Behavioural Processes 104 (2014) 44–52

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Pigeons exhibit contextual cueing to both simple and complex backgrounds☆

Edward A. Wasserman*, Yuejia Teng, Leyre Castro

University of Iowa, United States

ARTICLE INFO

Article history:
Received 9 October 2013
Received in revised form 16 January 2014
Accepted 20 January 2014
Available online 31 January 2014

Keywords:
Contextual cueing
Color backgrounds
Photo backgrounds
Pigeons

ABSTRACT

Repeated pairings of a particular visual context with a specific location of a target stimulus facilitate target search in humans. We explored an animal model of this *contextual cueing* effect using a novel Cueing–Miscueing design. Pigeons had to peck a target which could appear in one of four possible locations on four possible color backgrounds or four possible color photographs of real-world scenes. On 80% of the trials, each of the contexts was uniquely paired with one of the target locations; on the other 20% of the trials, each of the contexts was randomly paired with the remaining target locations. Pigeons came to exhibit robust contextual cueing when the context preceded the target by 2 s, with reaction times to the target being shorter on correctly-cued trials than on incorrectly-cued trials. Contextual cueing proved to be more robust with photographic backgrounds than with uniformly colored backgrounds. In addition, during the context-target delay, pigeons predominately pecked toward the location of the upcoming target, suggesting that attentional guidance contributes to contextual cueing. These findings confirm the effectiveness of animal models of contextual cueing and underscore the important part played by associative learning in producing the effect.

This article is part of a Special Issue entitled: SQAB 2013: Contextual Con.

As do other discriminative stimuli, environmental contexts can be said to set the occasion for operant behaviors to be reinforced. However, an even more active role may be played by contexts, especially when they give clear direction to the behavior in question (Kelly and Spetch, 2012). Several studies by Spetch, Cheng, Blaisdell, and their colleagues have shown that visual landmarks can effectively guide animals toward the location of an invisible target (Cheng and Spetch, 1995; Leising and Blaisdell, 2009; Spetch et al., 1992). Thus, a pigeon might learn to peck 2 cm to the left of a small red square projected on a computer monitor in order to receive food reinforcement, with the location of those pecks being pinpointed by a touchscreen just in front of the monitor.

Computer control and touch technology can also be deployed to study an important and related form of contextual control—so-called *contextual cueing*. Within the realm of human vision science, Chun and Jiang (1998) discovered that the spatial configuration of objects in a visual display can serve as a powerful contextual cue, facilitating an individual's search for a visible target item. Chun and Jiang found that, when the precise location of a target was consistently paired with a particular configuration of distractor items in the visual display, reaction times (RTs) to process the target became reliably shorter than when the target appeared in newly generated configurations of those same distractor items on each trial. This RT benefit defines the contextual cueing effect. Chun and Jiang went on to hypothesize that contextual cueing results from an observer's attention being directed toward the location of the target on consistently-paired trials, owing to learned associations between the context and the location of the target.

This emphasis on associative learning in contextual conditioning suggests an interesting question: Do nonhuman animals also exhibit contextual cueing? Although animal models of contextual cueing have been under development for several years (for pigeons: Brooks et al., 2008; for rhesus monkeys: Brooks et al., 2011), only the recent study by Goujon and Fagot (2013: for baboons) has so far been published.

Goujon and Fagot (2013) used the same basic methodology as Chun and Jiang. They trained 25 baboons to touch a single target stimulus (the letter T) embedded within configurations of seven distractor stimuli (the letter L) that either did or did not predict the target's location. Reliable contextual cueing—shorter RTs to predictive than to non-predictive configurations—was seen after only 24 training trials, and was retained after a 6-week delay.

Our own earlier work (Brooks et al., 2008) had found that pigeons too exhibit contextual cueing with the target-distractor paradigm of Chun and Jiang. So, in the present study, we report

☆ This research was supported by National Eye Institute Grant EY019781. The authors thank Daniel I. Brooks for helpful input in conducting this project.

* Corresponding author at: Department of Psychology, E11 Seashore Hall, University of Iowa, Iowa City, IA 52242, United States. Tel.: +1 3193352445.
E-mail address: ed-wasserman@uiowa.edu (E.A. Wasserman).

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http://dx.doi.org/10.1016/j.beproc.2014.01.021

the results of a different variant of the contextual cueing task, in the hope of shedding further light on the situational generality and comparative mechanisms of contextual cueing.

Specifically, we devised a novel Cueing–Miscueing design to explore contextual cueing in pigeons. We compared pigeons' latency to peck a target stimulus on two types of trials: correctly-cued trials and incorrectly-cued trials. We also compared two types of cueing contexts: solid color backgrounds which lacked any landmarks (Fig. 1, top four panels) and photographic scene backgrounds which provided rich landmarks (Fig. 1, bottom four panels).

We expected that pairing specific target locations with particular contexts would encourage faster detection when the target occurred in the correctly-cued location than when it appeared in one of three possible incorrectly-cued locations; this correct-versus-incorrect cueing tactic has proven to be very effective in the study of human visual processing (e.g., Posner et al., 1980). We also expected that the landmark-rich photographic scene backgrounds would support stronger contextual cueing effects than would the landmark-poor solid color backgrounds (Brockmole and Henderson, 2006). Landmarks close to *invisible* targets exert strong control over pigeons' pecking behavior (Spetch, 1995), so we expected the same to hold true for *visible* targets as well. Indeed, without any internal landmarks at all, there was a chance that no contextual cueing would occur with the uniform color backgrounds.

In addition, we conducted contextual cue training with a 2-s gap between presentation of the context and presentation of the context plus the target (an instance so-called Stimulus Onset Asynchrony or SOA). We correspondingly monitored pecking during the delay to see if any anticipatory responding occurred during the SOA that might provide useful clues as to the nature of contextual cueing. In a final stage of the experiment, we systematically varied the SOA to see what effects might be observed on both anticipatory responding and target-directed responding.

1. Method

1.1. Animals

We kept eight feral pigeons at 85% of their free-feeding weights. The pigeons were divided into two groups: Color (colored backgrounds as the context) and Scene (scene photographs as the context). The birds had participated in several unrelated studies before beginning this project. All housing and training procedures had been approved by the Institutional Animal Care and Use Committee at the University of Iowa.

1.2. Apparatus

We used eight 36-cm × 36-cm × 41-cm conditioning chambers (detailed by Castro et al., 2010) located in dark rooms with continuous white noise. Each chamber was equipped with a 15-in LCD monitor behind a resistive touchscreen. The viewable portion of the screen was 28.5 cm × 17 cm. Pecks to the touchscreen were processed by a serial controller outside the chamber. A rotary dispenser delivered 45-mg food pellets through a vinyl tube into a plastic cup in the center of the rear wall opposite the touchscreen. Illumination during experimental sessions was provided by a houselight on the upper rear wall of the chamber. The pellet dispenser and houselight were controlled by a digital I/O interface. Each chamber was controlled by an iMac computer. Programs were developed in MatLab with Psychtoolbox-3 extensions (Brainard, 1997; Pelli, 1997; http://psychtoolbox.org/).

1.3. Stimulus materials

In Pretraining, we taught the eight pigeons to peck a target stimulus in four possible positions on the computer monitor. For the four pigeons later trained with color contexts (Color group), the Pretraining context was an otherwise black screen; for the four pigeons later trained with photograph contexts (Scene group), the Pretraining context was a single color photograph (snow and ice).

For the Color group, the contexts were four different colored backgrounds: red, green, yellow, and purple (Fig. 1, top four panels). For the Scene group, the contexts were four different photographs: two (mountain and lake) depicted undeveloped nature scenes, whereas the other two (house and cemetery) also included human-made items (Fig. 1, bottom four panels). The 16.5-cm × 16.5-cm scenes were displayed in full color at a resolution of 555 × 555 pixels.

The same target stimulus was used in Pretraining and Training—an abstract shape consisting of nine white concentric circles superimposed on a dark gray square (3 cm × 3 cm). The target could appear in the top-left, top-right, bottom-left, and bottom-right corners of the Color and Scene contexts, 1.4 cm from the borders of the contextual image.

1.4. Pretraining

To familiarize the pigeons with the basic behavioral task before beginning Training, the birds were required to peck once at the target stimulus, which randomly appeared in one of four possible locations, in order to obtain food reinforcement. Pretraining comprised 240 trials (60 randomly scheduled presentations of the target in each corner of the contextual image) and continued for 2 or 3 days. Because of the pigeons' prior experimental histories, they had no difficulty completing Pretraining without special measures having to be taken.

1.5. Training design

Training involved two types of contextual cueing sessions: half of the sessions scheduled both correctly-cued and incorrectly-cued trials (Table 1), whereas the other half of the sessions scheduled only correctly-cued trials. In those sessions involving both correctly-cued and incorrectly-cued trials, the contextual cues correctly predicted the location of the target on 80% of the trials; on the remaining 20% of the trials, the contextual cues randomly and incorrectly predicted the target in one of the three remaining locations. Those incorrectly-cued trials were critical because they allowed us to see if the pigeons were faster to peck the target when it was presented in the most likely location than when it appeared in the other, much less likely locations. Of course, those incorrectly-cued trials necessarily weakened the predictive relation between the context and the target. That is precisely why we also trained the pigeons with interpolated sessions that provided unambiguous context-target information; we wanted to sustain the birds' context-target associations as best we could even though those correctly-cued sessions afforded us little useful data (indeed, we do

Table 1
Number of correctly-cued and incorrectly-cued trials in daily sessions.

Correct target location	Number of target presentations in four possible locations			
	Upper left	Upper right	Lower left	Lower right
Upper left	48	4	4	4
Upper right	4	48	4	4
Lower left	4	4	48	4
Lower right	4	4	4	48