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ORIGINAL PAPER

Re-evaluating birds' ability to detect Glass patterns

Jean-François Nankoo[1] · **Christopher R. Madan**[1] · **Douglas R. Wylie**[1,2] · **Marcia L. Spetch**[1]

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Abstract Glass patterns (GPs) are static stimuli that consist of randomly positioned dot-pairs that are spatially integrated to create the perception of a global form. However, when multiple independently generated static GPs are presented sequentially (termed 'dynamic' GP), observers report a percept of coherent motion, and data show an improvement in sensitivity. This increased sensitivity has been attributed to a summation of the form signals provided by the individual GPs. In Experiment 1, we tested whether pigeons also show a heightened sensitivity to dynamic GPs. Our results show that pigeons are significantly better at learning to discriminate dynamic GPs from noise compared with static GPs. However, in contrast to previous research, we found that pigeons did not perform well enough with our static GPs to extract sensitivity measurements. In Experiment 2, we compared our static GPs to those that have been used previously. We show that the difference in the comparison noise patterns is important. We used dipole noise patterns, while previous studies used uniform noise patterns that differ in mean dot spacing to the S+. We argue that prior findings from the use of GPs in pigeons should be re-evaluated using dynamic GP stimuli with noise that consist of dipoles.

Keywords Visual perception · Form perception · *Columba livia* · Glass pattern · Global form

Introduction

To perceive an object-filled scene, the visual system organizes the multitude of incoming signals through a process of integration and segregation of information. For instance, the analysis of complex shapes in the primate brain involves an integration stage in which local orientation signals from V1 neurons are pooled at higher cortical levels to derive global complex form of objects in the environment (Riesenhuber and Poggio 1999, 2000). To study the pooling mechanisms of the form signals, researchers frequently use Glass patterns (GPs) (Glass 1969). GPs are static moiré patterns that consist of randomly placed dot-pairs (dipoles) that are oriented in specific ways to generate different types of global forms. Orientation detectors in V1 and V2 respond to the dipoles in GPs, and the orientation information is pooled at higher cortical levels (e.g., V4) (Smith et al. 2002; Smith and Kohn 2007; Wilson and Wilkinson 1998). Thus, GPs are useful for studying the pooling mechanisms that ultimately extract complex shapes.

When presented with a rapid sequence of independently generated GPs with the same global form, termed 'dynamic' GPs, human observers report a salient percept of coherent motion (Ross et al. 2000). This occurs in spite of the fact that no coherent motion signals are present in the GPs. In addition, human observers appear to be significantly more sensitive in the detection of those dynamic GPs compared to static GPs (Nankoo et al. 2012; Burr and Ross 2006; Or et al. 2007). The mechanisms responsible for the perception of dynamic GPs remain a subject of

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✉ Jean-François Nankoo
nankoo@ualberta.ca

[1] Department of Psychology, University of Alberta, P217 Biological Sciences Bldg, Edmonton, AB T6G 2E9, Canada

[2] Neuroscience and Mental Health Institute, University of Alberta, Edmonton, Canada

investigation, but two possible explanations have been put forth. First, it has been suggested that the illusory coherent motion in dynamic GPs is the result of motion streak sensors interpreting dipoles as streaks that result from high velocity movement of objects across the retina (Day and Palomares 2014; Geisler 1999; Ross et al. 2000). Second, the improved sensitivity observed with dynamic GPs may be a consequence of summation of the greater number of unique global form signals present in dynamic GPs (Nankoo et al. 2012; 2015). Nankoo et al. (2012) showed that the relative detection thresholds of concentric, radial, vertical, horizontal, and spiral dynamic GPs are similar to those of static GPs and different from those of real motion (see Fig. 3 in Nankoo et al. 2012). Nankoo et al. (2015) provided evidence suggesting that the number of unique GPs frames is a more dominant factor than motion streak in facilitating the perception of form from dynamic GPs.

Birds, like mammals, appear to see and act upon an object-filled environment (Cook 2000). Indeed, evidence suggests that some birds have similar (and sometimes superior) visual capabilities compared to the most visually dependent mammals, primates (see Hodos 2012 for review). Several studies have demonstrated that pigeons, a common model organism for studies of avian vision, have the ability to see complex objects within a scene in a similar way to humans (e.g., Cavoto and Cook 2006; see Lazareva et al. 2012 for review). The capability of pigeons to perceive complex objects raises the question of whether a similar integration of form signals to that found in primates is present in the avian brain. Kelly et al. (2001) attempted to probe this question by comparing the detection thresholds for static GPs of different global forms (i.e., concentric, radial, vertical, horizontal, and spiral) in pigeons and humans. Kelly et al. (2001) reported that pigeons did not show any differential sensitivity to the types of GPs used. In contrast to birds, multiple studies, including Kelly et al. (2001), have shown that humans have a heightened sensitivity to concentric and radial GPs (Wilson and Wilkinson 1998; Anderson and Swettenham 2006; Nankoo et al. 2012; although see Dakin and Bex 2002). It has been suggested that the heightened sensitivity for concentric GPs in humans is due to the presence of specialized concentric detectors that feed into higher-level cortical areas, and is related to face perception (Wilson and Wilkinson 1998; Wilson et al. 1997; Fecko et al. 2014). Kelly et al. (2001) suggested that their results reflect the propensity for pigeons to rely more on local information than humans, and that unlike humans, they do not possess a specialized pooling mechanism for concentric form as they tend to use local cues for recognition of conspecifics (Cavoto and Cook 2001). A recent study by Qadri and Cook (2014) found similar results in starlings, suggesting that perhaps the bias for concentric and radial superiority is unique to primates (or mammals in general).

In order to further examine the potential differences in global form processes between the avian and mammalian visual system, we investigated the detection of dynamic GPs in pigeons. We initially aimed to compare the detection threshold of pigeons for concentric patterns of dynamic and static GPs. However, this was not possible as the majority of birds failed to reach a sufficient level of performance with static GPs to estimate thresholds. Thus, we instead analyzed acquisition of the discrimination to assess whether the birds were better able to discriminate global form from noise for dynamic or static GPs. Better performance in the dynamic GPs condition might suggest that the avian visual system processes dynamic GPs in a similar way to the primate visual system. That is, better performance with dynamic GPs might suggest that a form-summation mechanism, as suggested by Nankoo et al. (2012) for humans, is present in the avian visual system.

Experiment 1

Methods

Subjects

Six pigeons with previous unrelated touch screen experience served as subjects. Three birds were assigned to the dynamic GP group, and three birds were assigned to the static GP group. The birds were housed in individual cages under a 12-h light/dark cycle (light onset at 6:00 a.m.). All birds were maintained at approximately 85 % of their free-feeding weights. Water and grit were available adlib in the home cages.

Apparatus

The stimuli were displayed on a 22″ Viewsonic VX2268wm FuHzion LCD computer monitor (resolution 1680 × 1050 pixels; refresh rate 120 Hz). The experiment was conducted in touch screen operant chambers. The monitor was equipped with a 17″ Carroll Touch infrared touch frame. Each chamber contained two solenoid-type bird feeders on the side walls of the chamber. Lamps located within each feeder illuminated feeder presentations, and photocells measured the duration of head entries into the hoppers to limit feeding durations to 1 s per food presentation. The chambers were connected to computers located in an adjacent room. These computers controlled all of the experimental contingencies and recorded the responses.

Stimuli and design

Each stimulus was presented for two minutes or until the birds made a choice. Concentric patterns were used in both the static and dynamic conditions (see Fig. 1). Each stimulus consisted of multiple frames of GPs, each of which was updated at every second monitor refresh (image update rate 60 Hz). For the dynamic GP condition, each frame was a unique and independently generated GP, whereas in the static condition, each frame within a trial was identical, thus giving the impression of a static image; a sample dynamic GP is included as electronic supplementary material to the present paper.

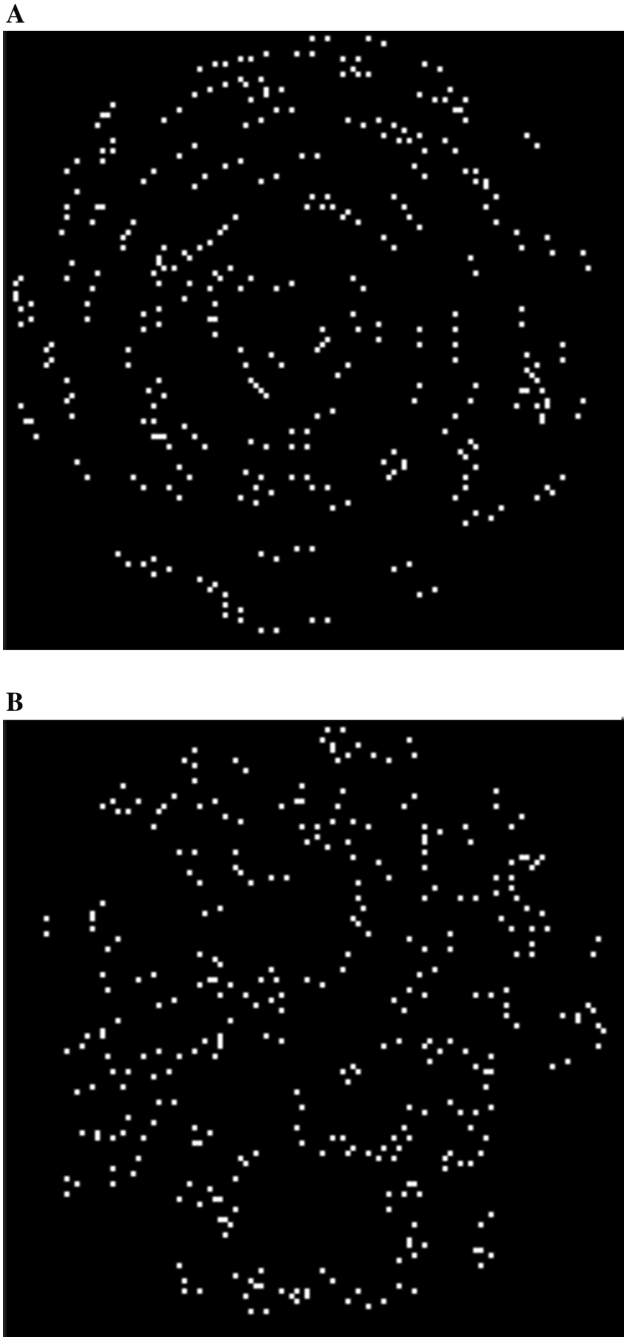

Fig. 1 Types of stimuli used in Experiment 1. **a** A concentric Glass pattern (100 % coherence) and **b** the noise pattern (0 % coherence)

Assuming an estimated 9 cm viewing distance (Bischof et al. 1999; also see Nankoo et al. 2014), each individual GP subtended a visual angle of 39.8° (232 pixels) and consisted of white square dots with an angular size of 0.36° × 0.36° (2 × 2 pixels) on a black background. The density of dots within each pattern was set at 3 %, and the dot separation was 1.07° (6 pixels). As shown in Fig. 1, the S+ pattern contained only signal dipoles (100 % coherence), whereas the S− pattern contained only randomly oriented dipoles (0 % coherence). Thus, there was no global form in the S−, but the distribution of dots in both the S+ and S− were equivalent.

Procedure

Pigeons were tested using a simultaneous two-alternative forced choice paradigm. The S+ and S− stimuli were presented simultaneously. The left–right location of the S+ and S− on the screen was randomized across trials. Each trial began when the birds pecked a gray start stimulus. Thereafter, a peck to the S+ resulted in access to food for one second. A peck to the S− resulted in no food reward. The birds completed as many trials as possible within 45-min sessions. In our data, this resulted in a minimum of 55 trials per session and an average of 150 trials per session. The criterion for completing the training was a mean of 75 % correct responses over three consecutive sessions. The performance for each session was calculated using a simple moving average of three sessions. A maximum of 45 training sessions were conducted.

Data analysis

Statistical analyses, using a binomial-sign test, were conducted for each session in order to establish whether the birds performed significantly better than chance. The accuracy measure was based on a moving average of three sessions.

Analysis of the overall performance of each bird was done by deriving a performance index (PI). The PI consisted of dividing the percent correct of the last session by the total number of sessions in order to account for the differences in number of sessions performed by the birds. Thus, a larger PI equates to better performance, incorporating both accuracy and speed of acquisition. Thereafter, analyses using independent *t* tests were conducted on the reciprocals of the PIs to avoid violating parametric assumptions (Fowler and Cohen 1990).

Effects were considered significant based on an alpha level of 0.05 on all statistical tests. All statistical analyses were conducted using SigmaPlot (Systat Software Inc., Chicago, IL).

Results

As shown in Fig. 2a, all three birds in the dynamic GP group reached criterion within 45 sessions (bird 1 = 11 sessions; bird 2 = 16 sessions; bird 3 = 32 sessions); in contrast, in the static group, all three birds failed to reach criterion within 45 sessions. Based on one-tailed binomial tests, all three birds in the dynamic GP group performed significantly greater than chance within nine sessions, whereas in the static GP group, the birds required a minimum of 11 sessions to perform better than chance (Fig. 2b).

Finally, the performance of the birds based on PI was found to be significantly higher in the dynamic GP condition (t (4) = 4.51, $p = 0.011$; see Fig. 2c).

Discussion

While the results from Experiment 1 shows that pigeons learn to discriminate dynamic GPs from noise more readily than static GPs from noise, it is unclear why our birds performed better with dynamic GPs. For instance, while it could be due to summation of the form signals as has been suggested by Nankoo et al. (2012, 2015), it is also possible that the performance increase should be attributed to other factors, such as dynamic GPs being attended to more because they 'moved' (i.e., changed rapidly over time). However, regardless of the mechanisms, the results suggest that dynamic GPs may be a more suitable stimulus to probe the avian global form mechanisms.

Our results from the static GP condition seem surprising in light of the discrimination of static GPs by pigeons and starlings in previous studies (Kelly et al. 2001; Qadri and Cook 2014). For example, Kelly et al. found that seven out of 11 birds were successful in learning the discrimination task. We therefore conducted a follow-up experiment to test whether the difficulty in learning the static GPs in our study could be due to our

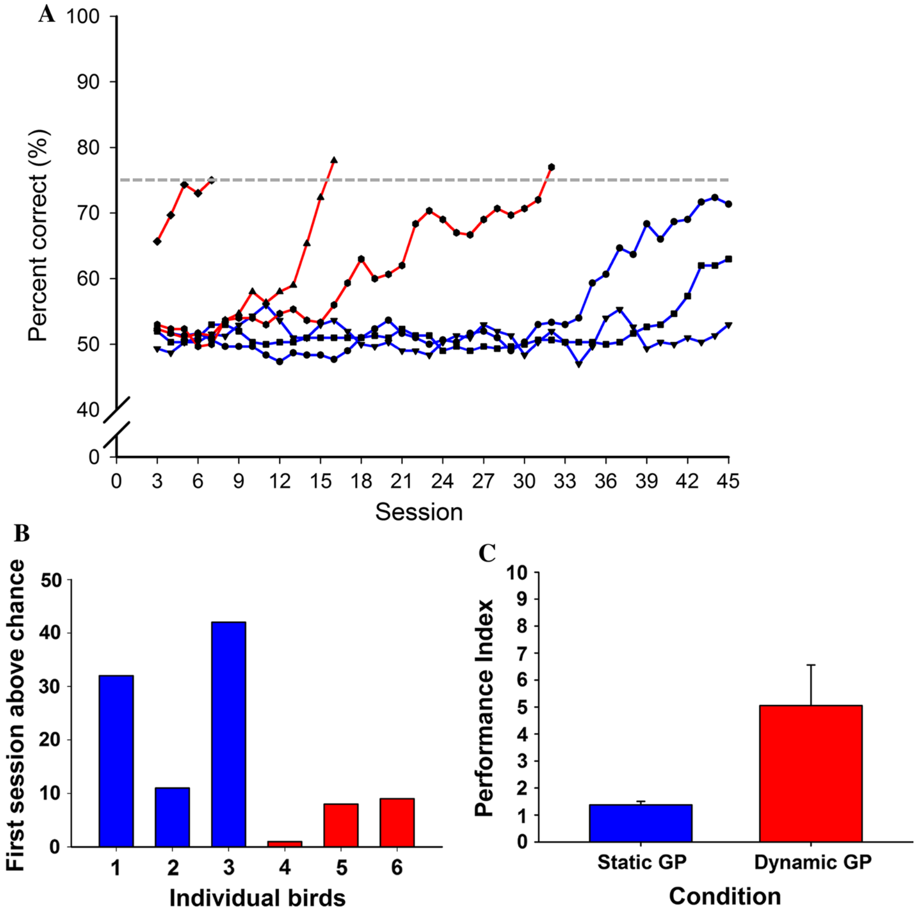

Fig. 2 **a** Mean performance of the birds in the dynamic GPs (in *red*) and the static GPs condition (in *blue*) as a function of session. **b** Number of sessions that each bird required to perform significantly above chance. **c** The mean PI for both the static and dynamic GPs. *Error bars* = SEM (color figure online)

stimuli parameters. Specifically, two noteworthy differences exist between the GPs used in Kelly et al. and ours (Fig. 1). First, Kelly et al. used black dots on a white background, whereas our GPs consisted of white dots on a black background. Second, the type of noise used in Kelly et al. consisted of randomly positioned single dots, whereas ours consisted of randomly oriented dipoles (e.g., Wilson and Wilkinson 1998).

In Experiment 2, we trained pigeons to discriminate between static GPs and randomly positioned single dots (Random-Uniform condition) as this was the type of noise used in Kelly et al. (2001), as well as between static GPs and dipole noise (Random-Dipole condition), as was done in our Experiment 1 (Fig. 3). Both conditions used black dots on a white background, eliminating dot polarity as a potential confound.

Experiment 2

Method

Subjects

Four pigeons with previous unrelated touch screen experience served as subjects for Experiment 2. Housing and feeding protocols were the same as in Experiment 1.

Apparatus, stimuli, and design

The apparatus was the same as in Experiment 1 except for the following differences: For both the Random-Dipole condition and the Random-Uniform condition, the dots were black, and the background was white. The Random-Dipole condition was identical to the static GP condition in Experiment 1 in every other aspect. That is, the S− consisted of randomly oriented dipoles (Fig. 3b). In the Random-Uniform condition, the S− (noise pattern) consisted of random dots (single dots) instead of randomly oriented dipoles (Fig. 3c). The stimuli, design, and procedure were similar to Experiment 1 in every other aspect. Unlike Experiment 1, we used a within-subject design whereby the birds completed both conditions sequentially. The condition order was counterbalanced across birds. Birds 1 and 2 completed the Random-Uniform condition first, while birds 3 and 4 completed Random-Dipole condition first. A paired-samples *t* test was used to test for differences between the two conditions.

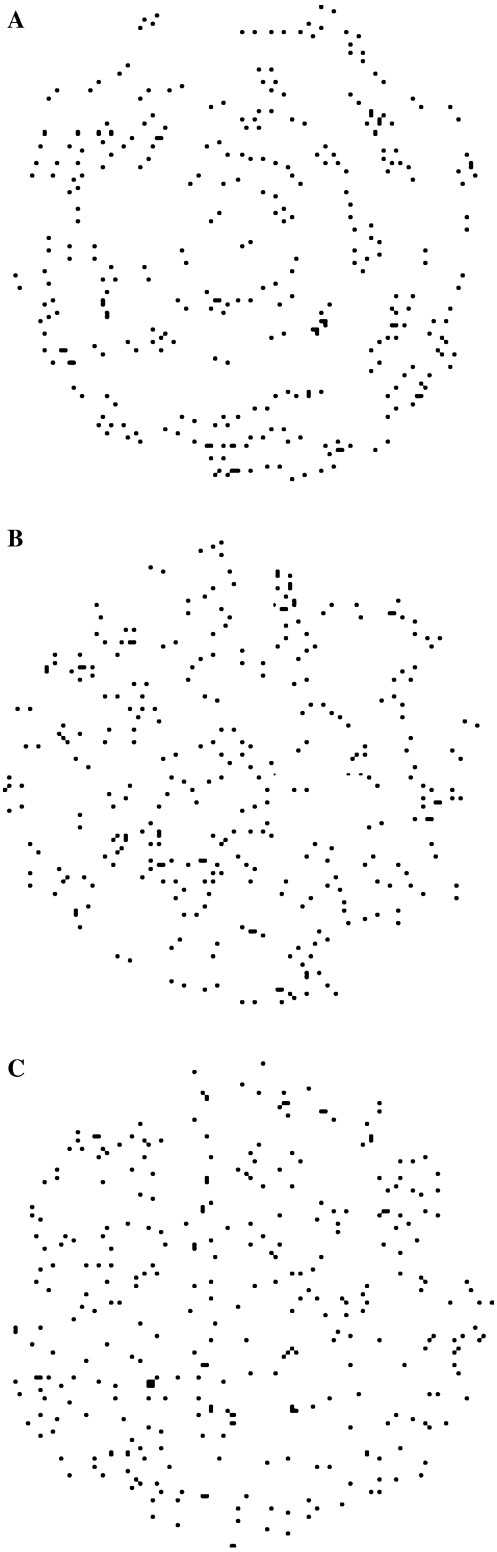

Fig. 3 Types of stimulus used in Experiment 2. **a** A concentric Glass pattern (100 % coherence) and **b** a dipole noise pattern (0 % coherence). **c** A uniform noise pattern

Results

The same performance index and accuracy criteria as Experiment 1 were used for analysis. As can be seen in Fig. 4a, three out of four birds passed the criterion for the discrimination between static GPs and uniform noise patterns within 45 sessions (bird 1 = 30 sessions; bird 2 = 14 sessions; bird 3 = 6 sessions; bird 4 = did not reach criterion). In contrast, *none* of the birds tested were able to reach criterion for the discrimination between GPs and dipole noise patterns. As shown in Fig. 4b, all the birds achieved a performance that was significantly higher than chance within 21 sessions (one-tailed binomial test, all *ps* $< .05$) in the Random-Uniform condition. These birds required, on average, 25 more sessions (SD = 7.38) to perform significantly above chance in the Random-Dipole condition.

The performance of the birds based on PI was significantly higher in the Random-Uniform condition ($t(3) = 5.37$; $p = .013$; see Fig. 4c).

Discussion

Our results support the hypothesis that the difficulty of our birds to learn the discrimination between GPs of 100 % coherence and 0 % coherence in Experiment 1 is likely to be due to difficulty resolving the global structure of GPs. Kelly et al. (2001) and Qadri and Cook (2014) reported that pigeons and starlings were able to discriminate GPSs from noise. However, it is clear that the use of random-uniform noise facilitates detection of the coherent GPs. The intention in using random dipole noise, rather than random uniform noise, is that the mean dot spacing should be matched to the coherent pattern. In Fig. 5, we show this quantitatively, by plotting the cumulative distribution function (CDF) of the distance of each dot to its nearest neighbor. As evident in this figure, for approximately 30 % of the dots, there is no difference in this distance between the two types of random patterns. However, for the concentric GPs and random-dipole noise, over half of the dots have their dipole partner as their nearest neighbor, whereas

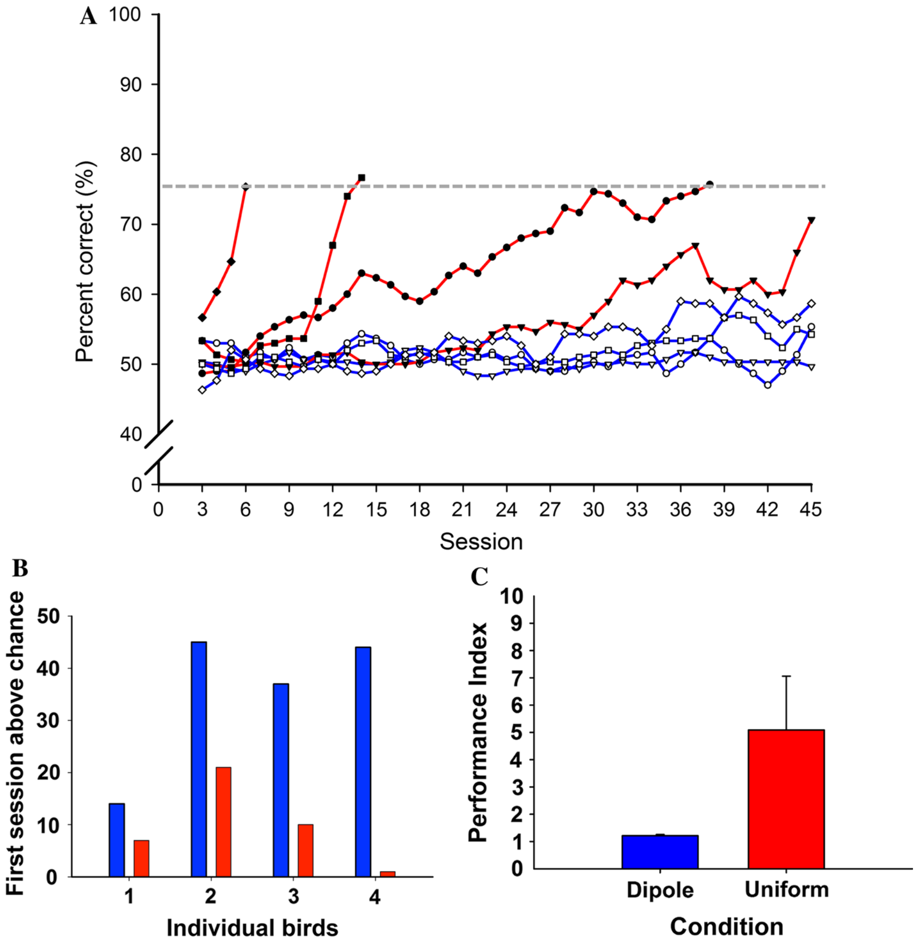

Fig. 4 **a** Mean performance of the birds in the Random-Uniform condition (in *red*) and the Random-Dipole condition (in *blue*) as a function of session. Each unique symbol represents a unique bird. **b** Number of sessions that each bird required to perform significantly above chance. **c** The mean PI for both the static and dynamic GPs. *Error bars* = SEM (color figure online)

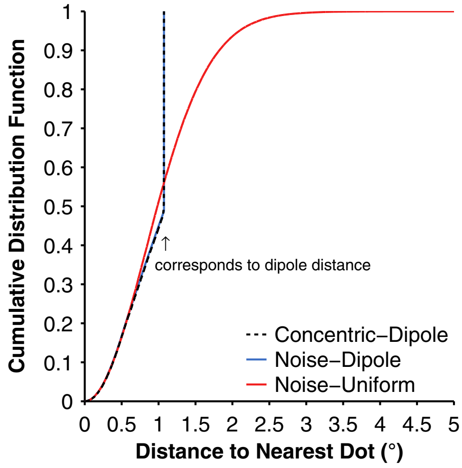

Fig. 5 Cumulative distribution function of distance to nearest dot for concentric, noise-dipole, and noise-uniform Glass patterns. Distributions calculated based on 1000 Glass patterns generated of each pattern type. Note that concentric and noise-dipole almost completely overlap

the sigmoid function simply continues to fall off for the random-uniform noise. This difference in distributions clearly illustrates a local statistic that random-dipole control for, as well as the strategy that could be used by pigeons to differentiate coherent versus random-uniform GPs instead of relying on global form processing. Thus, it is likely that the birds learned the potentially less demanding task of discriminating between dot distributions, as opposed to attempting to resolve the global structure of the patterns.

General discussion

The results from our study revealed two important aspects of investigating global pooling mechanisms for form perception in birds. In Experiment 1, we show that pigeons learn to discriminate dynamic GPs from noise better than static GPs from noise. This is congruent with the results from Nankoo et al. (2012) who showed that thresholds for dynamic GPs were lower than static GPs in humans (also see Burr and Ross 2006; Or et al. 2007). This result suggests that the use of dynamic GPs may be a more effective probe to investigate the global pooling of form information in pigeons and other species. Second, and perhaps more importantly, we found that our pigeons had difficulty discriminating globally coherent structured static GPs from globally incoherent static GPs. In contrast, the birds readily discriminated coherent static GPs from uniform noise, which provided an additional statistic of the mean dot spacing of the patterns that could be used to learn the discrimination. It therefore seems likely that our pigeons used the spatial distribution of the dots in the patterns to make their choice. We are not suggesting that the birds were unable to extract the global form of the patterns; rather that reliance on local strategy may be the favoured strategy.

Nankoo et al. (2012) showed that for humans, the relative ranking of thresholds with different dynamic GPs parallels the relative ranking of the thresholds for static GPs, and albeit thresholds were better with dynamic GPs across all patterns: In both dynamic and static GP conditions, the observers were best at detecting concentric, followed by radial, spiral, vertical, and were worst at horizontal. These relative rankings of thresholds differ from those observed when using random dot kinematograms (i.e., global motion), suggesting that global form mechanisms are dominant in the detection of dynamic GPs (see also Nankoo et al. 2015). Given that our birds exhibited a heightened performance for dynamic GPs relative to static GPs, it is possible that our birds' performance in the dynamic GPs condition is due to the greater amount of global form information as each frame consists of a unique static GP. In other words, the performance of the birds in the dynamic GPs condition may have been due to a summation mechanism of the global form signals.

The perception of global and local form has been extensively studied in birds (see Cook 2001 for review), and often local and global stimuli are put in conflict in order to extract the biases of birds. While these studies have shown that general birds are more likely to use local cues (at least given the stimuli and parameters tested) compared to humans, they also show that birds are clearly able to process stimuli globally (Cook 2001; Fremouw et al. 2003). Kelly et al. (2001) used GPs to investigate whether the avian global mechanism was similar to the human mechanism. However, they found that unlike humans, birds did not show a preference for concentric GPs. Indeed, performances of the birds with all patterns used were equivalent. More recently, Qadri and Cook (2014) have shown a similar set of results using starlings. However, both these studies used noise patterns that differed from the signal not only in global structure but also in dot distribution, as demonstrated in Fig. 5. Given the known bias to processing local information, it is likely that the birds in both studies ignored the global structure and made their choices based on the local information. Indeed, such a strategy would result in equivalent performance regardless of global structure. Here, we have shown that when the mean dot spacing of the noise were controlled to be the same as the signal patterns, the birds were significantly poorer at discriminating signal from noise. This finding reinforces the argument that the birds in Kelly et al. (2001) and Qadri and Cook (2014) may have attended to the differences at the local level as there was no need to globally integrate the orientation signals to solve the task, an alternative strategy noted in the discussion section of both of these papers.

Conclusions

GPs are useful for investigating the global mechanisms of form perception as they allow for control of local and global cues independently. Here, we found that birds can learn to discriminate between dynamic GPs and noise of equivalent mean dot spacing more readily than static GPs. The results of Experiment 2 showed that when the static GPs (S+) and the noise pattern (S−) differed in mean dot spacing, pigeons performed significantly better than when controlling for mean dot spacing, thus suggesting that birds in previous studies using static GPs may have been using a local strategy rather than relying on the global structure of the GPs. It is, however, unclear whether a summation of global form signals, like those suggested for human data (Nankoo et al. 2012), is responsible for the enhanced performance with dynamic GPs or whether this is due to an attention effect. For instance, Franconeri and Simons (2003) reported that translation and looming motion capture attention in a visual search task in humans. The effect of motion on attention was present even when the stimulus is not novel. Regardless, our results indicate that investigating the pooling mechanisms of form perception with static GPs in birds may be challenging. Our findings suggest that dynamic GPs are a suitable alternative to static GPs to investigate global form perception in birds.

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References

Anderson SJ, Swettenham JB (2006) Neuroimaging in human amblyopia. Strabismus 14:21–35

Bischof WF, Reid SL, Wylie DR, Spetch ML (1999) Perception of coherent motion in random dot displays by pigeons and humans. Percept Psychophys 61:1089–1101

Burr DC, Ross J (2006) The effects of opposite-polarity dipoles on the detection of Glass patterns. Vis Res 46:1139–1144

Cavoto KK, Cook RG (2001) Cognitive precedence for local information in hierarchical stimulus processing by pigeons. J Exp Psychol Anim B 27:3–16

Cavoto BR, Cook RG (2006) The contribution of monocular depth cues to scene perception by pigeons. Psychol Sci 17:628–634

Cook RG (2000) The comparative psychology of avian visual cognition. Curr Dir Psychol Sci 9:83–88

Cook RG (2001) Hierarchical stimulus processing in pigeons. In: Cook RG (ed) Avian visual cognition. http://www.pigeon.psy.tufts.edu/avc/cook/

Dakin SC, Bex PJ (2002) Summation of concentric orientation structure: seeing the Glass or the window? Vis Res 42:2013–2020

Day AM, Palomares M (2014) How temporal frequency affects global form coherence in Glass patterns. Vis Res 95:18–22

Feczko E, Shulman GL, Petersen SE, Pruett JR (2014) Interactions between concentric form-from-structure and face perception revealed by visual masking but not adaptation. J Vis 14:5

Fowler J, Cohen L (1990) Practical statistics for field biology. Wiley, England

Franconeri SL, Simons DJ (2003) Moving and looming stimuli capture attention. Percept Psychophys 65:999–1010

Fremouw T, Herbranson WT, Shimp CP (2002) Dynamic shifts of pigeon local/global attention. Anim Cognit 5:233–243

Geisler WS (1999) Motion streaks provide a spatial code for motion direction. Nature 400:65–69

Glass L (1969) Moiré effect from random dots. Nature 223:578–580

Hodos W (2012) What Birds See and What They Don't: Luminance, contrast, and spatial and temporal resolution. In: Lazareva OF, Shimizu T, Wasserman EA (eds) How animals see the world: comparative behavior, biology, and evolution of vision. Oxford University Press, London, pp 5–25

Kelly DM, Bischof WF, Wong-Wylie DR, Spetch ML (2001) Detection of glass patterns by pigeons and humans: implications for differences in higher-level processing. Psychol Sci 12:338–342

Lazareva OF, Shimizu T, Wasserman EA (2012) How animals see the world: Behavior, biology, and evolution of vision. Oxford University Press, London

Nankoo J-F, Madan CR, Spetch ML, Wylie DR (2012) Perception of dynamic Glass patterns. Vis Res 72:55–62

Nankoo J-F, Madan CR, Spetch ML, Wylie DR (2014) Perception of complex motion in humans and pigeons (*Columba livia*). Exp Brain Res 232:1843–1853

Nankoo J-F, Madan CR, Spetch ML, Wylie DR (2015) Temporal summation of global form signals in dynamic Glass patterns. Vis Res 107:30–35

Or CC-F, Khuu SK, Hayes A (2007) The role of luminance contrast in the detection of global structure in static and dynamic, same- and opposite polarity, Glass patterns. Vis Res 47:253–259

Qadri MA, Cook RG (2014) The perception of Glass patterns by starlings (*Sturnus vulgaris*). Psychon B Rev. doi:10.3758/s13423-014-0709-z

Riesenhuber M, Poggio T (1999) Hierarchical models of object recognition in cortex. Nat Neurosci 2:1019–1025

Riesenhuber M, Poggio T (2000) Models of object recognition. Nat Neurosci 3:1199–1204

Ross J, Badcock DR, Hayes A (2000) Coherent global motion in the absence of coherent velocity signals. Curr Biol 10:679–682

Smith M, Kohn A (2007) Glass pattern responses in macaque V2 neurons. J Vis 7:1–15

Smith MA, Bair W, Movshon JA (2002) Signals in macaque striate cortical neurons that support the perception of glass patterns. J Neurosci 22:8334–8345

Wilson HR, Wilkinson F (1998) Detection of global structure in Glass patterns: Implications for form vision. Vis Res 38:2933–2947

Wilson HR, Wilkinson F, Asaad W (1997) Concentric orientation summation in human form vision. Vis Res 37:2325–2330