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A test of receiver perceptual performance: European starlings' ability to detect asymmetry in a naturalistic trait

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There has been substantial interest in whether birds use small degrees of asymmetry (fluctuating asymmetry, FA) in visual communication. However, there is a scarcity of experimental evidence for the visual role of FA. Hence, there is still much debate as to whether FA could be a visual cue. We address this issue by exploring whether European starlings, *Sturnus vulgaris*, can perceive small asymmetries in digital representations of a visual communication trait: white plumage spots on dark throat and chest feathers. Through a series of operant learning trials, we trained starlings to discriminate symmetry from an initially large asymmetry (50% relative asymmetry in the position and number of dots) and then reduced the asymmetry through subsequent learning and unreinforced test trials. Six of seven birds could reliably detect a 25% asymmetry and one bird could detect a 15% asymmetry. There was no evidence for discrimination of a 10% asymmetry. Therefore, we propose that starlings express a limit for detection of asymmetry in this complex structured trait between 10 and 15% relative asymmetry. We discuss this limit in light of natural plumage asymmetries and conclude that most individuals in a wild population would probably be perceived as equally 'symmetric', rendering FA in such a trait an unlikely cue in visual communication. We also discuss the commonalities between this apparent limit to asymmetry detection and other reports of perception in European starlings and pigeons, *Columba livia*, and suggest that our findings could be applied cautiously to other avian systems.

Several authors have suggested that the small degree of asymmetry in bilaterally symmetric traits (fluctuating asymmetry, FA) could be a cue (or signal) of fitness differences among individuals (reviews in Swaddle 2003; Uetz & Taylor 2003). An FA–fitness relationship has been debated and there is no clear resolution as to whether these small morphological asymmetries reliably indicate fitness variation (Swaddle 2003; Pertoldi et al. 2006; Van Dongen 2006). Hence, despite over a decade of intense interest, the role of FA in behavioural communication is largely unresolved. This lack of resolution is partly due to the surprising lack of experimental investigations of the visual role of FA in mediating behavioural interactions. To date, there are

still fewer than a dozen published reports that have manipulated morphological asymmetry within natural ranges and monitored behavioural consequences (Swaddle 2003; Uetz & Taylor 2003).

Over the past few years, we have attempted to shed light on the generality of the visual communication properties of FA by investigating the abilities of a common passerine, the European starling *Sturnus vulgaris*, to detect and discriminate levels of ecologically relevant morphological asymmetry. So far we have quantified European starlings' abilities to detect length (Swaddle 1999a), size (Swaddle & Johnson 2007) and positional (Swaddle & Pruett-Jones 2001) and numerical asymmetries (Swaddle & Ruff 2004). If the European starling is a representative passerine and its asymmetry-detection abilities generally indicate those of other avian species, we can use our results to interpret the relevance of FA to visual communication

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in a broader group of birds. From the published reports we are aware of, European starlings' ability to discriminate variation in simple lengths of objects is similar to that reported in pigeons, *Columba livia* (Schwabl & Delius 1984); hence, we believe there is some generality to our data thus far.

Our current knowledge indicates that European starlings cannot reliably detect many of the length asymmetries present in nature, as many of the display-feather length asymmetries in nature are below an apparent visual detection threshold of approximately 2% relative asymmetry (Swaddle 1999a). However, European starlings' ability to detect size (two-dimensional area) asymmetries between paired, discrete patches does seem to be good enough to detect many natural size asymmetries (Swaddle & Johnson 2007). This is because published reports indicate that size asymmetries of plumage patches on birds are relatively much larger than length asymmetries (Møller & Höglund 1991; Balmford et al. 1993; Møller & Swaddle 1997; Swaddle & Johnson 2007). Interestingly, European starlings appear to be particularly poor at detecting large numerical asymmetries in random-dot displays (Swaddle & Ruff 2004). This was unexpected as humans seem to be able to outperform the birds easily at this task.

Our general approach of quantifying the abilities of European starlings to detect realistically small asymmetries can also help ascertain how general metric (e.g. length and size) and meristic (e.g. counts of elements) variation in cues and signals is detected visually (Guilford & Dawkins 1991; Swaddle 2003; Rowe & Skelhorn 2004). One way in which bilateral asymmetries could be assessed is by matching general length and size differences between the two sides of the same trait (Swaddle 1999b). Therefore, asymmetry-detection abilities could indicate the general upper bounds for discrimination of size and length differences among cues/signals in general. If our preceding assumptions are met, previous experiments indicate that starlings can do no better than discriminate length variation on the order of 2% differences (Swaddle 1999a), two-dimensional size (area) differences of approximately 5% (Swaddle & Johnson 2007) and numerical differences of 40% or greater, when the trait is composed of a large number of uncorrelated distinct elements (e.g. randomly placed dots) (Swaddle & Ruff 2004). As receivers' abilities partly define how a signalling system can evolve, these estimates of visual detection can help us further interpret the shape and strength of selection pressures acting on morphological variation of signals and cues (Rowe & Skelhorn 2004).

Previous investigations of visual cue detection by birds have been limited to fairly arbitrary and abstract cues (Delius & Habers 1978; Delius & Nowak 1982; Schwabl & Delius 1984; Blough & Franklin 1985; Aydin & Pearce 1994; Watanabe et al. 1995; Kirkpatrick-Steger et al. 1998; Swaddle 1999a; Swaddle et al. 2004; Swaddle & Johnson 2007), with a few exceptions (Cook et al. 1997; Jitsumori et al. 1999). Here, we provide the first experimental investigation of how European starlings detect asymmetry variation in representations of a natural cue—the light spots on dark starling throat and chest plumage. European starlings' throat and chest plumage

consists of long body feathers that are dark and iridescent (Bennett et al. 1997), but some feathers also have a large white distal tip that makes the chest appear spotted (Cabe 1993). A previous study showed that female European starlings respond to naturalistic among-individual variation (of approximately 12% differences in dot number between treatment groups) in this morphological cue (Swaddle & Witter 1995). Here, we digitized images of European starlings' throat and chest plumage and manipulated these representations to mimic realistic values of asymmetry in this complex visual trait. We then explored the abilities of European starlings to detect manipulated levels of asymmetry in these images. Based on the seeming difficulty that European starlings have in detecting and responding to fairly gross numerical asymmetries in random-dot patterns (Swaddle & Ruff 2004), we could predict that starlings would not show detection responses to asymmetries lower than 40% relative asymmetry. However, because individual elements within starlings' chest plumage are spatially correlated with one another (unlike in the random-dot displays used by Swaddle & Ruff 2004), it is possible that the correlated elements may give further cues to asymmetry differences, and detection may be better than that predicted by analogy with random-dot patterns (Jenkins 1983; Osorio 1996; Dakin & Hess 1997). As Swaddle & Witter (1995) indicated that female European starlings can adjust social dominance interactions based on 12% among-individual differences in the number of white spots on chest plumage, we predicted asymmetry detection in European starlings' chest plumage at approximately 12% relative asymmetry or lower.

METHODS

Production of Chest Plumage Images

To determine whether birds could discriminate levels of asymmetry from complex naturalistic images we designed stimuli that were based on digital photographs of female European starling throat and chest plumage. We photographed starlings with a Canon EOS digital camera (5 megapixels per image uncompressed) mounted onto a T stand, while the birds were held prostrate so the bird's chest was perpendicular to the camera lens and at a standard distance. We took multiple pictures of five female birds. For each bird, we selected the best picture based on the posture of the bird, the seemingly best overall picture quality (i.e. sharp focus and no blurriness to the image), and the most dots visible on the chest plumage. On average (mean ± SD) these model birds exhibited 176.2 ± 30.4 light dots on their plumage (after image cropping, see below).

We converted these five digital image files (one per bird) to greyscale, rotated and masked them by a trapezoidal shape (pixel dimensions: 640 long, 400 wide at top, 120 wide at bottom) to ensure that all images conformed to the same shape, size and orientation. We bisected each of the five selected images about a vertical midline and mirrored each half across this midline to create two unique chimerical symmetric images, one based on the

left side of the chest, the other based on the right side of the plumage. Therefore, we created 10 symmetric images from the original set of five.

To create parametrically asymmetric images, we either added or subtracted dots (randomly determined) from the left and right sides of the 10 symmetric images. We randomly selected Cartesian coordinates within the image to identify a pixel to manipulate. If the selected pixel fell on a white plumage spot, we coloured in that entire spot using neighbouring greyscale values selected by a dropper tool in Adobe Photoshop. If the selected pixel fell on a dark plumage area, we selected a random neighbouring plumage dot and copied it into that position. We selected a neighbouring dot by applying a six-section (3 × 2) grid over the image (three regions rostral to caudal, as spots are larger on the lower chest than on the throat, where each region had a left and right side). We generated random coordinates until we selected a dot in the same grid region as the previously defined coordinate. We followed this procedure to ensure that the added dot would match the general orientation and size of other dots in that region of the chest (left-side dots are oriented different from right-side dots). We extracted plumage dots using the magic wand tool in Photoshop with a tolerance setting of 75. We determined that this tolerance adequately extracted dots while retaining their original shape.

We restricted the selection of subsequent pixel locations within the same image so that the same dot could not be manipulated twice. We continued the plumage manipulation process until we altered (by addition or subtraction of dots) 5% of the total number of dots on the original image. At this point, we saved the image (as the 5% asymmetric version for this image) and continued the process in steps of 5% until we had produced 10, 15, 25 and 50% asymmetric images for each of the 10 original images. We repeated this entire process three times for each of 10 images, resulting in 30 asymmetric stimuli at each degree of asymmetry (0, 5, 10, 15, 25 and 50% asymmetry). We printed each of the sets of 30 images at 1200 dpi on white paper so that each stimulus image was approximately 3 × 3 cm. We laminated each stimulus image for ease of cleaning during the experiment.

By following this procedure, we produced a 'symmetric' (i.e. 0% asymmetry) and five 'asymmetric' (5, 10, 15, 25 and 50% asymmetry) representations of each of the 30 images. From the 30 manipulated plumage images (described above), we randomly selected 20 sets of images as 'learning images' and the remaining 10 sets as 'test images'. We used only the learning image sets in the learning trials and only the test image sets in unreinforced test trials (both described below).

Although we refer to symmetry and asymmetry it is possible that starlings could judge differences between these sets by using cues other than entire image symmetry, such as by counting dot elements on left and right sides of images. However, we know that starlings are particularly poor at matching numerical differences between the left and the right sides of random-dot displays (Swaddle & Ruff 2004). Our experiment was not designed to determine how starlings perceive asymmetry differences, but to illustrate that they can detect particular degrees of asymmetry—defined as mismatches in dot number and position on the left and right sides of chest plumage. We focused our stimuli manipulations on a vertical plane of symmetry (see Fig. 1) as the majority of natural avian plumage signals possess a vertical plane of symmetry. As birds viewing stimulus images could approach from all angles (see below), as would happen with cue/signal assessment behaviours in the wild, the starlings in this study could potentially perceive the manipulated chest images as possessing various orientations in their axis of symmetry. However, starlings' ability to detect asymmetry in achromatic dot patterns does not appear to be affected by the orientation of the axis of symmetry (Swaddle & Pruett-Jones 2001); therefore we did not attempt to assess how the orientation of the bird (perceiver) relative to the orientation of the axis of symmetry in the stimulus image affected asymmetry detection.

Animals and Housing

We studied the asymmetry-detection abilities of seven wild-caught adult European starlings (four females and three males). These birds were different from those we photographed to make the plumage images. When not in the experiment, the birds were housed in a large outdoor aviary (approximately 6 × 3 × 3 m) with a flock of 12 other wild-caught adult starlings. These birds had ad libitum access to food (nutritionally complete chick starter crumbs: Purina Mills' Start-and-Grow), drinking water, bathing water and perches. When the seven focal birds were in the experiment, they were housed in individual cages (approximately 1 × 0.6 × 0.5 m) on a short photoperiod (8:16 h light:dark) at approximately 20 °C with ad libitum access to food and water, except as noted below. No birds underwent moult while in the experiment.

Experimental Aviary and Pre-exposure Trials

The experimental room (approximately 5 × 4 × 3 m) was an empty, environmentally controlled flight room in which we marked a 1-m^2 grid on the floor (Fig. 2). Lighting and temperature conditions were the same as in the housing room. The grid marked on the floor contained 100 equally spaced locations (each 100 cm^2) upon which we placed 20 clear petri dishes (5 cm diameter) at randomly selected locations. Each dish was subdivided with a large transparent portion (under which we placed images in learning and test trials, see below) and a small food compartment to one side that held approximately 3 g of the starlings' standard food (chick starter crumbs). The food compartment was arranged so that the food did not block the view of images. We also placed two tall perches (1 m high) outside two opposite corners of the grid so that the birds could view the grid from above (Fig. 2).

We deprived the birds of food for 2 h before pre-exposure and all experimental trials (see below). This procedure increased the likelihood that the birds would eat during the trials but did not cause any observable
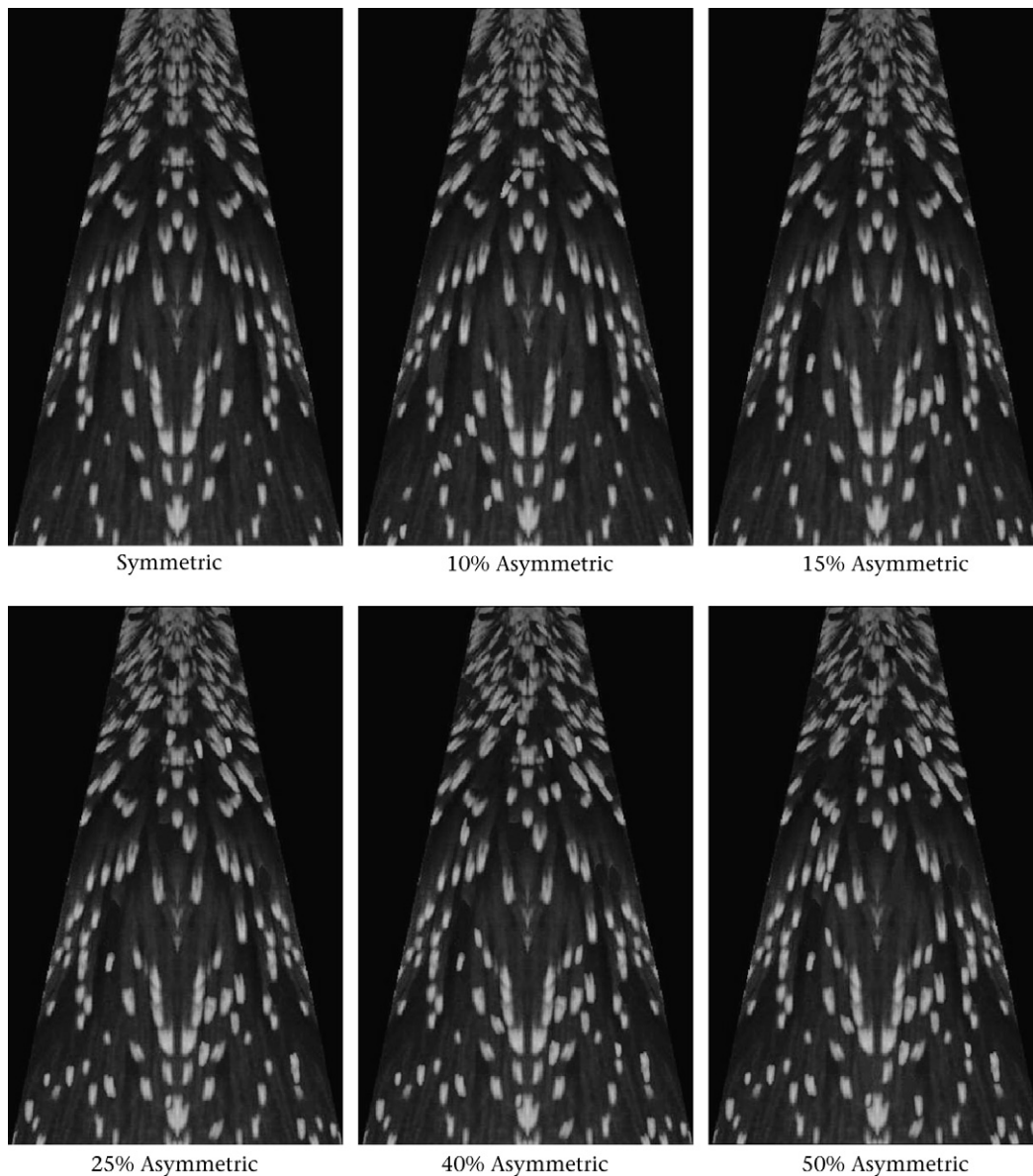
Figure 1. Examples of the manipulated chest plumage images used in learning trials. All of these images are based on the same symmetric template.

distress. Immediately following all pre-exposure and experimental trials, we returned the birds to their home cage and gave them ad libitum access to food until the next trial.

We pre-exposed each of the seven birds to the experimental room, in groups of either two or three a time, through a series of four daily trials. A pre-exposure trial lasted for 40 min, during which we monitored all feeding activity of the birds via a digital video camera through one-way glass (Fig. 2). Every bird ate from at least eight separate dishes (i.e. dishes at eight different locations on the grid) during each of these trials. We kept track of individuals' behaviour by placing unique combinations of coloured plastic bands on the birds' legs. Following this successful pre-exposure, the birds progressed to individual symmetry detection learning trials.

Symmetry Detection Learning Trials

Every bird began the learning phase of the experiment by being reinforced to detect the symmetric images from the 50% asymmetric images. Our intention was to train the birds first to detect symmetry (from asymmetry) using images with a large degree of asymmetry and then progressively decrease the degree of asymmetry in future sets of trials until the birds could no longer reliably detect the asymmetric images. The intended steps in reduction of this asymmetry were 50, 25, 15, 10, and 5%. If the birds could detect 5% asymmetry we intended to produce images with smaller degrees of asymmetry for use in further trials.

We positively reinforced feeding from dishes with symmetric images and negatively reinforced feedings from
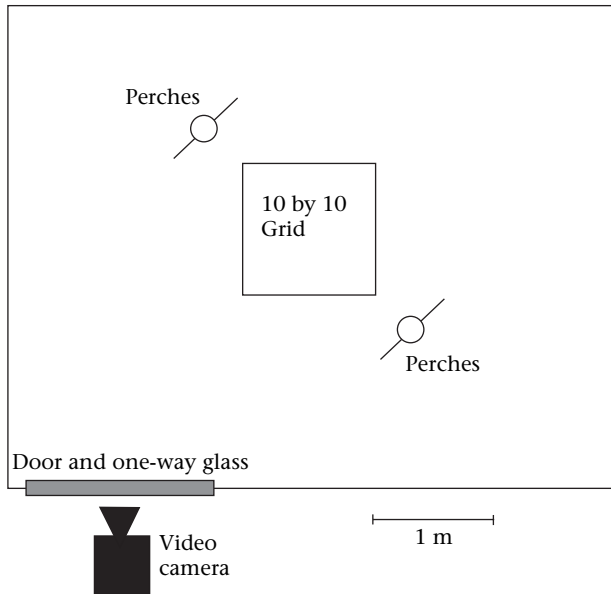
Figure 2. Plan view of the experimental room where we conducted learning, test and control trials.

asymmetric dishes. To achieve this we prepared two versions of their standard food, commercial chick crumbs. A distasteful version was prepared by spraying chick crumbs with a 15% aqueous solution of quinine hydroxide mixed with green food colouring. We used food colouring to mask any visual trace of a quinine residue. This distasteful food was bitter tasting but not harmful to the birds (Forsman & Herrstrom 2004; Swaddle et al. 2004; Swaddle & Johnson 2007) and was associated with asymmetric images in all learning trials. We also prepared a control food by spraying chick crumbs with an aqueous solution of the same green food colouring. This regular-tasting food was always associated with symmetric images. Once the two types of food dried, the experimenters could not visually distinguish between the distasteful and the control foods. We also explicitly tested whether birds could visually distinguish one type of food from the other in control trials (see below). A previous experiment using the same general methodology indicated that starlings could not visually discriminate between the two types of food (Swaddle & Johnson 2007). In addition, previous experiments have shown that the rate of learning to detect asymmetrical images is not affected by whether the negative reinforcement is associated with symmetric or asymmetric stimuli (Swaddle 1999a; Swaddle & Pruett-Jones 2001).

We began a learning trial by placing 10 randomly selected symmetric and 10 randomly selected 50% asymmetric images, from each set of 20 learning images, at 20 randomly selected locations on the experimental grid. We placed petri dishes containing approximately 3 g of control food over the symmetric images and dishes containing approximately 3 g of distasteful food over the asymmetric images. The images could clearly be seen through the dishes. A starling was released into the room and we recorded the proportion of symmetric dishes this starling fed from in a learning trial. A learning trial lasted for 40 min or until the bird had fed eight times

from the dishes, whichever occurred first. We allowed each test bird to revisit dishes within a trial to maintain the constant ratio of symmetric to asymmetric dishes that were available. We recorded revisits only if the subject had searched at least one other dish on the grid before returning to the original dish location. We conducted learning trials 3 to 5 days a week, once per day. After each learning trial, we returned the starling to its housing cage and provided it with ad libitum food.

We adopted a criterion for successful discrimination of symmetry as a bird feeding from symmetric dishes at least 75% of the time within a trial, in three consecutive learning trials. The cumulative probability of this sequence happening by chance is less than 5%. Each starling experienced 15 learning trials unless it reached this criterion sooner. Once a starling achieved the learning criterion or completed 15 learning trials, it progressed to successive test and control trials (described below) and then to a new set of learning trials with a smaller degree of asymmetry (i.e. 25% asymmetry after successful learning at the 50% asymmetry level).

In the subsequent learning trials (i.e. after successful learning, test and control trials at 50% asymmetry), we removed the starlings from the experiment if they did not learn within 10 trials. We adopted this stricter criterion in later learning trials as starlings had already learned the general symmetry detection task, and we had positive evidence that this learning transferred to new trials (described later). Hence, each subject should not have needed the extensive 15 trial learning condition to perform the next level of task. If a starling could discriminate a smaller degree of asymmetry (e.g. 25% asymmetry) it should be able to do so within 10 trials (and they all did) after learning the initial 50% asymmetry discrimination task. This methodology was successful in a previous experiment exploring size asymmetry detection in European starlings (Swaddle & Johnson 2007).

Symmetry Detection Test Trials

Once a starling had met the learning criterion, during the next trial we tested whether performance would generalize to novel images in an unreinforced test trial. These test trials were identical to learning trials except that we placed 10 new symmetric and 10 new asymmetric images at random locations on the grid. These were the images from the test set, described above. Also, we presented control food with both symmetric and asymmetric images in these 40-min test trials. As before, we recorded the proportion of feedings from symmetric versus asymmetric dishes. This procedure represented a generalization test without extinction.

Control Trials

Following a test trial, each starling experienced a control trial. This followed the same general protocol as learning trials except that we did not place any images under the 20 petri dishes on the grid. We recorded the proportion of feedings from control versus distasteful food dishes.

Hence, these trials were designed to test whether starlings could visually discriminate control from distasteful food.

Subsequent Learning Trials

Following completion of test and control trials, we presented the birds with further learning–test–control trial sequences using the same procedures as described above. However, these subsequent trials used progressively lower degrees of asymmetry in the asymmetric sets of stimuli: 25, 15 and 10%. No birds progressed beyond the 10% asymmetry level.

After completion of the experiment, we released the starlings back into the wild at the same location at which they were caught. All procedures were approved by our Institutional Animal Care and Use Committee and followed the ABS/ASAB *Guidelines for the Use of Animals in Research*.

Statistical Analyses

Although we defined a criterion for learning, we also tested statistically whether starlings had successfully learned to discriminate symmetry from asymmetry at each stage in the study. We did this by comparing the proportion of feedings from symmetric dishes in the last learning trial to the proportion of feedings from control dishes in the control trial, using a paired *t* test. Similarly, we tested whether any learned symmetry preference was transferred from the learning trials to the novel test images in the test trial by comparing the proportion of feedings from symmetric dishes in the test trial to the proportion of feedings from control dishes in the control trial, using a paired *t* test. All proportional data were arcsine square-root transformed to normalize their frequency distributions. We performed all analyses with SPSS version 13 for Windows, using two-tailed tests of probability.

RESULTS

All seven birds successfully completed the 50% asymmetry learning trials, performing 75% (or more) feeds from symmetric dishes in three consecutive trials. Performance in their last learning trial was better than in control trials ($t_6 = 14.72$, $P < 0.0001$; Fig. 3a), further indicating a robust level of learning and detection of symmetry from asymmetry. Also, performance in unreinforced test trials was better than in control trials ($t_6 = 3.17$, $P = 0.019$; Fig. 3a), indicating that the learned symmetry detection could be generalized and transferred to novel images.

All seven birds also successfully completed the 25% asymmetry learning trials. Performance in their last learning trial was better than in control trials ($t_6 = 6.86$, $P = 0.0005$; Fig. 3b), indicating successful learning of symmetry detection. In addition, performance in test trials was better than in control trials ($t_6 = 4.54$, $P = 0.004$; Fig. 3b), further indicating that learned symmetry preferences can be generalized to novel images.

Only one of the seven birds successfully completed the 15% asymmetry learning trials, indicating a general lack of
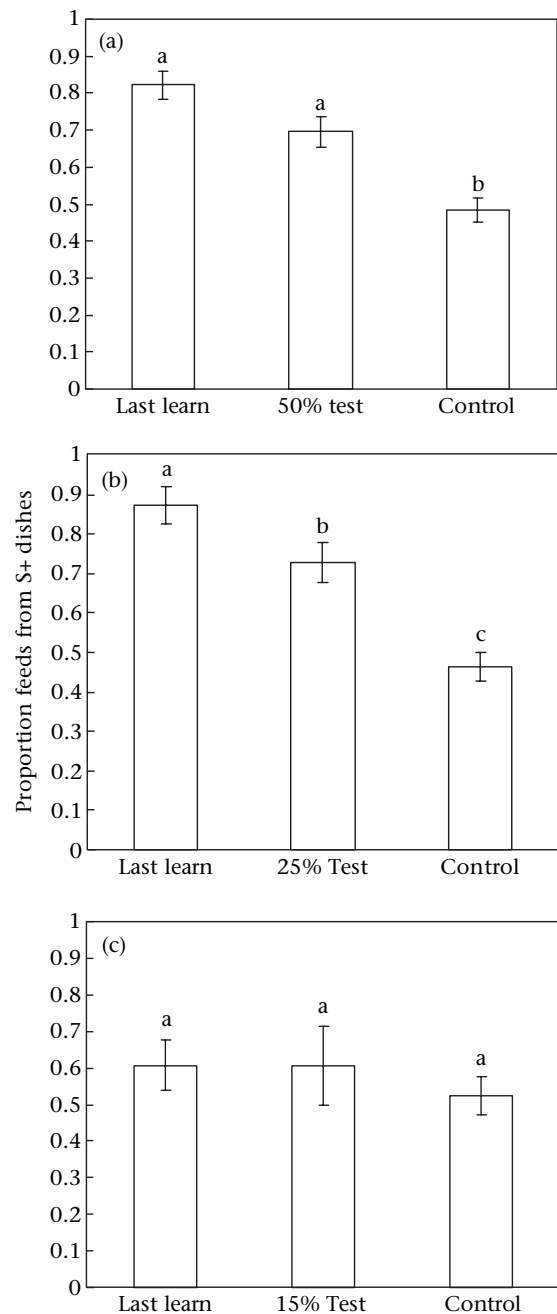

Figure 3. Mean (±SEM) proportion of feeds from symmetric (or positively reinforced) dishes. (a) For the last 10 learning trials with 50% asymmetric images, the single test trial at 50% asymmetry, and the respective control trial for the seven birds. (b) The same trials reported for the 25% and (c) the 15% asymmetric images. The letters indicate statistically significant ($P < 0.05$) differences between trials.

ability to detect and respond to this level of chest plumage asymmetry reliably. Throughout these (unsuccessful) learning trials, birds still ate from dishes, indicating that they had not lost general interest in feeding from the experimental grid. Additionally, performance in neither the last learning nor the associated test trials was notably different from performance in the control trials at this level of asymmetry ($t_6 < 1.15$, $P > 0.292$; Fig. 3c).

The single bird (a female) that progressed to the 10% asymmetry learning trials did not successfully complete this sequence. Therefore, we do not have evidence that European starlings can perceive asymmetries of 10% or less.

The sample sizes were too small to conduct meaningful analyses of sex differences in symmetry detection performance, although we are planning to pool results across previous experiments to investigate this possibility in a separate analysis.

DISCUSSION

All seven European starlings could reliably detect symmetry from 25% asymmetry in complex chest plumage patterns. One bird could also discriminate symmetry from 15% asymmetry, but no birds appeared to detect an asymmetry as small as 10% reliably. Therefore, we propose that our starlings expressed a limit to asymmetry detection, in this complex structured plumage trait, at somewhere between 10 and 15% relative asymmetry. This range of detection is similar to our a priori prediction for asymmetry detection and also close to the level of cue detection (12% dot differences among birds) shown in a previous study (Swaddle & Witter 1995). Interestingly, the average asymmetry displayed in our model birds (i.e. those that we photographed to make the stimulus images) was 10.9% ($\pm$0.09; median asymmetry = 8.7%), which is similar to that reported in a larger sample ($N = 35$; Swaddle & Witter 1995) and also similar to the limits of asymmetry perception that our data suggest. Therefore, it would seem that European starlings should be able to detect visually the most asymmetric individuals in a population, but most individuals would be perceived as being 'symmetric'. Based on a previous sample of 35 starling chest plumage patterns (Swaddle & Witter 1995), approximately 37% of individuals possessed a chest asymmetry of greater than 10%, and approximately 23% of individuals displayed a chest asymmetry of greater than 15% relative asymmetry. If most individuals are perceived as being equally symmetric, we question the effectiveness of visual communication by FA. At best, it would seem to select against (or for) only the fairly rare and highly asymmetric individuals.

Swaddle & Witter (1995) reported that female European starlings altered social interactions in response to approximately 12% changes in the average number of dots on the throat and chest plumage of conspecifics (females with more dots are more likely to be dominant). However, their starlings did not respond to a similar level of asymmetry differences among individuals. Our perception data confirm that European starlings are probably able to discriminate 12% asymmetry differences (although this may be close to their limit), hence further indicating that these birds simply do not use plumage asymmetry as a dominance-related cue. Hence, our new analysis adds to the growing evidence that social dominance interactions are not broadly mediated by asymmetry in visual cues and signals (review in Swaddle 2003).

To extrapolate our results beyond the European starling it would be helpful to compare our data to other species.

However, there are very few similar reports in the literature. Our only points of comparison are among-stimuli bar-length discrimination differences in pigeons (Schwabl & Delius 1984) compared with European starling within-stimuli length asymmetry discrimination (Swaddle 1999a). Both studies indicate that these birds can detect length differences of approximately 2%. Hence, there may be some generality in visual abilities between pigeons and European starlings. We can also challenge the generality of our findings by comparing the current data with reports of detection of other forms of asymmetry by European starlings. Recently, we have shown that these birds can detect size (area) asymmetries in paired, discrete patches of at least 5% asymmetry although many of the subjects detected no better than 10% asymmetry. Hence, European starlings seem to be able to discriminate smaller discrete area asymmetries than complex pattern asymmetries (reported in this study), but the two levels of performance are not that dissimilar. We predict that it would be more difficult for the birds to discriminate asymmetry accurately in the complex plumage traits; therefore it is not surprising that our current data suggest a generally poorer performance than responding to asymmetry in more simple patterns.

Overall, the studies in our emerging series appear consistent with one another and we tentatively suggest there may be commonality in the ways European starlings detect asymmetry among different types of cues (i.e. one-dimensional length asymmetries versus discrete area asymmetries versus numerical and positional asymmetries in complex structured patterns). As our only point of comparison with the pigeon also fits our general pattern, we further suggest that our data could be applied, with appropriate caution, as a starting point for interpreting asymmetry cue/signal detection in other similar avian species. However, if we know that another species has dramatically different visual properties, such as the increased visual acuity of many raptors, then we would not suggest that the European starling is a suitable model.

To interpret further the relevance of our perceptual data, it would also be useful to understand the range of natural asymmetries present in other avian cues/signals that have a structural complexity similar to that of the throat and chest plumage of European starlings. The dark and light throat bars of male zebra finches, *Taeniopygia guttata*, display an average relative asymmetry of a little over 10%, and these differences can be detected by females during preference trials (Swaddle & Cuthill 1994). This observation is consistent with our interpretations thus far. On average, peacock, *Pavo cristatus*, trains display relative asymmetry in eyespot number of approximately 5% (Manning & Hartley 1991). However, it is not clear whether peahens pay attention to complex peacock train asymmetry. We suggest that such asymmetries are at the lower end of perceptual limits and, hence, train asymmetry may not be an effective cue for discriminating among males. Overall train morphology (e.g. total eyespot number) appears more variable (Petrie & Halliday 1994) and, hence, would offer a less error-prone visual indicator of male quality. This is an example of how our perceptual data can be applied to formulate more specific hypotheses about the role of asymmetry in animal communication.

In general, the asymmetry of complex traits is rarely investigated, or if it is investigated, asymmetry metrics are rarely reported (e.g. Ligon et al. 1998). Hence, there are few studies that we can comment on directly at this point. However, we suggest that researchers can use the ballpark perceptual limits that we report here (and in the previous series of studies) to assess whether visual communication by asymmetry could occur within their avian study system.

If bird species use common perceptual and cognitive processes to assess plumage differences among individuals, as they do to determine the symmetry difference between the left and the right side of the same individual, then our results could also be interpreted in terms of general cue/signal detection levels. It is somewhat difficult to assess the validity of this assumption but, as we mentioned above, there are similarities in length discrimination among stimuli by pigeons (Schwabl & Delius 1984) and within stimuli by European starlings (Swaddle 1999a); hence, we feel our assumption has some support. If we accept our assumption, the results from the current study indicate a surprisingly coarse ability of European starlings to discriminate among-individual variation in complex plumage traits. Individuals would have to be approximately 10% different from each other to be reliably detected as possessing different plumage. This perceptual limit of detection will often be far more coarse than measurement error by a researcher. Therefore, we urge researchers to be cautious in interpreting whether birds can see subtle differences among individuals and, hence, whether selection is acting at the fine scale that many researchers can measure.

Our data also allow us to contrast aspects of avian and human symmetry detection. For example, Jenkins (1982) has shown that symmetry in dot patterns is detected by humans in a narrow strip (approximately 1° of the visual field) around the axis of symmetry. Our data do not generally corroborate this finding, as we manipulated symmetry in a much wider area and yet symmetry differences were detectable. Hence, birds may use different symmetry detection mechanisms compared to humans, and/or the very brief presentation of stimulus images commonly used in human asymmetry-detection studies (e.g. Jenkins 1982) results in the use of perceptual mechanisms different from those birds use when exposed to asymmetric images for longer periods (as in this study), and/or the autocorrelations (in particular the spatial correlations) among dots on a natural plumage patch may generate additional cues to symmetry detection that are not present on random-dot displays (Jenkins 1983; Osorio 1996; Dakin & Hess 1997; Wilson & Wilkinson 2002). Any one of these interpretations is interesting, as they indicate that the wealth of data exploring the mechanisms and limits of human visual symmetry detection in abstract (Tyler 1996; Wenderoth 1996; Herbert et al. 2002; Scognamillo et al. 2003) and biologically meaningful cues (Evans et al. 2000; Tjan & Liu 2005) may not be directly applicable to assessing whether birds can detect the same types and degrees of symmetry differences. We see a need to investigate systematically perception abilities in a range of taxa and to perform a comparative review of symmetry

detection or, perhaps more useful, general cue variation detection abilities (i.e. the abilities of animals to detect among-individual differences in cue expression). Several authors would predict widespread similarity of symmetry detection abilities, at least among vertebrates (e.g. Osorio 1996). However, our series of experiments with European starlings leads us to hypothesize that there may be fundamental differences between birds and mammals in their abilities to detect symmetry differences. However, we do agree that there may be commonalities among bird species (e.g. the European starling and the pigeon).

A recent model has suggested a nonlinear ability of humans to discriminate symmetry from asymmetry (Tjan & Liu 2005). In other words, it is far easier to detect symmetry when contrasted with a large asymmetry than with a small asymmetry. So far, through our series of experiments, we have indicated fairly abrupt thresholds of symmetry detection rather than a decreasing nonlinear function (e.g. Swaddle 1999a; Swaddle & Johnson 2007). However, it may be that with our relatively small sample sizes and discrete steps in the degree of asymmetry of learning cues, we do not have the resolution to detect the nonlinear function that Tjan & Liu (2005) suggest. On balance, our data suggest threshold effects of asymmetry discrimination in European starlings, which could indicate a further difference in the ways humans and birds perceive and detect subtle asymmetry differences.

Overall, our data indicate that European starlings have difficulty detecting relative asymmetries less than 10% in magnitude, when assessing a structured complex plumage trait. This limit suggests that many individuals in wild populations would be perceived as being equally symmetric and, at best, starlings may be able to select against the rare, very asymmetric individuals. Hence, these data, along with a series of previous studies (Swaddle 1999a; Swaddle & Ruff 2004; Swaddle & Johnson 2007), add to the growing view that FA in nature is often too small and invariable to be a reliable cue that mediates visual communication.

Acknowledgments

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