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Active Change Detection by Pigeons and Humans

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Abstract

Detecting change is vital to both human and non-human animals' interactions with the environment. Using the go/no-go dynamic change detection task developed by Hagmann and Cook (2011), we examined the capacity of four pigeons to detect changes in brightness of an area on a computer display. In contrast to the prior study, we reversed the response contingencies so that the animals had to actively inhibit pecking upon detecting change in brightness rather than its constancy. Testing eight rates of change revealed that this direct report change detection contingency produced results equivalent to the earlier indirect procedure. Corresponding tests with humans suggested that the temporal dynamics of detecting change were similar for both species. The results indicate the mechanisms of change detection in both pigeons and humans are organized in similar ways, although limitations in the operations of working memory may prevent pigeons from integrating information over the same time scale as humans.

Our continuous experience of a stable reality requires the coordinated integration of attention, perception, working memory, and long-term memory. How the brain accomplishes this apparently seamless integration has been of increasingly greater interest (Faw, 2003; Lamme, 2003; Naghavi & Nyberg, 2005; Tononi & Koch, 2008). The change detection task has been one widely used approach to assess this type of integration. In the change detection task, two different pictures are briefly shown in sequence, separated by a short visual mask (Rensink, 2002; Simons & Levin, 1997)., Studies using this approach have clearly demonstrated that we do not form complete representations of the entire visual input, often resulting in "change blindness" (Darriba, Pazo-Ãlvarez, Capilla, & Amenedo, 2012; Simons, Franconeri, & Reimer, 2000). Because of change blindness, a rather large change between the pictures is not detected until attention directly examines the changing portion of a display. Despite our stable experience of a continuous world, such findings suggest that little visual information is retained in memory from moment-to-moment.

Non-human animals also appear to experience a stable world during their extended interactions with each other and the environment. Accordingly, they face the same issues as humans in sequentially integrating past and current experiences. It is thus natural to ask if and how they also detect and integrate change and constancy over time. If they do, are the attention, perception, and memory mechanisms involved the same as those found in humans? This seems to be the case for primates, as studies have revealed functionally

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similar change detection behavior in visual short term memory (VSTM) between rhesus monkeys and humans (Elmore, et al., 2011; Heyselaar, Johnston, & Pare, 2011).

Only a few experiments have examined change detection in non-primate animals such as pigeons or directly compared their change detection abilities to those of humans. Wright et al. (2010) tested pigeons in a variant of the typical human change detection task. They showed the pigeons an array of two colored circles for 5 s. After a short 50 ms delay, a test array was presented in which the color of one of the two circles had changed. Pecking at the changed circle resulted in reinforcement. Following training with four colors in this two-item change detection task, the pigeons successfully transferred their discrimination to four novel colors. To evaluate whether this change discrimination was due to attentional capture or short-term memory for the stimuli, Wright et al. tested delays of up to 6.4 s between the initial and test arrays. The pigeons maintained performance above 70% accuracy with delays up to 1.6 s, and never dropped to chance at the longest delays. These results suggest pigeons were relying on working memory to mediate their detection of change, instead of attentional capture or other strictly perceptual mechanisms.

Gibson, Wasserman, and Luck (2011) tested VSTM in pigeons and humans with eight-icon displays. After viewing an initial array of eight icons, members of each species were shown a briefly delayed test array where between zero and eight icons changed, thus requiring appropriate responses to "change" or "no change" choice options. Both species showed similar declines with fewer changes, and the pigeons were overall less accurate than humans. Based on a computational model, Gibson et al. suggested that humans store more items and have fewer memory errors than pigeons, but otherwise may share similar VSTM mechanisms.

Recently, we examined change detection in pigeons using a different approach (Hagmann & Cook, 2011). Instead of presenting temporally separated sequences of discrete static images in order to isolate when a change had been detected, we used displays varied in their rate of continuous brightness change. Similar gradual techniques have been used to examine change blindness in humans (David, Laloyaux, Devue, & Cleeremans, 2006; Hollingworth & Henderson, 2004; Simons, et al., 2000). Using a grayscale stimulus that either changed slowly in brightness or was held at a constant brightness level, pigeons were trained in a go/no-go procedure to peck the display whenever a *change* in brightness was detected and to inhibit pecking when a *constant* stimulus was presented. The change condition consisted of continuously changing brightness values that oscillated at different rates between its dark and light extremes. The constant condition on any trial consisted of a randomly selected brightness value from the range of values tested on change trials.

We found that the pigeons could detect changes in brightness over time and their detection ability varied directly as a function of rate of change. Fast rates of changes were the easiest to discriminate from constant trials, with decreasingly slower rates of change becoming monotonically more difficult to detect. At the slowest rates tested, detection almost certainly required a short-term memory for an earlier value of brightness that was compared to the current perception of brightness. The results suggested that pigeons can retrospectively integrate past experiences over approximately 20 to 30 seconds. Several lines of evidence

suggested that perceptual mechanisms might have been used to detect rapidly changing displays and that working memory was used to compare values from different points in time when detecting slower rates of change.

In the current paper, we examined a potential limitation in Hagmann and Cook's (2011) approach. Go/no-go discriminations have a built-in asymmetry in their response contingences, with one class of stimuli indicated by pecking the display (the reinforced S+) and the other class reported by suppressing pecking to the display (the punished or extinguished S-). We have found that pigeons typically begin all trials by responding immediately upon stimulus presentation regardless of its reinforcement status and then gradually inhibit pecking to the S- condition over the course of a trial (Cook, Beale, & Koban, 2011; Cook & Roberts, 2007; Hagmann & Cook, 2010, 2011; Koban & Cook, 2009). Typically, S+ peck rates never change over a trial. As a result, the expressed discrimination between S+ and S- stimuli stems from the "active" inhibition of pecking behavior to the latter class rather than changes in peck rates to both classes. Because Hagmann and Cook's pigeons were tested with the change condition as the S+ component in their go/no-go procedure, the birds were actively suppressing their peck rates only when stimuli were being experienced as constant. As a result, it could be argued that pigeons were in fact directly expressing their capacity to detect *constancy*, rather than *change*. Therefore, the pigeons may have only been indirectly reporting whether a change was present. To determine whether something is constant, however, inherently requires a much longer sample of time than directly reporting whether something has changed. In the latter case, you can respond immediately, and with more certainty, upon a change being detected. You can be certain things are constant and unchanging only after a sufficiently long time has passed and the possibility of change has been ruled out. Consequently, our previous assignment of the S+/S- conditions to change and constant conditions respectively may have underestimated how quickly pigeons can detect change.

To examine whether the nature of the response and reinforcement assignment affected the measurement of change detection, we tested four pigeons in our continuous change detection task with the S+ and S– assignments for change and constancy reversed from those in Hagmann and Cook (2011). Here, the S+ condition in the go/no-go task was now assigned to be the constant condition and the S– condition was the change condition. Given the pigeons' active suppression of pecking in the S– condition, they could now immediately report their detection of change by response cessation and thus provide a direct and potentially more sensitive measure of change detection than before. Reversing the reinforcement assignments additionally allowed us to examine whether the discrimination of change detection exhibited any asymmetry in responding similar in some sense to that found in feature-positive/feature-negative stimulus discriminations (Jenkins & Sainsbury, 1970; Sainsbury & Jenkins, 1967; Wasserman & Anderson, 1974). The added presence of a distinctive feature in the S+ or S– condition controls the relative ease of learning in such discriminations. One possibility is that changing events may be distinctive in a similar way, and thus might be more easily associated with reinforcement than constant events (e.g. Dittrich & Lea, 1993).

Using this potentially more sensitive means of measuring change detection, the pigeons in the current experiment were tested similarly to those in Hagmann and Cook. Each 30-

session phase of testing examined increasingly slower rates of change that necessitated longer working memory spans to differentiate any changes in the displays relative to constancy. The major question of interest of was whether the pigeons would show a similar or different ability to detect change given this procedure's superior capacity to detect the birds' immediate response to changing events. Humans were also tested using the same stimuli in an analogous task for comparison.

Method

Animals

Four male White Carneaux pigeons (*Columba livia*) were tested. Previously used in other visual discriminations, they were naïve to this procedure. They were maintained at 80-85% of their free-feeding weights with free access to grit and water. Six adult human volunteers were also tested.

Apparatus

Pigeons were tested in in a computer-controlled chamber. Stimuli were presented on an LCD monitor (ViewSonic, 1024×768) visible behind a 26×18 cm infrared touchscreen (EloTouch; Harrisburg, PA) that recorded pecks. A ceiling houselight was illuminated at all times, except time-outs. A central food hopper was located under the touchscreen. Humans were comfortably seated in a chair directly in front of an LCD monitor (Dell, 1024×768) and used a mouse to interact with the experiment.

Procedure

Discriminative stimuli appeared as a 10.2×16.5 cm central rectangle on a salmon background (RGB: 255, 192, 192; used to minimize simultaneous contrast). Throughout a trial, the brightness of the rectangle was either held *constant* at a single grayscale value (gsv) or continuously *changing* in a sawtooth temporal pattern (see top left panel of Figure 1). The available 256 gsv (0=black; 255=white) ranged in brightness from 0.31 to 37.4 candelas per m² (Minolta Chromameter CS-100). Initial brightness values were randomly selected for each trial from within this range. Because the experiment was designed around the gsv controlling the video card, the results are described in these units.

Trials began with a peck to a 2.5 cm diameter circular green ready signal. The signal was then replaced by either a constant or changing rectangle for 30 s. Pecks on constant trials were reinforced (2.9 s of grain access) on a variable-interval 15-s schedule. Pecks on changing trials resulted in no reinforcement and a variable length timeout upon its termination (1 s per peck). A 5 s inter-trial-interval was used. To increase the sensitivity of our measurement and eliminate the role of cues from reinforcement during a trial, we randomly mixed into each session infrequent (<10%), non-reinforced, probe trials. Probe trials were identical to reinforced *constant* trials, except for the absence of reinforcement. Only data from change trials and constant probe trials were used in our analyses.

The experiment consisted of three 30-session phases. Each session consisted of 120 trials (60 constant/60 change; 20 per rate, 6 probes). Phase 1 used three rates (100, 33.3, & 20

gsv/s) that the pigeons in Hagmann and Cook (2011) easily perceived as changing. Phase 2 tested two slower rates (13.3 & 6.7 gsv/s) and one of the established fast rates (33.3 gsv/s). Phase 3 tested two new rates (4.4 & 2 gsv/s) slower than those previously tested, one retained medium rate (6.7 gsv/s), and the common fast rate (33.3 gsv/s). Because four rates were tested in Phase 3, each rate was instead tested 15 times per session to maintain the same 120-trial session organization. The number of constant trials remained 60, of which six were probe trials.

Six humans were tested with nine rates of change and the constant condition using an analogous go/no-go procedure. The stimuli were identical, except the range of change was 140 gsv with a minimum brightness of 30 gsv. At the time of their testing (for details see Hagmann and Cook, 2011), we were using a more restricted range of brightness to examine these questions than we typically used with the pigeons. Participants were seated in front of a computer and instructed to click the mouse cursor inside the warning signal to begin a trial. Once the stimulus appeared, a click with the mouse button indicated that a change in brightness had been detected and terminated the trial. No mouse response during the 40-s presentation was used to indicate that the humans detected no change. A 5 s inter-trial-interval separated trials. In a single session, forty trials were tested with four trials tested at nine rates (100, 33.3, 20, 13.3, 10, 6.7, 4.4 3.3 & 2.5 gsv/s) along with four constant trials.

Results

The pigeons' capacity to detect change was strongly controlled by rate of the brightness change across the different test conditions. The three panels of Figure 1 show the time course of change detection over the three phases of the experiment. Each panel shows mean normalized peck rate as a function of 2-s bins across a trial (adjusted relative to each bird's maximum mean 2-sec peck rate across all conditions). Both within and between all three test phases, as the rate of brightness change slowed, the time required for the pigeons to begin actively suppressing their pecking in these S– conditions correspondingly increased. Thus, as S– change trials slowed across phases and change presumably became more difficult to detect, peck rates increased to levels similar to that on S+ constant trials.

These patterns across rate conditions were confirmed for each phase by separate repeated measures ANOVAs (Brightness Rate × Time) as measured using the peck rates across the separate 2-s bins (an alpha level of p<0.05 was used to judge the significance of all tests). All phases yielded a significant Rate × Time interaction as difficulty of change detection increased with slower rates of change, Phase 1: F(42,126)=9.0; Phase 2: F(42,126)=18.4; Phase 3: F(56,168)=10.4. These interactions were not due to the inclusion of the constant condition, as a second set of ANOVAS testing just the change conditions also showed significant Rate × Time interactions, Phase 1: F(28,84)=4.5; Phase 2: F(28,84)=17; Phase 3: F(42,126)=11.3.

To measure when change detection occurred within a presentation, we determined the point in time when the peck rates for the change conditions significantly diverged from the peck rate recorded during constant condition. This determination of this divergence time consisted of a series of t-tests comparing peck rate across successive 2-s bins (*cf.* Hagmann

and Cook (2011)). The point of divergence was defined as the time when at least two or two of three consecutive bins exhibited significantly differences in peck rates between the change and constant conditions.

Figure 2 shows the mean divergence times as a function of the rate of change for the current experiment (black circles) and the analogous conditions from Hagmann and Cook (2011; white circles). Visual inspection suggests little difference between them. Both indicate that change detection became more difficult with slower rates of change regardless of the assignment of change and constancy to the reinforcement conditions. To evaluate performance across experiments, we tested the divergence times for the five common rates tested across the experiments and a sixth point that averaged the 3.3 and 4.4 gsv/s rates of Hagmann and Cook's study for comparison with the 4 gsv/s tested here. A between-groups ANOVA (Experiment × Rate) comparing divergence times across the six common rates tested in both experiments revealed a significant main effect of rate of change, F(5, 29)=6.6. Neither the main effect of Experiment nor its interaction with Rate, however, were found to be reliable. This pattern indicates that altering the direct or indirect nature of the report response to change had no significant effect on the pigeons' capacity to detect change as reflected in divergence times.

Figure 2 also shows the results of the human testing. In a very similar manner to the pigeons, humans took longer to report the slower rates of brightness change, F(8,40)=84.6, and their responses also progressively slowed with decreasing rates of change. Despite a task that may have been more difficult because of its smaller range of variation, humans reported change sooner at all rates than reflected in the divergence times of the pigeons. Consistent with superior human performance, an ANOVA (Species (combining both pigeon experiments) × six common/adjusted Rates) revealed significant main effects of both rate, F(5,65)=10.8, and species, F(1,65)=254.1, but no significant interaction between these factors. This suggests that the seven pigeons and six humans reacted in comparable ways to the different rates of presentation, although the pigeons always took more time to detect any change at the same rate. To further examine the similarity of the responses of the two species we fitted the resulting rate curves with power functions based on detection times from each experiment. The power function provided excellent approximations of both sets of data for the pigeons (r=0.97; 94.5% of the variance) and the humans (r=0.98; 96.2% of the variance).

Discussion

Here we tested for the first time a procedure allowing pigeons to directly report their immediate detection of dynamic change. The experiment revealed that pigeons exhibited the same rate-dependent change detection capacity regardless of whether this was measured using the new direct measure or the previous indirect measure (Hagmann & Cook, 2011). In both cases, we obtained the same functional relationship between rate of change and the measured time to detect a change. Humans were tested for the first time using comparable procedures. While the pigeons needed more time than humans to report their detection of the same rate of change, both species exhibited similar functional patterns of change detection that were well fit by a power function. These results suggest the mechanisms of detecting

change and constancy as tested using our continuous procedures are organized in analogous ways in pigeons and humans.

The pigeons' identical results independent of the testing procedure indicate that their capacity to detect and integrate constancy and change over time is not tied to the nature of the discriminative rule and its assignment as the S+ and S- responses. Whether the birds were actively suppressing their behavior to stimulus change or stimulus constancy, their ability to detect any difference between these physical conditions simply depended on the rate of change. The discrimination therefore exhibit none of the asymmetry found in some other stimulus discriminations when their stimulus-reinforcement assignments are reversed (Dittrich & Lea, 1993; Jenkins & Sainsbury, 1970; Sainsbury & Jenkins, 1967; Wasserman & Anderson, 1974). The absence of any performance asymmetry in the present research carries the implication that constancy and change are equally salient to the birds. Our results continue to suggest that pigeons update their memory for evaluating brightness changes from the recent past for about 20 to 30 seconds. The birds do not easily detect changes that require longer periods of integration to produce noticeable differences. This memory window for the integration and detection of change aligns reasonably well with independent estimates of the duration of pigeon working memory using discrete presentations (e.g., Blough, 1959; Cook & Blaisdell, 2006; Grant, 1976; Wixted, 1989).

We also found that humans reacted similarly to the pigeons in their ability to detect dynamic change, providing results consistent with earlier research using other gradual procedures (cf. David, et al., 2006; Hollingworth & Henderson, 2004). Power functions provided good fits in describing the psychophysics of rate-based change detection times for both species (Stevens, 1961). The smaller exponent found with the pigeons suggests sensitivity to change at slow rates decreased more rapidly than it did for humans (Krueger, 1989), and also makes the power function more easily confused with a logarithmic fit (cf, Hagmann & Cook, 2011). While this sensitivity difference may be related to species, it is also possible that it was partially a measurement issue. The humans could respond immediately to change by making a simple and rapid single click, while the pigeons may have needed more time to alter the motor dynamics and momentum of their ongoing pecking behavior sufficiently for us to detect it with our measure of divergence time. The humans may also have been motivated to respond more quickly because it terminated the trial at that point and moved the session along in a way that was not possible for the pigeons being tested with presentations of a fixed duration. If this were the case, however, one would have expected a high proportion of false alarms on constant trials in humans, which was not observed. Either way, the more important functional similarity in the form of the results raises the central question of how the pigeons and humans detect these changes in the recent past and whether the mechanisms involved are the same.

From available results on brightness detection and discrimination, the adjacent moment-tomoment changes in brightness were too small to be detected perceptually (Hodos & Bonbright, 1972). As a consequence, mechanisms capable of comparing brightness between different points in time are required for discrimination, with the current perception of brightness being compared to a maintained "trace" of an earlier experience. For rate-based change detection tasks, we previously suggested that a combination of visual perception and

working memory mechanisms are likely involved. For rapid changes in brightness, the timebased mechanisms expressly built to detect environmental change within the visual system, such as the detection of motion (e.g., Reichardt, 1987), are likely sufficient. Thus, one simply "sees" the change as mediated directly by the perceptual system. The time course of such mechanisms, however, is limited and typically assumed to operate only over short durations. At the point where the rate of change becomes too slow to detect with these mechanisms, the subject must be holding in memory some luminance value(s) encoded from the past in order to compare with the present value. When the difference between these points of time becomes great enough, the subject can once again report that a change must have occurred. Several lines of evidence are consistent with this multiple mechanism account.

The short gap between images in a typical change blindness experimental design, for example, is specifically included for the purpose of defeating or overriding such perceptual mechanisms and isolating and highlighting the effects of attention and memory. Studies of humans with brain lesions and psychological disorders further suggest dissociations between perception and working memory when it comes to detecting change. The profound disruption of working memory in a hippocampal patient, such as HM, would likely inhibit his ability to detect very slow changes in the present task. Nevertheless, HM had normal motion perception, so he would have been easily able to detect our most rapid changes (Corkin, 2002). Conversely, someone with akinetopsia, or motion blindness, faces the opposite problem. These people report that objects move suddenly to new locations without seeing any intervening motion (Zihl, Von Cramon, & Mai, 1983). Consequently, their intact working memory would likely mediate detection of slow changes, while rapid changes might be invisible, at least to the extent that they involve motion-based mechanisms. Thus any change detection would occur only by remembering and comparing separate instances in their disrupted visual stream.

It is still unknown exactly what and how information is stored and then updated for such longer time-based comparisons. Hollingworth and Henderson (2004) tested change detection in humans by presenting a sequence of incrementally different rotational perspectives of a visual scene. When the change was gradual, participants required a greater amount of change in order to detect it than when the increments of change were large and more abrupt. Their results suggested that humans were implicitly encoding earlier portions of the scenes to compare to their present view. They discussed three possible memory mechanisms. In the first, new values are being compared against a trace that is continuously replaced over time. In the second, new memories are constantly being created as a series of separate instances that are then compared to the current view. In the third, past experiences are integrated in some kind of average memory that is compared to the current value, perhaps weighted towards more recent ones. Future research will need to examine which of these memory-updating mechanisms is involved and whether they are the same in humans and pigeons.

These mechanisms would effectively determine the integrative time horizons of the past and the present and these might vary considerably across species. Some animals, like humans, might be able to focus, retain, and compare information over much longer periods of time than others. One reason why pigeons are generally not as good as humans in working

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memory tasks may be because they weigh events in the recent past more strongly, for instance. Investigating how different animals detect change at different time scales will provide fundamental insights into the evolution of event detection, working memory, cognition, and intelligence and how these mechanisms operate to produce coherent subjective realities for us and presumably in other animals as well.

If both perceptual and memory mechanisms are involved in change detection, it raises the interesting issue of their apparently seamless integration. When performing our task, for instance, the sensation is that the task only becomes very difficult at slower rates. There is no discernible transition or mediation between differences being detected by perceptual and then memory mechanisms. One possibility is that the stable integration of experience over time is so critical to the organization of behavior that evolution has ironed out the creases between these operations. Whether pigeons experience this same seamless cognitive integration is a compelling question, and the answer may depend on the role of executive cognition in the organization of their behavior. For instance, models of executive cognition in humans suggest the need for a brief storage time to encode perceived events and acts and thus integrate them into memory (e.g., Faw, 2003) with a synchronization of brain activity between the prefrontal and posterior association cortex appearing to serve this function in humans (Llinás & Steriade, 2006). If and how such executive functions are established in birds is only beginning to be examined (Emery, 2006; Güntürkün, 2005). Although the avian brain lacks a mammal-like cortex, contemporary anatomical and behavioral analyses have suggested the avian forebrain may have evolved to form a common hierarchical control organization similar to mammals. The examination of these issues and their implementation in birds, using procedure like those tested here, will surely offer new insights into the seamless organization of behavior across vertebrates and the role of convergent computational and functional neural organizations in generating such behaviors.

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Figure 1.

Diagram of experimental conditions (top left) and the results of the three different phases of testing. Each graph shows mean normalized peck rates within a trial as a function of different temporal rates of change. The unfilled symbols represent pecking behavior during change conditions (S-) of different rates and the filled circles represent pecking behavior during the positive constant condition (S+).

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Figure 2.

Sensitivity of change detection as a function of presentation rate for humans (gray circles), pigeons in the current experiment (black), and those tested in Hagmann and Cook (2011; white). The lines show the best-fitting power functions for the pigeon ($f=37.8*x^{-.55}$) and human ($f=35.3*x^{-.1.2}$) results.