Experimental evidence of receiver bias for symmetry

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This experiment provides the first empirical evidence that symmetry preferences may arise as a by-product of animals' recognition mechanisms. We used a computer touch screen to train domestic fowl, *Gallus gallus domesticus*, to discriminate between rewarding and nonrewarding stimuli. The rewarding stimuli consisted of two slightly asymmetrical crosses that were mirror images of each other. After training, all subjects preferred a novel symmetrical cross to the asymmetrical training stimuli. Naïve hens tested on the same symbols but without any previous training did not show any symmetry preferences. These results show that symmetry preferences can emerge after experiences with different stimuli that are asymmetrical but that are symmetrical when combined. A preference for symmetrical signals may thus arise as a consequence of generalization and without any link to, for instance, quality of the signal sender.

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Many studies have shown that animals, including humans, show preferences for a particular symmetry, for instance bilateral symmetry. The majority have investigated naturally occurring variation in symmetry. Thus pollinators prefer more symmetrical flowers (Møller 1995; Møller & Eriksson 1995) and females often prefer more symmetrical males, in insects, fish, birds and mammals including humans (see review by Møller & Thornhill 1997). There are, however, also studies that have failed to show any preference for more symmetrical partners, for instance in birds (Oakes & Barnard 1994; Jennions 1998; Ligon et al. 1998). Some studies have instead used artificial stimuli. In one, using bees as subjects, preference for symmetry was reported after previous experiences of symmetrical artificial patterns (Giurfa et al. 1996). Tests for spontaneous preferences for symmetry among novel artificial stimuli have, however, yielded mixed results in monkeys, birds, fish and insects (von Rensch 1957, 1958; Delius & Nowak 1982; Lehrer et al. 1995).

Why do symmetrical signals tend to evoke stronger responses in receivers? A currently popular hypothesis is that the degree of symmetry in a signal communicates the quality of the signal's sender (e.g. Møller 1990; Møller & Pomiankowski 1993; Watson & Thornhill 1994). Potential partners or flowers would signal their quality with their degree of symmetry. The rationale behind this

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idea is that it is costly to develop perfect symmetry and only high-quality individuals can do this successfully.

There is, however, another explanation. It may not be the symmetry per se, but a more efficient appearance of a signal, that is preferred. This appearance, from all the slight variations that normally exist of a signal, may in some cases be represented by symmetry. The preference may thus arise as a by-product of recognition mechanisms following specific experiences (Enquist & Arak 1994; Johnstone 1994; Enquist & Johnstone 1997). Recognition, which includes identification and categorization of a large range of visual stimuli, is a complex task. One difficulty is due to all the slightly different variants existing of a single kind of object (e.g. males of one species). Another arises because even when the same object is seen the image on the retina is neither static nor constant. The image moves when the animal moves its head, and changes in light conditions, distance and orientation also cause considerable variation of the retinal image. Since it is unlikely that exactly the same retinal image is experienced more than once, an animal has to generalize from one stimulus to the next in order to benefit from previous experiences.

Generalization, from previously encountered similar stimuli to novel stimuli, has been thoroughly studied and is usually described in terms of a generalization gradient. The gradient is often bell shaped with a maximum peak that corresponds to the training stimulus. Different models of gradient interaction can be used to anticipate the shape of the curve after training on several stimuli (Spence 1937; Hull 1939; Mackintosh 1974; Pearce 1994;

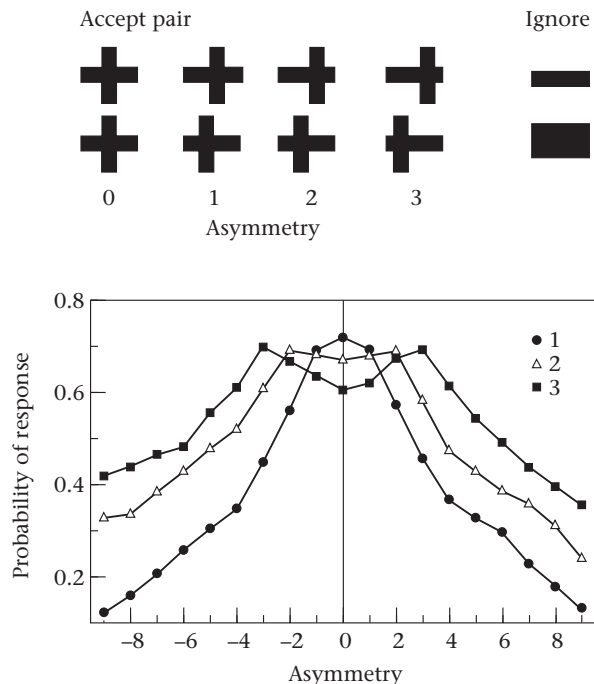Accept pair   Ignore

Figure 1. Generalization curves from neural network simulations, adapted from Enquist & Arak (1998a).

Ghirlanda & Enquist 1999). Such theories have also been applied to the issue of symmetry preferences (Enquist & Arak 1994; Johnstone 1994; Swaddle & Cuthill 1994). Enquist & Johnstone (1997) showed how gradient inter-action theory can be used to anticipate a generalization gradient that yields maximum response to a symmetrical stimulus.

The effect of generalization for development of sym-metry preferences has also been shown in simulations using artificial neural networks (Johnstone 1994; Enquist & Arak 1998). Johnstone (1994) trained by artificial selec-tion a network, representing the recognition system of a female bird, to recognize a set of images representing tails that showed varying degrees of fluctuating asymmetry, but were on average symmetrical. The procedure involved repeated mutation of the network to generate variants that differed slightly in their response to different pat-terns, and selection of those variants that tended to respond more strongly to the images in the training set than to random patterns. The selection procedure gave rise to preferences for symmetrical tail patterns. Enquist & Arak (1998) made a neural network simulation of a simple situation with a suite of stimuli varying in degree of symmetry along a single dimension (Fig. 1). All stimulus variants took the basic form of a cross but differed in the distance of the vertical bar from the centre of the hori-zontal bar. The two images may be thought of as variants of the same signal, for instance resulting from fluctuating asymmetries among individuals or the signal being viewed from different angles. When trained to recognize a pair of patterns that deviated only slightly from sym-metry (asymmetry 1 in Fig. 1), networks responded most strongly to patterns that displayed perfect symmetry. As the degree of asymmetry in the training patterns

increased, the generalization gradient became flatter, and eventually the network seemed to learn to recognize each pattern of the pair as a unique stimulus.

Our purpose in this study was to test the possible concordance of the Enquist & Arak (1998) network simu-lation above with the way living organisms react. Using a touch-sensitive computer screen gives a flexible way of presenting stimuli to a subject and previous work has shown that this approach works well for domestic fowl as test animals (Forkman & Enquist 2000). Therefore we did an experiment using this set-up and mimicking the training procedure in Enquist & Arak (1998). That is, we trained hens to recognize two asymmetrical mirror stimuli, and then measured their responses to a novel introduced symmetrical stimulus. We also did a second experiment testing hens for their spontaneous preferences of the same symbols.

METHODS

Subjects and Housing

Three roosters and six hens, *Gallus gallus domesticus*, 3 months old, participated in experiment 1. Two of the hens were later excluded from the experiment since they failed to reach the discrimination criterion (see Shaping procedure below). Six roosters, 1.5 months old, partici-pated in experiment 2. We obtained all birds newly hatched from a breeder. They were housed in cages measuring $1 \times 1 \times 1$ m, adult hens three per cage, adult roosters one per cage and young roosters six per cage. Each cage was equipped with sawdust bedding, a perch and a water bowl. All cages were placed in a laboratory room, at 20°C, with windows providing daylight in addition to a 12:12 h light:dark (artificial) light cycle. The birds were given free access to water, except during the sessions, and free access to food (commercial chicken pellets) after their daily session for the rest of the day. Food access was completely free during the session-free weekends. This is a very low restriction schedule, com-pared to those normally used in operant conditioning experiments, which typically involve keeping the animals at 80–90% of their ad libitum body weight. The use of the current schedule ensured that we were able to keep the birds at their ad libitum body weight and motivated to work for food at the same time (B. Forkman, unpub-lished data). The study was approved by Stockholms Norra försöksdjursetiska nämnd (the relevant Swedish authority).

Test Equipment

We tested the birds in an operant chamber placed in front of a computer equipped with a 15-inch touch screen. The chamber (40×50 cm and 44 cm high) was made of a wooden frame, coated with chicken wire. A feeding tray (12×3 cm), was fixed in the lower right corner of the computer screen. A feeder delivered food rewards. The computer registered all pecks to the touch screen. The symbols presented or the computer screen's background colour served as the only light source.
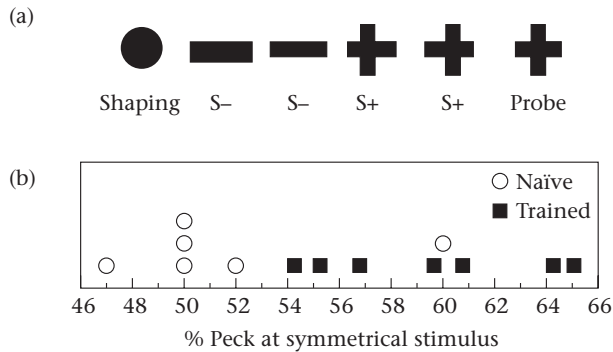
(a)

Shaping S− S− S+ S+ Probe

(b)

Figure 2. (a) Symbols presented during shaping, experimental training and probe trials. (b) Percentage symmetry preference of trained birds (experiment 1) and untrained birds (experiment 2).

Shaping Procedure

All birds were shaped daily except weekends. Sessions lasted 30 min or until the bird had stopped pecking for more than 5 min. During shaping a 5-mm red circle appeared randomly in any of six possible spots on a black screen background. Such spots were 7 or 13 cm from the top of the screen. In width the three possible locations were equally spread 7 cm apart. The birds were shaped to peck within an area of 20 mm from the circle. Pecking within the required area erased the circle and turned the screen background white, making the reward visible for 8 s. In experiment 1 the reward was 0.65 g of commercial pellets delivered from a feeder and in experiment 2 a mealworm. When a bird had pecked 70% of all pecks within the allowed area, in three consecutive sessions, we transferred it to the experiment.

Experiment 1

In experiment 1 we trained the birds to discriminate between one rewarding stimulus (S+) and one non-rewarding stimulus (S−; Fig. 2). The two stimuli were presented simultaneously at two of four possible locations on the screen. The rewarding stimulus occurred in two variants; the two mirror images of a slightly asymmetrical cross (each bar measuring 5.5×1.5 mm on the screen). The nonrewarding stimulus also occurred in two variants, rectangles of sizes 5.5×1.5 mm or 7.5×2.5 mm. The reason for using two S− was to prevent the birds from making their discrimination based on stimulus area (the area of the smaller rectangle was less than the cross while the larger rectangle had a bigger area). The location and version of S+ or S− were random except that S+ never appeared at the same spot twice in a row. This was to prevent birds from developing place preferences. The four possible locations were 8 cm from the top of the screen and equally spread (4.5 cm apart). Pecks within an area of 20 mm of each symbol were registered. If the bird did not peck at all the time between trials was 3 s. If the bird pecked at S−, the symbol disappeared while the screen background remained black for 8 s. If the bird pecked at S+, the symbol disappeared and 70% of the time the screen went white for 12 s, allowing the bird to

eat 0.65 g of commercial pellets, while 30% of the time the symbols disappeared for 5 s. We used this partial reinforcement schedule to avoid extinction effects during subsequent nonrewarded probe trials.

Probe trials were interspersed with discrimination training when the bird had achieved the criterion of pecking 70% to S+, for three consecutive sessions. The probe trials were inserted after every ninth reward. They consisted of a randomly chosen version of the asymmetrical cross together with a novel symmetrical cross of the same size (each bar measuring 5.5×1.5 mm; Fig. 2). The symbols were randomly presented in two of the four possible spots. Every probe trial, which never yielded any rewards, lasted for 10 s irrespective of any peck. When every bird had made a choice, by pecking at any of the symbols, in 50 probe trials the experiment was completed. All birds were trained and tested daily except weekends. Sessions lasted for about 30 min or until the bird had stopped pecking for more than 5 min.

Experiment 2

In experiment 2 we controlled for initial preferences for symmetry by testing for preferences among the same stimuli as in experiment 1 but without any previous discrimination training. Testing birds for initial preferences is a delicate matter. The chicks have to be inexperienced but not too inexperienced to be testable with the same equipment as in the other group. Initially, before a strong habit of pecking at the screen has developed, the chicks are less motivated to peck. To keep them motivated without training them more than necessary, we used mealworms in this experiment, which is a more stimulating reward than pellets. The birds were shown two images simultaneously, randomly presented at any of the four spots. For three birds, one image was a cross with a left asymmetry and the other a symmetrical cross. For three birds, one image was a cross with a right asymmetry and the other a symmetrical cross. The images were the same size as in experiment 1. Each peck within the area of 20 mm of each image erased the stimulus, yielded a white screen for 4 s and a mealworm. The symbols stayed on for 10 s if the bird did not peck. In the 3 s between trials the screen was black. Every bird had to make a choice 100 times, by pecking at any of the symbols. All birds were tested daily. Sessions lasted for about 30 min or until the bird had stopped pecking for more than 5 min.

Statistics

We used one-sample and two-sample t tests to analyse the results. Directional hypotheses are tested and thus one-tailed probabilities are given.

RESULTS

During the probe trials in experiment 1 all hens ($N=7$) showed a preference for the novel symmetrical cross over the familiar asymmetrical cross. The symmetrical cross was chosen in $59.5 \pm 1.59\%$ ($\bar{X} \pm$ SE; $N=7$) of cases. This is

Table 1. Distribution of pecks in probe trials with one symmetrical and one asymmetrical stimulus

Subject	On symmetrical stimulus (%)	Total
Trained		
T1	56.8	155
T2	65.1	218
T3	60.8	227
T4	55.3	208
T5	59.8	194
T6	64.3	221
T7	54.3	184
$\bar{X}\pm SE$	59.5±1.59*	201
t test (μ≤50%)	t_6=5.90, P<0.001	
Naïve		
N_1	52.0	100
N_2	47.0	100
N_3	50.0	100
N_4	50.0	100
N_5	50.0	100
N_6	60.0	100
$\bar{X}\pm SE$	51.5±1.82*	100
t test (μ≤50%)	t_5=0.82, P=0.22	

*Difference between groups: H_0: $\mu_T \leq \mu_N$, t_{11}=3.30, P=0.004.

significantly more than 50% (Table 1). In experiment 2, testing for initial preferences, the percentage of pecks at the symmetrical cross was $51.5 \pm 1.82\%$ (N=6) which is not significantly different from 50%, indicating no preference for the particular symmetry among naïve individuals (Table 1). The mean from experiment 1 was significantly larger than the mean from experiment 2 (Table 1). Together, these findings support the hypothesis that symmetry preferences can emerge from the training of the kind used in experiment 1.

DISCUSSION

The above experiment is to our knowledge the first to show that a preference for symmetry can emerge in real animals as a result of particular visual experiences. The training on two asymmetrical stimuli made the subjects respond more strongly to a symmetrical stimulus that was intermediate to the two training stimuli. The results support the hypothesis that symmetry preferences can result from receiver bias (Johnstone 1994; Enquist & Arak 1994, 1998; Enquist & Johnstone 1997). The result cannot be explained by any benefits being associated with responding to the symmetrical stimulus since completely artificial stimuli were used and the symmetrical stimulus was not rewarded.

According to the hypothesis we tested the preference is limited to the particular symmetry existing in the combination of the two training stimuli; no general preference for symmetry is expected. An alternative to this is the idea of symmetry detectors that could have been triggered by the training procedure. A symmetry detector could be based on the fact that symmetry has a characteristic pattern of phase relationships: they coincide at their peaks and troughs, that is, at 90° and 270° (Delius & Nowak 1982; Osorio 1996). This mechanism has also been implemented with a model showing how arrays of filters, operating locally across the visual image, can detect axes of symmetry by categorizing the spatial phase (Osorio 1996). This would make the visual system particularly sensitive to imperfection in bilateral symmetry. However, the relative phase model cannot explain the finding that symmetries in some categories of figures are harder to perceive than in others (Huber et al. 1999) or why our birds in experiment 2 did not show any spontaneous symmetry preference.

Using the present experimental set-up further insight could be gained by studying the generalization of animals trained to other variants of stimuli. One possibility would be to test subjects to only one of the asymmetrical training stimuli used in our experiment. According to the gradient interaction theory one would expect a gradient peaking at the asymmetrical training stimuli. Another suggestion is to test animals trained to highly asymmetrical examples on a variety of symmetrical patterns (see Enquist & Arak 1998 for artificial network results).

In conclusion, there is no need to assume the existence of a symmetry detector to explain our results, nor any links between symmetry and quality. Our study of domestic fowl shows that preferences for perfect bilateral symmetry can emerge as a consequence of experiences with asymmetrical exemplars that when combined are symmetrical.

References

Delius, J. D. & Nowak, B. 1982. Visual symmetry recognition by pigeons. *Psychological Research*, **44,** 199–212.

Enquist, M. & Arak, A. 1994. Symmetry, beauty and evolution. *Nature*, **372,** 169–172.

Enquist, M. & Arak, A. 1998. In: *Cognitive Ecology* (Ed. by R. Dukas), pp. 21–87. Chicago: University of Chicago Press.

Enquist, M. & Johnstone, R. A. 1997. Generalization and the evolution of symmetry preferences. *Proceedings of the Royal Society of London, Series B*, **264,** 1345–1348.

Forkman, B. & Enquist, M. 2000. Simulation of signal evolution in vivo. *Ethology*, **106,** 887–897.

Giurfa, M. B., Eichmann, B. & Menzel, R. 1996. Symmetry perception in an insect. *Nature*, **382,** 458–461.

Ghirlanda, S. & Enquist, M. 1999. The geometry of stimulus control. *Animal Behaviour*, **58,** 695–706.

Huber, L., Aust, U., Michelbach, G., Ölzant, S., Loidolt, M. & Nowotny, R. 1999. Limits of symmetry conceptualisation in pigeons. *Quarterly Journal of Experimental Psychology*, **4,** 351–379.

Hull, C. L. 1939. The problem of stimulus equivalence in behavior theory. *Psychological Review*, **46,** 9–30.

Jennions, M. D. 1998. The effect of leg band symmetry on female–male association in zebra finches. *Animal Behaviour*, **55**, 61–67.

Johnstone, R. A. 1994. Female preference for symmetrical males as a by-product of selection for mate recognition. *Nature*, **372**, 172–175.

Lehrer, M., Horridge, G. A., Zhang, S. W. & Gadagkar, R. 1995. Shape vision in bees: innate preference for flower-like patterns. *Philosophical Transactions of the Royal Society of London, Series B*, **347**, 123–137.

Ligon, D., Kimball, R. & Merola-Zwartjes, M. 1998. Mate choice by female red junglefowl: the issues of multiple ornaments and fluctuating asymmetry. *Animal Behaviour*, **55**, 41–50.

Mackintosh, N. J. 1974. *The Psychology of Animal Learning*. London: Academic Press.

Møller, A. P. 1990. Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Animal Behaviour*, **40**, 1185–1187.

Møller, A. P. 1995. Bumblebee preference for symmetrical flowers. *Proceedings of the National Academy of Sciences U.S.A.*, **92**, 2288–2292.

Møller, A. P. & Eriksson, M. 1995. Pollinator preference for symmetrical flowers and sexual selection in plants. *Oikos*, **73**, 15–22.

Møller, A. P. & Pomiankowski, A. 1993. Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology*, **32**, 167–176.

Møller, A. P. & Thornhill, R. 1997. A meta-analysis of the heritability of developmental stability. *Journal of Evolutionary Biology*, **10**, 1–16.

Oakes, E. J. & Barnard, P. 1994. Fluctuating asymmetry and mate choice in paradise whydahs, *Vidua paradisaea*: an experimental manipulation. *Animal Behaviour*, **48**, 937–943.

Osorio, D. 1996. Symmetry detection by categorisation of spatial phase, a model. *Proceedings of the Royal Society of London, Series B*, **263**, 105–110.

Pearce, J. M. 1994. Similarity and discrimination: a selective review and a connectionist model. *Psychological Review*, **101**, 587–607.

Spence, K. W. 1937. The differential response in animals to stimuli varying in a single dimension. *Psychological Review*, **44**, 430–444.

Swaddle, J. P. & Cuthill, I. C. 1994. Female zebra finches prefer males with symmetrically manipulated chest plumage. *Proceedings of the Royal Society of London, Series B*, **258**, 267–271.

von Rensch, B. 1957. Ästetische Faktoren bei Farb- und Formbevorzugungen von Affen. *Zeitschrift für Tierpsychologie*, **14**, 71–99.

von Rensch, B. 1958. Dir Wirksamheit ästhetischer Faktoren bei Wirbeltieren. *Zeitschrift für Tierpsychologie*, **15**, 447–461.

Watson, P. J. & Thornhill, R. 1994. Fluctuating asymmetry and sexual selection. *Trends in Ecology and Evolution*, **9**, 21–25.