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Dynamic shifts of pigeon local/global attention

Abstract It has previously been shown that pigeons can shift attention between parts and wholes of complex stimuli composed of larger, "global" characters constructed from smaller, "local" characters. The base-rate procedure used biased target level within any condition at either the local or global level; targets were more likely at one level than at the other. Biasing of target level in this manner demonstrated shifts of local/global attention over a time span consisting of several days with a fixed base rate. Experiment 1 examined the possibility that pigeons can shift attention between local and global levels of perceptual analysis in seconds rather than days. The experiment used priming cues the color of which predicted on a trial-by-trial basis targets at different perceptual levels. The results confirmed that pigeons, like humans, can display highly dynamic stimulus-driven shifts of local/global attention. Experiment 2 changed spatial relations between features of priming cues and features of targets within a task otherwise similar to that used in experiment 1. It was predicted that this change in cues might affect asymmetry but not the occurrence of a priming effect. A priming effect was again obtained, thereby providing generality to the claim that pigeons can learn that trial-by-trial primes predict targets at different levels of perceptual analysis. Pigeons can display perceptual, stimulus-driven priming of a highly dynamic nature.

Keywords Local/global attention · Pigeon · Priming effect · Attentional dynamics

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Introduction

Some species may have evolved highly dynamic attentional systems to deal with their dynamic and complex natural environments. An ability to shift attention rapidly to an important aspect of a complex stimulus might facilitate its processing and thereby provide a selective advantage. For instance, one important characteristic of complex environmental stimuli is spatial location, and humans can switch attention very rapidly between different spatial locations (Posner 1980). It has recently been shown that both pigeons and rats can also switch attention very rapidly between different spatial locations (Shimp and Friedrich 1993; Bushnell 1995; Ward and Brown 1996). Spatial attention is therefore a highly dynamic system in humans, pigeons, and rats.

Another important characteristic of complex environmental stimuli is the level of perceptual analysis they require. Complex stimuli may often be described in terms of a "local/global" distinction (Navon 1977, 1981) having its conceptual origins in Gestalt psychology. A common example of this distinction is that between the level of forests, on the one hand, and the level of trees, on the other. Humans can switch attention very rapidly between global and local perceptual levels. The defining evidence for these attentional shifts in humans has been faster responding to targets at either the local or global level following priming at that level (Kinchla et al.1983; Pomerantz 1983; Robertson et al. 1993). This priming effect has been demonstrated in either of two ways: (1) by blocking trials with a preponderance of targets at a particular level, a base-rate type of priming, or (2) by the use of a priming cue on individual trials to predict probabilistically a target at a particular level. The former method reveals that humans are capable of switching attention between perceptual levels but demonstrates this capacity only over a duration of time sufficient for humans to learn within any given blocking condition what the likelihoods of targets at different levels are. The latter method reveals that humans can rapidly switch attention on the basis of trial-by-trial cues that probabilistically predict the level of the following target.

Birds, like humans, may have evolved to benefit from the selective advantage of being able to attend to either local or global features of complex stimuli. An advantage might accrue to a pigeon if it were able to shift attention between different levels of visual analysis such as between a group of pigeons and a specific pigeon within the group. A number of researchers have demonstrated in the laboratory that the pigeon's attention to complex stimuli can be brought under the control of either parts or wholes (Maki and Leith 1973; Leith and Maki 1975). Cavoto and Cook (2001) more recently showed such control using hierarchically structured stimuli in which some complex stimuli having a particular shape were constructed from many smaller figures having a different shape. Fremouw et al. (1998) demonstrated with such hierarchical stimuli that pigeons can selectively attend either to wholes or to parts of hierarchically structured stimuli and can shift attention between these two levels. Their demonstration of local/global attentional shifts used the blocking procedure, wherein a bird learns over days to expect targets to appear at one level more frequently than at the other level. Thus, their demonstration does not fully address the dynamics of local/global attention in pigeons and it is unknown if pigeons can shift attention between local and global levels of analysis on a rapid, trial-by-trial basis the way humans can.

Clarification of whether birds are capable of very rapid, stimulus-driven priming is important for understanding the underlying mechanisms of local/global attentional shifts in nonhuman animals. Plaisted (1997) has suggested that at least some attentional shift phenomena in nonhuman animals may have little to do with attention per se and may derive simply from the fact that more recently seen stimuli have memory representations that have less fully decayed and are therefore those that can be more easily or more quickly remembered. The demonstration of local/global attention by Fremouw et al. (1998) is susceptible to such a criticism, at least in principle, because the more rapidly identified targets in their experiment were exactly those that were more frequently seen in the recent past. As a result, those memories would have decayed less and therefore would have been more accessible and more quickly retrieved. A demonstration that local/global attentional shifts are under stimulus control on a trial-by-trial basis would make such a time-based, memory-decay interpretation less tenable, or at least require that it be made substantially more complex.

Experiment 1

Experiment 1 was designed to determine whether pigeons can display the rapid shifts of attention that characterize the human local/global attentional system. For that purpose, we freely adapted the procedure of Robertson et al. (1993), who used the trial-by-trial cueing procedure to show that predictive cues can facilitate processing of subsequent targets, as revealed by shorter reaction times to those targets. We correspondingly asked if probabilistically cueing targets at a particular level can facilitate the speed at which pigeons respond to targets at that level. Specifically, on each trial, we cued the level at which the target appeared: just before a target appeared, a cue appeared, the color of which probabilistically predicted the level of the subsequent target.

Methods

Animals

Five male white carneaux pigeons (*Columba livia*) were housed individually in a colony room with a 14:10-h light:dark cycle. Birds were maintained at approximately 80% of their free-feeding weights and had continuous access in their home cages to water and grit. The birds had previously served in a study of the effects of base rate on attentional shifts with hierarchically structured stimuli (Fremouw et al. 1998). Experimental sessions occurred during the light cycle at approximately the same time 5–6 days a week.
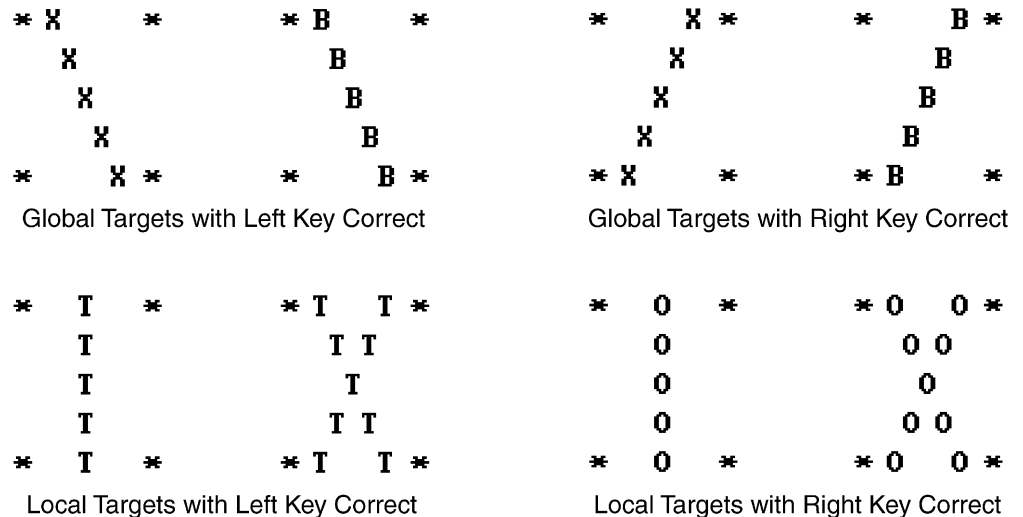
Apparatus

The experimental chamber (38×34.5×50 cm, length×width× height) contained three clear Plexiglas response keys (3.5×3.5 cm) mounted in a horizontal row within a clear Plexiglas viewing window (17×7 cm, width×height) in the front wall. The keys were 20 cm above the chamber floor. A food hopper was located just above the chamber floor beneath the center key. Stimuli were presented on a 15-inch CTX color monitor, 5 cm (birds 1–4) or 8 cm (bird 5) behind the front wall, and were visible through the response keys and Plexiglas viewing window. An IBM PS/2 model 95 computer controlled all experimental contingencies and recorded the data. A fan and white noise (93 dB, C scale, at approximately the position of a bird's head while pecking) helped mask extraneous sounds.

Stimuli

Stimuli were hierarchical in the loose sense that each stimulus consisted of a global character composed of smaller, local characters in a 5×5 grid that was approximately 15 mm wide and 34 mm high. The local characters were generated in standard VGA text mode (80×25 characters) from white ASCII characters (3×5 mm, width×height). Each stimulus had a target at one level and an irrelevant distractor at the other level; global targets were always composed of local distractors and local targets always formed a global distractor. For each bird there were two global targets paired with two local distractors and two local targets paired with two global distractors, resulting in a total of eight stimuli for each bird, as shown in Fig. 1. The stimuli were identical to those used in a previous experiment with these same birds (Fremouw et al. 1998).

Fig. 1 The star priming cues and all eight hierarchical local/global stimuli. Each hierarchical stimulus had a target stimulus at either the local or global level, and an irrelevant distractor stimulus at the other, nontarget level. As shown, the priming cue consisted of a *star* at each corner of the hierarchical stimulus. The targets appeared white and the stars appeared either red or green on a black/gray background. Because the local stimuli were presented on a video screen in standard VGA text mode (80×25 characters) the local characters were composed of small horizontal lines with slight gaps between the lines. Therefore, the stimuli displayed on the monitors were slightly different from the stimuli shown here even though we chose a printing font that in our judgment most closely matched the text mode screen characters

Primes and Stimuli for Birds 1 and 2

```
✳ X      ✳        ✳ B        ✳          ✳     X ✳       ✳       B ✳
   X                 B                      X                 B
   X                 B                      X                 B
   X                 B                      X                 B
✳     X ✳        ✳      B ✳           ✳ X      ✳        ✳ B         ✳
```
Global Targets with Left Key Correct   Global Targets with Right Key Correct

```
✳   T    ✳      ✳ T    T ✳           ✳   O   ✳        ✳ O    O ✳
    T             T  T                   O                O  O
    T             T                      O                O
    T             T  T                   O                O  O
✳   T    ✳      ✳ T    T ✳           ✳   O   ✳        ✳ O    O ✳
```
Local Targets with Left Key Correct   Local Targets with Right Key Correct

Primes and Stimuli for Birds 3, 4, and 5

```
✳ T    T ✳      ✳ E    E ✳           ✳ TTTT ✳        ✳   EEEE ✳
  T    T          E    E               T                E
  TTTTT           EEEEE                TTT              EEE
  T    T          E    E                 T                 E
✳ T    T ✳      ✳ E    E ✳           ✳ TTTT  ✳        ✳ EEEE   ✳
```
Global Targets with Left Key Correct   Global Targets with Right Key Correct

```
✳ HHHHH ✳       ✳ HHHHH ✳            ✳ SSSSS ✳        ✳ SSSSS ✳
   H              H                     S               S
   H              HHHH                  S               SSSS
   H              H                     S               S
✳  H    ✳       ✳ HHHHH ✳            ✳  S    ✳        ✳ SSSSS ✳
```
Local Targets with Left Key Correct   Local Targets with Right Key Correct

For birds 1 and 2, the two global targets were a "line tilted up to the left" (left key correct) or a "line tilted up to the right" (right key correct) composed of local distractor letters "B" or "X". The two local targets were the letters "T" (left key correct) or "O" (right key correct) arranged to form a global distractor "vertical line" or letter "X". For birds 3, 4, and 5, the two global targets were the letters "H" (left key correct) or "S" (right key correct) composed of local distractor letters "T" or "E". The two local targets were the letters "H" (left key correct) or "S" (right key correct) forming global distractor letters "T" or "E".

For birds 1–4, for which the screen was 5 cm from the response keys, the visual angle subtended by global stimuli was approximately 21° vertical and 9° horizontal, while local stimuli subtended approximately 3° vertically and 2° horizontally. For bird 5, for which the screen was 8 cm from the response keys, the visual angle subtended by global stimuli was approximately 16° vertical and 7° horizontal, while local stimuli subtended approximately 2° vertically and 1° horizontally.

Each of the two targets at a particular level occurred equally often, as did the two corresponding distractors. Thus, overall, all eight stimuli were equally likely to occur.

Priming cues

There were two cues, each consisting of four stars, all of which were either red or green. The four stars formed the

corners of a box slightly larger than the stimuli (as shown in Fig. 1). Individual stars (approximately 2×2 mm) subtended approximately 1° of visual angle both vertically and horizontally. The box formed by the four stars (26×32 mm, length×height) subtended approximately 20° vertically and 16° horizontally (birds 1–4) or 15° vertically and 12° horizontally (bird 5).

Each of the cues, either green stars or red stars, probabilistically predicted the level at which a target appeared. For birds 1 and 2, when the cue was red, local targets appeared on a random 85% of the trials and global targets appeared on the other 15% of the trials. In this sense, the red stars "primed" the local level. For these same two birds, the green stars "primed" the global level; targets appeared 85% of the time at the global level and 15% of the time at the local level. For birds 3, 4, and 5, the relation between color of primes and target level probabilities was reversed. Readers should note that a statement such as "when the local level was primed" simply refers to the trials in which the four-star cue probabilistically indicated that a local target was more likely to occur. Priming likelihoods of 0.85 and 0.15 were chosen to match those of Fremouw et al. (1998).

Procedure

Trial structure. On each trial, a pigeon observed one of the eight hierarchically structured stimuli. A bird's task was to respond to whichever key, left or right, was correct for the particular target present in the stimulus. Testing occurred for 35 days with each daily session consisting of 195 discrete trials.

Each trial began with a 2-s intertrial interval (ITI) with the houselight on and the screen blank. Following the ITI, one of the two priming cues, the red or green box, appeared on the screen behind the center key. The first center-key peck to the prime after 1 s elapsed turned on one of the eight stimuli behind the center key, and simultaneously, the two side keys were lit: two white rectangles, each 2.6× 2.4 cm (height×width), appeared on the screen, one behind the left key and one behind the right key. The priming cue remained on when the stimulus and side keys appeared.

The consequences of a peck to either lit side key depended on whether the peck was to the correct or incorrect key. If the peck was to the correct side key, reinforcement was delivered with a probability of 0.4: the hopper light came on and the food hopper was raised. (This partial reinforcement schedule for correct responses permitted a greater number of trials per day.) The 2-s ITI began immediately after food was delivered or after the correct response, if it was not reinforced. If the peck was to the incorrect side key, a correction procedure was initiated. The priming cue, the stimulus, and the side keys were turned off and the houselight blinked on and off every 0.5 s for 15 s. The same prime, the same stimulus, and the side keys then reappeared simultaneously. An error again produced the correction interval. This procedure continued until ultimately a correct response was made and a rein-

forcer was delivered with a probability of 0.4. Only the initial choice response in a trial was recorded and included in data analysis: any subsequent responses in the correction procedure were excluded.

If no peck to a lit side key occurred within 10 s of stimulus onset, a blank screen was presented for 2 s, after which the same prime, the stimulus, and the side keys were presented simultaneously. Such trials were extremely rare and were excluded from data analysis.

Pretraining. No special pretraining was required because of the birds' previous training with the same stimuli (Fremouw et al. 1998). Between this previous experiment and the beginning of the present research, the birds served in a variety of local/global tasks for durations ranging from 1 week to 2 months. To familiarize birds with the present task, and to establish an initial baseline performance, we therefore simply gave 15 days of initial training with easy-to-learn priming likelihoods of 0.95 and 0.05 rather than the values of 0.85 and 0.15 used in the experiment proper.

Results

Responses on the first five trials of each session were excluded from the analysis to reduce the impact of any possible warm-up effects. We grouped the 35 daily sessions into seven, 5-day blocks for data analysis. Following the recommendation of Keppel (1991), we evaluated significance using the Geisser–Greenhouse and Huynh–Feldt corrections where appropriate. Performance is described in terms of two indices, accuracy and reaction time.

We first consider accuracy. Figure 2A shows accuracy (percent correct responses) as a function of target level and primed level, averaged over all five birds and seven 5-day blocks. Figure 2A shows that overall accuracy (averaged over both target types) was very high: mean accuracy was 94.5%. Most critically, visual inspection of Fig. 2A suggests there was a priming effect: accuracy for global targets was higher after global priming than after local priming, and similarly, accuracy for local targets was higher after local priming than after global priming. Figure 2A also suggests that accuracy depended on target level, with accuracy higher for local targets.

A three-way within-subjects analysis of variance (ANOVA) with repeated measures (target level by primed level by block) indicated that there was a trend toward a target level by primed level interaction, $F_{(1,4)}=6.6$, $P=0.061$, and that accuracy was higher overall for local targets, $F_{(1,4)}=10.6$, $P=0.031$. There was also a significant target level by block interaction, $F_{(6,24)}=4.8$, $P=0.002$, resulting from an increase in accuracy for global targets over blocks (from 90.0 on the first 5-day block to 94.5 on the last). No other main effects or interactions were significant at the 0.05 level. In particular, there was no target level by primed level by block interaction, $F_{(6,24)}=0.3$, $P=0.931$.

In summary, accuracy was higher for local targets than for global targets, accuracy for global targets improved with training, and overall, accuracy was very high. The
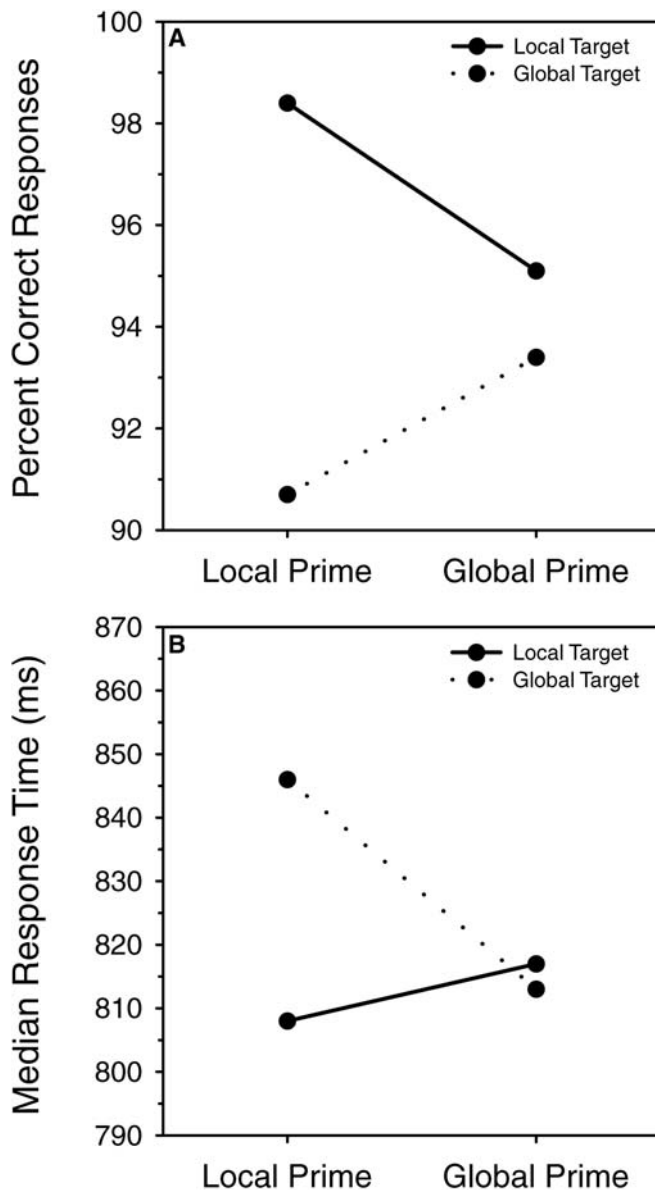
Fig. 2A, B Experiment 1. **A** Percent correct responses to local targets and to global targets as a function of primed level. **B** Reaction time to local targets and to global targets as a function of primed level

tion of Fig. 2B suggests that, on the average, priming a specific level did facilitate speed of responding to targets at that level. Reaction time was faster to stimuli with global targets when the global level was primed than when the local level was primed. Similarly, although to a much smaller degree, reaction time was faster to stimuli with local targets when the local level was primed than when the global level was primed.

Second, was reaction time to either target level faster than to the other? Mean median reaction time, averaged over the seven 5-day blocks, was faster for stimuli with local targets (812 ms) than for stimuli with global targets (830 ms).

A three-way within-subjects ANOVA with repeated measures (target level by primed level by block) indicates that there was a target level by primed level interaction, $F_{(1,4)}=13.7$, $P=0.021$, indicating that there was a priming effect. A Newman–Keuls post hoc test showed that reaction time was faster to global targets when the global level was primed than when the local level was primed, $P<0.05$. In addition, reaction time was faster to local targets than to global targets when the local level was primed, $P<0.05$. Finally, reaction time was faster to local targets when the global level was primed than to global targets when the local level was primed, $P<0.05$.

No other main effects or interactions were reliable at $P<0.05$. In particular, overall reaction time to stimuli with local targets was not significantly faster than reaction time to stimuli with global targets, $F_{(1,4)}=2.5$, $P=0.189$. In summary, the ANOVA shows that in terms of reaction time, there was a priming effect and neither level was, on the average, processed more quickly than the other.

Discussion

A previous demonstration that pigeons can switch attention between perceptual levels of analysis was limited to shifts of attention over a span of several days (Fremouw et al. 1998). This is a slow shift of attention. Here, pigeons shifted attention between different levels of perceptual analysis under trial-by-trial stimulus control and within a time span measured in approximately a second, or vastly shorter than in the several days of the previous demonstration. A priming effect was reliable in terms of reaction times, and a trend toward a priming effect was obtained in terms of accuracy.

The present demonstration shows that the avian local/global attentional system is both flexible, in the sense that it can be brought under stimulus control, and dynamic, in the sense that it can shift attentional resources within the time frame of a single trial. A flexible and dynamic local/global attentional system is therefore not uniquely human.

Plaisted (1997), it will be recalled, suggested that priming-like attentional phenomena appearing in experiments using the blocking procedure might emerge for targets with higher base rates within a block of trials merely because more likely targets are more likely to have been recently seen, and therefore to have any residual memory

absence of a reliable priming effect in terms of accuracy is perhaps to be expected, given the very high overall accuracy and given that shifts of local/global attention in analogous human tasks is typically defined, in part because of this same ceiling effect, in terms of facilitation of response time, not accuracy.

Let us then consider the results in terms of the more typical measure, reaction times for correct responses. We report the mean median reaction times typically used to represent central tendency of reaction-time distributions that are often asymmetric (see, for example, Robertson et al. 1993).

First, did priming a level (local or global) facilitate speed of responding to targets at that level? Visual inspec-

representations more highly activated. The present experiment, however, shows that local/global shifts of attention can be brought under momentary stimulus control, and it is unclear how a purely time-based, decay-of-target-memory process could account for the present results. We therefore now have at least one demonstration of rapid, perceptual priming of avian local/global attention.

We hasten to note that although the present results make a purely time-based, memory-decay explanation of some local/global attentional phenomena in nonhuman animals virtually untenable, they leave for future research to determine just what the underlying mechanisms are. We agree with Cavoto and Cook (2001) that the underlying mechanisms that generate such shifts of local/global attention probably depend on the particular behavioral and perceptual context. For example, it is possible that a decay-of-memory process may have played a role in Fremouw et al. (1998), given the blocking procedure used in that experiment. We note that the contemporary human literature upon which the present research is based is itself in the process of articulating and evaluating competing possibilities involving spatial frequency analysis (Shulman and Wilson 1987; Lamb et al. 1999), the activation of level-specific neural mechanisms (Lamb et al. 1998), and an attentional spotlight (Lamb and Robertson 1988). We expect that the mechanisms underlying local/global attention will be found to involve the dynamic interaction of several processes, including basic memory processes.

Experiment 2

Experiment 1 demonstrated that pigeons can switch attention between levels of perceptual analysis on a trial-by-trial basis, as a function of stimulus-driven priming. The time frame over which this priming was obtained, a fraction of a second, was vastly shorter than in a previous demonstration by Fremouw et al. (1998) of local/global attentional switching, where attentional switches occurred only over periods of several days. A single demonstration of a new phenomenon may raise as many new questions as it answers old ones. In particular, it was judged prudent to conduct an additional experiment to examine further some possible effects of the relations between specific features of a priming stimulus and those of a target. In general, the relation between priming stimulus and target stimulus might affect various details of priming.

Consider that in experiment 1 the priming effect was asymmetric in the sense that global primes facilitated responding to global targets but local primes did not have the correspondingly reliable facilitating effect on responding to local targets. Asymmetric priming has been observed previously in the human literature (Robertson et al. 1993) and is a feature of priming that might depend on specific relations between priming stimulus and target stimulus. The present priming cues, like those used in some corresponding human research (Robertson et al. 1993), consisted of four objects located at the corners of the spatial region within which global stimuli appeared. The priming objects therefore closely identified the spatial region where global targets appeared. Thus, from the perspective of an "attentional spotlight," according to which attentional resources tend to be allocated to spatial regions where targets are likely (Robertson et al. 1993), one might expect more effective global than local priming, simply because the spatial locations of the primes more accurately identified spatial locations of global than of local targets. Alternatively, the global nature of the star prime might produce divided attention between two global stimuli, the star prime and a global target, and might thereby reduce overall attention to a global target. In short, the specific nature of a prime might idiosyncratically affect attentional switching in ways difficult to anticipate or interpret.

We wish to emphasize, however, that although the details of priming in experiment 1 might have been affected by the spatial features of the primes used there, the fact that priming occurred at all is not likely to have depended on these features. Thus, in experiment 1, it was not possible for the observed priming effects to have resulted simply from the specific spatial features of the primes, because the same spatial configuration of four stars was used as the priming stimulus in the two different conditions associated with opposite biases: the only difference between the primes for conditions with opposite biases was the color of the primes. Thus, the same spatial configuration successfully primed opposite levels of perceptual analysis in the two conditions, although reliably so in only one direction.

Experiment 2 varied structural aspects of one of the two priming stimuli: this experiment used two very different kinds of primes. On half of the trials, a star prime identical to that in experiment 1 was used. On the other half of the trials, however, a blank computer monitor was used to prime the other target level. Experiment 2 therefore asked if a prime consisting of a blank screen signaling the same information as a star prime, but having drastically different features, would still facilitate responding to the level it predicted, relative to responding to the other level. If so, then rapid attentional switching between levels of perceptual analysis would have been displayed for two very different kinds of primes, and the generality of rapid local/global attentional priming would be substantially increased.

Experiment 2 also explored the values of stimulus onset asynchrony (SOA) over which avian local/global shifts of attention may be obtained because experiment 1 used only a fixed minimum SOA of 1 s. Since nothing was known about suitable values of SOA, we varied it over a range of approximately 50–450 msec, a range suggested by a somewhat analogous spatial attention literature (Shimp and Friedrich 1993).

Methods

Animals and apparatus

The animals and apparatus were the same as in experiment 1.

Stimuli

The target stimuli and the star prime stimulus were the same as in experiment 1.

Procedure

The procedure was different from that of experiment 1 in three ways. First, a prime for one level consisted of four stars, and a prime for the other level consisted of a blank screen. It will be recalled that in experiment 1, both levels were primed by stars, with different colors of stars associated with different levels. Second, a prime was presented in advance of the target for different durations on different trials: the three randomly selected SOAs were 50 msec, 250 msec, and 450 msec. As in experiment 1, the prime remained on when the target appeared. Both prime and target remained on until a bird pecked a side key. (Of course, on trials when the prime consisted of a blank monitor, only the target appeared on the monitor.) Notice that the effective duration of the prime depended on a bird's reaction time to respond to the prime–target compound stimulus; the longer the reaction time, the longer the prime duration.

Trial structure. The trial structure was exactly the same as in experiment 1: on each trial, a pigeon observed one of eight possible hierarchically structured stimuli, randomly selected, and its task was to respond to whichever key, left or right, was correct for the particular target present in the randomly selected stimulus.

A trial began with a 2-s ITI with the houselight on and the screen blank. Following the ITI, a white warning cue, 2.6×2.4 cm (height×width), appeared on the screen behind the center key. The first center-key peck to the warning cue after 1 s elapsed turned it off, began one of two equally likely types of trials, star prime trials or blank prime trials, and began one of three equally likely prime durations of 57.1, 256.8, or 456.5 ms. On a star prime trial, immediately after the warning cue turned off, a star prime appeared behind the center key. In condition 1, the star prime consisted of green stars, and in condition 2, red stars. On a blank prime trial, the termination of the warning cue presented a blank screen. Minimum durations of both types of prime were determined by the same three presentation intervals described above. When the prime presentation time elapsed, one of the eight stimuli was randomly selected and presented behind the center key, and simultaneously, the two side keys were lit.

Experimental conditions

Both primes probabilistically predicted, in identical manners, the level at which a target appeared. In condition 1, a star prime predicted a global target on 85% of the trials and a local target on only 15% of the trials. A blank prime predicted a global target 15% of the time and a local tar-

get 85% of the time. In condition 2, the priming likelihoods were reversed, so that a star prime predicted a local target 85% of the time and a global target 15% of the time, and a blank prime predicted a global target 85% of the time and a local target 15% of the time. In short, in condition 1, a star prime primed global targets and a blank prime primed local targets, and in condition 2, a star prime primed local targets and the blank prime primed global targets.

Each of the two primes occurred equally often, as did stimuli at the two target levels. Each of the two targets at a particular level occurred equally often, as did the two corresponding distractors. As a result, overall, all eight stimuli were equally likely. Condition 1 and condition 2 were each conducted for 50 days.

Pretraining. No special pretraining was required because the basic procedure was similar to that in experiment 1. Birds were simply familiarized with the task by giving them 15 days of training before each of the two conditions with relatively easy-to-learn priming likelihoods of 0.95 and 0.05 rather than the values of 0.85 and 0.15 used in the experiment proper.

Results

Responses on the first five trials of each session were excluded from the analysis to reduce the impact of any possible warm-up effects. We grouped the 50 daily sessions in each condition into five, 10-day blocks for data analysis. Performance is described in terms of two indices, accuracy and reaction time.

First consider accuracy. Figure 3A shows accuracy (percent correct responses) as a function of target level and primed level for the two conditions averaged over all five birds and the five 10-day blocks. Figure 3A shows that overall accuracy was very high: overall percent correct was 94.8. Visual inspection of Fig. 3A suggests that there was a priming effect in terms of accuracy; accuracy to global targets was higher after global than after local primes, and similarly, accuracy to local targets was higher after local than after global primes. Figure 3A also suggests that accuracy depended on target level: accuracy was higher for local targets than for global targets regardless of the bias or primed level.

A five-way within-subjects ANOVA with repeated measures (condition by target level by primed level by SOA by block) corroborates visual inspection. There was a significant target level by primed level interaction, $F_{(1,4)}=8.1$, $P=0.046$, indicating that there was a priming effect. A Newman–Keuls post hoc test showed that accuracy was higher for local targets than for global targets when the local level was primed, $P<0.05$. No other interactions involving both target level and primed level were significant.

The main effect of target level was not significant, $F_{(1,4)}=6.7$, $P=0.061$. A target level by block interaction, $F_{(4,16)}=3.5$, $P=0.031$, indicated that accuracy was significantly higher for local targets in individual blocks. A Newman–Keuls post hoc test showed that accuracy was
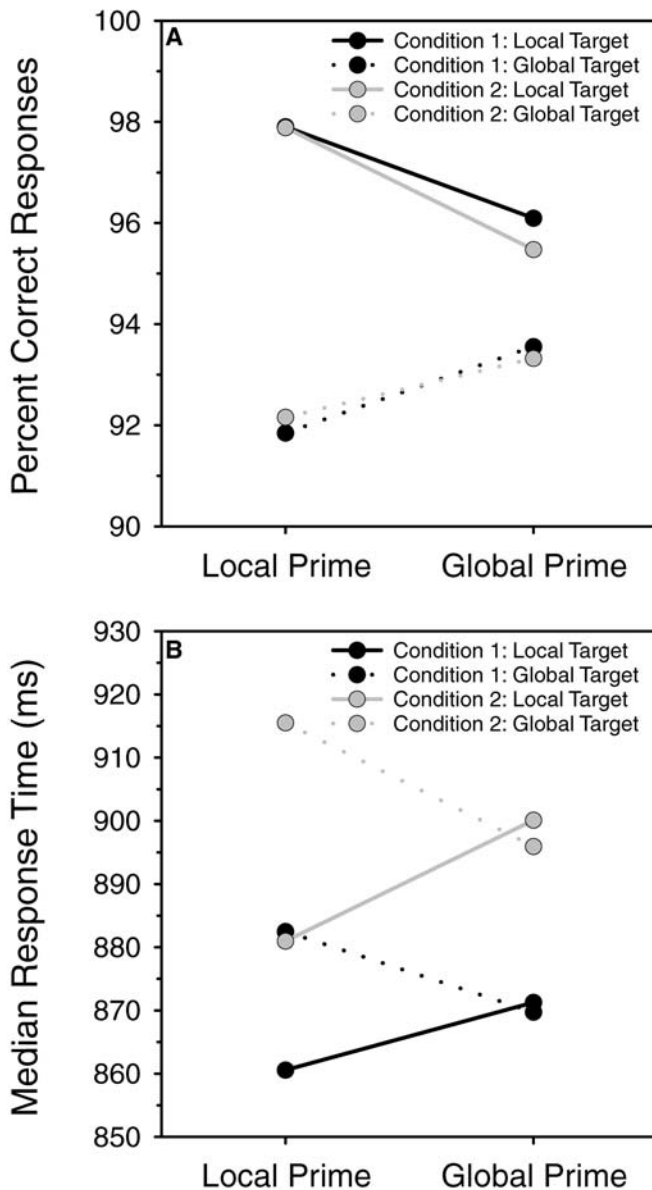
Fig. 3A, B Experiment 2. **A** Percent correct responses to local targets and to global targets as a function of primed level for the two different priming conditions. **B** Reaction time to local targets and to global targets as a function of primed level for the two different priming conditions

significantly higher for local targets than for global targets during all blocks, *P*<0.05. The ANOVA also indicated that there was a significant condition by target level by SOA interaction, $F_{(2,8)}=5.2$, *P*<0.04. A Newman–Keuls post hoc test showed that in condition 2 accuracy was higher to local targets than to global targets for all three SOAs, *P*<0.05. However, in condition 1 accuracy was higher for local targets for the 250- and 450-ms SOAs but not for the 50-ms SOA, *P*<0.05. Thus, in general, accuracy was higher for local targets than for global targets.

The ANOVA indicated that there was a significant block main effect, $F_{(4,16)}=6.1$, *P*=0.003, resulting from an approximately 1% drop in accuracy during blocks 4 and 5.

The ANOVA also indicated that there was a significant primed level by block interaction, $F_{(4,16)}=5.4$, *P*=0.006.

In conclusion, in terms of accuracy, there was a priming effect, accuracy was very high, accuracy was generally higher for local targets than for global targets, and SOA had little effect.

Now consider the more traditional measure, reaction times for correct responses. Mean median reaction times are displayed because reaction times often are asymmetric (see, for example, Robertson et al. 1993). Figure 3B shows mean median reaction time as a function of target level and primed level for the two conditions averaged over all five birds and five 10-day blocks. Figure 3B suggests that in both conditions there was a priming effect: reaction time to global targets was faster after global than after local primes, and similarly, reaction time to local targets was faster after local than after global primes. Figure 3B suggests that reaction time was faster overall, averaged over both global and local targets, in condition 1 than in condition 2.

A five-way within-subjects ANOVA with repeated measures (condition by target level by primed level by SOA by block) corroborates visual inspection. There was a target level by bias interaction, $F_{(1,4)}=10.8$, *P*=0.030, indicating that there was a priming effect. A Newman–Keuls post hoc test showed that reaction time was faster to local targets than to global targets when the local level was primed, *P*<0.05. Overall, reaction time was faster in condition 1 than in condition 2, $F_{(1,4)}=30.0$, *P*=0.005. No other main effects or interactions were reliable at *P*<0.05. Specifically, the SOA by target by bias interaction was not reliable, $F_{(2,8)}=0.67$, *P*=0.538, so that SOA had no reliable effect on priming as measured by reaction time.

In summary, in terms of reaction time, there was a priming effect in both conditions and reaction time, overall, was faster in condition 1 than in condition 2. We feel the simplest explanation for the overall change in speed is that response topography drifted with training for some birds such that absolute response speeds changed accordingly. This appeared to be the case for at least two of the birds.

Discussion

Experiment 2, like experiment 1, demonstrated that pigeons are capable of trial-by-trial stimulus-driven local/global shifts of attention such that priming cues that diagnosed different likelihoods of targets at different levels of perceptual analysis affected responding to those targets. Experiment 2 produced a priming effect with a relation between the spatial configuration of priming cue and target stimulus that was radically different from that in experiment 1. In experiment 2, the priming stimulus on half of the trials consisted of a star prime as in experiment 1 but on the other half of the trials it consisted merely of a blank computer monitor. The fact that priming was still observed despite these procedural changes corroborates experiment 1, where different levels were cued by different colors, and shows pigeons are capable of rapid, per-

ceptual shifts of local/global attention with importantly different kinds of relations between priming and target stimuli.

General discussion

The results of experiments 1 and 2 differ in specific detail but agree on the critical fact that pigeons are capable of displaying trial-by-trial, stimulus-driven priming of local/global attention: priming cues that predict the perceptual level at which a subsequent target will appear can affect processing of that target. Fremouw et al. (1998) demonstrated priming of local/global attentional shifts over a period of days. The present experiments demonstrated such priming over a period of a fraction of a second. Although we cannot with absolute certainty rule out the possibility that a bird solved the task of attending either to local or to global levels by looking for a specific feature or set of features across levels that permitted the bird to perform accurately, we believe this possibility is highly unlikely. First, Fremouw et al. (1998) showed that replacing the local and global distractors with novel characters had little effect on performance. Second, in experiment 2 reported here the physical relationship between the priming cues and the local/global stimuli was changed yet the priming effect was similar. Taken together these results suggest that the birds attended to local and global features of the stimuli. We discuss the implications of these results for the basic nature of avian local/global shifts of attention, for the dynamics of search images, and for precedence of one level over the other.

An implication for the basic nature of avian local/global attention

Experiments 1 and 2 combined strongly suggest that a simple form of memory-trace decay is not a sufficient explanation of all priming of local/global attentional switching. The memory-decay account of Plaisted (1997) may apply admirably to priming-like attentional phenomena appearing in experiments using the blocking procedure, where responding may be faster to targets with higher base rates within a block of trials merely because more likely targets are more likely to have been recently seen, and therefore to have any residual memory representations more highly activated. The combined results of experiments 1 and 2, however, show local/global attentional priming under momentary stimulus control and therefore the purely time-based memory-decay account is not generally adequate.

A possible implication for the dynamics of a search image

When birds forage for cryptic prey, they sometimes develop a temporary selection bias for prey that are tem-

porarily more likely to occur. This bias for prey having high base rates of occurrence can be said to reflect the facilitation of search behavior by a "search image" (Tinbergen 1960; Pietrewicz and Kamil 1981; Blough 1989, 1991). Langley et al. (1996) suggested that "a search image is a perceptual expectancy set by repeated encounters with a particular type of prey" (p. 150). The results of Fremouw et al. (1998) suggested that the "perceptual expectancy" to which Langley et al. (1996) referred can involve levels of perceptual analysis as well as specific features of specific stimuli. The present results further suggest that a local/global perceptual expectancy can be brought under control of the momentary stimulus context. Accordingly, if a search image is a perceptual expectancy, then a bird might be able to rapidly shift the perceptual level at which a search image facilitates processing of a cryptic prey.

The nature of precedence

Navon (1977) found that humans identified global targets faster than local targets and suggested that humans prioritize the global level over the local. Such a prioritization is termed "global precedence." Subsequently, it has been shown that humans can show precedence at either level (Kinchla and Wolf 1979; Kinchla et al. 1983; Pomerantz 1983; Lamb and Robertson 1990). Pigeons and baboons have also been shown to display precedence for one level or the other when identifying targets in compound stimuli (Fulbright-Cavoto 1994; Fagot and Deruelle 1997; Cavoto and Cook 2001), although available evidence suggests that the level for which precedence is obtained depends critically on highly particularistic and as yet not fully understood methodological variables (Cook 1992a, b; Fulbright-Cavoto 1994; Cook et al. 1996; Fagot and Deruelle 1997; Fremouw et al. 1998; Cavoto and Cook 2001).

Despite these disparate past results, it was of some interest to determine if any such precedence might be obtained under the specific experimental conditions of experiments 1 and 2. In experiment 1, responding was reliably more accurate to local than to global targets, and also faster, but not reliably so, for local than to global targets. The results therefore generally conformed to the results obtained by Cavoto and Cook (2001), who also found a general local precedence in their study of local/global attention in pigeons. In experiment 2, there was a similar, but not quite reliable, tendency for responses to be more accurate to local than to global targets. Responses in experiment 2 were not generally faster to local than to global targets.

Precedence has been viewed as involving either the order of processing of different levels or some general predisposition to attend to one level more than to the other. Evidence is accruing from our specific experimental arrangement that sheds light on which of these two underlying mechanisms might produce precedence. Consider that in Fremouw et al. (1998) there was a trend toward local precedence in terms of accuracy and no precedence in terms of reaction times and similarly, in the present experiments there was overall greater evidence of local

precedence in terms of accuracy than in terms of reaction times. A tentative conclusion may therefore be emerging about precedence's basic nature. We know that reaction times are sensitive to priming through blocked trials (Fremouw et al. 1998) and in our present demonstration with trial-specific primes, so that it is unlikely the failure to obtain precedence in terms of reaction times is due merely to that measure's general insensitivity (for other evidence of the sensitivity of reaction times, see Blough and Blough 1990). Thus, it would appear that in our experimental arrangement, local precedence is not completely, or even primarily, due to a temporal advantage accruing to processing information at the local level. A local precedence therefore does not necessarily imply that processing of local information precedes processing of global information.

Future research

There are several contemporary perspectives on local/global attention that the present methodology could be used to address in future research. One such perspective involves the issue of spatial frequency and automatic versus controlled processing (Lamb et al. 1998, 2000; Kim et al. 1999). The present method could also be used to address the issue of costs and benefits of priming. Jonides and Mack (1984) showed that cost/benefit analyses are orthogonal to the question we posed in the present experiments, that is, whether stimulus-driven trial-by-trial priming can be demonstrated. As they noted, no neutral condition is required for such a demonstration. Nevertheless, cost/benefit analyses are of considerable interest in their own right, and the methodology described here opens up this and other important issues for future empirical analyses using nonhuman animals.

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