Generalization and the evolution of symmetry preferences

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SUMMARY

Biological displays are often symmetrical, and there is growing evidence that receivers are sensitive to these symmetries. One explanation for the evolution of such sensitivity is that symmetry reflects the quality of the signaller. An alternative is that the sensitivity may arise as a by-product of general properties of biological recognition systems. In line with the latter idea, simulations of the recognition process based on simple, artificial neural networks have suggested that generalization can give rise to preferences for particular symmetrical stimuli. However, it is not clear from these studies exactly how the preferences emerge, and to what extent the results are relevant to biological recognition systems. Here, we employ a different class of recognition models (gradient interaction models) to demonstrate more clearly how generalization can generate a preference for symmetrical variants of a display. We also point out that the predictions of the gradient interaction and network-based models regarding the effects of generalization closely match the results from empirical studies of stimulus control. Our analysis demonstrates that the effects of generalization cannot be ignored when studying the evolution of symmetry preferences and symmetric signals.

1. INTRODUCTION

Biological displays are often strikingly symmetrical. Moreover, there is growing evidence that receivers are sensitive to symmetries of various kinds. Female preferences for male symmetry have been demonstrated in a number of species, ranging from earwigs (Radesäter & Halldórsdóttir 1993) to humans (Berlyne 1971; and, see Møller 1992, 1993; Swaddle & Cuthill 1994 for other examples), and similar biases have also been found in non-mating contexts (Rensch 1957; Lehrer *et al*. 1995; Møller 1995). Why have so many different organisms evolved the same kind of preference? One possible reason is that symmetry may often provide information about the quality of a signaller. The most symmetrical males, for example, may make the best partners (Møller 1990; Møller & Pomiankowski 1993), while the most symmetrical flowers may provide foraging bees with the richest nectar supplies (Møller 1995). An alternative and potentially more general explanation is that sensitivity to particular symmetries may arise as a by-product of common properties of biological recognition systems (Enquist & Arak 1994; Johnstone 1994).

Recognition of a particular display may appear to be a simple task, but it is one that requires the receiver to respond in a similar way to a large range of different stimuli. There are two reasons for this. First, many slightly different variants of the display are likely to be found in the population. Due to instabilities during development, for instance, bilaterally symmetrical display traits suffer random deviations from perfect symmetry (see Ludwig 1932; van Valen 1962; Parsons 1990) that give rise to a range of asymmetrical variants (Johnstone 1994). Second, even a single variant will be encountered in many different positions and orientations, and under different conditions, giving rise to many different retinal images (Enquist & Arak 1994).

Although individual images and variants are typically asymmetrical, there are likely to be symmetries present within the full set of stimuli associated with a display. For example, while individuals exhibit fluctuating asymmetries due to developmental stress, these deviations are random in direction, so that the average phenotype remains symmetrical. Equally, many retinal images correspond to rotations, translations and reflections of each other, so that even for an asymmetrical display, there will be symmetries hidden among the images of the signal. Generalization over the range of stimuli associated with a display might thus give rise to a preference for symmetry (Johnstone 1994; Enquist & Arak 1994).

2. THE CONSEQUENCES OF GENERALIZATION

The phenomenon of generalization was first described by Pavlov, and has been extensively studied in relation to animal learning (e.g. Kalish 1969; Mackintosh 1974). In learning theory the term refers to the fact that when an animal is conditioned to react to a particular individual training stimulus, it will also react to

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stimuli that are somewhat different. The strength of response is described by a generalization gradient (over some stimulus dimension) that is often bell-shaped, with a maximum response at the training stimulus. Innate forms of recognition also seem to yield similar patterns of response (e.g. Baerends & Kruijt 1973; Baerends 1982).

Hull (1943), Spence (1937), and others (e.g. Mackintosh 1974) proposed that the generalization gradient formed after training with several stimuli could be calculated by constructing separate gradients for each stimulus alone, and combining these according to some simple rule. According to Spence's (1937) classical model, for example, the generalization gradient (considering only a single dimension of stimulus variation) produced by training with one positive and one negative stimulus can be predicted simply by summing the excitatory and inhibitory gradients that training with each stimulus alone would produce. By this method, Spence was able to anticipate the widespread finding of peak-shift, in which the peak response after training is elicited by a stimulus shifted away from the positive stimulus in a direction opposite to that of the negative stimulus (Mackintosh 1974; Rilling 1977). In conclusion, gradient-interaction models may be used to investigate biases emerging from biological recognition mechanisms (see Leimar *et al.* (1986) for a previous use of this approach in the context of signal evolution).

Here, we are not concerned with the interaction between excitatory and inhibitory factors, but with generalization over several positive stimuli, namely the different variants and/or images of a display. Nevertheless, we can still make use of the gradient interaction approach. For the sake of simplicity, we consider the consequences of generalization over just a single pair of asymmetrical stimuli; one stimulus being the mirror image of the other. This could represent phenotypic variants of a single display arising from instabilities in development (i.e. fluctuating asymmetry), or views of a single, asymmetric display from different directions. We calculated overall generalization gradients for such pairs of stimuli, along an axis of signed asymmetry, ranging from left-asymmetry (negative values) to right-asymmetry (positive values), assuming that the excitatory gradients around each combine additively and are both given by a normal curve with a maximum at the relevant stimulus (Mackintosh (1974) reviews empirical evidence for gradients of similar shape). We varied both the standard deviation of the excitatory gradients, denoted σ, and the degree of asymmetry of the stimuli, in order to examine the effects of this variation on the shape of the final gradient.

The results are shown in figure 1. The final generalization gradient may be single- or double-peaked, with the latter more likely when the stimuli are strongly asymmetrical and/or individual excitatory gradients are narrow. In either case, however, the maximum probability of response is always for test stimuli that are closer to the intermediate value of perfect symmetry than are the training stimuli (and around each peak, with a double-peaked curve, response declines more slowly towards the intermediate value than in the opposite direction).
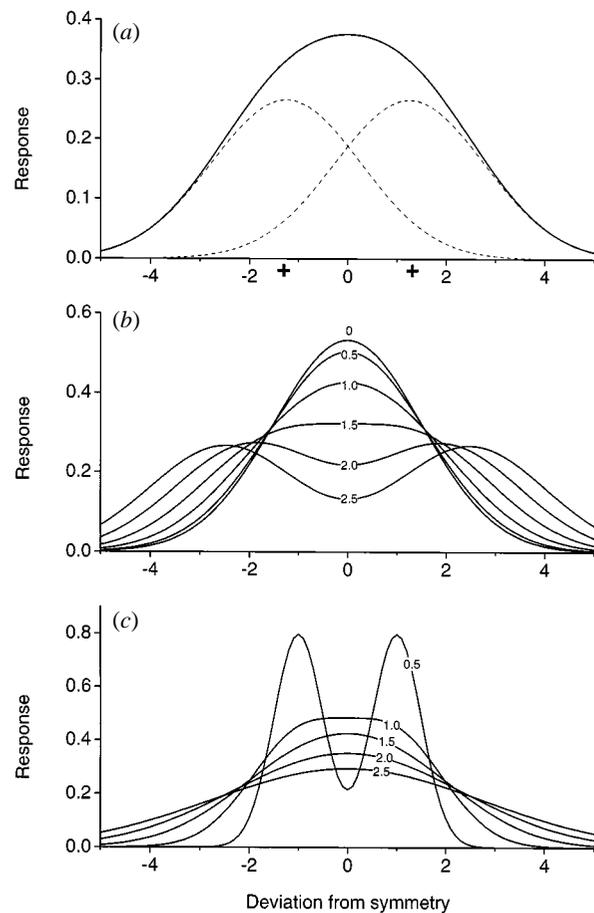

Figure 1. Generalization gradients calculated using the gradient-interaction approach (see main text). Graph (*a*) describes how two hypothetical individual generalization gradients are combined to form the final gradient. Graph (*b*) shows gradients calculated using a fixed value of $\sigma = 1.5$, but varying the distance between the positive stimuli (the distance of each stimulus from the midpoint is given for every gradient). Graph (*c*) shows results for a fixed distance, but varying the value of *s* (which is given for every gradient).

3. DISCUSSION

The above analysis suggests that generalization over two (or more) stimuli or images will result in heightened responsiveness to intermediate test stimuli, especially if these are not too different. This is simply because such intermediates fall in the region of overlap between the generalization gradients surrounding each training stimulus, i.e. they are similar to both training stimuli. If the training stimuli are mirror-symmetric images, the result will be a preference for test images closer to the symmetrical intermediate of the two (and provided that the training stimuli are not too asymmetrical, and/or the individual generalization gradients are not too narrow, this preference will extend as far as perfect symmetry).

While there have been no attempts to date to determine experimentally whether generalization can give rise to preferences for particular symmetries, we can compare the above predictions with the results of studies examining generalization over other kinds of

positive stimuli (Mackintosh 1974). Kalish & Guttman (1957, 1959), and Blough (1969) studied how generalization gradients were formed when pigeons were trained to react with the same response to several mono-chromatic colours. All three studies yielded very similar results despite some differences in experimental method (e.g. figure 2). When the training stimuli were similar the generalization gradient had a single peak, indicating that stimuli of intermediate wavelength, which were not included in the training sets, could evoke a response at least as strong as the training stimuli. Further, response was found to drop off quickly on either side of the peak. When the difference between the training stimuli was increased, a two-peaked gradient emerged. However, the intermediate value still tended to be rather efficient as long as the training stimuli were not too far apart. In all cases the gradients were symmetrical around the intermediate value.

It should be pointed out that generalization does not give rise to a 'universal symmetry detector', but merely sensitivity to particular symmetrical stimuli. Many species, however, do appear to possess specialisations for dealing with symmetries in general, and with transformations related to symmetry such as rotations and reflections. For instance, both humans and pigeons are capable of mental rotation in match to sample tests (see e.g. Hollard & Delius 1982). Humans are also particularly sensitive towards bilateral (mirror) symmetry along a vertical axis (Barlow & Reeves 1979). Osorio (1996) has suggested that mechanisms operating early in the visual system resembling line detectors would be particularly sensitive to imperfection in bilateral symmetry. It is likely that these adaptations also play a part in generating sensitivities to symmetry, but as the present results demonstrate, preference for symmetrical variants of a particular display need not imply the existence of such a specialized mechanism.

The emergence of a preference for the symmetrical intermediate of paired asymmetrical images is likely to give rise to selection favouring increasing display symmetry. A single-peaked response curve, of the sort expected when asymmetries in the paired training stimuli are small (figure 1), clearly favours stimuli that more closely approach perfect symmetry (within the dimension studied), because these elicit a stronger response. When a double-peaked curve is obtained (symmetrical around the intermediate value of the training stimuli), it may appear that selection for symmetry would be weak or absent. However, selection for a display that is more symmetrical may still occur. Deviation from the level of asymmetry that provokes the peak response will have less severe consequences when it is in the direction of greater rather then lesser symmetry (figure 1). This will be important when con-sidering a larger number of stimuli which vary in their degree of symmetry (representing, for instance, individual display variants differing in their level of fluctuating asymmetry). In such a case, the most symmetrical variants would fare slightly better than the most asymmetrical ones, resulting in selection for more symmetrical patterns. A further increase in realism would be to allow the stimuli to vary in more dimensions. A particular symmetry can be manifested
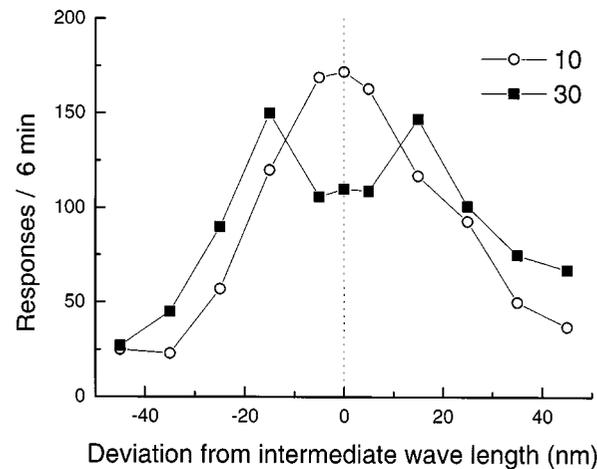
Figure 2. The graph shows data on colour generalization in pigeons extracted from Kalish & Guttman (1957). Pigeons were trained to respond to two different monochromatic colours deviating by 10 nm and 30 nm in wavelength. When the difference between the two colours was small, subjects responded most strongly to a colour that was inter-mediate, but when the difference was large, they behaved as if they had formed two separate representations of each colour.

in a pattern in many ways (e.g. a cross and a bar are both symmetrical under reflection) and a recognition system may exhibit stronger preferences for some of these patterns than others. Thus, if we found a weak preference for symmetry in one dimension, a stronger preference for the same symmetry may exist in another dimension, as simulation using artificial neural networks (these models generalize in a similar way) suggests (Enquist & Arak 1994).

To conclude, sensitivity to increasingly symmetrical variants of a display is likely to emerge in any recognition system (biological or artificial) that exhibits generalization, provided that symmetries are hidden among the set of variants and images associated with the display. Consequently, increased sensitivity towards particular symmetries can appear in the absence of direct selection for such a response, and signals with corresponding symmetries may arise as a result of coevolution between senders and receivers. These simple and robust findings should not be ignored when discussing the functions of symmetry preferences and symmetries found in signals.

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