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Integrity/Separability of Stimulus Dimensions and Multidimensional Generalization in Pigeons

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Abstract

We present a quantitative framework for interpreting the results of multidimensional stimulus generalization experiments in animals using concepts derived from the geometrical approach to human cognition. We apply the model to the analysis of stimulus generalization data obtained from pigeons trained with different sets of stimuli varying along two orthogonal dimensions. *Separable* pigeons were trained with stimuli varying along the dimensions of circle size and line tilt, dimensions found to be separable in previous human research; *Integral* pigeons were trained with stimuli varying along two dimensions of rotation in depth, dimensions which are intuitively integral and which hold special interest for theories of object recognition. The model accurately described the stimulus generalization data, with best fits to the City-Block metric for *Separable* pigeons and to the Euclidean metric for *Integral* pigeons.

Keywords

Multidimensional generalization; integrity; separability; metric; pigeon

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The objects and scenes that organisms encounter in their natural environments are often extraordinarily complex and they vary along multiple dimensions. For this reason, a key question in the study of animal visual cognition is how different dimensions of a stimulus interact with each other. One way to investigate this dimensional interaction is through studies of multidimensional stimulus generalization.

Consider the simple case in which a training stimulus is changed along two dimensions. If it is possible to find a *combination rule* to predict generalization after a *bidimensional* change in the stimulus from generalization after *unidimensional* changes along each dimension alone, then this rule might provide important insights into how these dimensions are processed, represented, and combined.

In human research, the distinction between *separable* and *integral* stimulus dimensions has been of considerable value in the study of dimensional interaction (Garner, 1974; Shepard, 1991). Separable dimensions are those that can be attended to and processed independently of each other; here, the dimensional structure itself determines the similarity between stimuli. Integral dimensions are those that cannot be attended to and processed independently of each other; here, the similarity between stimuli is directly perceived and the notion of multiple

dimensions loses meaning. Instead, the stimuli can be envisioned as varying along a single, “integral” dimension.

One approach to the study of multidimensional stimulus generalization in humans has used generalization measures as input to *multidimensional scaling* (MDS) procedures, which yield as output a representation of similarities between the stimuli in terms of their distance along a small number of orthogonal dimensions in psychological space (for a review, see Nosofsky, 1992). A central question concerning these spatial representations is how to compute the distance between points from their coordinates in the dimensions of this space. One alternative is to compute the distance between points as the sum of their distances along each dimension, in what is commonly called the *City-Block* metric. A second alternative is to use the Pythagorean formula to compute the straight-line distance between points, in what is commonly called the *Euclidean* metric.

Separable dimensions are conceptually related to the City-Block metric; in this case, the dimensional structure of the similarity space completely determines the distances between different stimuli in the coordinate system. Integral dimensions are conceptually related to the Euclidean metric; in this case, the distances between different points in the similarity space are indifferent to the specific dimensions that are chosen to describe the stimuli. In line with this well-known dichotomy, good empirical accord as to the separability or integrality of different stimulus dimensions has emerged from work deploying MDS as well as from work analyzing how different dimensions interact during classification tasks (Gardner, 1974; Shepard, 1991).

Early animal research on multidimensional stimulus generalization adopted a more descriptive approach to finding a combination rule to describe the behavioral data (e.g., Butter, 1963; Fink & Patton, 1953; Rohrbaugh, Brennan, & Riccio, 1971). Guttman (1956) first suggested that the study of bidimensional stimulus generalization might prove helpful in distinguishing his “Discrimination Hypothesis,” which proposed that stimulus generalization results from the failure to discriminate between training and testing stimuli, from Hull’s (1943) “Excitation Hypothesis,” which proposed that stimulus generalization results from the immediate spread of excitation from the training stimulus to the testing stimuli, with no need of discrimination training. According to Guttman (1956), Hull’s Excitation Hypothesis implies that a bidimensional stimulus generalization gradient can be obtained by rotating a unidimensional stimulus generalization gradient around its peak. The bidimensional gradient should thus have the same shape regardless of the means by which a stimulus is changed: along one dimension, along a second dimension, or along both dimensions. Guttman’s Discrimination Hypothesis predicts a different bidimensional stimulus generalization gradient, in which the combined changes along two dimensions should produce more pronounced drops in responding than changes along a single dimension.

Jones (1962) linked each of these hypotheses to a different quantitative combination rule for multidimensional stimulus generalization. And, Cross (1965) associated each of these hypotheses and their combination rules with work in multidimensional scaling; he proposed that the Excitation Model be considered equivalent to the Euclidean metric and that the Discrimination Model be considered equivalent to the City-Block metric.

These early analyses assumed that stimulus generalization gradients could be made linear and of equivalent slope through appropriate scaling of *physical* dimensions (Cross, 1965; Jones, 1962). One of the most appealing aspects of the geometrical approach to human cognition is that it represents stimulus generalization data through the concept of *psychological* distance; here, the focus is on what stimulus generalization behavior tells us about the underlying representation of similarity between stimuli, instead of trying to describe the stimulus generalization data as a function of some physical index of similarity.

Although the usual multidimensional stimulus generalization study does not yield enough data to conduct MDS, it does offer ways in which the behavioral data can support inferences about dimensional interaction. We next show how this analysis can be accomplished using our own *spatial model*. The main idea behind this model is to transform the observed stimulus generalization data into measures of psychological distance and to use these distances to find the metric in psychological space that best reproduces the observed behavior. This metric depends on the value of a single free parameter, r , which determines how the distance between points in psychological space can be computed from their distance along each axis in the space.

A Model of Multidimensional Stimulus Generalization

A commonly used task to study generalization in animals is one in which a single stimulus is reinforced and all other stimuli are not reinforced. This simple procedure allows one to obtain estimates of the probability of responding to each stimulus. These generalization measures can be transformed into estimates of psychological distance if we make some assumptions about the function relating both variables. Once this function is identified, distances can be computed using the inverse transformation over the generalization data.

There is substantial evidence that an exponential function relates psychological distance to stimulus generalization behavior (Shepard, 1987). This relation has been found in both human and animal generalization studies and using stimuli which are varied along many different dimensions, including the generalization gradients obtained by Guttman and Kalish (1956) in their pioneering work with the pigeon (Shepard, 1965). If the assumption is correct that generalization is an exponential function of psychological distance, then the natural logarithm of the generalization data should provide a good estimate of distance in psychological space:

$$d_{ij} = -\ln(g_{ij}) \quad (1)$$

where d_{ij} stands for psychological distance and g_{ij} represents the measure of stimulus generalization behavior.

Once obtained, these distances must be arranged in a spatial configuration in which the manipulated stimulus dimensions are represented as continuous and orthogonal dimensions in psychological space. For this task, we must assume: correspondence, interdimensional additivity, and intradimensional subtractivity (see Beals, Krantz, & Tversky, 1968; Dunn, 1983). Correspondence assumes that stimuli which vary along a physical dimension are represented as varying along a psychological dimension as well, falling along a straight line which is parallel to one of the main axes of psychological space. Interdimensional additivity assumes that all of the psychological dimensions are orthogonal to each other, allowing one to compute distances between stimuli as a function of the additive combination of their distances along each dimension. Intradimensional subtractivity assumes that the distance between points along a single dimension can be computed by subtracting the distances of those points to the origin from each other.

In this way, all of the stimuli that vary along only one dimension from the target can be represented as lying along one of several orthogonal straight lines in psychological space, thereby forming a coordinate system. All of the other stimuli (those that differ in more than one dimension from the target) can be correspondingly positioned in this coordinate system and their distances to the target at the origin can be computed using the well-known Minkowski metric:

$$d_{ij} = \sqrt[r]{\sum_{k=1}^K d_{ik}^r} \quad (2)$$

Equation 2 indicates how the distance between stimuli i and j (d_{ij}) can be computed from the distance between those stimuli along each dimension k (d_{ik}). The value of parameter r determines the specific metric that is used to compute distances in psychological space from distances along each dimension. When $r = 1$, the distance between points is simply the sum of their distance along each dimension, that is, the City-Block metric. When $r = 2$, the distance is computed using the Pythagorean theorem, that is, the Euclidean metric. Replacing (1) in (2), and solving for g_{ij} , we obtain a model to predict generalization after combined changes in stimulus dimensions from generalization after changes in each dimension alone:

$$g_{ij} = \exp \left(-\sqrt[r]{\sum_{k=1}^K (-\ln(g_{ik}))^r} \right) \quad (3)$$

The inputs to equation (3) are measures of generalization to stimuli which are changed in only one dimension from a target. The resulting values are predictions of generalization to stimuli which are changed in multiple dimensions from the target, and which can be compared to the actual generalization data to find the value of free parameter r that best fits with the observed generalization gradients. In this way, the search for a combination rule becomes a matter of discovering the metric of a spatial model that best describes the generalization data.

Several of the combination rules that have been proposed in the animal learning literature are special cases of equation (3). The multiplicative rule (Butter, 1963), according to which the probability of responding to a stimulus that is changed in two dimensions is equal to the product of the probabilities of responding to stimuli that are changed in each dimension alone, is equivalent to the City-Block metric, because the multiplication operation is equivalent to addition along a logarithmic scale. Thus, the City-Block metric is related to statistical independence in the processing of both dimensions of the stimulus (Blough, 1972) and to the Discrimination Model of generalization in animal learning theory (Cross, 1965; Guttman, 1956). The Euclidean metric, which predicts greater generalization values than those that are expected from the City-Block metric, is related to the excitation model of generalization in animal learning theory (Cross, 1965; Hull, 1943). Finally, a value of $r \approx \infty$ leads to what has been called the dominance metric, which translates into a behavioral rule predicting that generalization after changes in several dimensions equals the smaller level of generalization after changes in each of the dimensions alone, a rule also known as the “better criterion” model (Jones, 1962) and which has been studied in the animal literature as well (Warren, 1954).

The advantages of our spatial model are clear. It offers both mathematical precision and theoretical generality, as it contains most of the combination rules that have been proposed in the animal literature plus several other intermediate rules. Because our model can adopt several combination rules depending on the value of r , it captures the idea that different dimensions of a visual stimulus can interact with each other in multiple ways and that there is no single combination rule that can describe multidimensional generalization for all possible stimulus sets. Our model also implies that combination rules do not vary categorically. Instead, there is a gradual shift from one combination rule to the other—depending on changes in the continuously-valued parameter r —and any of the intermediate rules may describe the generalization data for a particular set of stimulus dimensions. Thus, our spatial model goes

well beyond previous approaches to the study of multidimensional stimulus generalization, which assumed that a single combination rule can describe generalization for several different sets of dimensions and which focused on seeking the best rule among several candidates through a purely trial-and-error process (e.g., Blough, 1972; Jones, 1962).

Instead, we suggest that a better strategy involves trying to understand the way in which specific stimulus dimensions interact with each other in a discrimination task and to characterize the relation between this dimensional interaction and the combination rules that are identified in the generalization data. Our model makes explicit the relation between different combination rules and the various metrics of psychological space that would produce them, including the City-Block and Euclidean metrics. Because these two metrics have been related to the key concepts of dimensional separability and integrality in human research, we expect that stimuli which vary along separable dimensions should produce generalization data that better fit with the City-Block metric ($r = 1$) than with the Euclidean metric ($r = 2$) and vice versa for stimuli which vary along integral dimensions.

In the remainder of this paper, we evaluate the utility of our model by applying it to the description of generalization data obtained from different sets of visual stimuli. We created these stimulus sets by manipulating dimensions that are believed to be separable and integral in order to test the prediction that a spatial model should point toward a City-Block metric when tested with the former kinds of dimensions and toward a Euclidean metric when tested with the latter.

Experiment 1

Our first experiment assessed the utility of our spatial model by applying it to the description of stimulus generalization gradients which were obtained after manipulating very different dimensions of multidimensional visual stimuli. One group of pigeons (*Group Separable*) was trained with stimuli varying along the dimensions of size and line tilt, dimensions that are known to be separable from previous human research (e.g., Garner & Felfoldy, 1970) and to yield a City-Block metric in MDS (Hyman & Well, 1967; Shepard, 1991). The second group of pigeons (*Group Integral*) was trained on a discrimination involving more complex dimensions and more naturalistic stimuli. The visual images were computer renderings of a three-dimensional object (an airplane) which was rotated in depth. Rotation in depth is especially interesting because of its relevance to theories of object recognition (Biederman & Gerhardstein, 1993; Tarr & Bülthoff, 1995) and because viewpoint is intuitively a single integral dimension that can nevertheless be varied along innumerable pairs of orthogonal axes.

Our straightforward prediction was that the generalization data of these two groups should produce disparate best-fitting values of parameter r , indicating that the specific dimensions that are chosen to build the stimulus set in a generalization experiment materially affect the combination rule that is used by the animals, even when all other aspects of the experimental task are kept constant. This result would suggest that there is no single combination rule which can account for multidimensional generalization along all stimulus dimensions.

We also expected that the generalization data from Group Separable would better be described by the City-Block metric than by the Euclidean metric, whereas the reverse would be true for Group Integral. This expectation does not require the best-fitting values of r to be exactly 1 or 2, which are relatively arbitrary values chosen in the literature from all possible values that this parameter might take. The prediction for Group Separable was based on results from the human literature. To the best of our knowledge, data supporting this prediction have not been reported in the animal literature. There are no previous data, human or animal, on which to base our prediction for Group Integral; but, we see no reason to believe that arbitrarily chosen axes of rotation in depth should impose their dimensional structure to the representation of viewpoint.

Instead, we believe that viewpoint is represented by the pigeons as a single, integral dimension of a complex stimulus. Because the two dimensions of rotation are arbitrarily selected to produce changes in viewpoint, they should not interact with one another in the same way as do the more analyzable dimensions of line tilt and circle size.

Method

Subjects—Eight feral pigeons (*Columba livia*) were kept at 85% of their free-feeding weights by controlled daily feeding. The birds had previously participated in unrelated research.

Apparatus—The experiment used four $36 \times 36 \times 41$ cm operant conditioning chambers (Gibson, Wasserman, Frei, & Miller, 2004), located in a dark room with continuous white noise. The stimuli were presented on a 15-in. LCD monitor located behind an AccuTouch® resistive touchscreen (Elo TouchSystems, Fremont, CA) which was coated with mylar for durability. A food cup was centered on the rear wall of the chamber. A food dispenser delivered 45-mg food pellets through a vinyl tube into the cup. A houselight on the rear wall of the chamber provided illumination during sessions. Each chamber was controlled by an Apple® eMac® computer and the experimental procedure was programmed using Matlab Version 7.0.4 (© The MathWorks, Inc.) with the Psychophysics Toolbox extensions (Brainard, 1997). Images were displayed in a 6.7 cm square in the middle of the screen; the rest of the screen was black at all times.

Stimuli—For Group Separable, the stimuli were 36 images of a circle bisected by a line through its center, which resulted from factorially combining 6 different circle sizes with 6 different line orientations. The circle varied in size from 100 to 150 pixels in 10-pixel steps and the line varied in orientation from 0° to 25° in 5° steps (Figure 1, top). These shapes were centered on a grey square background, 300×300 pixels in size, and were created using Canvas 9.0.4 (© ACD Systems Inc.).

For Group Integral, the stimuli were 36 renderings of a three-dimensional object (an airplane) rotated in depth by 12° intervals along both its x- and y-axes. There were 6 possible values of rotation along both axes, ranging from 0° to 60° ; the resulting set of 36 stimuli represented all possible combinations of these values. The images were rendered over a white background using Carrara V. 5.0.1 (© Eovia Corporation) and each image had a size of 300×300 pixels. Two criteria were used to choose the particular rendered viewpoints of the airplane: (1) all of the views avoided occlusion of one or more of the main parts of the airplane by one another and (2) there were no extreme disparities in total brightness among the 36 images, as judged by human observers. Two main sources of light were used: one locked to the camera and the second positioned to the top-left of the airplane. There was an angle of 45° between the top of the airplane and the latter light source (Figure 1, bottom).

Procedure—For each of the two groups ($n = 4$), a different target stimulus was randomly selected for each pigeon from a set of four possible images. In Group Integral, this set included computer renderings of the airplane at the following combinations of rotation along the x- and y- axes: (0° , 0°), (0° , 60°), (60° , 0°) and (60° , 60°). In Group Separable, the set included the circle with the following combinations of size and line tilt: (100 px, 0°), (150 px, 0°), (100 px, 25°) and (150 px, 25°). Each of the stimuli in these two sets corresponded to the images positioned in each of the four corners of the stimulus sets shown in Figure 1.

All trials began with the presentation of a white square in the center display area of the screen. A single peck anywhere within the square led to the presentation of the stimulus. On a reinforced trial, the stimulus was presented and remained on for 15 s; the first response after this interval turned the display area black and led to the delivery of food. On a nonreinforced

trial, the stimulus was presented and remained on for 15 s, after which the display area automatically darkened and the intertrial interval began. On both reinforced and nonreinforced trials, scored responses were recorded only during the first 15 s in which the stimulus was displayed on the screen. The intertrial interval randomly ranged from 6 to 10 s. Reinforcement consisted of 1 to 3 food pellets scheduled randomly from trial to trial.

The experiment began with a Baseline Training phase during which all of the trials were reinforced. Each daily session of Baseline Training was composed of 3 blocks of 60 trials each, for a total of 180 trials. In each block, there were 24 unscored presentations of the target stimulus and 1 scored presentation of each of the 36 visual stimuli, including the 1 future target stimulus and the 35 future non-target stimuli. This trial organization was intended to equilibrate the block structure of this Baseline phase and the following Discrimination Training phase. The order of trial presentation was randomized within each block.

Pigeons were kept on Baseline training until the mean rate of response to each of the 36 stimuli fell within 80% and 120% of the overall mean rate of response. This mean response rate was updated daily taking into account all of the scored trials of the past 6 sessions; thus, all of the scored responses in the last 18 trials of each stimulus were considered. After the pigeons met criterion, they started Discrimination training.

Each daily session of Discrimination Training was composed of 3 blocks of 60 trials, for a total of 180 trials. In each block, there were 24 reinforced and unscored presentations of the target stimulus and 1 nonreinforced and scored presentation of each stimulus, including the 1 target stimulus and the 35 non-target stimuli. This procedure of reinforcing 40% of all of the trials assured sustained responding across discrimination training. Reinforcement of 96% of the target stimulus trials fostered high rates of responding to this stimulus, while equilibrating the total number of nonreinforced and scored presentations of the 1 target stimulus and the 35 non-target stimuli for data analysis. The order of trial presentation was randomized within each block.

A global measure of discrimination performance (Overall Discrimination Ratio, ODR) was computed by taking the mean response rate to all 35 of the non-target stimuli and dividing it by the mean response rate to the 1 target stimulus. We analyzed the data from all sessions from the inception of discrimination training until an ODR less than .30 was obtained across 5 sessions; at this point, the discrimination between all non-target stimuli and the target stimulus was quite strong. Including later sessions in the data analysis added no useful information because discrimination performance was too good.

Model Fit—To fit the behavioral data to our spatial model, the mean rate of responding to each stimulus across all of the scored training sessions was used as the behavioral measure of stimulus generalization. These data were transformed to a scale ranging from 0 to 1, by dividing them by the mean rate of responding to the target stimulus. As Shepard (1957) has pointed out, in most behavioral studies, the floor of the generalization measure tends to be higher than 0, because of an initial phase of learning in which subjects tend to respond randomly. Therefore, each observed generalization measure G_{ij} is assumed to be equal to the true generalization measure g_{ij} plus a constant value C . The value of C is constant for each subject, but it is reasonable to believe that it varies for different subjects and for tasks of differing difficulty; therefore, the value of C must be estimated from the data. Several approaches have been used for this estimation (Blough, 1988; Shepard, 1957). Here, we took the simple approach of defining C as the smallest observed value of G_{ij} . In this way, the obtained stimulus generalization data were re-scaled separately for each pigeon through the following linear transformation:

$$g_{ij} = (1 + \min(G_{ij})) G_{ij} - \min(G_{ij})$$

We used the resulting stimulus generalization measures to find the best-fitting value of r in our model, utilizing the Gauss-Newton method of least-squares estimation with step halving added in the statistical package JMP IN Version 5.1 (SAS Institute Inc.). For comparison purposes, lack-of-fit measures were also computed for the model using values of r equal to 1 and 2, corresponding to the City-Block and Euclidean metrics, respectively.

Results

Baseline training took between 6 and 19 sessions for pigeons in Group Separable and between 6 and 16 sessions for pigeons in Group Integral. Discrimination training took between 22 and 42 sessions for pigeons in Group Separable and between 9 and 16 sessions for pigeons in Group Integral.

Generalization gradients are shown in Figure 2, with the data averaged across all four of the subjects in each group. To test the statistical reliability of our observations about the mean gradients, the data that are shown in Figure 2 were entered in a 6 (Dimension 1: Rotation in x-axis for Group Integral; circle size for Group Separable) $\times$ 6 (Dimension 2: Rotation in y-axis for Group Integral; line tilt for Group Separable) $\times$ 2 (Group) ANOVA.

The same data are plotted in two different ways. The left part of Figure 2 shows a three-dimensional surface graph, in which mean response proportion is plotted against change steps in both stimulus dimensions. For each group, response proportion dropped monotonically as a function of changes in both dimensions; as well, changes in two dimensions produced a more marked generalization decrement than did changes in either dimension alone. This pattern of results was supported by significant effects of Dimension 1, $F(5, 30) = 72.19, p < .0001$, Dimension 2, $F(5, 30) = 28.05, p < .0001$, and the Dimension 1 $\times$ Dimension 2 interaction, $F(25, 150) = 14.39, p < .0001$. The main effect of Group was not significant, $F(1, 6) = .93, p > .10$.

Beyond these effects, there was a visible disparity between the groups: in Group Integral changes in the two dimensions supported similar generalization gradients (which can be taken as evidence that both dimensions similarly controlled behavior), whereas in Group Separable responses showed a more marked decline across changes in circle size than across changes in line tilt. Thus, the interaction between Dimension 1 (which reflects averages across the levels of line tilt in Group Separable) and Group was found to be significant, $F(5, 30) = 5.54, p < .001$, whereas the interaction between Dimension 2 and Group was not significant, $F(5, 30) = .17, p > .10$. Still, both dimensions exerted strong control over the pigeons' pecking behavior.

What is more interesting for the present purposes is how the two dimensions interacted with one another to produce changes in mean response proportion and whether this interaction differed between the groups. This matter is easier to visualize in the circle plots that are shown in the right side of Figure 2.

The x- and y-axes in these plots represent the relevant stimulus dimensions. The center of each circle is determined by the combination of values of a stimulus along those two dimensions. The size of each circle represents the mean response proportion to each stimulus. The circles are also shaded differently depending on the mean response proportion to each stimulus. White circles represent a mean response proportion higher than .5, black circles represent a mean response proportion lower than .2, and grey circles represent a mean response proportion between .2 and .5. The most important aspect of these data is the relation between the level of

responding to those stimuli that are changed along *one* dimension alone and the level of responding to those stimuli that are changed along *both* dimensions.

The right side of Figure 2 shows that the mean *unidimensional* generalization decrement was more precipitous in Group Integral than in Group Separable (excluding the target stimulus at Point 0/0, these data appear in the leftmost columns and bottommost rows of each group's circle plots). In Group Integral, the mean response proportion fell below .5 very quickly for both dimensions combined (7/10 scores were below .5); in Group Separable, the mean response proportion fell more slowly below .5 for both dimensions combined (only 3/10 scores were below .5). On the other hand, the mean *bidimensional* generalization decrement exhibited the opposite trend, being more precipitous in Group Separable than in Group Integral. Notice that in Group Separable the mean response proportion dropped quickly below .2 for stimuli changed in two dimensions (11/25 scores are below .2), whereas in Group Integral the mean response proportion dropped more slowly below .2 for stimuli changed in two dimensions (only 4/25 scores are below .2). These disparities in the generalization gradients produced by both groups were supported by a significant interaction between Dimension 1, Dimension 2, and Group, $F(25, 150) = 4.39, p < .001$.

The main results of our critical model-fitting procedure are shown in Table 1 for each individual pigeon as well as for the pooled data of each group. The pooled data consisted of all of the data from each bird in the group; these data do not represent the means across birds. Thus, the best-fitting value of r for the pooled data is constrained by each generalization data point from all four birds.

The three bottom rows in Table 1 show the Root Mean Squared Error (RMSE) values that were obtained for the best-fitting value of parameter r and for the predictions generated by our model with the City-Block metric ($r = 1$) and with the Euclidean metric ($r = 2$). The RMSE values for the best-fitting solution tend to be low and similar across pigeons, with a better fit to the data from Group Separable than to the data from Group Integral. The same disparity in fit was observed from the correlation between the observed stimulus generalization values and the stimulus generalization values predicted by our model fitted to the pooled group data. The correlations between the predicted and observed data were strong and significant for both groups according to Pearson's product-moment coefficient: 0.947 ($p < .0001$) for Group Separable and 0.846 ($p < .0001$) for Group Integral. In sum, our model reproduced the obtained generalization data in both groups with high accuracy.

A possibly more interesting comparison may entail the best-fitting values of parameter r , which are detailed in the first line of Table 1. The obtained values for each individual pigeon in Group Separable are all closer to a value of 1, indicative of the City-Block metric, than to a value of 2, indicative of the Euclidean metric; the same is true for the value of r obtained from fitting the pooled data of this group. This result is further confirmed by the fact that RMSEs obtained from the predictions of the City-Block metric are all lower than those obtained from the predictions of the Euclidean metric.

The results for Group Integral are different, with the best-fitting group value of r closer to the Euclidean metric of 2 than to the City-Block metric of 1. A closer look at the data reveals that the individual fits are not as straightforward as those in Group Separable. Two of the birds (38B and 89B) show values of r that are clearly closer to the Euclidean metric than to the City-Block metric, but this trend is not true for the other two birds which show values that are either intermediate between the metrics (51Y) or closer to the City-Block metric (93W). Analysis of the predictions obtained with the City-Block and Euclidean metrics reveals that the RMSEs for three out of the four pigeons are lower with the Euclidean metric, with only Bird 93W exhibiting the opposite pattern. So, although Bird 51Y shows a best-fitting value for parameter

r that is slightly closer to the City-Block metric, its data are better fit by the Euclidean model. The pooled data are also better fit by the Euclidean metric than by the City-Block metric.

A Wilcoxon rank sum test indicated that the best-fitting values of parameter r were significantly different between the groups ($z = 2.17$, $p < 0.05$), reflecting the fact that, regardless of any individual differences within each group, there was no overlap between the scores of pigeons in Group Integral and pigeons in Group Separable. These results are further depicted in Figure 3, which shows the SSE profiles that were obtained for values of parameter r ranging from 1 to 2, representing the City-Block and the Euclidean metrics, respectively. The SSE profiles of all four pigeons in Group Separable rise with higher values of r , whereas they fall for three of the four pigeons in Group Integral.

Discussion

The results of Experiment 1 suggest that different combination rules may underlie multidimensional generalization to stimuli which are varied along different physical dimensions. The best-fitting values of parameter r for pigeons in Group Integral were reliably higher than those for pigeons in Group Separable. This key finding supports our main hypothesis that the particular dimensions that are selected to build the stimulus set in a generalization experiment may have a strong influence on the combination rules used by animals, even when all other aspects of the experimental method are kept constant. Thus, these results offer firm empirical support for the assumption that only a flexible account, like the spatial model that we have proposed here, can explain multidimensional generalization to different sets of visual stimuli.

A second aspect of our proposal is that devising such a general model using concepts from the spatial approach to human cognition is highly advantageous, because it opens the door to linking different spatial metrics in the model to the central concepts of integrality and separability of stimulus dimensions (Garner, 1974; Shepard, 1991). Thus, we hypothesized that those stimuli that varied along separable dimensions would produce generalization gradients that better fit with the City-Block metric, whereas those stimuli that varied along integral dimensions would produce generalization gradients that better fit with the Euclidean metric.

The data from Group Separable, that was trained with stimuli which varied along dimensions that human research suggests are separable, were better fit by the City-Block metric in our model. Although the best-fitting values of r observed in Table 1 were all below 1, the fit provided by the City-Block metric was always better than the fit provided by the Euclidean metric. Furthermore, best-fitting values lower than 1 have also been reported for separable dimensions in the human literature (Dunn, 1983; Tversky & Gati, 1982), a point to which we will return later (see General Discussion).

Finally, we found some evidence to support our prediction that the Euclidean metric would better fit the generalization data from Group Integral than the City-Block metric. This result was true for three out of the four pigeons in Group Integral. However, the data of one pigeon in this group was better fit by the City-Block metric and a second pigeon produced results which might also be interpreted as providing only equivocal evidence for the Euclidean over the City-Block metric. Such findings are not unique to our study; they have been reported in the human literature as well (Dunn, 1983; Ronacher & Bautz, 1985).

These final results and the small number of subjects that were trained in Group Integral may raise doubts as to whether the Euclidean metric provides a suitably good description of generalization for stimuli varied along viewpoint. Perhaps training more pigeons would produce the opposite pattern of results, with a tendency for most birds to behave as predicted

by the City-Block metric. Furthermore, although the results for Group Separable were expected on the basis of previous human research, the same was not true for Group Integral. We are unaware of any prior research attempting to test the integrality of viewpoint dimensions. So, there are no other data, beyond those we collected in Experiment 1, to support a solid conclusion about the best model to describe multidimensional generalization for the dimensions of rotation in depth.

We therefore decided to conduct a second experiment. The main goals of Experiment 2 were to see whether the results of Group Integral were reliable and to determine whether the Euclidean metric indeed provides a robust description of the generalization data of most pigeons that are trained with images of an object which is rotated in depth. Finally, in order to test the ability of our model to describe the generalization data that are obtained with different training procedures, Experiment 2 used a Forced-Choice task instead of a Go/No-Go task to train the pigeons in the discrimination between target and non-target stimuli.

Experiment 2

Method

Subjects and apparatus—The subjects were four pigeons. One of the birds (39Y) had served in Group Separable of Experiment 1, but it (and the other three birds) did not have any prior experience with the particular stimuli and the Forced-Choice methods used in this experiment. The apparatus was the same as in Experiment 1 and the stimuli were those previously used for Group Integral (see the bottom panel of Figure 1).

Procedure—As in Experiment 1, different target stimuli were randomly assigned to each pigeon from the same set of four images.

All trials began with the presentation of a white square in the center display area of the screen. A single peck anywhere within the square display area led to the simultaneous presentation of the target stimulus plus 1 of the 35 possible distracter stimuli. The stimuli were displayed in two 6.7-cm square boxes vertically centered in the screen and with their horizontal midpoint equally spaced to the left and right of the screen midpoint. After a fixed presentation time of 5 s, the pigeons had to make a single peck to one of the two stimuli. The stimulus to which the response was made remained on the screen for 2 s; the other stimulus disappeared. If the response was made to the target stimulus (S+), then reinforcement consisting of 1 to 3 pellets was delivered and a fixed intertrial interval of 5 s followed. If the response was made to the S-, then the houselight darkened and a variable (5- to 30-s) Timeout (TO) followed. After the TO elapsed, a correction trial identical to the previous trial was given to the pigeon. Correction trials were given until the correct response was made, but only the first choice response of a trial was recorded and used in data analyses.

Daily sessions of Discrimination Training were composed of 2 blocks of 70 trials each, for a total of 140 daily trials. The target stimulus was presented along with each of the 35 possible distracter stimuli twice in each block, with the left-right location counterbalanced. The order of presentation of trials within each block was randomized.

Model Fit—The data analysis included all of the sessions from the start of training until the birds reached 90% correct responses on 3 non-consecutive days. The data from these sessions were fit to the model described in Equation 3, using the procedure described in Experiment 1. The specific scores that were used to fit the model involved the proportion of trials, across all of the training sessions, in which the pigeon erroneously pecked the non-target stimulus. This proportion was separately computed for each non-target stimulus and then divided by .5 to transform it to a scale ranging from 0 to 1. This final measure was then re-scaled according to

the same linear transformation described in Experiment 1. This experiment did not include any trials which presented the target stimulus twice on the screen, because the data produced by such trials could not be interpreted as “errors.” Such data were simply replaced by a score of .5 for each of the pigeons, representing the probability of responding to each duplicate of the target view across a large number of trials, which yielded a value of 1 in the final generalization measure.

Results

It took the pigeons between 6 and 21 sessions to reach criterion. Both versions of the pigeons’ stimulus generalization gradients—surface plots and circle plots—are shown in Figure 4, depicted as functions of rotational steps from the training view. It can be seen that the response proportion fell as a function of changes across the two dimensions and that conjoint changes in both dimensions tended to produce a more marked generalization decrement than did changes in either dimension alone. However, the shapes of the gradients were not as regular as those obtained with the Go/No-Go procedure in Experiment 1 and the level of generalized responding was lower than that observed for Group Integral in that experiment. Perhaps the opportunity to simultaneously compare the target and non-target stimuli was responsible for this lower level of generalized responding.

These data were entered into a 6 (Rotation in x-axis) $\times$ 6 (Rotation in y-axis) ANOVA, which revealed a significant main effect of Rotation in the x-axis, $F(5, 15) = 21.03, p < .0001$, a significant main effect of Rotation in the y-axis, $F(5, 15) = 60.54, p < .0001$, and a significant interaction between these factors, $F(25, 75) = 8.14, p < .0001$.

The relation between the observed generalization data and the values that were predicted by our model was computed via a Pearson’s product-moment coefficient. The result was a moderately strong and significant correlation of 0.654 ($p < .0001$). This value was somewhat lower than the correlations that were obtained in Experiment 1, possibly because of the lower level of generalized responding that was supported by the choice task that was used in the present experiment than the Go/No-Go procedure that was used in Experiment 1.

Table 2 shows the key results of our model-fitting procedure for each pigeon and for their pooled data. It can be seen that the best-fitting value of r for all four of the pigeons was closer to a value of 2, indicative of the Euclidean metric, than to a value of 1, indicative of the City-Block metric. Furthermore, the best-fitting value of r for the pooled data was 2.14, very close to the perfect Euclidean metric of 2. These results were consistent with the RMSE values that are shown in the lower part of the table, which indicate that for each individual pigeon and for the pooled data, the Euclidean metric provided a better fit to the data than did the City-Block metric.

Figure 5 provides different look at these fits, with SSE plotted as a function of values of parameter r ranging from 1 to 2. The SSE profiles of all four pigeons fall with higher values of parameter r .

Discussion

The results of Experiment 2 lend further support to the hypothesis that stimulus generalization across different dimensions of rotation in depth is better described by a spatial model using the Euclidean metric than by the City-Block metric. This result leads us to conclude that the findings in Experiment 1 for Group Integral were not due to chance, but instead reflect the particular combination rule that is fostered by the stimuli used to train those birds. Only one of eight pigeons trained with these stimuli yielded generalization data that were fit better by the City-Block metric, suggesting that this subject was an outlier in an otherwise consistent

group of pigeons which behaved as predicted by the Euclidean model. Furthermore, these results show that it is possible for our model to point consistently toward the same combination rule used by pigeons when they are tested with a specific set of stimuli, regardless of the discrimination task—Go/No-Go vs. Forced-Choice—that is deployed to gather the generalization data.

General Discussion

This paper developed a quantitative model of multidimensional stimulus generalization based on a set of concepts which were derived from the geometrical approach to human cognition (Nosofsky, 1992). Our model includes focal combination rules that have been suggested in the literature (Blough, 1972; Butter, 1963; Cross, 1965; Jones, 1962; Warren, 1954) and it links each of these rules to different spatial metrics as well as to the twin concepts of dimensional separability and integrality. The combination rule that is adopted by the model depends on a single free parameter, making the search for a suitable rule a matter of fitting this parameter to data instead of looking for the best rule among a handful of possibilities by a trial-and-error process, as in previous explorations of this problem (e.g., Blough, 1972; Jones, 1962).

In the first experiment, generalized responding to stimuli which varied along dimensions that are believed to be separable (circle size and line tilt) was better described by the City-Block metric, just as in human studies using MDS (Hyman & Well, 1967; Shepard, 1991). On the other hand, generalized responding to stimuli which varied along intuitively integral dimensions (orthogonal dimensions of rotation in depth) was better described by the Euclidean metric in three of four subjects, just the result found with other sets of dimensions in human studies (see Shepard, 1991). The latter conclusion was confirmed by the results of Experiment 2. The good fit of our model to the generalization data that we obtained from very different stimuli and dimensions coupled with the fact that our results mirrored previous findings from human research suggest that the assumptions underlying the model are valid. So, despite obvious anatomical disparities between avian and mammalian visual and nervous systems, the study of dimensional interaction can lead to similar conclusions for both classes of organisms.

As well, some aspects of our generalization data warrant further discussion, because they might be deemed to be problematic for our interpretation of the results. The most obvious issue is that, in Experiment 1, the City-Block metric better described the data of one pigeon in Group Integral than did the Euclidean metric. This same pattern of results has been reported in human research as well, where individual similarity judgments fit well with a variety of metrics regardless of the specific dimensions that were manipulated to create the stimulus set (Dunn, 1983; Ronacher & Bautz, 1985). These studies found that a minority of subjects trained with integral dimensions generated data that were better fit by the City-Block metric.

The relation between integrality and the Euclidean metric, on the one hand, and between separability and the City-Block metric, on the other, appears to be far from perfect; that relation may only reflect a general tendency to deploy one form of processing visual information over another depending on the dimensions along which the stimuli vary. As Shepard (1991, p. 61) concluded from his review of the human literature: “pure integrality is more or less approximated, if perhaps never strictly achieved. Some directions through the stimulus space [...], although not fully separable, may always be somewhat more psychologically salient [...] Integrality and separability may define a continuum rather than a dichotomy.” Furthermore, several other factors, such as individual differences or task demands, could also affect the way in which stimulus dimensions interact (e.g., Foard & Kemler Nelson, 1984; Ronacher, 1984).

Nonetheless, despite the fact that one pigeon in Group Integral may have used a combination rule unlike that used by the other pigeons, the best-fitting value of parameter r for *every* pigeon

in Group Separable was lower than the value of r for *every* pigeon in Group Integral, thus attesting to the strong effects that our stimulus manipulations had on pigeons' discrimination performance in Experiment 1. This is evidence that the combination rules that are used in multidimensional generalization vary in a predictable way depending on stimulus factors, even when training conditions are kept constant. Only a flexible model like the one that we presented here can capture such variability.

As to the possible effect of task demands on the pigeons' behavior, note that we used two different *discrimination* tasks for obtaining stimulus generalization gradients, in which only responses to the target stimulus were reinforced; responses to all other non-target stimuli were never reinforced during discrimination training. Under both of these conditions, response efficiency can be maximized by reducing the number of non-target responses. This reduction in responding would be better accomplished if pigeons were to *separately* evaluate changes in both dimensions than if they were to *integrally* evaluate stimulus similarity. Why?

The City-Block metric always locates two stimuli that are changed in more than one dimension at a greater distance from one another than does the Euclidean metric. In other words, the City-Block metric predicts greater discriminability between stimuli, which translates into less generalized responding between them. Under reinforcement contingencies that thus ought to have favored lower levels of generalization between the target and non-target stimuli, it is surprising that, in Experiment 1, the data for most of the pigeons in Group Integral were better fit by the Euclidean metric than by the City-Block metric (see Table 1 and the bottom panel of Figure 3), and that the same was true for all of the pigeons in Experiment 2 (Table 2 and Figure 5); this observation is consistent with the notion that these birds could not separately attend to changes in the two manipulated dimensions.

A related aspect of our results that merits further consideration is the fact that the best-fitting values for pigeons in Group Separable in Experiment 1 disclosed systematic deviations from the City-Block metric. Specifically, these values of r were all lower than 1, pointing to violations of the triangle inequality axiom of metric spaces and suggesting that the data could better be described by a non-metric model (see Tversky & Gati, 1982). Concretely, this result suggests that the observed generalization decrements after changes in two dimensions were larger than those predicted by the City-Block metric.

This result too has been reported in human studies involving the dimensions of circle size and line tilt (Dunn, 1983). Furthermore, this may be yet another case in which the specific task that is used to gather the stimulus generalization data could have exaggerated the steepness of the stimulus generalization gradient for combined changes along the two dimensions. As suggested above, the contingencies of reinforcement favored the pigeons' adopting a strategy using the information about changes in both dimensions in a way which encourages lower levels of stimulus generalization. Future experiments, gathering stimulus generalization data via other procedures, might help to resolve this issue.

A final concern is the fact that the best-fitting values of parameter r in Experiment 1 showed disparities between groups not only in their *magnitude*, but also in their *variability*. The values of r obtained for pigeons in Group Integral were not only larger, but they were also more variable than those obtained in Group Separable.

Here, it should be noted that two Minkowski metrics with a constant disparity in exponent translate into more similar spaces as their exponents increase. Assuming that the pigeons' confusion errors include random variations, a constant amount of variation in these values should lead to a broader distribution of exponent values for larger exponents, because shifting a point at a particular distance in psychological space requires a larger shift in the exponent (Ronacher & Bautz, 1985). Thus, this result can be explained as a consequence of using a model

based on the Minkowski metric, although differences in the stimulus sets that were given to each group could also underlie the between-group disparities in individual variability and the fit of the model to the generalization data.

To conclude, we wish to observe that the study of dimensional interaction in information processing may yield important insights into the processes underlying visual object recognition and categorization. The study of multidimensional stimulus generalization, in general, and the use of spatial models to investigate this matter, in particular, have not been popular in the animal behavior literature. At least one reason for this neglect might be the difficulty of obtaining sufficient generalization data to deploy MDS techniques using traditional animal discrimination learning tasks. But, the use of scaling methods is only one approach to the problem of representing similarity data through spatial models.

A different approach assumes that the component dimensions of the model are known and it infers the combinatorial rule or spatial metric that better describes the way in which the subjects actually use these dimensions (Hyman & Well, 1967). The work presented here illustrates how this second approach can be successfully applied to the study of multidimensional stimulus generalization gradients, which are easily obtainable using common animal discrimination learning tasks.

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References

- Beals R, Krantz DH, Tversky A. Foundations of multidimensional scaling. *Psychological Review* 1968;75:127–142. [PubMed: 4870550]
- Biederman I, Gerhardstein PC. Recognizing depth-rotated objects: Evidence and conditions for three-dimensional viewpoint invariance. *Journal of Experimental Psychology: Human Perception and Performance* 1993;19:1162–1182. [PubMed: 8294886]
- Blough DS. Quantitative relations between visual search speed and target-distractor similarity. *Perception & Psychophysics* 1988;43:57–71. [PubMed: 3340500]
- Blough DS. Recognition by the pigeon of stimuli varying in two dimensions. *Journal of the Experimental Analysis of Behavior* 1972;18:345–367. [PubMed: 16811632]
- Brainard DH. The psychophysics toolbox. *Spatial Vision* 1997;10:433–436. [PubMed: 9176952]
- Butter CM. Stimulus generalization along one and two dimensions in pigeons. *Journal of Experimental Psychology* 1963;65:339–346. [PubMed: 14017413]
- Cross, DV. Metric properties of multidimensional stimulus generalization. In: Mostofsky, DI., editor. *Stimulus Generalization*. Palo Alto, CA: Stanford University Press; 1965. p. 72–93.
- Dunn JC. Spatial metrics of integral and separable dimensions. *Journal of Experimental Psychology: Human Perception and Performance* 1983;9:242–257. [PubMed: 6221069]
- Fink JB, Patton RM. Decrement of a learned drinking response accompanying changes in several stimulus characteristics. *Journal of Comparative and Physiological Psychology* 1953;46:23–27. [PubMed: 13034948]
- Foard CF, Kemler DG. Holistic and analytic modes of processing: The multiple determinants of perceptual analysis. *Journal of Experimental Psychology: General* 1984;113:94–111. [PubMed: 6242409]
- Garner, WR. *The Processing of Information and Structure*. New York: Lawrence Erlbaum Associates; 1974.
- Garner WR, Felfoldy GL. Integrality of stimulus dimensions in various types of information processing. *Cognitive Psychology* 1970;1:225–241.

- Gibson BM, Wasserman EA, Frei L, Miller K. Recent advances in operant conditioning technology: A versatile and affordable computerized touchscreen system. *Behavior Research Methods, Instruments, & Computers* 2004;36:355–362.
- Guttman N. The pigeon and the spectrum and other perplexities. *Psychological Reports* 1956;2:449–460.
- Guttman N, Kalish HI. Discriminability and stimulus generalization. *Journal of Experimental Psychology* 1956;51:79–88. [PubMed: 13286444]
- Hull, CL. *Principles of Behavior: An Introduction to Behavior Theory*. New York: Appleton-Century-Crofts; 1943.
- Hyman R, Well A. Judgments of similarity and spatial models. *Perception and Psychophysics* 1967;2:233–248.
- Jones JE. Stimulus generalization in two and three dimensions. *Canadian Journal of Psychology* 1962;16:23–36. [PubMed: 14452285]
- Nosofsky RM. Similarity scaling and cognitive process models. *Annual Review of Psychology* 1992;43:25–53.
- Rohrbaugh M, Brennan JF, Riccio DC. Control of two-way shuttle avoidance in rats by auditory frequency and intensity. *Journal of Comparative and Physiological Psychology* 1971;75:324–330. [PubMed: 5087381]
- Ronacher B. Human pattern recognition: Evidence for a switching between strategies in analyzing complex stimuli. *Biological Cybernetics* 1984;51:205–210. [PubMed: 6518182]
- Ronacher B, Bautz W. Human pattern recognition: Individually different strategies in analyzing complex stimuli. *Biological Cybernetics* 1985;51:249–261. [PubMed: 3970985]
- Shepard, RN. Approximation to uniform gradients of generalization by monotone transformations of scale. In: Mostofsky, DI., editor. *Stimulus Generalization*. Palo Alto, CA: Stanford University Press; 1965. p. 94–110.
- Shepard RN. Stimulus and response generalization: A stochastic model relating generalization to distance in psychological space. *Psychometrika* 1957;22:325–345.
- Shepard RN. Toward a universal law of generalization for psychological science. *Science* 1987;237:1317–1323. [PubMed: 3629243]
- Shepard, RN. Integrality versus separability of stimulus dimensions: From an early convergence of evidence to a proposed theoretical basis. In: Pomerantz, J.; Lockhead, G., editors. *The Perception of Structure: Essays in Honor of Wendell R. Garner*. Washington, DC: American Psychological Association; 1991. p. 53–71.
- Tarr MJ, Bülthoff HH. Is human object recognition better described by geon structural descriptions or by multiple views? Comment on Biederman and Gerhardstein (1993). *Journal of Experimental Psychology: Human Perception and Performance* 1995;21:1494–1505. [PubMed: 7490590]
- Tversky A, Gati I. Similarity, separability, and the triangle inequality. *Psychological Review* 1982;89:123–154. [PubMed: 7089125]
- Warren JM. Perceptual dominance in discrimination learning by monkeys. *Journal of Comparative and Physiological Psychology* 1954;47:290–293. [PubMed: 13192221]
- Wasserman EA, Gagliardi JL, Cook BR, Kirkpatrick-Steger K, Astley SL, Biederman I. The pigeon's recognition of drawings of depth-rotated stimuli. *Journal of Experimental Psychology: Animal Behavior Processes* 1996;22:205–221. [PubMed: 8618103]

Figure 1.

Stimulus sets used to gather the stimulus generalization data. The stimuli shown to pigeons in Group Separable were circles that varied in size and diameter tilt (top). The stimuli shown to pigeons in Group Integral were renderings of a three-dimensional airplane that were rotated in depth along two orthogonal axes (bottom).

Group
Separable

Group
Integral

Figure 2.

Multidimensional generalization gradients plotting the mean response proportion to each of the stimuli presented to Group Separable (top) and to Group Integral (bottom) in Experiment 1. The same information is plotted as a surface plot at the left and as a circle plot at the right. See text for detailed description.

Figure 3.

Lack of fit of the model's predictions to the empirical data of Experiment 1 (SSE) as a function of r values ranging from 1, representing the City-Block metric, to 2, representing the Euclidean metric. The data from Groups Separable and Integral are presented in the top and bottom portions, respectively.

Figure 4.

Multidimensional generalization gradients plotting the mean response proportion to each of the stimuli presented to the pigeons in Experiment 2. The same information is plotted as a surface plot to the left and as a circle plot to the right. See text for detailed description.

Figure 5.

Lack of fit of the model's predictions to the empirical data of Experiment 2 (SSE) as a function of r values ranging from 1, representing the City-Block metric, to 2, representing the Euclidean metric.

Table 1

Best-fitting values of parameter r and RMSE values, both for the individual pigeon data and for the pooled data of each group in Experiment 1: Separable and Integral.

Bird	Group Separable					Group Integral				
	28W	39Y	60Y	8B	Group	38B	89B	93W	51Y	Group
Best-fitting r	0.82	0.61	0.54	0.62	0.64	7.39	2.22	1.01	1.47	1.72
RMSE										
Best fit	0.09469	0.05426	0.05615	0.04766	0.07643	0.09295	0.12524	0.08987	0.09975	0.11007
City-Block	0.09956	0.07463	0.15644	0.10392	0.11264	0.15023	0.13144	0.08806	0.10071	0.12015
Euclidean	0.14137	0.08939	0.22608	0.16094	0.16201	0.10166	0.12285	0.11477	0.09861	0.10991

Table 2

Best-fitting values of parameter r and RMSE values, both for the individual pigeon data and for the pooled data of the Integral pigeons in Experiment 2.

Bird	15W	24W	34R	39Y	Group
Best-fitting r	1.86	1.53	1.88	4.24	2.14
RMSE					
Best fit	0.14999	0.14372	0.16394	0.13374	0.14715
City-Block	0.15867	0.14503	0.17198	0.16091	0.15943
Euclidean	0.14704	0.14154	0.16068	0.13542	0.14647