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15. Cells within the superficial layers discharge primarily to visual stimuli, while cells in the deeper layers discharge mainly in relation to eye movements [R. H. Wurtz and J. E. Albano, *Annu. Rev. Neurosci.* **3**, 189 (1980)].
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20. For example, activity in the visually stimulated compared to the visually deafferented hemisphere is more than 200 percent greater in layer IV of area OC, 100 percent greater in the superficial layer of the superior colliculus, but only 50 percent greater in the dorsal lateral geniculate nucleus. The latter value is about the same as the value not only in area TE, another exclusively visual structure, but also in area PG, known to be a polysensory area. These differences in the quantitative contribution of visual input to the metabolic activity of the various structures related to vision have no known explanation at present and therefore pose an intriguing new question for future research.
21. Abbreviations used: AB, basal nucleus of the amygdala; ABA, basal accessory nucleus of the amygdala; AL, lateral nucleus of the amygdala; Cd, caudate nucleus (b, body; ha, anterior part of head; hp, posterior part of head; t, tail); CI, inferior colliculus; Cl, claustrum (d, dorsal part; v, ventral part); Cm, nucleus (N.) centrum medianum; CS, superior colliculus (d, deep layers; s, superficial layers); E, entorhinal cortex; FA, precentral cortex; FB, dorsal precentral cortex; FBA, posteroventral premotor cortex; FCB, anteroventral premotor cortex; FD$_\Delta$, posterior prefrontal cortex; GlP, globus pallidus; GL, corpus geniculatum laterale (d, dorsal); GM, corpus geniculatum mediale; H, hippocampal formation; IA, anterior insular cortex; IB, posterior insular cortex; LD, N. lateralis dorsalis; LP, N. lateralis posterior; MD, N. medialis dorsalis; NO, N. occulomotorii; NR, N. ruber; NSTH, N. subthalamicus; OA, anterior prestriate cortex; OB, posterior prestriate cortex; OC$_{IV}$, layer IV of striate cortex; OC$_{-IV}$, striate cortex, excluding layer IV; PE, superior parietal cortex; PF, anterior inferior parietal cortex; PG, posterior inferior parietal cortex; Pi, piriform cortex (t, temporal); Pul, N. pulvinaris (i, inferior; m, medial; l, lateral); Put, putamen (a, anterior; p, posterior); SN, substantia nigra; TA, superior temporal cortex, lateral surface; TC, superior temporal cortex, supratemporal plane; TE, anterior inferior temporal cortex (a, anterior; p, posterior); TEO, posterior inferior temporal cortex; TF, fusiform cortex; TG, temporal polar cortex (v, ventral); TH, parahippocampal cortex; T Opt, optic tract; VL, N. ventralis lateralis; VPL, N. ventralis posterolateralis.

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Pigeon Perception of Letters of the Alphabet

Abstract. *In a three-choice discrimination task three pigeons learned to distinguish each letter of the alphabet from all other letters. Errors during learning were based on 54 presentations of each target letter with every other letter. The errors were used to scale letters in a multidimensional similarity space and to associate them in hierarchical clusters. The results resembled those generated from similarity judgments by humans, suggesting cross-task and cross-species generality in processes of letter discrimination.*

Does the world look the same to pigeons and people? Herrnstein and coworkers (*1*) found that pigeons can identify categories such as "tree" and "fish" in photographs. However, the perception of such complex and variable stimuli is difficult to analyze. The birds in the present experiment learned instead the letters of the alphabet. These relatively simple stimuli yielded similarity patterns that are well correlated with comparable data for human subjects. The method may be useful in further studies of form perception in animals.

Each pigeon was placed in a box with a small television monitor screen set in one wall. On this screen an Atari home computer generated black letters on a white ground. The letters were formed within a five by seven dot matrix 2.0 mm wide and 2.8 mm high and were of the same format as those used by Podgorny and Garner (*2*) in a recent study of letter perception in humans. Three letters appeared in each experimental trial; they were horizontally aligned and spaced 2.3 cm apart, each behind a key made from a glass microscope slide.

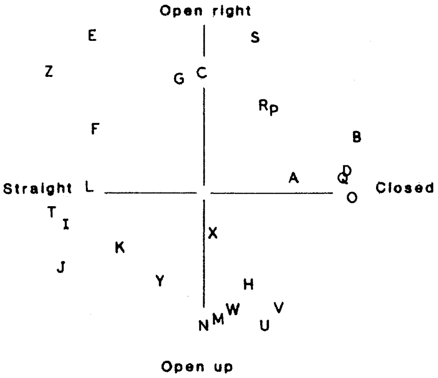

Fig. 1. Two-dimensional representation by ALSCAL of the similarity of letters perceived by the pigeons. In general, where two letters are far apart, the pigeon made few errors when discriminating them; where two letters are close together, it made many errors. Ideally, the closest pair would have the most errors, the next closest the next most, and so on. The names near the dimensional extremes call attention to common features of nearby letters.

Three white Carneaux pigeons were trained by standard methods to eat from a feeder located below and to the left of the display screen and to peck at randomly selected single letters appearing behind any of the three response keys. In the test procedure the bird was rewarded for pecking at a single letter—the target letter—on four successive daily sessions. This letter appeared equally often behind each of the glass keys on 675 test trials each day, while one of the other letters appeared behind both of the other keys. Each of the 25 nontarget letters appeared on one trial in each successive block of 25 trials. If the target letter was pecked, all the letters on the screen became white (higher in luminance than the background) for 0.5 second and then disappeared; at the same time, the feeder was illuminated. These changes signaled a "correct" response. With a probability of one in ten, correct responses were followed by access to food (mixed grain) for 3 seconds. After a correct response the screen remained blank white for 1.5 seconds; a new trial followed (*3*). If one of the nontarget keys was pecked, the letters disappeared, and after 1.5 seconds the target letter reappeared on the same key as before while black blocks (five by seven dot matrices) replaced the nontarget letters. This "correction" procedure was repeated until the target letter was pecked. Each session began with 25 trials in which the target letter was

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accompanied only by black blocks behind the incorrect response keys. After each target letter had been used for four sessions, it was replaced by a new target letter selected randomly under several restrictions (*4*).

Results were tabulated for test trials on the last two of the four sessions devoted to each target letter. During these sessions each pair of letters (target and nontarget) appeared 54 times and a percentage of correct responses was determined. Since each letter occurred as a target and as a nontarget, the resulting matrix of percentages contained two measures of confusion for each pair of letters. Data were omitted for pairs of letters in which the nontarget had served as a target during the immediately preceding series of four test days. Product-moment correlations between these matrices for the three birds taken in pairs were .64, .66, and .62. To represent overall performance, the matrices were averaged after multiplying by constants to make the mean value the same for each bird. The resulting matrix was then "folded," combining the two confusion values for each letter pair. The resulting half-matrix of means was used in the remainder of the data analysis.

The pigeons' view of the letters was first explored by mapping the data in a multidimensional space where similarity between forms is represented by relative proximity (*5*). The half-matrix was used as input for ALSCAL, a widely used scaling program (*6*). The two-dimensional output from ALSCAL appears in Fig. 1. This representation makes some sense to the human observer, and the dimensions discovered by ALSCAL can be roughly characterized, as suggested in Fig. 1. This picture is similar to pictures based on human data (*2*); in fact, ALSCAL provided a better fit (*6*) to the pigeon data than to the human data from the Podgorny and Garner study.

However, neither set of data fits with precision in a space with few dimensions. The similarity among letters need not be, and probably is not, well represented on dimensions that can be visualized. Fewer constraints are provided by an alternative representation in which computed distances between letters are used to form clusters of similar forms (*5*). To do this, the pigeon data were input to CLUSTER, a hierarchical cluster analysis program (*6*). The result is pictured in Fig. 2. Here, letters that showed similar confusion patterns are clustered together. In general, the lower the position of the cluster, the more confused were its letters. For example, U and V, which form the lowest cluster, were the letters most frequently confused with each other. They were distinguished correctly on only 34 percent of the test trials, just above the frequency attributable to chance (33 percent). In contrast, D and Z are among a number of letter pairs that share only the topmost cluster; D and Z were distinguished correctly on 92 percent of the test trials. The extent to which pigeon errors and human judgments correspond is suggested by the degree of similarity among letters in the clusters shown (although Fig. 2 does not duplicate the letter format in the experiment). The clusters, unconstrained by the dimensions present in Fig. 1, suggest even more definitive crucial features, such as "open up" and "small closed loop."

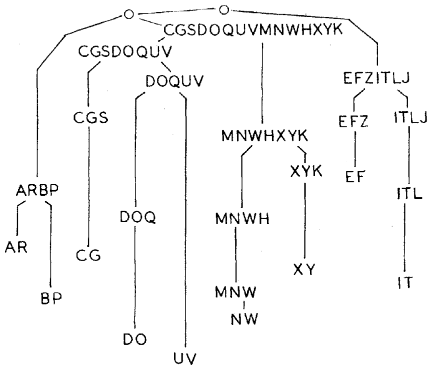

Fig. 2. Hierarchical arrangement of letters produced by the CLUSTER procedure. The abscissa is arbitrary; distance up the ordinate is proportional to the logarithm of the greatest "distance" within a cluster at that level. For example, since the *UV* cluster is the lowest, U and V were perceived as the two most similar letters. The topmost two clusters are represented by circles.

Correlation provides a quantitative measure of the relation between similarity matrices. The correlation between the pigeon data and the data based on similarity judgments by humans (*2*) was .68, comparable to correlations among different sets of human data (*7*). Together with the intuitive sense that the pigeon data in Figs. 1 and 2 make to the human viewer, this correlation suggests that the perceptual processes involved have much in common. Perhaps similar feature or spatial frequency analysis underlies the correlation, or perhaps adaptive pressures have generated similar perceptual mechanisms of a higher order. In any event, animal subjects may help to call attention to universal or fundamental aspects of recognition processes and may permit manipulations of training or physiological variables that would be difficult with human subjects. The present results suggest that a fruitful line to follow in such studies might use confusion matrices generated by the classic choice method.

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References and Notes

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2. P. Podgorny and W. R. Garner, *Percept. Psychophys.* **26**, 37 (1979). The present letters differed from those in the human study in size, ratio of height to width, and in being black on white rather than white on black.
3. Pigeon pecks are not well controlled by stimuli to which the birds respond very rapidly [D. Blough, *J. Exp. Anal. Behav.* **30**, 163 (1978)]. Such fast pecks were discouraged by withholding reward for any response that occurred less than 0.3 second after the appearance of the letters. The intertrial interval was randomly longer than 1.5 second by as much as 1 second, depending on the search time of the computer trial randomizer.
4. Targets were selected with the following restrictions: each was used only once with each bird; the order of targets differed across birds, such that a letter preceded or followed any letter as target only once at most; and each new target was among the ten letters with which the previous target had been least confused.
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6. Both ALSCAL and CLUSTER were run in versions provided by the SAS computer system for data analysis (SAS Institute, Inc.). ALSCAL used a Euclidean option to provide a nonmetric analysis (ordinal data) and an optimal procedure to break ties. The program was run, with identical options, on the Podgorny and Garner (*2*) data; the pigeon data fitted better than the human. For two dimensions, Kruskal formula 1 stress was 0.196 for humans and 0.234 for pigeons. Spaces of higher dimensionality provided a better fit, but the pigeon advantage was maintained. In averaging across birds, averages for two rather than three birds were used when data were missing for reasons described in the text.
7. Podgorny and Garner (*2*) report a correlation of .59 between human judgments of letter similarity and human reaction times in a letter discrimination task. The similarity judgments are correlated .57 with human data for letters of similar format [G. C. Gilmore, H. Hersh, A. Caramazza, J. Griffin, *Percept. Psychophys.* **25**, 425 (1979)].
8. Supported in part by PHS grant MH-02456 and NSF grant BNS-8025515.

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