



REVIEWS

A century of generalization

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We review data from both ethology and psychology about generalization, that is how animals respond to sets of stimuli including familiar and novel stimuli. Our main conclusion is that patterns of generalization are largely independent of systematic group (evidence is available for insects, fish, amphibians, reptiles, birds and mammals, including humans), behavioural context (feeding, drinking, courting, etc.), sensory modality (light, sound, etc.) and of whether reaction to stimuli is learned or genetically inherited. These universalities suggest that generalization originates from general properties of nervous systems, and that evolutionary strategies to cope with novelty and variability in stimulation may be limited. Two major shapes of the generalization gradient can be identified, corresponding to two types of stimulus dimensions. When changes in stimulation involve a rearrangement of a constant amount of stimulation on the sense organs, the generalization gradient peaks close to familiar stimuli, and peak responding is not much higher than responding to familiar stimuli. Contrary to what is often claimed, such gradients are better described by Gaussian curves than by exponentials. When the stimulus dimension involves a variation in the intensity of stimulation, the gradient is often monotonic, and responding to some novel stimuli is considerably stronger than responding to familiar stimuli. Lastly, when several or many familiar stimuli are close to each other predictable biases in responding occur, along all studied dimensions. We do not find differences between biases referred to as peak shift and biases referred to as supernormal stimulation. We conclude by discussing theoretical issues.

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The study of how external stimuli affect behaviour has been referred to as the theory of stimulus selection in ethology and stimulus control in experimental psychology, and has played a key role in both disciplines during the 20th century. A key finding of such research is generalization: if a behaviour has been established in response to a stimulus, novel stimuli resembling the first one will usually elicit the same response. Usually, modified stimuli are less effective than familiar ones, but sometimes they are even more potent in evoking the response. This finding has been referred to as 'supernormal stimulation' by ethologists, 'peak shift' by psychologists, and more recently 'response bias' (see, respectively, Tinbergen 1951; Mackintosh 1974; Enquist & Arak 1998). Interest in theories of generalization seems to have faded in recent years, although our understanding is still unsatisfactory (Mackintosh 1974; Ghirlanda & Enquist 1999). Behaviour is often 'explained' by merely empirical rules

of generalization or theories that more or less directly summarize observations (for example by incorporating observed features of generalization into the theory, Hull 1943; Mackintosh 1974). In this review we aim to organize existing data in a way useful to develop and test theories of generalization. We also point out findings that conflict with existing theories, and we conclude with a discussion of theoretical issues. Finally, we hope that this review will be helpful as a guide of what to expect when reactions to novel stimuli are important, for example in experimental design.

APPROACHES TO THE STUDY OF GENERALIZATION

Ethology and Experimental Psychology

Data about generalization come primarily from ethological and psychological studies of behaviour. Within experimental psychology, animals are typically trained to perform a response to one stimulus, called the positive stimulus (S^+), and not to a second, negative stimulus

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(S^-). The S^- may be absence of S^+ or a stimulus differing from S^+ in characteristics such as visual size or sound frequency. More complex arrangements, with several positive and negative stimuli, have also been used. After training, the animals' reactions to a set of test stimuli are recorded. These are usually chosen from a 'stimulus dimension' obtained by varying a physical variable such as wavelength of light or intensity of sound. Data can thus be represented in the form of a response gradient along the dimension; this is the chief analytical tool of the psychological tradition, from which key concepts such as 'peak shift' and 'stimulus control' are defined (e.g. Terrace 1966). The test stimuli typically include S^+ . If S^- lies on the test dimension, too, it is customary to speak of an 'intradimensional' discrimination, for example when light wavelength generalization is studied after a discrimination between two wavelengths. If S^- cannot be placed on the test dimension, the term 'interdimensional' discrimination is used, for instance if the test dimension is sound frequency and S^- is silence or white noise. The same discrimination can be both intra- and interdimensional depending on the test stimuli chosen. We thus prefer to speak of inter- and intradimensional tests, rather than discriminations.

Whereas psychologists are almost exclusively based in the laboratory, ethologists have mainly studied behaviour in nature. Although animals are seldom trained by the researcher, discriminations are common in the wild as well. For example, to incubate their eggs birds must discriminate between the egg and the nest background; to pursue females male butterflies must discriminate their presence from their absence, and so on. The main research tool in ethology has been the use of dummies resembling natural stimuli but with added, removed or modified features. For instance, the egg retrieval behaviour of the herring gull, *Larus argentatus*, has been studied using dummy eggs of different sizes, colours and shapes (Baerends 1982).

We can thus summarize both the ethological and the psychological methods as the recording of animals' reactions to stimulus sets including novel and familiar stimuli. In interpreting results from such experiments, it is important to remember that behaviour is influenced both by individual experiences and by the evolutionary history of the species. Even if the stimuli used in the laboratory have little significance for animals in the wild, pre-existing responses and predispositions can influence behaviour. For instance, novel stimuli can elicit fear. Thus, laboratory experiments only approximate the ideal situation of an empty memory modified by experience with only one or two stimuli, even when 'naive' individuals are used. The analysis of natural behaviour is even more complex, both because the animals' evolutionary history more directly influences behaviour and because experimental control over individual experiences is at most partial.

Analysis of Stimulus Dimensions

In both ethology and comparative psychology, results of generalization tests are most often analysed in terms of

Table 1. Contribution of rearrangement and intensity of stimulation along common stimulus dimensions

Stimulus dimension	Contribution of	
	Rearrangement	Intensity
Intensity of sound		L
Intensity of light		L
Chemical concentration (smell, taste)		L
Object size	L	L
Complex sound spectra	L	L
Complex light spectra	L	L
Object shape	L	S
Tone frequency	L	S
Monochromatic light	L	S
Object orientation	L	
Object location	L	

L: Large contribution; S: small contribution, or varying contribution depending on the exact stimuli used; no symbol means negligible contribution.

objective properties of stimuli. One drawback of this approach is that it ignores how stimuli are received by the sense organs. For instance, focusing on wavelength of light does not explain why ultraviolet light cannot control behaviour in some animals. But if we consider photoreceptors, we discover that some animals have none that react to ultraviolet light. Here we focus on two aspects of sense organ activation patterns. The first is the intensity of stimulation, by which term we mean the total activation of receptors. This is related to physical intensity but is not identical with it; for instance, a sound of 100 kHz does not elicit any activation in human ears regardless of its physical intensity. The second aspect is how a given amount of stimulation is distributed among receptors. We refer to stimulus dimensions along which intensity does not change as 'rearrangement dimensions', since different stimuli along such dimensions correspond to a different arrangement of the same amount of stimulation on the sense organs. Table 1 shows how common stimulus dimensions can be classified according to this scheme. The rationale for such a classification is that variation in intensity has significantly different behavioural effects, compared with rearrangement of stimulation (see below).

DATA SELECTION

Although experimental paradigms in generalization research can be summarized succinctly in their main points, countless variations exist. We have tried to include as many studies as possible in our analyses, but we deemed some unsuitable. Our guidelines may be summarized as follows. First, we included no study with fewer than three subjects per treatment, except when we considered the effect of group size. Second, responding should be probed at a sufficient number of stimulus locations to make inferences about gradient shape. When fitting a curve to the data, we required that more than 10 stimulus locations be probed. One exception is the

analysis of response biases, where responding to a single test stimulus may serve to estimate a bias. Third, we have not included studies whose outcome was importantly affected by unusual features of training or testing, apart from when we discuss the specific effects of such features (see especially intensity dimensions below). Fourth, we could not include some studies in quantitative analyses because they reveal generalization indirectly, for instance by studying how reproduction or position in a social hierarchy is affected by signals used in social interactions (e.g. Burley et al. 1982; Burley 1986; Johnson et al. 1993). Nevertheless, these are powerful examples of the biological significance of generalization. Lastly, we do not include temporal generalization, owing to our lack of familiarity with the field and the additional space it would require.

We turn now to reviewing the available data on generalization, considering rearrangement dimensions first, then intensity gradients, and lastly dimensions along which both the amount and the arrangement of stimulation on the sense organs vary. In order not to burden the text with the description, results and data sources of statistical tests, we have collected this information in Appendices 1 and 2. In the following, we refer to tests by their number in Appendix 1. A short summary concludes each major section.

REARRANGEMENT DIMENSIONS

Generalization gradients peaking at or near the positive stimulus are considered the prototypical finding about generalization (Fig. 1). Such gradients have been found along diverse stimulus dimensions such as light wavelength, tone frequency, object orientation and object location (Table 2). Stimuli along these dimensions are best described as corresponding to a rearrangement of stimulation with respect to the S^+ , without much change in the total activation of sense organs. For instance, all positions and orientations of lines or squares in the (centre of the) visual field give rise to the same amount of stimulation in the eye. This is also true of tones of the same physical intensity and not too different frequencies (e.g. human hearing, Coren et al. 1999). Variation in light wavelength can be classified as a rearrangement dimension as well, that is, total receptor activation is approximately constant over considerable wavelength ranges in many species.

Gradient Shape

Spence (1937), in his pioneering work on stimulus control, used parabolic functions to introduce the concept of a generalization gradient. In later work, he also assumed bell-shaped gradients (Spence 1942). He acknowledged that these choices were purely illustrative, lacking at the time reliable data. Hull (1943), based on Hovland's (1937) data, incorporated an exponential function into his theory of behaviour. Nowadays researchers mostly hold gradients to be either exponential or Gaussian (e.g. Blough 1975; Shepard 1987;

Staddon & Reid 1990; Cheng et al. 1997). We analysed 223 rearrangement gradients and found that Gaussian curves account for about 3% more of the variance in observed data (estimated by r^2 ; appendix 2 describes the fitting procedure). This difference is small, but significant (Test 1, $P < 10^{-10}$). Both Gaussians and exponentials account for more than 90% of the variance in most cases, and about 25% of the gradients conform better to the exponential shape. Figure 2 illustrates these results.

The experiments we surveyed were designed to give an overall picture of generalization gradients rather than to decide between two specific hypotheses. The region around the peak, most important to discriminate exponentials from Gaussians, is often poorly sampled. Better sampling appears to favour Gaussian fits, as shown in Fig. 3 relative to light wavelength generalization in the pigeon, *Columba livia* (see for instance the data from Blough 1975 in Fig. 1). Note also that fitting attempts are evaluated only in the light of sampled values. Strictly, we cannot say anything about other values. Yet we do not expect the actual gradient to depart systematically from a good fit. Inspection of Gaussian and exponential fits (e.g. Fig. 1) shows that exponential fits often predict a considerably taller gradient than actually observed (an average of 20% higher, Fig. 4a). Predictions from Gaussian fits, on the other hand, are distributed around the observed values (Fig. 4b). This suggests that Gaussian fits estimate gradient height more accurately. There is instead no difference between predictions of Gaussian and exponential fits about the location of the peak (Test 3, NS). Finally, we note that gradients that are clearly neither exponential nor Gaussian exist (e.g. the bottom gradients in Fig. 1; Hoffman & Fleshler 1964; Blough 1972).

Gradient Symmetry

Nearly all theories of generalization assume or predict that gradients obtained from interdimensional tests are symmetrical around the S^+ (Spence 1937; Hull 1943; Blough 1975; Shepard 1987). However, reproducible asymmetries have been reported. When data from all subjects taking part in an experiment are published, we can test whether they are consistently skewed towards one or the other side of the S^+ (see Appendix 2 for details). For instance, individual gradients in Hearst et al. (1964, pigeon, line orientation, S^+ = vertical line, S^- = no line) are skewed on the side of clockwise rotations (Test 4, $P < 0.05$).

When individual data are not published, we can gather group averages from different studies conducted under similar conditions, and look for a systematic across-study asymmetry. We can thus confirm that the the skewed gradient reported by Hearst et al. (1964) has been consistently observed in other studies (Test 4, $P < 10^{-4}$); responses to anticlockwise tilted lines are on average 92% of responses to clockwise tilted ones (range 76–104%). Similarly, an analysis of studies of light wavelength generalization in pigeons reveals that generalization around $S^+ = 550$ nm is consistently skewed (Test 5, $P < 10^{-6}$). Wavelengths shorter than 550 nm total an average of 67% of the responses to longer wavelengths

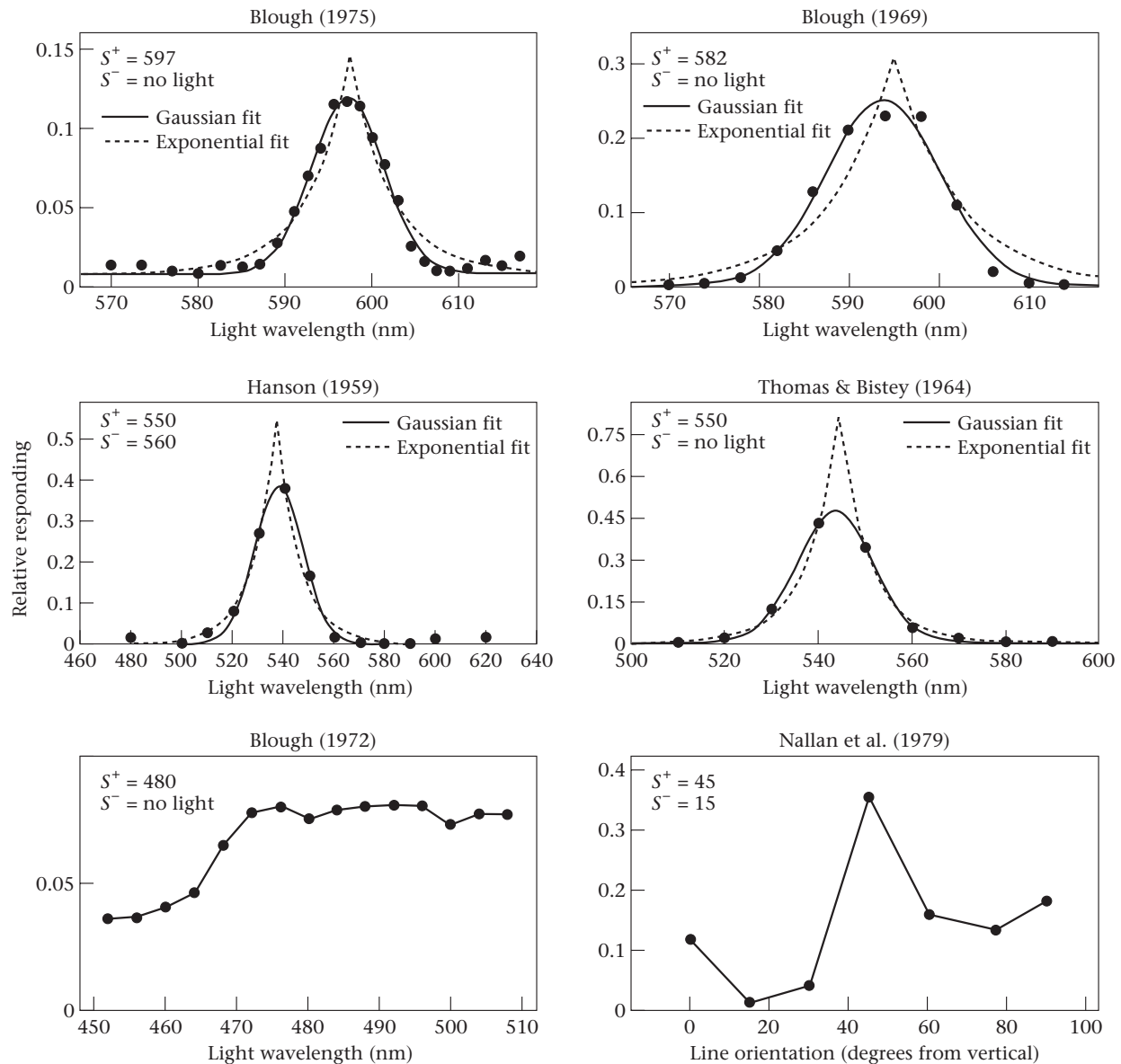


Figure 1. Examples of rearrangement generalization gradients, with Gaussian and exponential fits where appropriate. Sources are given above each graph.

(range 48–94%). Observations of asymmetrical gradients also exist for humans. For instance, Kalish (1958), Thomas & Mitchell (1962) and Thomas & Bistey (1964), reported marked asymmetries in every one of 12 groups of 20 subjects each generalizing along the dimension of light wavelength. Some gradients even show strong response biases, despite resulting from interdimensional tests (see e.g. the data from Thomas & Bistey 1964 in Fig. 1). Furthermore, Thomas & Bistey (1964) reported increasing asymmetry as more of the test dimension was sampled (symmetrically around the S^+), a challenging result for theories of generalization (analysis of variance in the original study: $F_{4,95}=11.00$, $P<0.001$).

Obviously, gradient symmetry depends on the scale chosen along a dimension. Symmetry on a linear scale will be destroyed passing to a logarithmic one, and vice

versa. Considering the sense organs can help us understand why a gradient is symmetrical on a given scale. For instance, in the case of sound, gradients appear most symmetrical on a logarithmic frequency scale, in keeping with physiological evidence that sound frequency must change exponentially to yield changes in activation patterns of constant magnitude in the ear (Kandel et al. 1991; Coren et al. 1999). For many dimensions de facto standards about which scale to use have emerged that agree with these considerations based on sensory physiology. We return to this issue below.

Response Biases

After training a discrimination between two stimuli differing along the test dimension (intradimensional

Table 2. Examples of generalization along rearrangement dimensions

Dimension	Response bias	Species	Source
Light spectra Monochromatic light	No data	Human	Kalish 1958
	Yes	Pigeon, <i>Columba livia</i>	Hanson 1959
	Yes	Goldfish, <i>Carassius auratus</i>	Ames & Yarczower 1965
Nonmonochromatic light*	Yes	Goldfish	Ohinata 1978
	Yes	Glow-worm, <i>Lampyrus noctiluca</i>	Schaller & Schwalb 1961
Colour of female dummy*	Yes	Glow-worm, <i>Phausis splendidula</i>	Schaller & Schwalb 1961
	No	Butterfly, <i>Argynnis paphia</i>	Magnus 1958
Colour of egg dummy*	Yes	Herring gull, <i>Larus argentatus</i>	Baerends 1982
Orientation of Line	Yes	Pigeon	Bloomfield 1967
	Yes	Fish, <i>Haplochromis burtoni</i>	Heiligenberg et al. 1972
	Yes	Human children	Nicholson & Gray 1971
Sound frequency	No data	Goldfish	Fay 1970
	Yes	Rat, <i>Rattus r. norvegicus</i>	Brennan & Riccio 1972
	Yes	Human	Baron 1973; Galizio 1985
	Yes	Pigeon	Klein & Rilling 1974
Location in space	Yes	Pigeon	Cheng et al. 1997
	No data	Honeybee, <i>Apis mellifera</i>	Cheng 1999, 2000

For laboratory studies, the column 'Response bias' refers to intradimensional tests. See the main text for information about biases in other conditions.

*Nonmonochromatic lights cannot be meaningfully aligned along a single dimension, and intensity effects may be caused by different sensitivity of the receptors to different wavelengths of light.

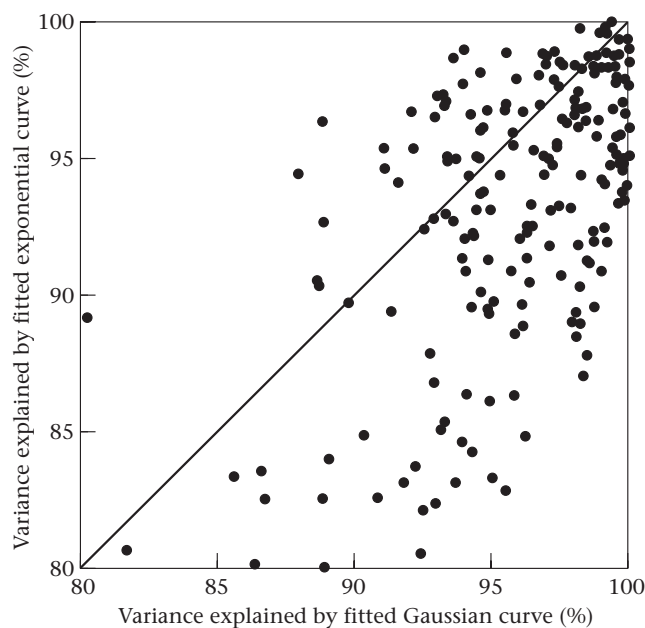


Figure 2. Comparison of Gaussian and exponential fits with empirical generalization gradients. Points above (below) the diagonal represent empirical gradients better fitted by exponential (Gaussian) curves.

tests), authors have often found response biases (Table 2). That is, there exist stimuli that elicit stronger responding than S^+ (Fig. 5a). These stimuli are, almost invariably, located further away from S^- . Recall that response biases can also appear in interdimensional tests (e.g. Kalish 1958; Thomas & Bistey 1964), a finding that has received

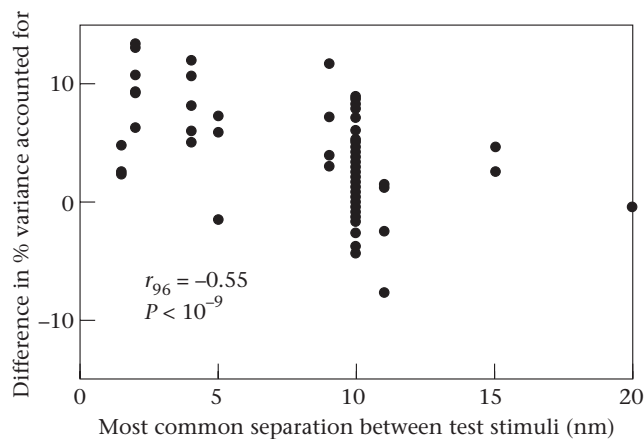


Figure 3. Differences in percentage of variance accounted for between Gaussian and exponential fits to light wavelength generalization data in pigeons, as a function of separation between test stimuli (see Test 2, Appendix 1, for data sources and statistics). Similar results are obtained when considering average separation between test stimuli rather than the most common one. Note that most studies adopt a sampling step of about 10 nm, where a large variation is observed.

little attention. Sometimes a 'negative' bias is also observed, that is, lower responding than to S^- to stimuli that are further away from S^+ . This effect is apparent when S^- elicits a considerable number of responses even after discrimination training (Fig. 5b; Stevenson 1966; Wills & Mackintosh 1998). Response biases along rearrangement dimensions also occur in nature, as reported in the ethological literature about 'supernormal stimuli' (Tinbergen 1951; Eibl-Eibesfeldt 1975; cf. Table 2 and

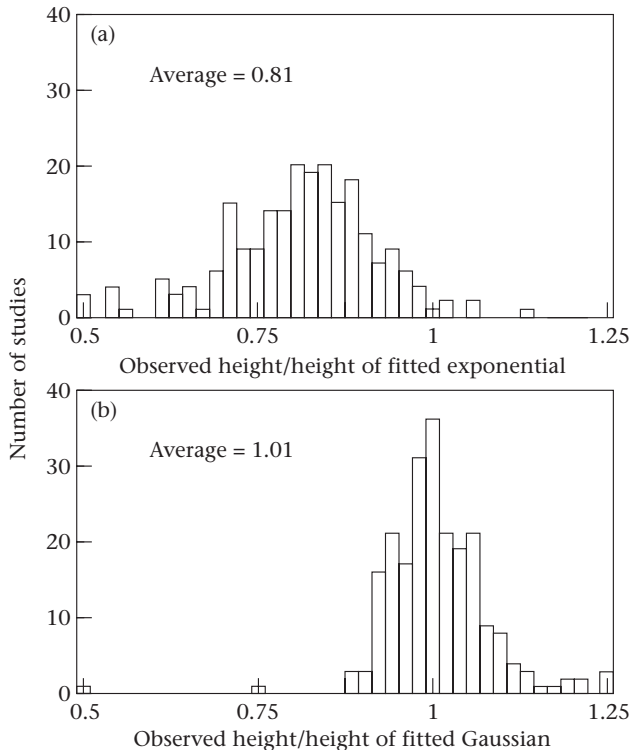


Figure 4. Predictions about gradient height by (a) exponential and (b) Gaussian fits to rearrangement gradients, compared with the observed height. Data sources in Test 1, Appendix 1.

Generalization of inherited and learned behaviour, below).

In field studies it is often difficult to know what experience an animal has had. Under laboratory conditions, however, there are a few well-established facts about the effects of previous experience on biases. A general finding is that both the strength of the bias (maximum responding relative to S^+) and the distance of the most effective stimulus from S^+ increase when the S^+ and S^- come closer. In Fig. 6 we show these effects in the pigeon, along the light wavelength dimension. The pattern is the same in all studies where the separation between S^+ and S^- has been varied. Examples are Hearst (1968, line-tilt, pigeon), Ohinata (1978, wavelength, goldfish), Baron (1973, tone frequency, humans) and Cheng et al. (1997, spatial location, pigeon).

The variation in Fig. 6 reveals that similarity between test stimuli is not the sole determinant of response biases. There are ample indications that training and testing procedures, as well as the characteristics of stimuli used, are important factors (Purtle 1973; Mackintosh 1974). For instance, the so-called 'errorless' discrimination training, where the intensity of the S^- is increased gradually, does not seem to produce response biases (Terrace 1964, 1966). An example of how testing can affect generalization is the finding that biases tend to recede when the test phase is very long (Crawford et al. 1980; Cheng et al. 1997). This may be the effect of the subjects learning that the test stimuli are not reinforced (see also Blough 1975).

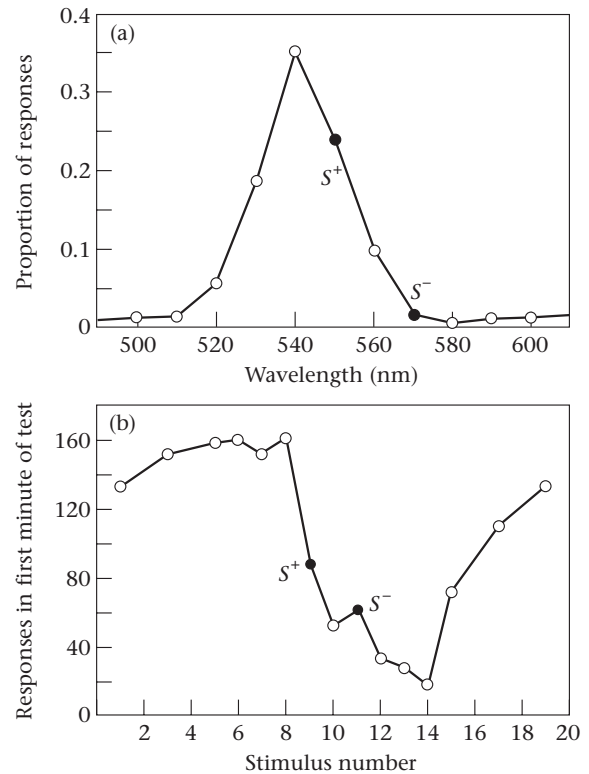


Figure 5. Examples of response biases along rearrangement dimensions. (a) Hanson's (1959) classical study. Pigeons were trained to peck a key for food when it was lit with a 550-nm light, but not when the wavelength was 570 nm. In a subsequent generalization test the maximum number of responses occurred at the 540-nm light. (b) A gradient showing response biases both left of S^+ and right of S^- , from Guttman (1965). He first trained pigeons to peck at all the wavelengths to be tested, then introduced a discrimination training by presenting only S^+ (still reinforced) and S^- (unreinforced). The following generalization tests reveal that some stimuli to the right of S^- are reacted to less than S^- .

Conclusions

(1) Generalization gradients along rearrangement dimensions are described better by Gaussian than by exponential functions (Test 1, Fig. 4).

(2) When the rearrangement dimension includes one S^+ but no S^- , the gradient typically peaks at S^+ (but not invariably, Fig. 1), and the gradient is typically symmetrical around S^+ ; however, reproducible asymmetries exist, and may be more common than usually assumed (Tests 4, 5).

(3) When the rearrangement dimension includes both one S^+ and one S^- , responding is biased: gradients typically peak at a stimulus that is further away from S^- than S^+ (Fig. 5); and closer S^+ and S^- produce gradients whose peak is both higher and further away from S^+ (Fig. 6).

INTENSITY DIMENSIONS

It has long been noted that, in contrast to rearrangement dimensions, intensity dimensions yield strongly

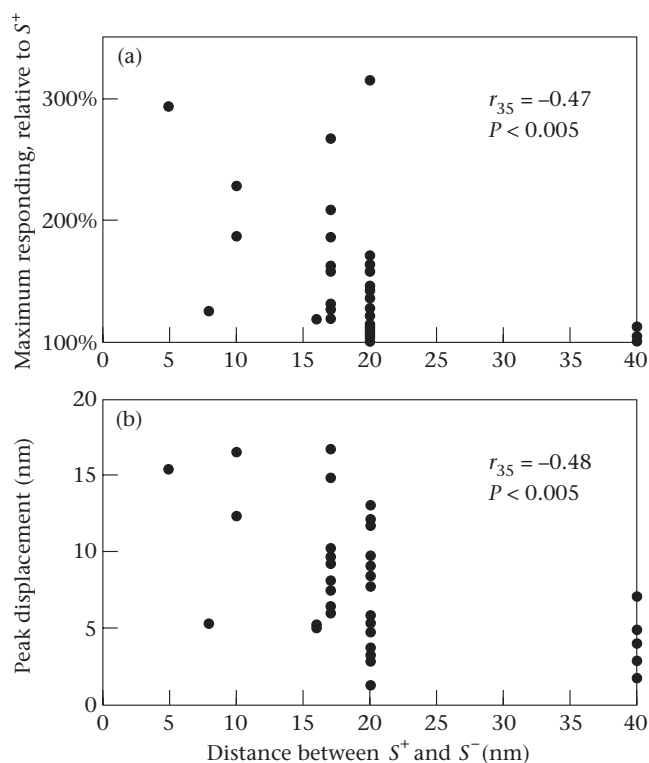


Figure 6. Dependence of response biases on the difference between S^+ and S^- . Data come from studies in which pigeons were trained to discriminate between two monochromatic lights (sources in Test 6, Appendix 1). (a) Ratio between peak responding and responding to the positive stimulus. (b) Displacement of gradient peak from the S^+ . Peak responding, peak position and responding to S^+ are estimated from fitted Gaussians.

asymmetrical gradients and strong response biases (Mackintosh 1974; Fig. 7, Table 3). This was once attributed to an ‘energizing’ effect of intensity on behaviour (Hull 1949). However, it is not intensity per se that controls responding, since gradients that are higher at lower intensities can follow from experiences with a faint S^+ and an intense S^- (Fig. 7b; Pierrel & Sherman 1960; Zielinski & Jakubowska 1977).

The shape of intensity generalization gradients has been a debated subject. Claims that variations in intensity produce monotonic gradients (i.e. ever-increasing or ever-decreasing) have been contrasted with findings of non-monotonic gradients (Ernst et al. 1971; Thomas & Setzer 1972). It is clear that intensity gradients cannot grow or fall forever; for instance, intensities that are too high will harm the sense organs, and those that are too low cannot be detected. However, important differences between intensity and nonintensity gradients exist independent of statements about gradient shape. For instance, in 30 of 38 intensity gradients surveyed, responding beyond S^+ does not drop below S^+ levels, even when the gradient is not monotonic (intradimensional rearrangement gradients: 2 of 93, Test 7 (1), $P < 10^{-6}$). Furthermore, a quantitative analysis shows that response biases along intensity dimensions are significantly stronger than along rearrangement dimensions (Test 8, $P < 10^{-6}$; Fig. 8).

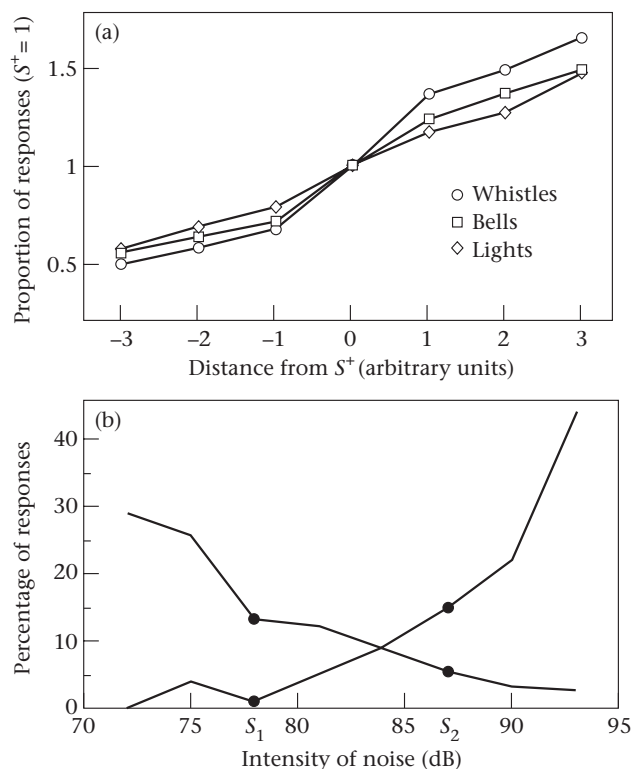


Figure 7. (a) Intensity generalization in dogs conditioned to salivate to a light, whistle or bell (position 0 on the horizontal axis). Responding is expressed in terms of proportion of responses relative to the S^+ . Data from Razran (1949), summarizing over 250 studies from Pavlov’s laboratory. (b) Intensity generalization in rats following training with two noise intensities, $S_1=78$ dB and $S_2=87$ dB. The gradient is reversed when the weaker stimulus is the positive one (data from Huff et al. 1975).

Returning to gradient shape, if we consider ‘monotonic’ a gradient that does not drop past S^+ (see below), we find 16 out of 38 monotonic intensity gradients, but none in 93 intradimensional rearrangement gradients (Test 7 (2), $P < 10^{-6}$).

Theories of generalization must thus explain a number of differences between intensity and rearrangement generalization. The only models that so far have met with some success (reviewed by Ghirlanda 2002) predict monotonic intensity gradients ‘under ideal conditions’ (that is, in idealized generalization experiments probing a memory modified by experiences with only two stimuli), and may be able to explain nonmonotonic intensity gradients by appealing to determinants of gradient shape other than stimulus dimension (S. Ghirlanda, unpublished data). In the following we discuss three such determinants.

First, sampling errors lead to underestimates of the number of monotonic intensity gradients. An inaccurate estimate of responding at a single point can transform a monotonic curve into a nonmonotonic one, but it is less likely that the reverse occurs. The above definition of ‘monotonicity’, considering only the S^+ and stimuli further away from S^- , reduces but does not eliminate the effects of sampling. Indeed, monotonicity of intensity

Table 3. Examples of generalization along intensity dimensions

Intensity dimension	Monotonicity	Response bias	Species	Source
Sound Tone	Yes	Yes	Rat, <i>R. norvegicus</i>	Pierrel & Sherman 1960
	Yes/no*	Yes	Rat	Thomas & Setzer 1972
	Yes/no*	Yes	Guinea pig, <i>Cavia porcellus</i>	Thomas & Setzer 1972
	Yes	Yes	Rat	Brennan & Riccio 1973
	Yes	Yes	Rabbit, <i>Oryctolagus cuniculus</i>	Scavio & Gormezano 1974
Bell	Yes	Yes	Dog, <i>Canis familiaris</i>	Razran 1949
Whistle	Yes	Yes	Dog	Razran 1949
White noise	Yes	Yes	Rat	Huff et al. 1975
	Yes	Yes	Rat	Zielinski & Jakubowska 1977
Light White light	Yes	Yes	Dog	Razran 1949
	Yes/no*	Yes	Pigeon, <i>C. livia</i>	Ernst et al. 1971
	No	Yes	Pigeon	Lawrence 1973
	Yes	Yes	Rat	Brown 1942
	No data	Yes	Earthworm, <i>Lumbricus terrestris</i>	Gilpin et al. 1978
Brightness of egg dummy	Yes	Yes	Herring gull, <i>L. argentatus</i>	Baerends 1982
Brightness of female dummy	Yes	Yes	Butterfly, <i>Eumenes semele</i>	Tinbergen et al. 1942
	Yes	Yes	Glow-worm, <i>P. splendidula</i>	Schaller & Schwalb 1961
	No	No	Glow-worm, <i>L. noctiluca</i>	Schaller & Schwalb 1961
Chemical concentration Odour	No data	Yes	Bee, <i>A. mellifera</i>	Bhagavan & Smith 1997
	No data	Yes	Rat	Tapper & Halpern 1968

*Both monotonic and nonmonotonic gradients were found.

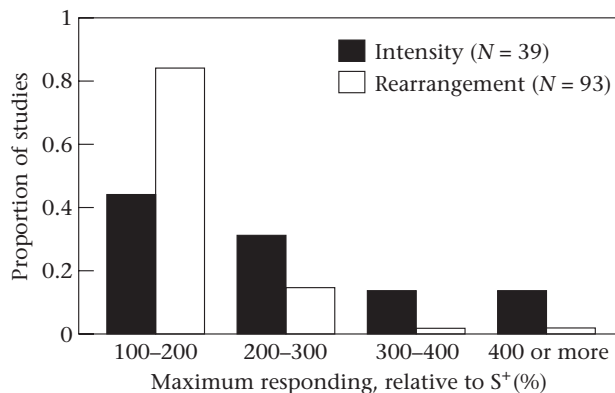


Figure 8. Distribution of response biases along intensity and rearrangement dimensions. The strength of bias is measured as the ratio of observed maximum responding to responding to S^+ . Note that strength of bias is underestimated along intensity dimensions, since responding often does not start decreasing within the probed stimulus range. Data sources in Test 8, Appendix 1.

gradients increases with better sampling, that is, with larger experimental groups (Test 9, $P < 0.01$).

Second, a number of studies reporting nonmonotonic intensity generalization were designed to explore the effects of very long test sessions (e.g. Newlin et al. 1979; Thomas et al. 1991, 1992, excluded from the analyses above; this research is summarized in Thomas 1993). Under these conditions, gradients can change from monotonic to peaked during the test (Fig. 9). Such a shape change appear analogous to the disappearing or waning of response biases in the course of long test sessions, along rearrangement dimensions (e.g. Crawford et al. 1980, Cheng et al. 1997).

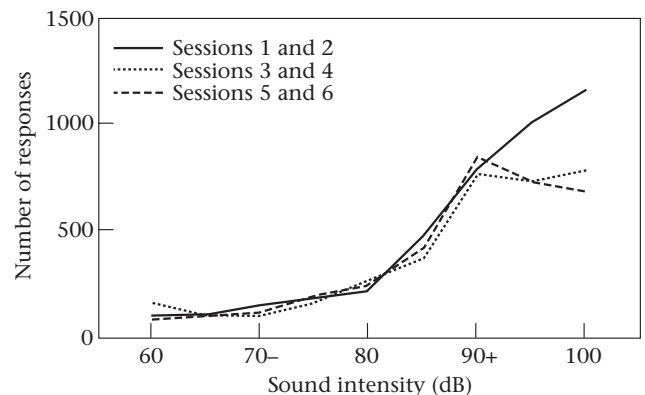


Figure 9. Data on sound intensity generalization in rats (Pierrel & Sherman 1960), collected over 6 days of testing in extinction. Gradients from test days 1 and 2 are both monotonic (their average is shown in the figure); gradients from subsequent days are not.

Third, laboratory data are often analysed by taking into account only experimentally controlled stimuli. However, responding to both the low and high ends of intensity continua is likely to be influenced by factors beyond experimental control. Stimuli of high intensity, for example very loud sounds or very bright lights, are often avoided by animals. Similarly, stimuli of very low intensity (silence, a dark response key) are usually not reacted to. In addition to such generic reactions, specific responses may interfere. For instance, Baerends (1982) reported that lightly coloured egg dummies are preferentially retrieved by herring gulls, *Larus argentatus*, but this preference does not extend to white dummies. Studies with related species have shown that gulls usually remove

Table 4. Examples of generalization along size dimensions

Size dimension	Response bias	Species	Source
Circle	No data	Rat, <i>R. r. norvegicus</i>	Grice & Saltz 1950
	No data	Pigeon, <i>C. livia</i>	Jenkins et al. 1958
	No data	Toad, <i>Bufo bufo</i>	Ewert 1980
	Yes	Horse, <i>Equus caballus</i>	Dougherty & Lewis 1991
	Yes	Butterfly, <i>E. semele</i>	Tinbergen et al. 1942
	Yes	Human	Berlyne 1950
Square	No data	Toad	Ewert 1980
Rectangle	No data	Human	Rosenbaum 1953
Egg	Yes	Herring gull, <i>L. argentatus</i>	Baerends 1982
	Yes	Black-headed gull, <i>L. ridibundus</i>	Baerends et al. 1975
	Yes	Oystercatcher, <i>Haematopus ostralegus</i>	Tinbergen 1951
	Yes	Ringed plover, <i>Charadrius hiaticula</i>	Koehler & Zagarus 1937
Tail	Yes	Widowbird, <i>Euplectes progne</i>	Andersson 1982
	Yes	Swordtail fish, <i>Xiphophorus helleri</i>	Basolo 1990; Basolo & Delaney 2001
Food item	Yes	Newborn chicks, <i>Gallus g. domesticus</i>	Gamberale & Sillen-Tullberg 1998; Gamberale-Stille 2000
Female dummy	Yes	Butterfly, <i>Argynnis paphia</i>	Magnus 1958
Female lantern	Yes	Glow-worm, <i>P. splendidula</i>	Schaller & Schwalb 1961
	No	Glow-worm, <i>L. noctiluca</i>	Schaller & Schwalb 1961

white objects from the nest (a likely antipredatory defence; Tinbergen et al. 1962; Baerends 1982).

Conclusions

(1) Gradients obtained along intensity dimensions show larger response biases than rearrangement gradients (Fig. 8).

(2) Many intensity gradients are monotonic (rather than peaked) over large ranges of intensity; more specifically: responding increases with intensity when S^+ is more intense than S^- (including when S^- is S^+ 'turned off', e.g. a dark versus an illuminated key); and responding decreases with intensity when S^+ is less intense than S^- .

(3) Observed departures from monotonicity can, at least in some cases, be ascribed to: errors in sampling the gradient (Test 9); long test sessions, leading to changes in gradient shape (Fig. 9); and pre-existing reactions (both inherited and learned) to very intense stimuli (often avoided) or very weak ones (often ignored).

VARIATION IN SIZE AND OTHER DIMENSIONS

Along size dimensions, both the amount of stimulation and its arrangement on the sense organs vary. Consider a familiar stimulus of a given size. A bigger stimulus will act on more sensory cells than the familiar one, providing more stimulation. On the other hand, it will also provide a different arrangement of stimulation. We can try to understand size gradients as a trade-off between these two components. One immediate consequence is that the gradient may be asymmetrical, higher on the side of

bigger sizes. This is because the intensity and rearrangement components have contrasting effects for bigger stimuli (stimulating more receptors, but in a different pattern), but work together in reducing responding to smaller stimuli (stimulating fewer receptors and in a different pattern). This prediction is confirmed by available data (Test 10, $P < 0.05$). The same data suggest that size gradients are described better by Gaussian than by exponential curves (Test 11, $P = 0$). Both conclusions should be viewed as tentative in light of the small number of studies examined ($N = 7$ and $N = 8$, respectively). Another element in support of a rearrangement/intensity analysis of size dimensions is that size gradients show larger response biases than rearrangement gradients (Test 8, $P < 0.02$). In the small sample collected, biases towards bigger sizes appear comparable with biases along intensity dimensions (Test 8, NS).

Table 4 gives examples of response biases along size dimensions. Similar regularities as those reported above for rearrangement dimensions seem to apply. For instance, Weinberg (1973) found a stronger bias when S^+ and S^- were closer in size.

If a simple consideration of the arrangement and intensity of stimulation is helpful in analysing size dimensions, it is not so for many other dimensions (Table 5). In some cases, we do not know enough about the sense organs underlying perception along some dimensions, for example floor tilt (Lyons et al. 1973) or arm movement (Hedges 1983; Dickinson & Hedges 1986). In other cases, for example complex variations in shape (Ferraro & Grisham 1972; Wasserman et al. 1996), distinguishing between intensity and nonintensity effects is simply not sufficient. When we lack information about underlying

Table 5. Examples of generalization along dimensions that cannot be classified with the rearrangement/intensity scheme

Dimension	Response bias	Species	Source
Visual shape			
Female dummy	Yes	Butterfly, <i>A. paphia</i>	Magnus 1958
Polygon	Yes	Pigeon, <i>C. livia</i>	Ferraro & Grisham 1972
Egg	No	Herring gull, <i>L. argentatus</i>	Baerends 1982
Visual contrast	Yes	Herring gull	Baerends 1982
	Yes	Chicks, <i>Gallus g. domesticus</i>	Osorio et al. 1999
Length of movement	Yes	Human	Hedges 1983
	No data	Human	Dickinson & Hedges 1986
Click rate	Yes	Pigeon	Farthing & Hearst 1972
	Yes	Rat, <i>R. r. norvegicus</i>	Weiss & Schindler 1981
Flicker rate	Yes	Pigeon	Sloane 1964
	Yes	Butterfly, <i>A. paphia</i>	Magnus 1958
Floor tilt	Yes	Pigeon	Lyons et al. 1973
	Yes	Pigeon	Riccio et al. 1966
Calls/songs	Yes	Monkey, <i>Callimico goeldii</i>	Masataka 1983
	Yes	Blackbird, <i>Turdus merula</i>	Wolffgramm & Todt 1982
Human faces	Yes	Human	Rhodes 1996; Rhodes & Zebrowitz 2002
	Yes	Chickens	Ghirlanda et al. 2002
Checkerboard patterns	Yes	Human	McLaren et al. 1995
Icon sets	Yes	Human	Wills & Mackintosh 1998
Drawings of rotated objects	No data	Pigeon	Wasserman et al. 1996
'Aggressiveness' of verbal stimuli	No data	Human	Buss 1961; 1962
'Fearfulness' of snake pictures	No data	Human	Buss et al. 1968

sensory processes, we can try to infer some characteristics of such processes by analysing the experimental data in the light of what we know from other, better studied dimensions. For example, Dickinson & Hedges (1986) let blindfolded humans move a sliding handle for a given distance, and tested them with movements of different lengths by asking if they matched the training one. Their results seem to suggest that length of movement is perceived as a rearrangement dimension. Monotonic gradients have been reported along dimensions that cannot be readily identified as intensity ones (Ghirlanda & Enquist, 1999); for instance rate of stimulus presentation (Magnus 1958; Weiss & Schindler 1981) or femininity/masculinity of human faces (Enquist et al. 2002b). The case of changes in shape is particularly interesting. For instance, Magnus (1958), studying *Argynnis paphia* butterflies, found that certain shapes attract males more than female-shaped dummies, but also that males respond very little to other shapes (Fig. 10). Data of this kind can be used to explore how similarity is perceived across species.

Conclusions

(1) Both peaked and monotonic gradients have been found along dimensions where both the intensity and the arrangement of stimulation vary.

(2) Response biases have been found along all dimensions investigated so far.

(3) Generalization along size dimensions is influenced by both intensity and rearrangement effects: size generalization gradients are typically peaked; they are better approximated by Gaussian than by exponential functions (Test 11); they exhibit larger biases than gradients along rearrangement dimensions, and comparable to intensity gradients (Test 8); and when S^- is the absence of S^+ , responding is biased towards bigger sizes (Test 10).

FACTORS AFFECTING THE AMOUNT OF GENERALIZATION

A fundamental question is what regulates the amount of generalization along a dimension. The width of a peaked gradient provides a measure of the amount of generalization, and one factor related to gradient width is discriminability. Guttman & Kalish (1956) noted that generalization is measured by the change in behaviour arising from a change in stimulation, whereas discriminability is defined as the change in stimulation necessary to yield a behavioural change (cf. Lashley & Wade 1946). They thus suggested that generalization and discriminability should be inversely related, but because they lacked reliable data on discriminability they failed to

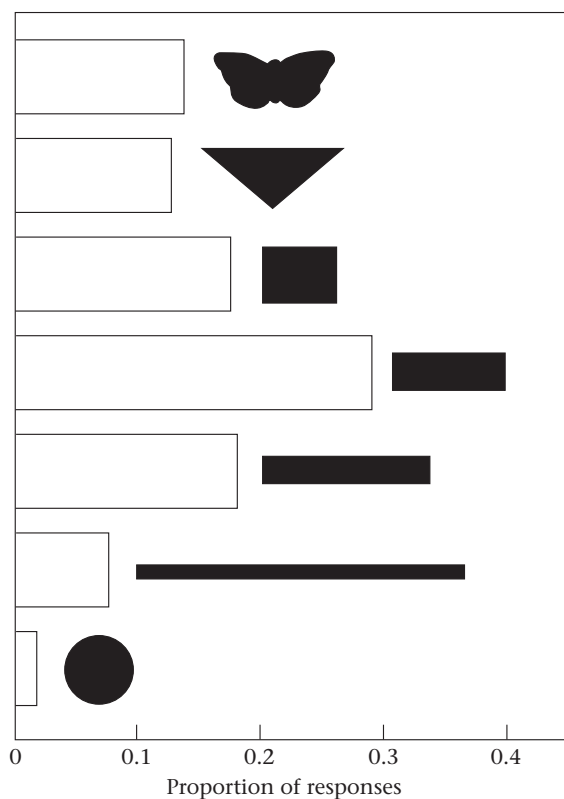


Figure 10. Reactions of male *Argynnis paphia* butterflies to female models of different shapes (data from Magnus 1958). The effectiveness of each model is expressed as the proportion of flights towards it on a total of 135 flights, in an open area where all models were visible simultaneously. All models had an area of approximately 22 cm² and were of the same colour (orange-red).

observe this relation studying light wavelength generalization in the pigeon. Later work has confirmed that pigeons generalize more in regions of the light spectrum where discriminability is poorer (reviewed in Honig & Urcuioli 1981). The same conclusion was reached by Kalish (1958) in a study of wavelength generalization in humans. Similarly, Fay (1970) showed that width of sound frequency generalization gradients in goldfish increases approximately linearly with the frequency of the S^+ , in line with the decreasing discriminability along this dimension (Hawkins 1981). Furthermore, discriminability can change differently on the two sides of the S^+ , thus affecting gradient symmetry (Blough 1972; Honig & Urcuioli 1981). We stress that discriminability and generalization are both behavioural measures, and thus one cannot explain the other. Rather, we should understand how both emerge from characteristics of nervous systems such as the response properties of receptors and how signals from receptors are processed.

A second factor influencing the amount of generalization is the experiences an animal had along the test dimension. Gradients obtained from interdimensional tests along the same dimension can vary considerably in width. An analysis of light wavelength generalization in the pigeon, for instance, shows that the standard deviation of Gaussian fits varies from about 2.5 nm (Blough

1969) to about 27 nm (Thomas & King 1959), indicating that choice of stimuli and details of experience have a large impact on amount of generalization. Adding negative stimuli along the test dimensions tends to make gradients narrower. For instance, pigeons generalize less after discrimination between two wavelengths than after discrimination between one wavelength and a dark stimulus (Test 12, $P < 0.001$). This effect has also been observed in goldfish, along the wavelength dimension (Ames & Yarczower 1965; Ohinata 1978), and in humans, along the dimension of sound frequency (Baron 1973).

So far we have mainly discussed generalization after experiences with only one S^+ and one S^- . In reality, a particular external condition, such as presence of food, produces many different stimuli on the sense organs (many positive stimuli for feeding behaviour). For example, food items differ in appearance and a single food item gives rise to different receptor activations because of variations in distance, light conditions, orientation and so on. In such situations there is variation within as well as between the sets of positive and negative stimuli. Despite the obvious biological importance of the subject, our knowledge of generalization following experiences with many stimuli is unsystematic. Relevant data come from a variety of sources such as studies of summation, generalization, memory and perceptual constancy (Walsh & Kulikowski 1998). In Fig. 11 we show some data from studies of generalization. When two or more positive stimuli are close enough we may observe stronger reactions to intermediate stimuli (Fig. 11a), a result found also in studies of summation and stimulus compounds (Wagner 1971; Weiss 1972; Kehoe 1986) and in evaluations of the prototype model of memory (Rosch et al. 1976; Homa et al. 1981; Shanks 1995). When the positive stimuli are more distant the intermediate ones may result in less responding (Fig. 11a). This may be the same as the failure of revealing prototype effects in some memory studies (Lea & Harrison 1978; Pearce 1987; Watanabe 1988). A fundamental question, for both behaviour and evolution, is whether response biases are found after the same amount of experience with many stimuli (Enquist & Johnstone 1997; Enquist & Arak 1998). Flat gradients (Fig. 11c) and small (Fig. 11b) and large biases (Fig. 11d) have all been reported. The strongest biases seem to appear along intensity dimensions (Fig. 11d, from Scavio & Gormezano 1974; see also Kessen 1953; Bass 1958; Murray & Kohfeld 1965; Birkimer & James 1967; Blue et al. 1971).

Conclusions

(1) Gradient width and symmetry can be related to discriminability along the test dimension: finer discriminability is correlated with narrower gradients; and when discriminability is different on the two sides of S^+ asymmetrical generalization gradients are observed.

(2) Along rearrangement dimensions, discriminations between stimuli leads to decreased generalization (narrower gradients).

(3) Along rearrangement dimensions, training on several or many equally rewarded S^+ increases generalization

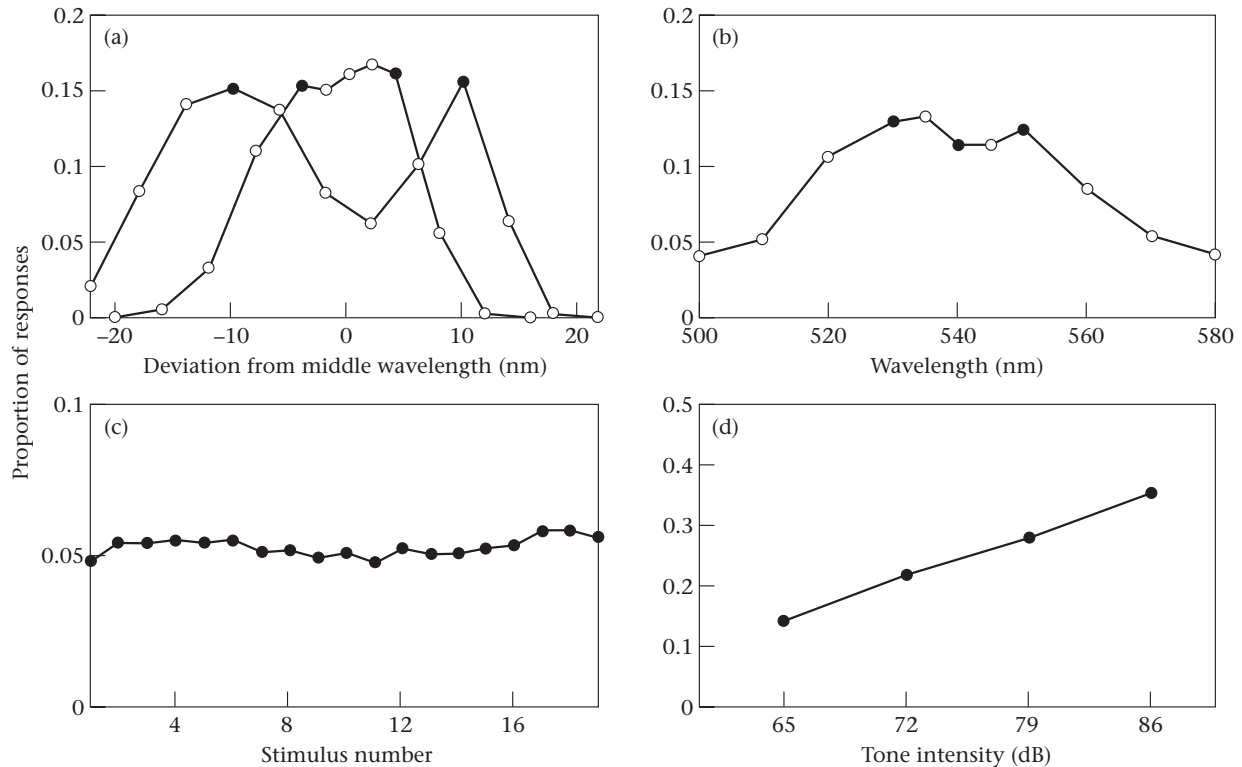


Figure 11. Four examples of generalization after experience with many stimuli. ●: Training stimuli; ○: test stimuli. Subjects had the same experience with all training stimuli. (a) Two-stimulus training can yield gradients with both one or two peaks depending on the difference between stimuli (data from Blough 1969, pigeon, wavelength). (b) Three-stimulus training can produce less responding to the intermediate stimulus (data from Kalish & Guttman 1959, pigeon, wavelength). (c) In this case no response biases are found after extensive experience with a set of contiguous stimuli (data from Guttman 1965, pigeon, wavelength). (d) Responding can be stronger to more intense stimuli, even when all stimuli were followed by the same consequences during training (data from Scavio & Gormezano 1974, rabbit, tone intensity).

(broader gradients): if the S^+ 's are close to each other, a flat or almost flat gradient develops over the range covered by the training stimuli; departing from the S^+ on both sides, the gradient falls down (Fig. 11a, b, c); the gradient shows multiple peaks if the distance between training stimuli is sufficiently increased (Fig. 11a); and responding to all training stimuli is the same or similar (small biases, Fig. 11b, c).

(4) Along intensity dimensions, substantial biases in responding persist even when two or more stimuli are equally rewarded. The more intense S^+ 's elicit stronger reactions (Fig. 11d; Kessen 1953; Bass 1958; Murray & Kohfeld 1965; Birkimer & James 1967; Blue et al. 1971).

GENERALIZATION OF INHERITED AND LEARNED BEHAVIOUR

Both genetically inherited and individually learned responses generalize to novel stimuli (Tables 2–5). Within ethology, however, there has been a tendency to separate the study of innate and learned generalization. For instance, ethologists have often claimed that supernormality and peak shift are distinct phenomena, at the same time that similarities have been acknowledged (Baerends & Krujtit 1973; Hogan et al. 1975; Staddon 1975; Dawkins & Guilford 1995). Within psychology, the question is seldom addressed explicitly; however, defini-

tions of generalization typically make direct reference to individual learning (Kalish 1969). These attitudes probably stem from early ideas within the two disciplines: classical psychologists often ignored innate determinants of behaviour (Watson 1924), and early ethologists claimed that inherited and learned behaviour are governed by different mechanisms (Von Uexkull 1928; Lorenz 1937).

Although such rigid ideas have been abandoned (Hogan & Bolhuis 1994; Bolhuis & Hogan 1999), the idea that inherited and learned behaviour generalize differently seems to have survived longer (Baerends & Krujtit 1973; Dawkins & Guilford 1995). In particular, it has been claimed that innate behaviour results in 'open-ended' generalization (i.e. monotonic gradients), while individual learning does not (Baerends & Krujtit 1973; Hogan et al. 1975; Lorenz 1981). The data do not support this statement. Note first that ethological studies of supernormality are not always about behaviour that is independent of individual learning (e.g. egg retrieval in gulls, Baerends 1982). Furthermore, some dimensions cannot by their nature result in open-ended generalization, regardless of ontogeny of behaviour. For instance, the response of male *Haplochromis burtoni* cichlids to the orientation of the head stripe (Heiligenberg et al. 1972) can only come back to its original value after the stripe has turned a full circle.

Pure rearrangement dimensions are rare in ethological studies, as test stimuli most often vary in complex ways. One exception is the just cited study by Heiligenberg et al. (1972), where the supernormal effect of a rotated head stripe decreases after only a 90° rotation. In other cases a rearrangement dimension can be defined by varying only one characteristic of a complex stimulus. For instance, many of the stimuli in Fig. 10 are rectangles of different length and constant area. It is clear that the preferences of *A. paphia* males along this rearrangement dimension are not open ended. The case of colour is more complex. First, different light spectra of the same physical intensity can elicit different amounts of activation in receptors (and differences between species exist). Second, physical intensity is seldom controlled for in ethological studies. Anyway, ethologists report that dummies of unnatural colour can be both more and less effective in eliciting an innate behaviour (Magnus 1958; Schaller & Schwab 1961). In some cases the most effective colour is clearly not at the extremes of the spectrum (*L. noctiluca* glow-worms: Schaller & Schwab 1961; herring gulls: Baerends 1982) or closely matches the natural colour (*A. paphia* butterflies: Magnus 1958).

Open-ended generalization of innate behaviour has been reported almost exclusively along intensity dimensions, for instance by Tinbergen et al. (1942, brightness of female butterfly dummy), and Schaller & Schwab (1961, brightness of glow-worm female dummy), with a few exceptions along size dimensions (where strong biases are expected, see above). For example, Baerends (1982) showed that oversized eggs are preferred by incubating gulls up to giant sizes. Magnus (1958) provided mixed evidence, showing that male *A. paphia* butterflies prefer four-fold enlarged female dummies to dummies twice the normal size when the dummies are stationary, but not when they imitate flight. Similarly, Schaller & Schwab (1961) reported that in glow-worms, *P. splendidula* males prefer dummy female lanterns four times bigger than normal, but *L. noctiluca* males do not. There are further reports that the supernormal effect of bigger stimuli often quickly ceases. One instance is the response of male *P. splendidula* and *L. noctiluca* to circular lights, which declines for circles several times bigger than the female's lantern (Schaller & Schwab 1961). The same authors showed that *L. noctiluca* males prefer a dummy lantern containing three horizontal segments to one with six (two is normal). Koehler & Zagarus (1937) found that ringed plovers, *Charadrius hiaticula*, retrieve eggs weighing 17 g, but not those above 35 g (normal eggs weigh about 11.5 g). In this last case individual learning may play a role (cf. Baerends 1982). Finally, Ewert (1980) has shown that both naive and experienced toads, *Bufo bufo*, clearly prefer catching objects within a restricted size range.

Conclusions

We could find no difference between generalization of genetically inherited and individually learned behaviour, with respect to either gradient shape or response biases: the distinction between the effects of intensity and

rearrangement of stimulation appears valid for both inherited and learned behaviour; and the claim that biases in inherited behaviour are open ended (monotonic) whereas biases in learned behaviour are limited is unsupported.

DISCUSSION

Empirical data gathered in about 100 years of research establish generalization as a fundamental behavioural phenomenon, whose basic characteristics appear universal. Birds and mammals are most studied, but fish, insects, amphibians and reptiles generalize in the same ways. It seems to matter little, for generalization, whether a behaviour has been acquired phylogenetically or through individual learning, and the nature of sensory continua is an important determinant of gradient shape. Furthermore, generalization seems little dependent on the context in which a given behaviour is used. That is, if a discrimination between green and red is established, generalization to other colours will follow independent of whether the discrimination is about food items or potential partners (e.g. Ghirlanda et al. 2002), or on whether behaviour is performed by children to obtain 'points' or by pigeons pecking for food. The generality of the findings reviewed suggests that generalization arises from basic and universal characteristics of behaviour mechanisms (cf. Hogan 1994).

This review has focused on empirical findings, but we end with some theoretical considerations. A number of attempts have been made to understand the causes of generalization (reviewed in Kalish 1969; Mackintosh 1974). Theorizing about mechanisms has considered properties of stimuli, sense organs and neural processing, and how these factors interact. Physical similarity between stimuli is one cause of generalization. Stimuli may be similar because they share common components, and generalization may follow because novel stimuli include components also present in familiar stimuli (e.g. Thorndike 1911; Guthrie 1930, 1935; Blough 1975; Rescorla 1976). However, not all stimuli are made up of 'components' in this sense (e.g. light and sound spectra). In general, what is similar and different to an organism depends also on properties of receptors and the organization of sense organs (including early processing of neural signals within sense organs). These factors determine how physical similarity translates into similarity of nervous signals to the brain, and will thus contribute to generalization. Receptors and sense organs have often been ignored, especially in contemporary psychological models (but not always in early ones, Hull 1943; Schlosberg & Solomon 1943; Hebb 1949). By considering them it may be possible to account for both rearrangement generalization and intensity generalization within the same model, by recognizing that similarity depends upon which receptors are stimulated and to what degree (Ghirlanda 2002).

Generalization is also modulated centrally in the nervous system. Suggestion about how this occurs vary in detail, but the core idea is that processing of stimuli that are distinctly different can rely, at least to some extent, on

Table 6. Basic predictions by models of generalization

Theory	Rearrangement generalization			Intensity generalization			Source
	Bell shape	Biases along dimensions including S^+ and S^-	Monotonic increase ($S^+ > S^-$)	Monotonic decrease ($S^+ < S^-$)	Stronger biases		
Early ideas suggesting overlap or interactions among nerve cells*		Consequences unclear or not studied				Pavlov 1927; Hebb 1949; Horne 1965; Thompson 1965; Lorenz 1981; Baerends 1982	
Gradient interaction, original formulation	Assumed	Yes†	No	No	No	Spence 1937; Hull 1943	
Gradient interaction, later developments	Assumed	Yes†	Assumed	No	Assumed	Hull 1949; Perkins 1953; Logan 1954	
Exponential generalization in 'psychological space'§	No	No	No	No	No	Shepard 1987; Cheng et al. 1997	
Gaussian generalization in 'psychological spaces'§	Assumed	Yes	No	No	May be assumed	Shepard 1987	
Configural theory	Assumed	Yes	No	No	May be assumed	Pearce 1987	
Blough's model, original formulation	Assumed	Yes	No	No	May be assumed	Blough 1975	
Blough's model, reinterpretation*	Yes	Yes	Yes	Yes	Yes	Ghirlanda & Enquist 1999; Ghirlanda 2002	
Feed forward networks, with idealized inputs‡	No/assumed	No/yes	No	No	No	Gluck 1991; Pearce 1994; S. Ghirlanda, unpublished data	
Feed forward networks, with realistic inputs*	Yes	Yes	Yes	Yes	Yes	Ghirlanda & Enquist 1998	
Overlap theory, based on receptor activations*	Yes	Yes	Yes	Yes	Yes	Ghirlanda & Enquist 1999	

Derivations for some of these predictions not in the original sources can be found in Ghirlanda & Enquist 1999; Ghirlanda 2002.

*Empirical knowledge about the nervous system is used.

†Responding underestimated.

‡See cited papers for details of assumed stimulus representations.

§For possible improvements, see Ennis (1988), Shepard (1988), Staddon & Reid (1990), Shepard (1990).

the same nerve cells and connections (Pavlov 1927; Hebb 1949; Horne 1965; Thompson 1965; Baerends & Kruijt 1973; Blough 1975; Lorenz 1981). Distinct stimuli may thus come to elicit similar responses. Generalization of this kind is strongly dependent on experience (including the species' experience, coded in the genes). Often generalization is substantial along dimensions with which the organism has little experience (Peterson 1962; Rubel & Rosenthal 1975; Kerr et al. 1979). Along familiar dimensions organisms generalize less: latent learning, perceptual learning and discriminations between similar stimuli all decrease generalization (Mackintosh et al. 1991; Bennett et al. 1994; see also above). Discrimination learning, in particular, can substantially lower generalization, presumably up to sensory limits.

There is of course also a functional side to generalization. Evolution has favoured those behaviour mechanisms that are 'intelligent' towards the real world. For instance, stimuli that are similar to one another often share some causal relation with events in the outside world. Animals detect and use such regularities, generalizing knowledge about familiar situations to novel ones. In addition, animals use general methods to cope with novelty, including exploratory and avoidance behaviour. Observed similarities in generalization across taxa may indicate that evolutionary strategies to deal with novelty are limited. Note that, without generalization, learning itself would be seriously limited: by trying out different responses to novel stimuli animals can adapt by learning, but without generalization possibly productive responses would never be tested. Whether everything about generalization is functional is more uncertain (Enquist & Arak 1998; Enquist et al. 2002a). Characteristics that seem difficult to explain as adaptive include, for instance, the two- or three-fold increase in responding along intensity dimensions, and biases within sets of stimuli with the same consequences.

A number of models provide predictions about generalization (Table 6). Gradient interaction models predict responding after training on several stimuli by combining gradients relative to each training stimulus (Spence 1937; Hull 1943; Kalish & Guttman 1957, 1959). The latter, however, are not predicted by the model but assumed or obtained from experiments. Similar assumptions about generalization are also present in other models (Pearce 1987; Shepard 1987). This incompleteness is avoided in some recent 'artificial neural network' models. Here gradient shapes emerge from the interaction of input patterns with model mechanisms that attempt to capture properties of real nervous systems. Some earlier models, originally based on assumptions about generalization, can also be reinterpreted as network models taking into account actual perceptual processes (for instance, the model in Blough 1975; see Ghirlanda & Enquist 1999, Ghirlanda 2002). Artificial neural networks are promising to students of behaviour (Haykin 1999; Arbib 2003). In combination with models of sense organs, neural networks can potentially integrate all the factors discussed above: properties of stimuli, reception, neural processing and learning. Preliminary results indicate that

these models provide a powerful explanation for how generalization is generated, including the consequences of learning (Blough 1975; Ghirlanda & Enquist 1998; Ghirlanda 2002).

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Appendix 1: Statistical Tests

Data from the sources listed below were acquired from published tables, by millimetre paper readouts or by computer scanning and readout with the g3data software (freely available from <http://beam.helsinki.fi/~frantz/software/g3data.php>). The number following the year in each citation indicates the number of data sets in the cited study relevant to the test. Statistical tests were computed using the statistical package for the GNU/Octave software (freely available from <http://www.octave.org>). All tests are two tailed.

Test 1

Gaussian fits to rearrangement gradients account for about 3% more of the variance than exponential fits (Appendix 2). Sign test: $Z=163$, $N=223$, $P<10^{-10}$. Sources: Akins et al. (1981, 2), Ames & Yarczower (1965, 2), Baron (1973, 6), Bloomfield (1967, 2), Blough (1969, 3), Blough (1972, 11), Blough (1975, 3), Brown et al. (1951, 2), Brown et al. (1958, 2), Cheng et al. (1997, 15), Crawford et al. (1980, 4), Dukhayyil & Lyons (1973, 1), Dysart et al. (1974, 5), Fay (1970, 6), Friedman (1963, 3), Frieman & Thomas (1970, 2), Galizio (1980, 2), Galizio (1985, 24), Gewirtz et al. (1956, 7), Ghirlanda et al. (2002, 2), Grusec (1968, 4), Guttman & Kalish (1956, 4), Guttman (1959, 2), Hall & Honig (1974, 4), Hanson (1959, 5), Hanson (1961, 2), Hearst et al. (1964, 4), Hearst & Poppen (1965, 3), Hearst (1968, 4), Hearst (1969, 6), Honig et al. (1959, 12), Honig et al. (1963, 2), Jenkins & Harrison (1960, 1), Kalish (1958, 4), Kalish & Haber (1963, 7), Klipec et al. (1979, 6), Lyons et al. (1973, 8), Marsh (1972, 2), Marx & McLean (1971, 1), Mednick & Lehtinen (1957, 2), Moye & Thomas (1982, 2), Nallan et al. (1979, 1), Ohinata (1978, 5), Penkower Rosen & Terrace (1975, 1), Tempone (1965, 3), Terrace (1964, 3), Thomas & King (1959, 5), Thomas et al. (1960, 3), Thomas (1962, 3), Thomas & Bistey (1964, 3), Thomas & Switalski (1966, 2), Wheatley & Thomas (1974, 4), Wilkie (1972, 1). Total: 223 gradients. These studies comprise both inter- and intradimensional tests, as well as tests where two positive stimuli were subject to different reinforcement schedules (e.g. Dysart et al. 1974; Wheatley & Thomas 1974), producing a gradient with a single peak.

Test 2

Advantage of Gaussian fits to light wavelength generalization gradients in pigeons increases with finer sampling. $r_{96} = -0.55$, $P < 10^{-9}$. Sources: Akins et al. (1981, 2), Blough (1969, 3), Blough (1972, 11), Blough

(1975, 3), Dukhayyil & Lyons (1973, 1), Dysart et al. (1974, 5), Friedman (1963, 3), Frieman & Thomas (1970, 2), Grusec (1968, 4), Guttman & Kalish (1956, 4), Guttman (1959, 2), Hanson (1959, 5), Hanson (1961, 2), Honig et al. (1959, 12), Kalish & Haber (1963, 7), Klipec et al. (1979, 6), Marsh (1972, 2), Marx & McLean (1971, 1), Moye & Thomas (1982, 2), Penkower Rosen & Terrace (1975, 1), Terrace (1964, 3), Thomas & King (1959, 5), Thomas et al. (1960, 3), Thomas (1962, 3), Thomas & Switalski (1966, 2), Wheatley & Thomas (1974, 4). Total: 98 gradients.

Test 3

Gaussian and exponential fits do not make different predictions about peak location in rearrangement gradients. Wilcoxon signed-ranks test: $Z = -0.87$, $N = 223$, $P = 0.38$. Sources: as Test 1.

Test 4

Line-tilt generalization around a vertical line in pigeons is skewed towards clockwise rotations. One-sample t test: $t_9 = -2.37$, $N = 10$, $P < 0.05$. Sources: individual gradients from the 0° group in Hearst et al. (1964). One sample t test, $t_{19} = -5.21$, $N = 20$, $P < 10^{-4}$. Sources: average group gradients from Bloomfield (1967, 1), Hall & Honig (1974, 4), Hearst et al. (1964, 3), Hearst & Poppen (1965, 3), Hearst (1968, 4), Hearst (1969, 3), Honig et al. (1963, 2). Total: 20 gradients.

Test 5

Light wavelength generalization around 550 nm in pigeon is skewed towards longer wavelengths. One-sample t test: $t_{17} = -8.40$, $N = 18$, $P < 10^{-6}$. Sources: average group gradients from Friedman (1963, 3), Guttman & Kalish (1956, 1), Hanson (1959, 1), Hanson (1961, 1), Honig et al. (1959, 4), Marsh (1972, 1), Thomas & King (1959, 5), Thomas & Switalski (1966, 2). Total: 18 gradients.

Test 6

(1) Strength of response bias (measured as the ratio of maximum responding to S^+ responding) in light wavelength intradimensional tests with pigeons increases as separation between S^+ and S^- decreases. $r_{35} = -0.47$, $P < 0.005$.

(2) Distance of gradient peak from S^+ in light wavelength intradimensional tests with pigeons increases as separation between S^+ and S^- decreases. $r_{35} = -0.48$, $P < 0.005$.

Sources: Akins et al. (1981, 2), Dukhayyil & Lyons (1973, 1), Frieman & Thomas (1970, 2), Grusec (1968, 4), Guttman (1959, 1), Hanson (1959, 4), Honig et al. (1959, 4), Klipec et al. (1979, 6), Marsh (1972, 1), Marx & McLean (1971, 1), Moye & Thomas (1982, 2), Terrace (1964, 3), Thomas et al. (1960, 3), Thomas (1962, 3). Total: 37 gradients.

Test 7

(1) Responding along intensity dimensions keeps above S^+ levels, for stimuli further away from S^- , more often

than along rearrangement dimensions. Fisher's exact probability test: $P < 10^{-6}$. Along intensity dimensions, responding to the most extreme intensity sampled was above S^+ level in 30 of 38 gradients, and along rearrangement dimensions in two of 93.

(2) More monotonic intensity gradients are found along intensity dimensions than along rearrangement ones. Fisher's exact probability test $P < 10^{-6}$. Along intensity dimensions, 16 of 38 gradients were monotonic, and along rearrangement dimensions none of 93. A gradient is considered monotonic if it never drops beyond S^+ (see text).

Sources of intensity data: Baron & Harris (1968, 1), Bartoshuk (1964, 1), Brennan & Riccio (1973, 4), Ernst et al. (1971, 4), Huff et al. (1975, 2), Lawrence (1973, 4), Olson & King (1962, 4), Pierrel & Sherman (1960, 2), Razran (1949, 3), Rohrbaugh et al. (1971, 1), Steinhneider et al. (1966, 2), Thomas & Setzer (1972, 4), Wills & Mackintosh (1998, 3), Zielinski & Jakubowska (1977, 3). Total: 39 gradients. Sources of rearrangement data: Akins et al. (1981, 2), Ames & Yarczower (1965, 1), Baron (1973, 4), Bloomfield (1967, 1), Cheng et al. (1997, 8), Crawford et al. (1980, 4), Dukhayil & Lyons (1973, 1), Frieman & Thomas (1970, 2), Galizio (1985, 14), Ghirlanda et al. (2002, 2), Grusec (1968, 4), Guttman (1959, 1), Hanson (1959, 3), Hearst (1969, 2), Honig et al. (1959, 8), Kalish & Haber (1963, 1), Klipec et al. (1979, 6), Lyons et al. (1973, 8), Marsh (1972, 1), Marx & McLean (1971, 1), Moyer & Thomas (1982, 2), Nallan et al. (1979, 1), Ohinata (1978, 4), Terrace (1964, 3), Thomas et al. (1960, 3), Thomas (1962, 2), Wilkie (1972, 1), Wills & Mackintosh (1998, 3). Total: 93 gradients.

Sources of size data: Andersson (1982, 1), Baerends (1982, 1), Basolo & Delaney (2001, 1), Dougherty & Lewis (1991, 1), Magnus (1958, 3), Pryke & Andersson (2002, 1), Schaller & Schwab (1961, 2). Total: 10 gradients.

Test 8:

(1) Intensity generalization produces stronger response biases than rearrangement dimensions. Mann-Whitney U test: $Z = 4.89$, $N_1 = 38$, $N_2 = 93$, $P < 10^{-6}$.

(2) Size dimensions produce stronger biases than rearrangement dimensions. Mann-Whitney U test: $U = 4.21$, $N_1 = 10$, $N_2 = 93$, $P < 10^{-4}$.

(3) Size and intensity dimensions appear to produce biases of comparable size. Mann-Whitney U test: $U = -0.61$, $N_1 = 10$, $N_2 = 38$, $P = 0.54$.

Sources: see Test 7. Strength of bias is measured as the ratio of maximum observed responding to S^+ responding.

Test 9

Better sampling of the gradient (more experimental subjects) leads to higher degree of monotonicity in intensity gradients. $r_s = 0.58$, $N = 11$, $P < 0.01$. Sources: Baron & Harris (1968, 1), Bartoshuk (1964, 1), Brennan & Riccio (1973, 4), Ernst et al. (1971, 4), Hall & Prokasy (1961, 1), Huff et al. (1975, 2), James & Hughes (1969, 1), Lawrence (1973, 4), Olson & King (1962, 4), Pierrel & Sherman (1960, 2), Rohrbaugh et al. (1971, 1), Steinhneider et al.

(1966, 2), Thomas & Setzer (1972, 4), Wills & Mackintosh (1998, 5), Zielinski & Jakubowska (1977, 3). Total: 39 gradients. 'Degree of monotonicity' is defined as the absolute Spearman rank correlation between responding observed to a stimulus and its position along the stimulus dimension (absolute values are used to cover both increasing and decreasing gradients). The correlation reported above is the Spearman rank correlation between group size and average degrees of monotonicity. The value $N = 11$ reported above refers to the number of group sizes found in the surveyed studies (in the range 2–45).

Test 10

Size generalization gradients obtained in inter-dimensional tests appear to peak at sizes larger than S^+ . Wilcoxon signed-ranks test: $T = 2.20$, $N = 7$, $P < 0.05$. Sources: Brush et al. (1952, 1), Buss & Daniell (1967, 3), Dougherty & Lewis (1991, 1), Grant & Schiller (1953, 1), Tosti & Ellis (1964, 1). Total: 7 gradients. The result holds when peak position is estimated by either Gaussian or exponential curves. The linear dimensions of the stimuli were used as the independent variable (e.g. circle diameter or square side). Using stimulus area, which is another natural choice for size dimensions, would have yielded even bigger asymmetries.

Test 11

Gaussian fits to size gradients account for about 3% more of the variance than exponential fits (Appendix 2). Sign test: $Z = 8$, $N = 8$, $P = 0$. Sources: Brush et al. (1952, 1), Buss & Daniell (1967, 3), Dougherty & Lewis (1991, 2), Grant & Schiller (1953, 1), Tosti & Ellis (1964, 1). Total: 8 gradients. These studies comprise both inter- and intradimensional tests.

Test 12

Pigeons generalize less, along the light wavelength dimension, after a discrimination between two wavelengths than between one wavelength and a dark stimulus. Kolmogorov-Smirnov two-sample test: $Z = 1.67$, $N_1 = 48$, $N_2 = 40$, $P < 0.001$. Sources: Akins et al. (1981, 2), Blough (1969, 3), Blough (1972, 11), Blough (1975, 3), Dukhayil & Lyons (1973, 1), Dysart et al. (1974, 1), Friedman (1963, 3), Frieman & Thomas (1970, 2), Grusec (1968, 4), Guttman & Kalish (1956, 4), Guttman (1959, 1), Hanson (1959, 5), Hanson (1961, 1), Honig et al. (1959, 12), Kalish & Haber (1963, 7), Klipec et al. (1979, 6), Marsh (1972, 2), Marx & McLean (1971, 1), Moyer & Thomas (1982, 2), Penkower Rosen & Terrace (1975, 1), Terrace (1964, 3), Thomas & King (1959, 5), Thomas et al. (1960, 3), Thomas (1962, 3), Thomas & Switalski (1966, 2). Total: 88 gradients.

Appendix 2: Data Analysis

Fitting procedure

We describe briefly the fitting procedure leading to the results on gradient shape reported in the main text.

By 'exponential' and 'Gaussian' shapes we mean the following functions, respectively:

$$f_E(x) = a \exp(-|x - b|/c) + d \quad (1)$$

$$f_G(x) = a \exp(-(x - b)^2/2c^2) + d \quad (2)$$

where, in both functions, the maximum value of the function is $a+d$, the peak position is b , c determines how quickly the gradient drops from the peak, and d is the minimum function value (approximately reached very far from the peak). The parameter d has been included because not all empirical gradients fall to zero within the probed stimulus range. However, d was not fitted; rather, it was set equal to the minimum gradient value, consistent with its meaning in equations (1) and (2). Using a , b and c as fitted parameters, we fitted both equations (1) and (2) to the studies listed as sources for Test 1. For fitting we used the Marquardt–Levenberg algorithm provided with the Gnuplot software, version 3.7.1. (available via anonymous ftp from <ftp://ftp.ucc.ie/pub/gnuplot>). For each data set and each fit, we then computed the Pearson correlation r , and we used r^2 as an estimate of how much of the variance in empirical data is accounted for by the fitted curve (a measure of goodness of fit). We thus had two samples of r^2 's, from the exponential and

Gaussian fits to each gradient. These can be used in statistical tests as detailed in Appendix 1.

Testing for gradient symmetry

To test for symmetry of gradients obtained from inter-dimensional tests, we divided the gradient into a 'left' and a 'right' side, using S^+ as the reference point. We then summed all responses to stimuli on the same side, obtaining a left sum L and a right sum R (responses to S^+ are excluded from both L and R). R and L were combined as follows to yield the test statistics:

$$I = \frac{L}{L+R}$$

which has the meaning of proportion of responses to the left of S^+ . By construction, its value is independent of whether published data are reported as absolute numbers of responses or as proportions of responses to each stimulus. Under the null hypothesis that a set of gradients shows no systematic asymmetry, the expected value of I is 0.5. In testing this hypothesis by one-sample t tests (see Appendix 1), we considered the same number of stimuli on each side of S^+ (a few times discarding a data point), and covering the same range.