A century of generalization[*]

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Abstract

We review empirical data from both ethology and psychology about generalization, that is how animals respond to sets of stimuli including familiar as well as novel stimuli. Our main conclusion is that many characteristics of generalization are universal behavioural phenomena, suggesting that they originate from general properties of nervous mechanisms and/or that evolutionary strategies to cope with novelty and variability in stimulation are limited. We also reach the following conclusions. First, 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, orientation, etc.), modality (light, sound, etc.) and of whether reaction to stimuli is learned or genetically inherited. Second, 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. When the dimension involves increase or decrease of the intensity of stimulation, the gradient is often monotonic, and responding to some novel stimuli is considerably stronger than responding to familiar stimuli, compared to non-intensity dimensions. Third, rearrangement gradients are better described by Gaussian curves, rather than exponentials as often suggested. Fourth, when several or many familiar stimuli are close to each other interferences occur, giving rise to predictable response biases such as peak shift or supernormality (interference between positive and negative stimuli), and stretched bell shaped curves (several positive stimuli). Lastly, no principle differences between biases referred to as peak shift and biases referred to as supernormal stimulation are found. The paper ends with a discussion of theoretical issues.

Introduction

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). The 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 summarise observations (for example by incorporating observed features of generalization into the theory, see Hull, 1943; Mackintosh, 1974). This review aims to organise existing data in a way useful to develop and test theories of generalization. We will also point out findings that contrast with existing theories, conclude the paper with a discussion 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 (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 employed. Following training, the animals' reactions to a set of test stimuli are recorded. These are usually chosen from a 'stimulus dimension' obtained by changing a physical variable such as wavelength of light or intensity of sound. Data can be thus 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 'intra-dimensional' discrimination, for example when light wavelength generalization is studied following a discrimination between two wavelengths. If S^- cannot be placed on the test dimension, the term 'inter-dimensional' discrimination is used, for instance if the test dimension is sound frequency and S^- is silence or white noise. Note that the same discrimination can be both intra- and inter-dimensional depending on the test stimuli chosen. We prefer thus to speak of inter- and intra-dimensional tests, rather than discriminations.

While 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; males must discriminate females from other stimuli, 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 summarise both the ethological and the psychological methods as the recording of animals' reactions to stimulus sets including novel as well as 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, preexisting 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 'naïve' individuals are employed. The analysis of natural behaviour is even more complex, both because the animals' evolutionary history more directly influences behaviour and because control over individual experiences is at most partial.

The analysis of stimulus dimensions

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

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

Stimulus dimension	Contribution of:	
	rearrangement	intensity
Intensity of sound		●
Intensity of light		●
Chemical concentration (smell, taste)		●
Object size	●	●
Complex sound spectra	●	●
Complex light spectra	●	●
Object shape	●	○
Tone frequency	●	○
Monochromatic light	●	○
Object orientation	●	
Object location	●	

Note: ● large contribution; ○ small contribution, or varying contribution depending on the exact stimuli employed; no symbol means negligible contribution.

the total activation of receptors. This is related to physical intensity but 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 will 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 to 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 less than three subjects per treatment, unless when focusing on the very effects 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 re-

sponding to a single test stimulus may serve to estimate a bias. Third, we have not included studies whose outcome is importantly affected by unusual features of training or testing, apart when discussing the specific effects of such features (see especially intensity generalization below). Fourth, we could not include some studies in quantitative analyses because they reveal generalization very indirectly, for instance by studying how reproduction or position in a social hierarchy is affected by signals employed 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, due to our lack of familiarity with the field and the additional space it would require.

We will turn now to reviewing 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 Appendix and Appendix . In the following, tests will be referred to by their progressive number in Appendix . 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 as diverse stimulus dimensions as light wavelength, tone frequency, object orientation, 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 (see e.g. Coren et al., 1999, for human hearing). 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, employed 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

Table 2: Examples of generalization along rearrangement dimensions

Dimension	Response bias	Species	References
Light spectra:			
monochromatic light	no data	human	Kalish (1958)
	yes	pigeon (*Columba livia*)	Hanson (1959)
	yes	goldfish (*Carassius auratus*)	Ames & Yarczower (1965)
non-monochromatic light[a]	yes	goldfish	Ohinata (1978)
colour of female dummy[a]	yes	glow-worm (*Lampyris noctiluca*)	Schaller & Schwalb (1961)
	yes	glow-worm (*Phausis splendidula*)	Schaller & Schwalb (1961)
	no	butterfly (*Argynnis paphia*)	Magnus (1958)
colour of egg dummy[a]	yes	herring gull (*L. argentatus*)	Baerends (1982)
Orientation of:			
Line	yes	pigeon	Bloomfield (1967)
Head stripe	yes	fish (*Haplochromis burtoni*)	Heiligenberg et al. (1972)
Rocket picture	yes	human children	Nicholson & Gray (1971)
Sound Frequency:			
	no data	goldfish	Fay (1970)
	yes	rat (*Rattus r. norvegicus*)	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	honey bee (*Apis mellifera*)	Cheng (2000, 2002)

Note: for laboratory studies, the column 'Response bias' refers to intra-dimensional tests. See main text for information about biases in other conditions.

[a] Non-monochromatic lights cannot be meaningfully aligned along a single dimension, and intensity effects may occur due to different sensitivity of the receptors to different wavelengths of light.
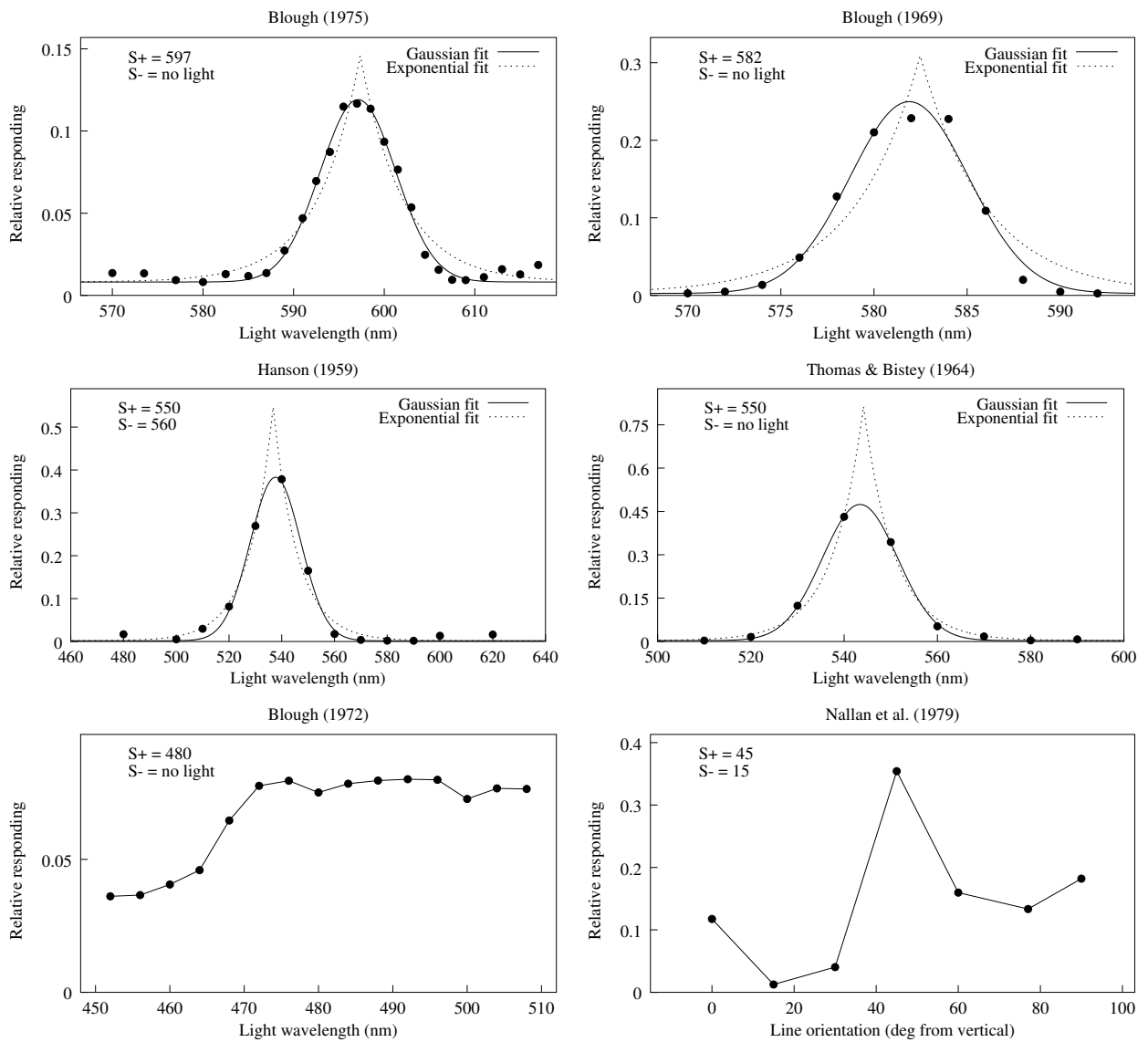
Figure 1: Examples of rearrangement generalization gradients, with Gaussian and exponential fits where appropriate. See the original studies for training and testing procedures.
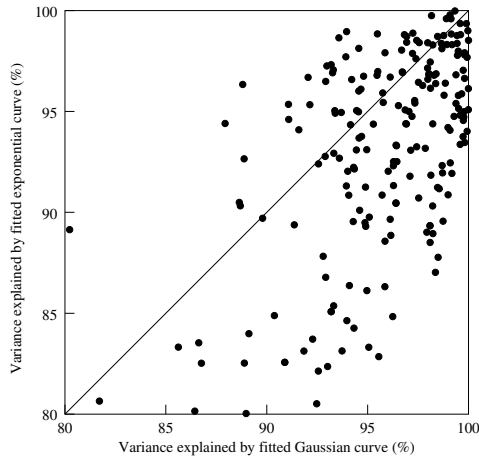
Figure 2: Comparison of Gaussian and exponential fits to empirical generalization gradients. Points above (below) the diagonal represent empirical gradients better fitted by exponential (Gaussian) curves.
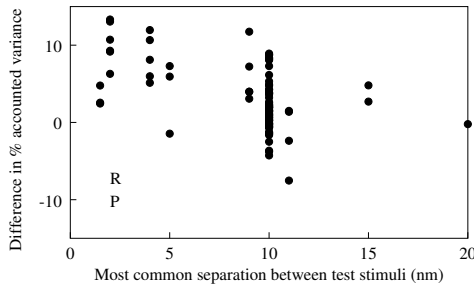

Figure 3: Differences in percentage of accounted variance between Gaussian and exponential fits to light wavelength generalization data in pigeons, as a function of separation between test stimuli (see Test 2 for data sources and statistics). Entirely similar results are obtained when considering average separation between test stimuli rather than the most common one.
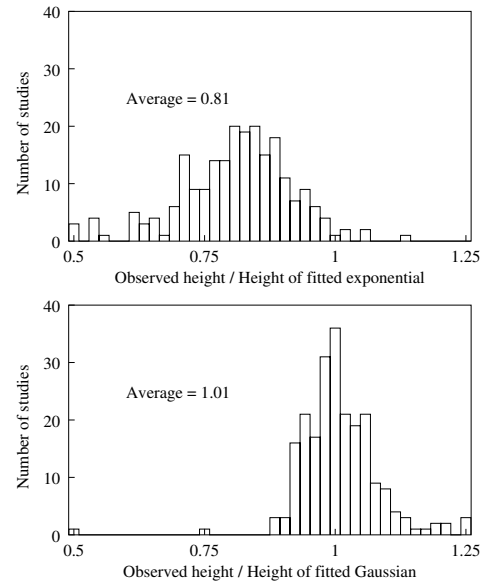

Figure 4: Predictions about gradient height by Gaussian and exponentials fits to rearrangement gradients, compared with the observed height. Data sources in Test 1.

the data by Hovland (1924), incorporated an exponential generalization function into his theory of behaviour. Nowadays most researchers hold gradients to be either exponential or Gaussian (see e.g. Blough, 1975; Shepard, 1987; Staddon & Reid, 1990; Cheng et al., 1997). We have analysed 223 rearrangement gradients, finding that Gaussian curves account, on average, for about 3% more of the variance in observed data (estimated by r^2; Appendix 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 actually conform better to the exponential shape. Fig. 2 illustrates these results.

Note that surveyed experiments 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 (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 (see e.g. Fig. 1) shows that the latter ones often predict a considerably taller gradient than actually observed (an average of 20% higher, Fig. 4, left). Predictions from Gaussian fits, on the other hand, distribute around the observed values (Fig. 4, right). 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, n.s.). Finally, we should note that gradients which are clearly neither exponential nor Gaussian exist (e.g. the bottom gradients in Fig. 1, see also Hoffman & Fleshler, 1964; Blough, 1972).

Gradient symmetry

Nearly all theories of generalization assume or predict that gradients obtained from inter-dimensional tests be symmetrical around the S^+ (Spence, 1937; Hull, 1943; Blough, 1975; Shepard, 1987). However, reproducible asymmetries have been reported. When data from all experimental subjects are published, we can test

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whether they are consistently skewed towards one or the other side of the S^+ (see Appendix 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 across-study asymmetries. We can thus confirm that the skewed gradient reported by Hearst et al. (1964) has been consistently observed in other studies (Test 4, $P < 10^{-4}$); responses to counter-clockwise 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 emitedd to longer wavelengths (range 48%–94%). Observations of asymmetrical gradients also exist for humans. For instance, Kalish (1958), Thomas & Mitchell (1962) and Thomas & Bistey (1964) report 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 inter-dimensional tests (see e.g. the data from Thomas & Bistey (1964) in Fig. 1). Moreover, Thomas & Bistey (1964) report 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 understanding why a gradient is symmetrical on a given scale. For instance, in the case of sound frequency 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 (Coren et al., 1999; Kandel et al., 1991). For many dimensions, *de facto* standards about which scale to use have emerged, that agree with considerations based on sensory physiology. We will return to this issue in *Factors affecting the amount of generalization* below.

Response biases

After training a discrimination between two stimuli differing along the test dimension (intra-dimensional tests), response biases are often found (Table 2). That is, there exist stimuli which elicit stronger responding than S^+ (Fig. 5a). These stimuli are, almost invari-
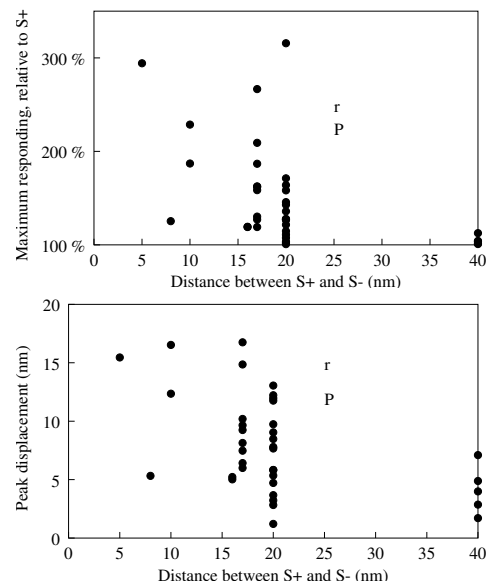

Figure 6: Dependence of response biases on the difference between S^+ and S^-. Data come from studies in which pigeons where trained to discriminate between two monochromatic lights (sources in Test 6). Left: ratio between peak responding and responding to the positive stimulus. Right: displacement of gradient peak from the S^+. Peak responding, peak position and responding to S^+ are estimated from fitted Gaussians.

ably, located further away from S^-. Recall also that response biases can appear also in inter-dimensional tests (e.g. Thomas & Bistey, 1964; Kalish, 1958), a finding which has received little attention. Sometimes a 'negative' bias is also observed, that is lower responding than to S^- to stimuli which 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 *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 responding 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 were the separation between S^+ and S^- was varied. Examples are: Hearst (1968, line-tilt, pigeon), Ohinata (1978, wavelength, goldfish), Baron (1973, tone frequency, hu-
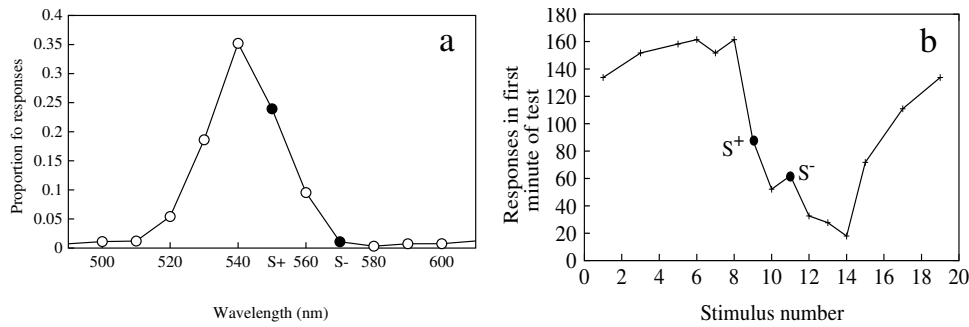
Figure 5: Examples of response biases along rearrangement dimensions. a) Hanson's (1959) classical study. Pigeons were trained to peck a key for food when it was lit with a 550 nm light, but not when the wavelength was 570 nm. In a subsequent generalization test the maximum number of responses occurred 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 wavelength to be tested, then introduced a discrimination training by presenting only S^+ (still reinforced) and S^- (unreinforced). The following generalization tests reveals that some stimuli right of S^- are reacted to less than S^-.

mans), Cheng et al. (1997, spatial location, pigeon).

The variation in Fig. 6 reveals that similarity between training stimuli is not the sole determinant of response biases. There are indeed ample indications that training and testing procedure, as well as the characteristics of stimuli used, are important factors (Purtle, 1973; Mackintosh, 1974). For instance, the so-called 'errorless' training procedure, 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' experience with the unreinforced test stimuli (see also Blough, 1975).

Conclusions

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

- When the rearrangement dimension includes one S^+ but no S^-:

  - the gradient typically peaks at S^+ (but not invariably, Fig. 1);

  - the gradient is typically symmetrical around S^+;

  - however, reproducible asymmetries exist, and may be more common than usually assumed (Test 4, Test 5).

- 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);
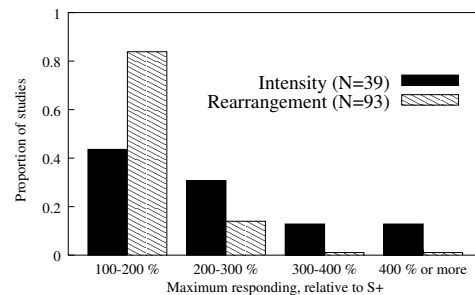

Figure 8: Distribution of response biases along intensity and rearrangement dimensions. The strength of bias is measured as the ratio of osberved maximum responding to responding to S^+. Note that strength of bias is understimated along intensity dimensions, since often responding does not start decreasing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

  - closer S^+ and S^- produce gradients whose peak is both higher and further away from S^+ (Fig. 6).

Intensity dimensions

It has been since long noted that, in contrast with rearrangement dimensions, intensity dimensions yield strongly asymmetrical gradients and strong response biases (Mackintosh, 1974, cf. Fig. 7; Table 3 lists some studies). This was once attributed to an 'energising' effect of intensity on behaviour (Hull, 1949). However, it is not intensity *per se* that controls responding, since gradients which 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 inten-

Table 3: Examples of generalization along intensity dimensions

Intensity dimension	Monotonicity	Response bias	Species	References
Sound:				
tone	yes	yes	rat (*R. r. norvegicus*)	Pierrel & Sherman (1960)
	yes/no[a]	yes	rat	Thomas & Setzer (1972)
	yes/no[a]	yes	guinea pig (*Cavia porcellus*)	Thomas & Setzer (1972)
	yes	yes	rat	Brennan & Riccio (1973)
	yes	yes	rabbit (*Oryctolagus cuniculus*)	Scavio & Gormezano (1974)
bell	yes	yes	dog (*Canis familiaris*)	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[a]	yes	pigeon (*C. livia*)	Ernst et al. (1971)
	no	yes	pigeon	Lawrence (1973)
	yes	yes	rat	Brown (1942)
	no data	yes	earthworm (*Lombricus terrestris*)	Gilpin et al. (1978)
brightness of egg dummy	yes	yes	herring gull (*L. argentatus*)	Baerends (1982)
brightness of female dummy	yes	yes	butterfly (*Eumenis semele*)	Tinbergen et al. (1942)
	yes	yes	glow-worm (*P. splendidula*)	Schaller & Schwalb (1961)
	no	no	glow-worm (*L. noctiluca*)	Schaller & Schwalb (1961)
Chemical concentration:				
odour	no data	yes	bee (*A. mellifera*)	Bhagavan & Smith (1997)
taste	no data	yes	rat	Tapper & Halpern (1968)

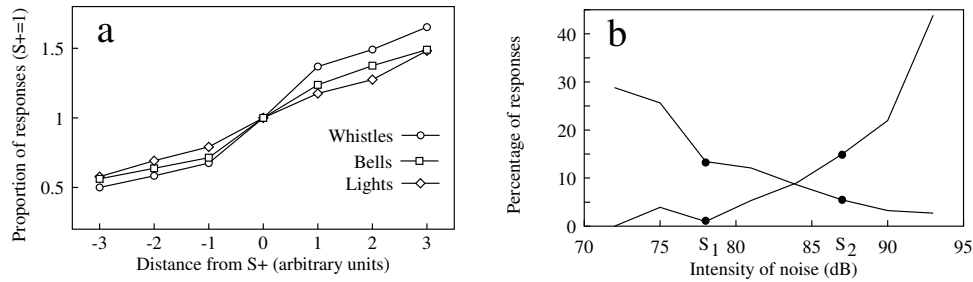[a] Both monotonic and non-monotonic gradients where found.

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), summarising 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).

sity produce monotonic gradients (i.e., ever-increasing or ever-decreasing) have been contrasted with findings of non-monotonic gradients (see Ernst et al., 1971; Thomas & Setzer, 1972). It is clear that intensity gradients cannot grow or fall forever; for instance, too high intensities will harm the sense organs, and too low ones cannot be detected. However, important differences between intensity and non-intensity gradients exist independent of statements about gradient shape. For instance, in 31 of 39 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 7a, $P < 10^{-6}$). Moreover, a quantitative analysis shows that response biases along intensity dimensions are significantly stronger than along rearrangement dimensions (Test 8, $P < 10^{-6}$, see Fig. 8). Returning to gradient shape, if we consider 'monotonic' a gradient that does not drop past S^+ (see below), we find 17 out of 39 monotonic intensity gradients, but none in 93 intra-dimensional rearrangement gradients (Test 7b, $P < 10^{-6}$).

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

First, sampling errors lead to underestimate the number of monotonic intensity gradients. An inaccurate estimate of responding at a single point can transform a monotonic curve into a non-monotonic one, but it is less likely that the reverse occurs. The above definition of 'monotonicity', considering only the S^+ and stim-
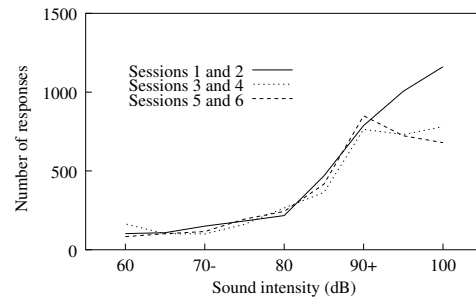

Figure 9: Data about sound intensity generalization in rats (Pierrel & Sherman, 1960), collected over six days of testing in extinction. Average data from the first two test sessions show a monotonic gradients (data from both days do), while gradients from subsequent sessions have lost monotonicity.

uli further away from S^-, reduces but does not eliminate the effects of sampling. Indeed, it can be shown that monotonicity of intensity gradients increases with better sampling, i.e. larger experimental groups (Test 9, $P < 0.01$).

Second, a number of studies reporting non-monotonic 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, as reported by Pierrel & Sherman (1960, see Fig. 9). Such shape changes appears analogous to the disappearing or waning of response biases in the course of long test sessions, along rearrangement dimensions (e.g. in Crawford et al., 1980; Cheng et al., 1997).

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, e.g. 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) reports that lightly coloured egg dummies are preferentially retrieved by herring gulls (*L. argentatus*), but this preference does not extend to white dummies. Studies with related species have shown that gulls usually remove white objects from the nest (a likely anti-predatory defense, see Tinbergen et al., 1962; Baerends, 1982).

Conclusions

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

- 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 vs. an illuminated key);

    - responding decreases with intensity when S^+ is less intense than S^-.

- 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);

    - 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 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 less receptors and in a different pattern). This prediction is confirmed by
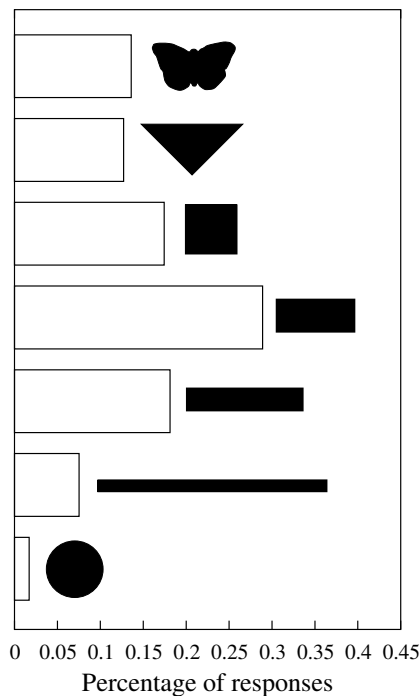
Figure 10: Reactions of male *Argynnis paphia* butterflies to female models of different shapes (data from Magnus, 1958). The effectiveness of each model is expressed as percentage of flights towards it on a total of 135 flights, in an open area where all models were visible simultaneously. All models had an area of approximately 22 cm^2 and were of the same colour (orange-red).

available data (Test 10, $P < 0.05$). The same data suggest that size gradients are better described by Gaussian rather than 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 8b, $P < 0.02$). In the small sample collected, biases towards bigger sizes appear comparable with biases along intensity dimensions (Test 8c, n.s.). Examples of response biases along size dimensions are reported in Table 4. 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 analyzing size dimensions, it is not so for many other dimensions. Table 5 lists studies relative to some such dimensions. In some cases, we do not know enough about the sense organs underlying perception along some dimensions, e.g. floor tilt (Lyons et al., 1973) or arm movement (Hedges, 1983; Dickinson & Hedges, 1986). In other cases, e.g. complex variations in shape (Ferraro & Gr-

Table 4: Examples of generalization along size dimensions

Size dimension	Response bias	Species	References
circle	no data	rat (*R. r. norvegicus*)	Grice & Saltz (1950)
	no data	pigeon (*C. livia*)	Jenkins et al. (1958)
	no data	toad (*Bufo bufo*)	Ewert (1980)
	yes	horse (*Equus caballus*)	Dougherty & Lewis (1991)
	yes	butterfly (*E. semele*)	Tinbergen et al. (1942)
	yes	human	Berlyne (1950)
square	no data	toad (*B. bufo*)	Ewert (1980)
rectangle	no data	human	Rosenbaum (1953)
egg	yes	herring gull (*L. argentatus*)	Baerends (1982)
	yes	black-headed gull (*L. ridibundus*)	Baerends et al. (1975)
	yes	oystercatcher (*Haematopus ostralegus*)	Tinbergen (1951)
	yes	ringed plover (*Charadrius hiaticula*)	Koehler & Zagarus (1937)
tail	yes	widowbird (*Euplectes progne*)	Andersson (1982)
	yes	swordtail fish (*Xiphophorus helleri*)	Basolo (1990); Basolo & Delaney (2001)
food item	yes	newborn chicks (*Gallus g. domesticus*)	Gamberale & Sillen-Tullberg (1998), Gamberale-Stille (2000)
female dummy	yes	butterfly (*Argynnis paphia*)	Magnus (1958)
female lantern	yes	glow-worm (*P. splendidula*)	Schaller & Schwalb (1961)
	no	glow-worm (*L. noctiluca*)	Schaller & Schwalb (1961)

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

Dimension	Response bias	Species	Studies
Visual shape:			
female dummy	yes	butterfly (*A. paphia*)	Magnus (1958)
polygon	yes	pigeon (*C. livia*)	Ferraro & Grisham (1972)
egg	no	herring gull (*L. argentatus*)	Baerends (1982)
Visual contrast	yes	herring gull (*L. argentatus*)	Baerends (1982)
	yes	chicks (*G. g. domesticus*)	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 (*R. r. norvegicus*)	Weiss & Schindler (1981)
Flicker rate	yes	pigeon	Sloane (1964)
	yes	butterfly (*A. paphia*)	Magnus (1958)
Floor tilt	yes	pigeon	Lyons et al. (1973)
	yes	pigeon	Riccio et al. (1966)
Calls / songs	yes	monkey (*Callimico goeldii*)	Masataka (1983)
	yes	blackbird (*Turdus merula*)	Wolffgramm & Todt (1982)
Human faces	yes	human	Rhodes (1996); Rhodes & Zebrowitz (2002)
	yes	chickens (*G. g. domesticus*)	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)

isham, 1972; Wasserman et al., 1996), distinguishing between intensity and non-intensity effects is simply not sufficient. When we lack information about underlying 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; for instance rate of stimulus presentation (Magnus, 1958; Weiss & Schindler, 1981) or femininity/masculinity of human faces (Enquist et al., 2002b, see also Ghirlanda & Enquist, 1999). 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

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

- Response biases have been found along all dimensions investigated so far.

- Generalization along size dimensions is influenced by both intensity and rearrangement effects:

    – size generalization gradients are typically peaked;

    – they are better approximated by Gaussian rather than exponential functions (Test 11);

    – they exhibit larger biases than gradients along rearrangement dimensions, and comparable to intensity gradients (Test 8);

    – 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. One factor related to gradient width is discriminability. Guttman & Kalish (1956) noted that,

while generalization is measured by the change in behaviour due to a change in stimulation, discriminability is defined as the change in stimulation necessary to yield a behavioural change (cf. also Lashley & Wade, 1946). They thus suggested that generalization and discriminability should be inversely related, but due to lack of reliable data on discriminability they failed to observe this relationship studying light wavelength generalization in the pigeon. Later work has confirmed that pigeons generalize more in regions of the wavelength spectrum where discriminability is poorer (reviewed in Honig & Urcuioli, 1981). The same conclusion is 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 inter-dimensional tests along the same dimension can vary considerably in width. An analysis of light wavelength generalization in the pigeon, for instance, reveals 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 studying tone frequency generalization in humans (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). First, because food items differ in appearance. Second, because a single food item gives rise to different receptor activations due to variations in distance, light conditions, orientation and so on. In such situations there is variation within as well as between the sets of
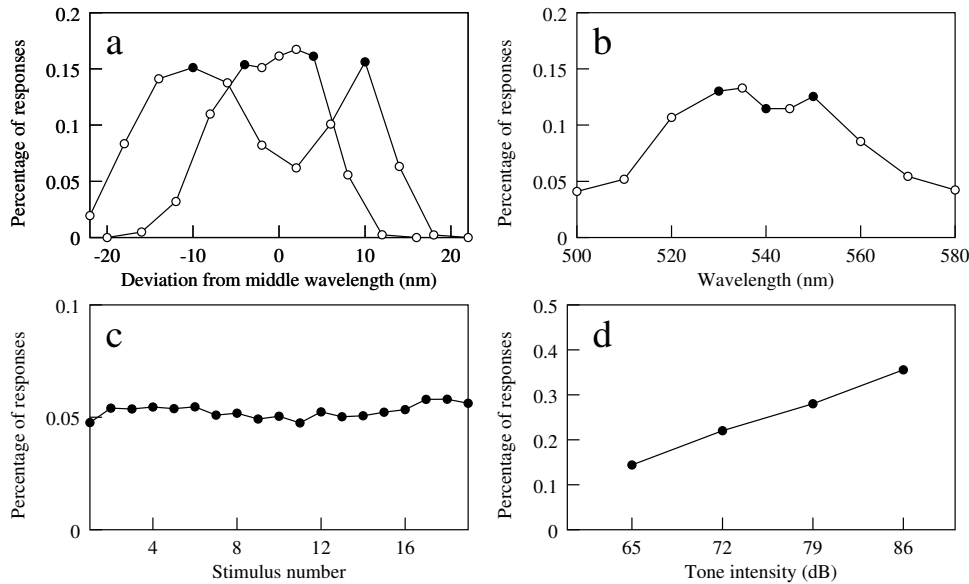
Figure 11: Four examples of generalization after experience with many stimuli. Subjects had the same experience with all training stimuli (closed circles). a) Two-stimulus training can yield gradients with either one or two peaks depending on the difference between stimuli (data from Blough, 1969, pigeon, 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).

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 (Weiss, 1972; Wagner, 1971; 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 yield 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). Both flat gradients (Fig. 11c), small (Fig. 11b) and large biases (Fig. 11d) have been reported. Interestingly, 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

- Gradient width and symmetry can be related to discriminability along the test dimension:

  – finer discriminability is correlated with narrower gradients;

  – when discriminability is different on the two sides of S^+ asymmetrical generalization gradients are observed.

- Along rearrangement dimensions, discriminations between stimuli lead to decreased generalization (narrower gradients).

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

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– responding to all training stimuli is the same or similar (small biases, Fig. 11b,c).

- 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 & Krujit, 1973; Hogan et al., 1975; Staddon, 1975; Dawkins & Guilford, 1995). Within psychology the question is seldom addressed explicitly; however, definitions 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), while early ethologists claimed that inherited and learned behaviour be governed by different mechanisms (Von Uexküll, 1928; Lorenz, 1937).

While 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 & Krujit, 1973; Dawkins & Guilford, 1995). In particular, it has been claimed that innate behaviour yields 'open ended' generalization (i.e. monotonic gradients), while individual learning does not (Baerends & Krujit, 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 which is independent of individual learning (e.g. egg retrieval in gulls, Baerends, 1982). Moreover, some dimensions cannot by their nature yield open ended generalization, irrespective of ontogeny of behaviour. For instance, the response of male *Haplochromis burtoni* cichlids to the orientation of the head stripe of male conspecifics (Heiligenberg et al., 1972) will necessarily come back to its starting 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 (Schaller & Schwalb, 1961; Magnus, 1958). In some cases the most effective colour is clearly not at the extremes of the spectrum (Schaller & Schwalb 1961, *L. noctiluca* glow worms; Baerends 1982, herring gulls) or closely matches the natural colour (Magnus, 1958, *A. paphia* butterflies).

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 & Schwalb (1961, brightness of glow-worm female dummy), with a few exceptions along size dimensions (where strong biases are expected, see above). For example, Baerends and coworkers showed that oversized eggs are preferred by incubating gulls up to giant sizes (Baerends, 1982). Magnus (1958) provides mixed evidence, showing that male *A. paphia* butterflies prefer four-fold enlarged female dummies to dummies two times the normal size when the dummies are stationary, but not when they imitate flight. Similarly, Schaller & Schwalb (1961) report that male *P. splendidula* glow-worms prefer dummy female lanters four times bigger than normal, but male *L. noctiluca* do not. There are further reports that the supernormal effect of bigger stimuli often ceases rather soon. One instance is the responses of male *P. splendidula* and *L. noctiluca* to circular lights, which declines for circles several times bigger than the females' lantern, again in Schaller & Schwalb (1961). The same authors show that *L. noctiluca* males prefer a dummy lantern containing three horizontal segments to one with six (normal is two). Koehler & Zagarus (1937) found that ringed plovers (*Charadrius hiaticula*) retrieve eggs weighting 17 g, but not those above 35 g (normal eggs weight about 11.5 g). In this last case individual learning may play a role (cf. Baerends, 1982). Finally, Ewert (1980) has shown that both naïve and experienced toads exhibit a clear preference for catching objects within a restricted size range.

Conclusions

- We could find no difference between generalization of genetically inherited and individually

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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;
- 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 phenomena, 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, while 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 would like to end with some theoretical considerations. A number of attempts have been made to understand the causes of generalization (see Kalish, 1969; Mackintosh, 1974, for reviews). Theorising 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 (see 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 organisation of sense organs (including early processing of neural signals within sense organs, see e.g. Dudel 1983). 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, see 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 recognising that similarity depends upon which receptors are stimulated and to what degree (Ghirlanda 2002).

Generalization is also modulated centrally in the nervous system. Suggestions 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 the same nerve cells and connections (Pavlov, 1927; Hebb, 1949; Horne, 1965; Thompson, 1965; Baerends & Krujit, 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 favours those behaviour mechanisms that are 'intelligent' towards the real world. For instance, stimuli that are similar to one another often share some causal relationship 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 behaviour 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 exist that 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

Table 6: Basic predictions by models of generalization

Theory	Rearrangement generalization		Intensity generalization			References
	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), 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)

Note: * empirical knowledge about the nervous system is employed; † responding under-estimated; ‡ see cited papers for details of assumed stimulus representation; § for possible improvements, see Ennis (1988); Shepard (1988); Staddon & Reid (1990); Shepard (1990). Derivations for some predictions not in the original works can be found in Ghirlanda & Enquist (1999), Ghirlanda (1999), Ghirlanda (2002).

1957, 1959). The latter ones, however, are not predicted by the model but assumed or obtained from experiments. Similar assumptions about generalization are also present in other models (Shepard, 1987; Pearce, 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 system. 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 very promising to students of behaviour (Haykin, 1994; Arbib, 1995). In combination with models of sense organs, neural networks can potentially integrate all 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).

Acknowledgements

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Statistical tests

Data from the sources listed below where acquired from published tables, by millimeter paper readouts of published graphs 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 performed using the statistical package of 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% of the variance more than exponential fits (see Appendix).

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 & K. (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.

Note: The studies above comprise both inter- and intra-dimensional tests, as well as tests where two positive stimuli where subject to different reinforcement shcedules (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.

$r = -0.55$, $N = 98$, $P < 10^{-9}$.

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 matched-pair test, $z = -0.87$, $N = 223$, $P = 0.38$.

Sources: same as Test 1.

Test 4: Line-tilt generalization around a vertical line in pigeons is skewed towards clockwise rotations.

- one-sample t test, $t = -2.37$, $N = 10$, $P < 0.05$.
  Sources: individual gradients from the $0°$ group in Hearst et al. (1964).

- one sample t test, $t = -5.21$, $N = 20$, $P < 10^{-4}$.
  Sources: average group gradients from Bloomfield (1967, 1), Hall & K. (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, $t = -8.40$, $N = 18$, $P < 10^{-6}$.

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:

a) Strength of response bias (measuread as the ration of maximum responding to S^+ responding) in light-wavelength intra-dimensional tests with pigeons increases as separation between S^+ and S^- decreases.
$r = -0.47, N = 37, P < 0.005$.

b) Distance of gradient peak from S^+ in light-wavelength intra-dimensional tests with pigeons increases as separation between S^+ and S^- decreases.
$r = -0.48, N = 37, P < 0.005$.

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:

a) Responding along intensity dimensions keeps above S^+ levels, for stimuli further away from S^-, more often than along rearrangement dimensions.
$P < 10^{-8}$, Fisher's exact probability test with contingency table:

	Above S^+	Below S^+
Intensity	30	8
Rearrangement	2	91

b) More monotonic intensity gradients are found along intensity dimensions than along rearrangement ones.
$P < 10^{-8}$, Fisher's exact probability test with contingency table:

	Monotonic	Peaked
Intensity	16	22
Rearrangement	0	93

Note: 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 (1962, 4), Pierrel & Sherman (1960, 2), Razran (1949, 3), Rohrbaugh et al. (1971, 1), Steinshneider et al. (1966, 2), Thomas & Setzer (1972, 4), Wills & Mackintosh (1998, 3), Zielinski & Jakubowska (1977, 3). Total: 38 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), Dukhayyil & 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), Moye & 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 & Schwalb (1961, 2). Total: 10 gradients.

Test 8:

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

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

c) Size and intensity dimensions 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.

Note: Strength of bias is measured as the ration 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 (1962, 4), Pierrel & Sherman (1960, 2), Rohrbaugh et al. (1971, 1), Steinshneider et al. (1966, 2), Thomas & Setzer (1972, 4), Wills & Mackintosh (1998, 5), Zielinski & Jakubowska (1977, 3). Total: 39 gradients.

Note: '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 groups size and average degrees of monotonicity. The value $N = 11$ reported above refers to the number of group sizes found in surveyed study (in the range from 2 to 45).

Test 10: Size generalization gradients obtained in inter-dimensional tests appear to peak at sizes larger than S^+.

Wilcoxon matched-pair test, $z = -2.20$, $N = 7$, $P < 0.05$.

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.

Note: 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% of the variance more than exponential fits (see Appendix).

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.

Note: These studies comprise both inter- and intra-dimensional 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.

Kolmogorow-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), Dukhayyil & 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), 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). Total: 88 gradients.

Data analysis

Fitting procedure

We describe briefly the fitting procedure leading to the results about gradient shape reported in the main text. By 'exponential' and 'Gaussian' shapes we mean the following functions, respectively:

$$f_E(x) = a\exp(-|x-b|/c) + d \qquad (1)$$
$$f_G(x) = a\exp(-(x-b)^2/2c^2) + d \qquad (2)$$

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 departing from the peak, and d is the minimum function value (approximately reached very far from the peak). The parameter d has been included since 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 equation (1) and equation (2). Using therefore a, b and c as fit parameters, whe have fitted both equation (1) and equation (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 compute Pearson's correlation r, and we use 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 have thus 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 .

Testing for gradient symmetry

To test for symmetry of gradients obtained from inter-dimensional tests, we divide the gradient in a 'left' and a 'right' side using S^+ as reference point. We then sum all responses emitted 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 are combined as follows to yield the test statistics:

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

which has the meaning of proportion of responses emitted to the left of S^+. By construction its value is independent on 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 l is 0.5. In testing this hypothesis by one-sample t tests (see Appendix), we have considered the same number of stimuli on each side of S^+ (a few times discarding a data point), and covering the same range.