
Amodal completion of moving objects by pigeons

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Abstract. In a series of four experiments, we explored whether pigeons complete partially occluded moving shapes. Four pigeons were trained to discriminate between a complete moving shape and an incomplete moving shape in a two-alternative forced-choice task. In testing, the birds were presented with a partially occluded moving shape. In experiment 1, none of the pigeons appeared to complete the testing stimulus; instead, they appeared to perceive the testing stimulus as incomplete fragments. However, in experiments 2, 3, and 4, three of the birds appeared to complete the partially occluded moving shapes. These rare positive results suggest that motion may facilitate amodal completion by pigeons, perhaps by enhancing the figure–ground segregation process.

1 Introduction

The broad spatial pattern of our visual world projects onto a small two-dimensional (2-D) retina in each eye. Our visual system extracts useful information from these retinal patterns and reconstructs them into a meaningful visual scene representing the three-dimensional (3-D) world. During this complex reconstructive process, the visual system appears to interpolate the features (contour, color, and texture) of an object that are partially hidden from view. This interpolation process is called amodal or visual completion (Kanizsa 1979; Michotte et al 1964/1991; Palmer 1999; for a review, see Sekuler and Murray 2001).

Several behavioral studies (Nakayama et al 1989; Rensink and Enns 1998), physiological investigations (Bakin et al 2000; Corballis et al 1999; Giersch et al 2000; Murray et al 2002; Schiller 1995; Sugita 1999), and an analytical model (Grossberg 2003) all suggest that the process of amodal completion begins in the early stages of visual processing. It is, therefore, plausible to expect that the system responsible for amodal completion in human adults may be shared with human infants and even non-human animals.

Developmental research has shown that infants do not exhibit amodal completion behavior immediately after birth. The groundbreaking study of amodal completion in infants was conducted by Bower (1967), who tested 1-month-old infants with operant conditioning methods. The results showed that infants trained with a partially occluded triangle exhibited generalization to a complete triangle. However, Kellman and Spelke (1983) later failed to replicate this result with 4-month-old infants, using visual habituation and response recovery methods. Nevertheless, Kellman and Spelke (1983; Kellman et al 1986) did find common motion between the visible parts of an occluded rod to be a strong cue for the perception of object unity by 4-month-old infants; these infants appeared to perceive two commonly moving rods as a single object, implying that they amodally completed the rod when it was placed behind a box.

Subsequent to the Kellman and Spelke (1983) project, most studies of amodal completion behavior in infants have been conducted in the context of ‘object unity’. Jusczyk et al (1999) confirmed that common motion is a better cue for object unity than edge

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alignment, synchronous color change, or synchronous brightness change of an occluded rod. The results of these and other studies of infants' perception of amodal completion—or object unity (for summaries, see Johnson 2003)—are consistent with each other in that completion occurred in 4-month-old and older infants, and that common motion was required to support amodal completion behavior (see also Quinn et al 1997).

In several non-human primate studies, empirical evidence suggests that squirrel monkeys (Nagasaka and Osada 2000), Japanese macaques (Sugita 1999), rhesus macaques (Bakin et al 2000; Fujita 2001; Osada and Schiller 1994; Schiller 1995), baboons (Deruelle et al 2000; Fagot et al 2006), and chimpanzees (Sato et al 1997) may amodally complete a partially occluded object. Moreover, other studies have explored amodal completion behavior in non-primate species. Bengalese finches (Okanoya and Takahashi 2000), chickens (Forkman 1998; Forkman and Vallortigara 1999; Lea et al 1996; Regolin and Vallortigara 1995; Regolin et al 2004), and mice (Kanizsa et al 1993) may also exhibit amodal completion behavior.

The subjects in these non-human animal experiments cover a very wide range of species; peculiarly, all but one species in those studies have shown evidence of amodal completion behavior. Despite at least ten research efforts in over 20 years, no positive evidence has ever been obtained for amodal completion behavior in pigeons (Aust and Huber 2006; Cerella 1980; DiPietro et al 2002, experiment 1; Fujita 2001; Fujita and Ushitani 2005; Sekuler et al 1996; Shimizu 1998; Ushitani and Fujita 2005; Ushitani et al 2001; Watanabe and Furuya 1997).

Although pigeons have thus far failed to show evidence of amodal completion behavior, it may be premature to conclude that they cannot do so. Most prior pigeon studies were conducted with static stimuli. As noted above, common motion facilitates amodal completion behavior of 4-month-old human infants. Perhaps common motion also plays a similarly important role in amodal completion for pigeons. The present study explored pigeons' capacity to exhibit amodal completion behavior by training and testing the birds with moving stimuli.

We examined pigeons' amodal completion behavior by using moving stimuli depicted in figure 1. We created these stimuli by the methods of Lorenceau and Shiffrar (1992; Shiffrar and Lorenceau 1996). In general, human observers report that a square is moving in a circular trajectory behind four occluders when they view the rightmost display in the first row of figure 1 (*occluded* stimulus in experiment 1). However, if the hue and luminance of the occluders are equal to those of the background and only the visible portions of the occluded shape are presented (*incomplete* stimulus in experiment 1), then the perception of the stimulus is dramatically changed; when human observers view the center display in the first row of figure 1, they do not report seeing a square, but, instead, report seeing two pairs of parallel lines with the opposite pairs moving in unison. This experimental task has been productively deployed in studying 'motion integration' or 'motion interpretation'.

Here, we used these stimuli to see if pigeons spontaneously exhibit 'motion integration' or 'motion interpretation'. That is, we aimed to see whether or not pigeons perceive a complete shape when they are presented with a partial shape moving behind occluders, thereby suggesting the involvement of amodal completion. We report four experiments in which we asked whether object motion supports amodal completion behavior in pigeons. We initially trained pigeons to discriminate two movie stimuli: one of a *complete* object (left column of figure 1) and the other of an *incomplete* object (center column of figure 1). We then showed them the *occluded* object movie (right column of figure 1). If the pigeons were to classify the *occluded* object movie as 'complete', then this would constitute evidence that pigeons can amodally complete partially occluded moving objects.

Experiment

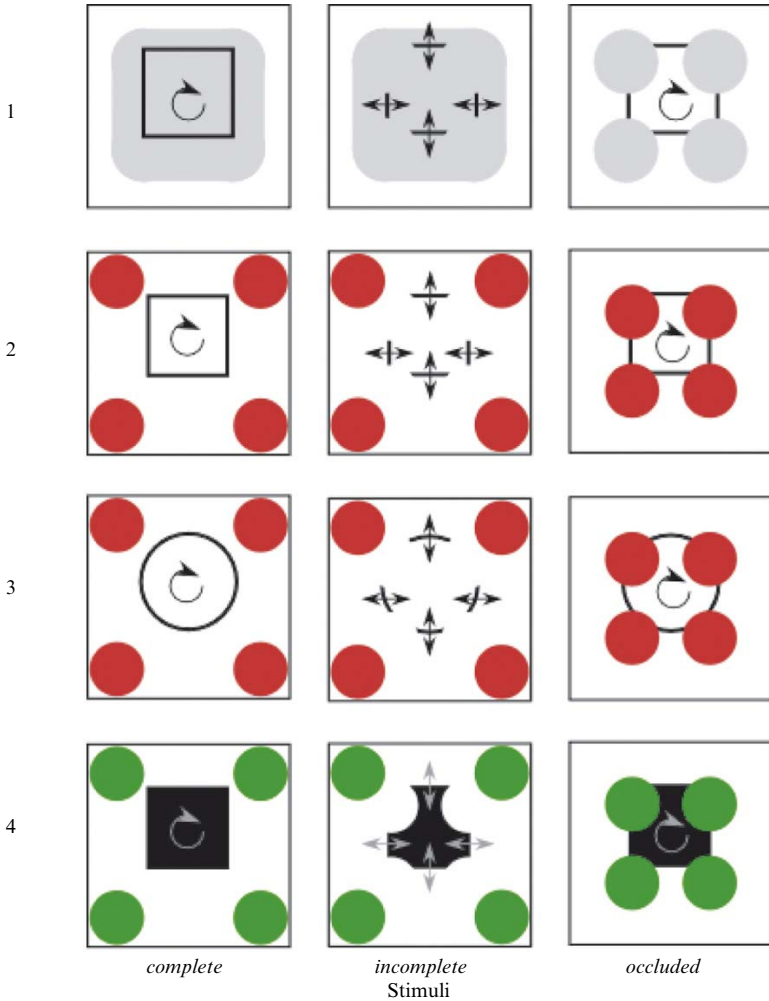


Figure 1. [In color online, see <http://dx.doi.org/10.1068/p5899>] The four sets of stimuli used in the study. Each set comprised three movies (*complete*, *incomplete*, and *occluded*). The *complete* and *incomplete* stimuli were presented in training and testing. The *occluded* stimuli were presented only in testing. The arrows depict the movement of the shapes and were not shown in the actual stimuli. The full set of stimuli in color can be seen at: <http://www.psychology.uiowa.edu/Faculty/Wasserman/ACMovies/Figure1.html> and on the Perception website.

2 Experiment 1

2.1 Method

2.1.1 Subjects. The subjects were four feral pigeons (*Columba livia*) kept at 85% of their free-feeding weights by controlled daily rations. The pigeons participated earlier in amodal completion studies in which static 2-D stimuli were used; they then failed to show evidence of amodal completion in much the same way as pigeons in all of the previously published research reports reviewed earlier. The birds had never before seen moving stimuli in the experimental apparatus.

2.1.2 Apparatus. The pigeons were trained in four operant conditioning boxes detailed by Gibson et al (2004). The boxes were located in a dark room with continuous white noise. The stimuli were presented on a 15-inch LCD monitor located behind

an AccuTouch[®] resistive touchscreen (Elo TouchSystems, Fremont, CA). A food cup was centered on the rear wall, level with the floor; a rotary food dispenser delivered 45 mg Noyes food pellets through a vinyl tube into the cup. A houselight on the rear wall provided illumination during the session. Each chamber was controlled by an Apple eMac[®] computer. The experimental procedure was programmed in HyperCard (Version 2.4, Apple Computer, Inc., Cupertino, CA).

2.1.3 Stimuli. The stimuli consisted of three movies: *complete* square, *incomplete* square, and *occluded* square (top row of figure 1). The movies were made with Flash MX (Version 7.2, Macromedia, Inc., San Jose, CA) and were composed of 35 frames. Each stimulus (4.0 cm high \times 4.0 cm wide) was placed in the center of the screen. The choice keys were two 2.7 cm \times 2.4 cm white rectangles, each containing distinctive Macintosh icons, which were located above and below or left and right of the movie stimulus; those placements were counterbalanced across the birds. The rest of the screen was black.

The *occluded* stimulus consisted of two parts: an outline of a square (19 mm high \times 19 mm wide, 0.6 mm thick) and four occluders. The *occluded* stimulus was drawn in black on a white background; the inside of the square was also white. The square moved in a circular trajectory behind the four occluders during each presentation; the occluders (13 mm in diameter) were gray circles placed over the four corners of the square. The *complete* stimulus showed the full contour of the square; the *incomplete* stimulus showed the same portions of the square that were visible in the *occluded* stimulus. Both *complete* and *incomplete* stimuli were drawn on a round-cornered gray square on a white background. The luminance of the square was the same as that of the occluders in the *occluded* stimulus. All movies that were used in our study can be found on the web (see figure 1).

2.1.4 Procedure: Pretraining. During pretraining, the pigeons were taught to peck at a square that was placed in the center of the display or at one of four smaller squares that were placed around the central square. After the birds reached an 'observing response' criterion (fixed ratio 20 for each square), the birds proceeded to training.

Training. The pigeons were trained on a standard two-alternative forced-choice task. Figure 2 shows the sequence of events in the course of a training trial. The trial began with the presentation of a black cross centered on a white square (7 cm \times 7 cm) in the middle of the display. After a peck at the square, either the *complete* or *incomplete* moving stimulus appeared. The birds were required to peck at the stimulus a fixed number of times ('observing responses'), which varied for different birds from 7 to 15 pecks per trial. After the final peck, two choice report keys ('complete' and 'incomplete') appeared. After a choice response to either of the keys, the moving stimulus and the keys were removed from the screen. A correct choice was followed by a food-pellet reinforcer and an intertrial interval (ITI) which ranged from 6 to 10 s (mean of 8 s); then a new trial followed. If the bird chose the incorrect response, then the house light darkened from 6 to 10 s (mean of 8 s) and the bird had to complete one or more correction trials until it made the correct choice. The correction trials were identical to the choice trials. The correction trials and occasional incomplete sessions were not used in data analysis.

Each daily training session contained 80 blocks of 2 trials (total of 160 trials) and each trial presented either a *complete* or an *incomplete* moving stimulus. Training continued until the pigeons reached a criterion of at least 80% correct for each stimulus and 85% correct overall for 2 consecutive sessions.

Testing. During each testing session, the pigeons received 184 trials. The first 40 trials involved 20 presentations of each training stimulus and were treated as warm-up trials, which were not used in data analysis. The following 144 trials contained 16 blocks; each block (9 trials) included 4 presentations of the 2 training stimuli plus 1 'occluded'

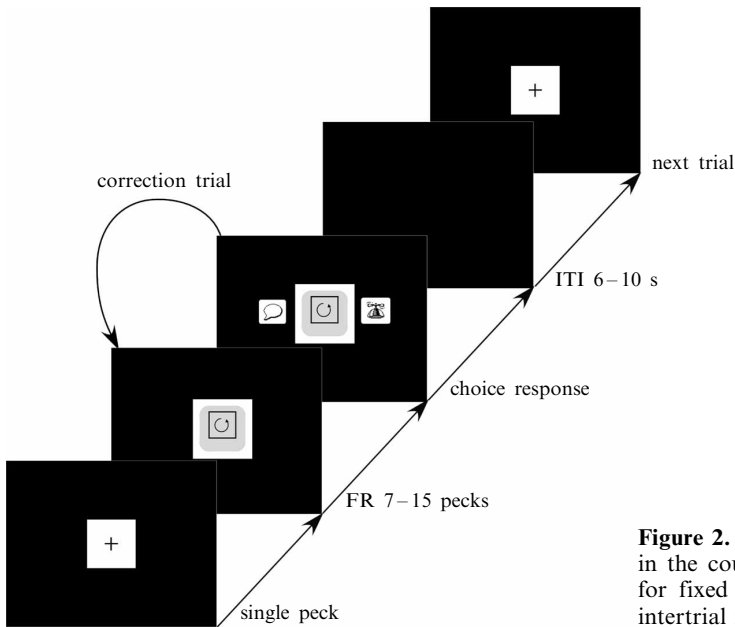


Figure 2. The sequence of events in the course of a trial. FR stands for fixed ratio and ITI stands for intertrial interval.

testing stimulus. The trials in each block were randomly presented. The birds received reinforcement for any responses (nondifferential reinforcement) on the testing trials. Testing sessions continued for 3 days. If a pigeon failed to complete a testing session, then it was returned to training until it again reached criterion.

2.1.5 Behavioral measures. The percentage of choices of the ‘complete’ key (number of responses to ‘complete’ key divided by total number of responses to both ‘complete’ and ‘incomplete’ key times 100) during testing was our dependent measure. For all statistical tests, α was set at 0.05.

2.2 Results and discussion

The pigeons took a mean of 13.3 sessions (range: 8 to 16 sessions) to finish discrimination training. Figure 3a shows the percentage of correct responses to the training stimuli during the testing sessions; these scores were near or above 90% correct, indicating that the birds’ responding to the training stimuli was substantially free of interference from the interpolated testing trials. Figure 3a also shows the percentage of choice responses to the ‘complete’ report key when the pigeons were presented with an *occluded* testing stimulus. If the birds perceived a square moving behind occluders in the *occluded* testing stimulus, then these scores should have been reliably higher than chance (50%). But, the pigeons responded in just the opposite fashion; they predominantly chose the ‘incomplete’ key rather than the ‘complete’ key. This trend was statistically significant for all four birds. Two-tailed *t*-tests revealed that the percentages of ‘complete’ responses made to the *occluded* testing stimulus were lower than the 50% chance level (bird 6Y: $t_{47} = -4.92$; 80Y: $t_{47} = -15.73$; 81Y: $t_{47} = -7.77$; 97W: $t_{47} = -8.88$). These results suggest that the pigeons did not amodally complete the square in the *occluded* testing stimulus, despite the fact that motion has been reported to be a robust cue for object unity in human infants.

In most prior studies, pigeons categorized a partially occluded object as neither complete nor incomplete (Cerella 1980; Ushitani and Fujita 2005, experiment 2; Watanabe and Furuya 1997); that is, they showed no systematic perception of the stimulus. But, in this experiment we found that the birds classified the *occluded* square as ‘incomplete’.

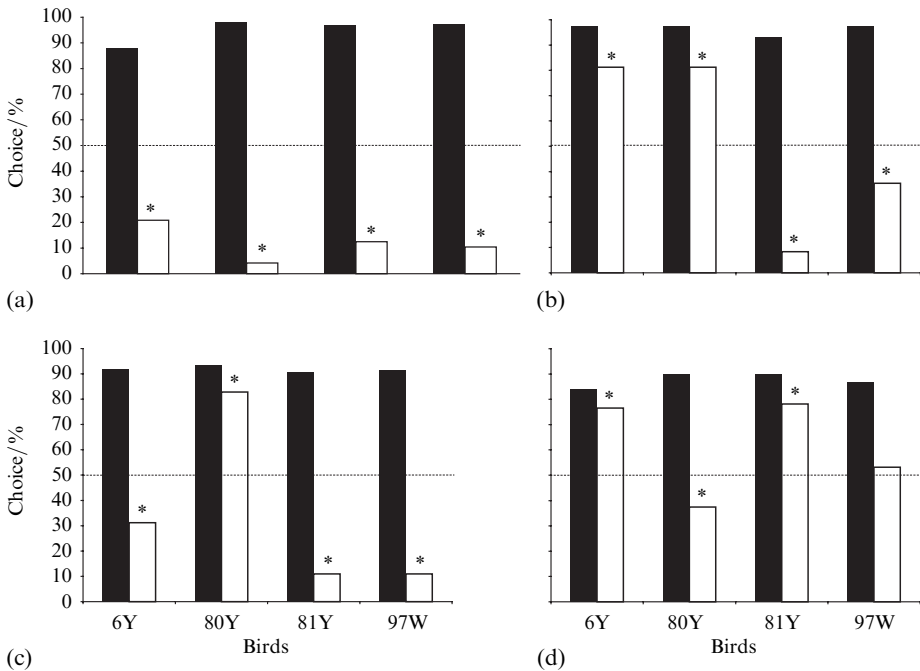


Figure 3. The percentage of each bird's choice responses in (a) experiment 1, (b) experiment 2, (c) experiment 3, and (d) experiment 4. Solid bars show the percentage of correct responses to the training stimuli. Open bars show the percentage of choices on *occluded* testing trials made to the 'complete' report key. The dashed line shows chance responding (50%). The asterisks represent choice scores that were significantly above or below chance ($p < 0.05$).

The difference between the *incomplete* stimulus and the *occluded* stimulus was the presence of the occluders; perhaps the birds ignored the occluders altogether when they viewed the testing display. Indeed, in this experiment, the occluders were painted gray on a white background (figure 1, experiment 1). Therefore, the *occluded* testing stimuli used here might not have provided a distinct enough contrast for the pigeons to perceive the circles as occluders. Also, the interior of the square in the *occluded* stimulus was white, whereas it was gray in the *complete* stimulus. If the birds encoded and remembered the moving gray square in the *complete* stimulus, then they might have discriminated the *occluded* stimulus from the *complete* stimulus and failed to report the presence of the *occluded* square. We addressed these concerns in experiment 2.

3 Experiment 2

In experiment 1, all of the birds reported the *occluded* stimulus as 'incomplete'. This result might have been due to particular features of the *occluded* stimulus, such as the brightness of the background, the brightness of the square, and the shading of the occluders. Thus, the birds might not have seen the four circles in the *occluded* stimulus as occluders obstructing the moving square; amodal completion requires recognition of the occluded object and the occluding object. In experiment 2, we used stimuli in which the occluders were painted red. This modification of adding color contrast to luminance contrast between the occluders and the background should enhance the salience of the occluders, which in turn might facilitate amodal completion behavior. In addition, we painted the interior of the square objects with the same white color in all three versions of the movies, in order to make the stimuli more similar to each other. This change too might facilitate the pigeons' discriminative transfer of 'complete' responses to the *occluded* testing stimulus.

3.1 Method

3.1.1 *Subjects.* The same four pigeons from experiment 1 continued to serve.

3.1.2 *Apparatus.* The apparatus was the same as that used in experiment 1.

3.1.3 *Stimuli.* The second row in figure 1 shows the three movie stimuli that were used in this experiment. The *occluded* stimulus consisted of two parts: an outline of a square (13 mm high \times 13 mm wide, 0.6 mm thick) and four occluders. The square was drawn in black on a white background (33 mm high \times 13 mm wide); the inside of the square was also white. The square moved in a circular trajectory behind the occluders during each stimulus presentation. The occluders (9 mm in diameter) were red circles placed over the four corners of the square. The *complete* stimulus showed the full contour of the square; the *incomplete* stimulus showed the same portions of the square that were visible in the *occluded* stimulus. Both *complete* and *incomplete* stimuli were drawn on a white background (33 mm high \times 33 mm wide); the same occluders in the *occluded* stimulus were placed in the corners of the background.

3.1.4 *Procedure.* The training and testing procedures were the same as in experiment 1.

3.1.5 *Behavioral measures.* The behavioral measures were the same as in experiment 1.

3.2 Results and discussion

The pigeons took a mean of 2.8 sessions (range: 2 to 4 sessions) to finish discrimination training. Figure 3b shows the percentages of correct responses to the training stimuli during the testing sessions; these scores all exceeded 90% correct. Figure 3b also shows the percentages of choice responses to the 'complete' key when the pigeons were presented with *occluded* testing stimuli. Two birds (6Y and 80Y) robustly responded to the 'complete' key and the other two birds (81Y and 97W) reliably responded to the 'incomplete' key to different degrees when they viewed the *occluded* testing stimulus.

Two-tailed *t*-tests confirmed that the percentage of 'complete' key choices made to the *occluded* testing stimuli was significantly higher than the 50% chance level for birds 6Y and 80Y (6Y: $t_{47} = 5.49$; 80Y: $t_{47} = 5.49$). These results suggest that the two pigeons amodally completed the moving square when it was occluded by the red circles. These data represent rare signs of amodal completion behavior in pigeons. But, statistical analysis also disclosed that birds 81Y and 97W chose the 'complete' key significantly less often than the 50% chance level when they viewed the *occluded* testing stimulus (81Y: $t_{47} = -10.34$; 97W: $t_{47} = -2.09$). These results suggest that these two birds classified the *occluded* testing stimulus as 'incomplete', just as they had in experiment 1.

Why did the pigeons exhibit such inconsistent trends? Perhaps the pigeons simply expressed a spatial report-key preference when they were shown the *occluded* testing stimulus; thus, these results might not truly reflect the transfer of discriminative responding to the *occluded* testing stimuli. We addressed this matter in experiment 3.

4 Experiment 3

In experiment 2, two birds classified the *occluded* testing stimulus as 'complete', whereas the other two birds classified it as 'incomplete'. The method used in experiment 2 could not rule out the possibility that the birds responded on the *occluded* testing trials with strong spatial report-key preferences. In experiment 3, we randomized the placements of the 'complete' and 'incomplete' report keys in an effort to discourage the birds from displaying a spatial report-key preference. In addition, we also explored the effect of two different types of reinforcement procedures on *occluded* testing trials.

4.1 Method

4.1.1 *Subjects.* The same four pigeons from experiments 1 and 2 continued to serve.

4.1.2 *Apparatus.* The apparatus was the same as in experiments 1 and 2.

4.1.3 *Stimuli.* The third row in figure 1 shows the stimuli that were used in this experiment. The *occluded* stimulus consisted of two parts: an outline of a circle (16 mm in diameter, 0.6 mm thick) and four occluders. The circle was drawn in black on a white background (33 mm in diameter); the interior of the circle was also white. The circle moved in a circular trajectory behind the occluders during each stimulus presentation. The occluders (9 mm in diameter) were red circles placed over the circle. The *complete* stimulus showed the full contour of the circle; the *incomplete* stimulus showed the same portions of the circle that were visible in the *occluded* stimulus. Both *complete* and *incomplete* stimuli were drawn on a white background (33 mm high \times 33 mm wide); the same occluders in the *occluded* stimulus were placed in the corners of the background.

The choice keys were two 2.7 cm \times 2.4 cm rectangles painted blue or yellow, located above and below or left and right of the movie stimulus; those placements were counterbalanced across birds. The blue key was assigned to 'complete' reports and the yellow key was assigned to 'incomplete' reports for two pigeons (6Y and 80Y); the assignments were reversed for the other two pigeons (81Y and 97W). The placements of the blue and yellow keys were randomized on each trial.

4.1.4 *Procedure.* Each bird took part in 4 testing sessions after training to criterion. The birds did not receive reinforcement for any report responses (extinction) on *occluded* testing trials for the first 2 testing days; for the following 2 testing days, the birds received reinforcement for any report responses (nondifferential reinforcement) on *occluded* testing trials. The rest of the procedure was conducted in the same way as in experiment 2.

4.1.5 *Behavioral measures.* The behavioral measures were the same as in experiments 1 and 2.

4.2 Results and discussion

The pigeons took a mean of 8.25 sessions (range: 5 to 12 sessions) to complete discrimination training. As the overall trends in the birds' responding were similar for both types of testing conditions, we consolidated the data for the following data analysis. Figure 3c shows the percentages of correct responses to the training stimuli during the testing sessions. These scores were near or above 90% correct. Figure 3c also shows the percentages of choice responses to the 'complete' key when the pigeons were presented with an *occluded* testing stimulus. One bird (80Y) robustly responded to the 'complete' key when it viewed an *occluded* testing stimulus; but the other three birds (6Y, 81Y, and 97W) robustly responded to the 'incomplete' key when they viewed an *occluded* testing stimulus. Two-tailed *t*-tests confirmed that the percentage of choices made to the 'complete' key was reliably higher than the 50% chance level for bird 80Y ($t_{63} = 6.9$), whereas the other three birds chose the 'complete' key reliably less often than the 50% chance level (6Y: $t_{63} = -3.2$; 81Y: $t_{63} = -9.9$; 97W: $t_{63} = -9.9$).

These results suggest that one pigeon amodally completed the moving circle, but that the other three birds did not. They further suggest that one of the pigeons (6Y) that predominantly chose the 'complete' key in experiment 2, may have been expressing a spatial report-key preference when the bird was shown the *occluded* testing stimuli.

5 Experiment 4

In the three preceding experiments, the pigeons were presented with an 'outline' of a shape in the movie stimuli. However, the objects in our visual world also have salient surfaces; only rarely do we perceive the bar outlines of objects. Therefore, objects with a discriminable surface should be more natural in pigeons' visual experience than line-drawn objects. Kellman (2003) proposed two processes for visual interpolation in studies of human perception (Kellman and Shipley 1991; Yin et al 1997, 2000): contour interpolation and surface interpolation. He argued that the contour interpolation process connects oriented edges across a gap and that surface interpolation integrates visible regions. Moreover, his studies showed that these two interpolation systems are separately operative for visual interpolation. So, we surmised that adding surface properties might prove to be a practical cue for pigeons' amodal completion behavior. We thus devised this final investigation (experiment 4), in which filled objects were used, in order to explore the effect of surface cues on pigeons' amodal completion behavior.

5.1 Method

5.1.1 *Subjects.* The same four pigeons from experiments 1, 2, and 3 continued to serve.

5.1.2 *Apparatus.* The apparatus was the same as in experiments 1, 2, and 3.

5.1.3 *Stimuli.* The fourth row of figure 1 depicts the stimuli that were used in this experiment. The *occluded* stimulus consisted of two parts: a square (13 mm high \times 13 mm wide, 0.6 mm thick) and four occluders. The square was painted black on a white background (33 mm high \times 33 mm wide). The square moved in a circular trajectory behind the occluders during each presentation. The occluders (9 mm in diameter) were green circles placed over the four corners of the square. The *complete* stimulus showed the whole shape of the square; the *incomplete* stimulus showed the same portion of the square that was visible in the *occluded* stimulus. Both *complete* and *incomplete* stimuli were drawn on a white background (33 mm high \times 33 mm wide); the same occluders in the *occluded* stimulus were placed in the corners of the background.

The choice keys were two 2.7 cm \times 2.4 cm white rectangles, each containing a triangular picture (an upright triangle with a texture of vertical lines or an inverted triangle with a texture of horizontal lines), were located at the top-left and bottom-right or at the top-right and bottom-left of the movie stimulus; these placements were counter-balanced across birds. The key containing the upright triangle was made the 'complete' report response and the key containing the inverted triangle was made the 'incomplete' report response for two birds (81Y and 97W); the assignments were reversed for the other two birds (6Y and 80Y). The placements of the keys were randomized on each trial.

5.1.4 *Procedure.* The procedure was the same as in experiment 3.

5.1.5 *Behavioral measures.* The behavioral measures were the same as in the three prior experiments.

5.2 Results and discussion

The pigeons required many more sessions (6Y: 38; 80Y: 30; 81Y: 156; 97W: 31) to complete discrimination training than in the earlier experiments. Figure 3d shows the percentages of correct responses to the training stimuli during the testing sessions. These scores were near or above 90% correct. Figure 3d also shows the percentages of choice responses to the 'complete' key when the pigeons were presented with an *occluded* testing stimulus. Two birds (6Y and 81Y) responded predominantly to the 'complete' key, one bird (80Y) responded predominantly to the 'incomplete' key, and the remaining bird (97W) responded indiscriminately to both keys when presented with the *occluded* testing stimulus.

Two-tailed t -tests confirmed that the percentages of report responses made to the 'complete' key were significantly higher than the 50% chance level for birds 6Y and 81Y (6Y: $t_{63} = 5.0$; 81Y: $t_{63} = 5.4$). These results suggest that these two pigeons amodally completed the moving square when it was presented along with surface cues. But statistical analysis also disclosed that bird 97W equivalently chose the 'complete' and 'incomplete' keys ($t_{63} = 0.5$, $p = 0.6$) and that bird 80Y chose the 'complete' key significantly less often than the 50% chance level ($t_{63} = -2.0$). Curiously, bird 80Y had been the only pigeon in experiment 3 to exhibit reliable choice of the 'complete' key to the *occluded* testing stimulus.

6 General discussion

In the present series of four experiments, we explored pigeons' amodal completion behavior with moving visual stimuli (figure 1). In experiment 1, we found that the pigeons perceived broken lines instead of a complete square in the *occluded* testing stimulus. We suspected that the birds might have ignored the gray occluders because of the weak contrast disparity between the light-gray occluders and the white background. In experiment 2, in which we painted the occluders red, the results indicated that two of the birds that had not done so in experiment 1 now perceived a complete square in the *occluded* testing stimulus; the other two birds still appeared to have seen broken lines in the *occluded* testing stimulus. Because of the experimental procedures used in experiment 2, this pattern of results could have arisen from the pigeons exhibiting a spatial report-key preference when they were shown the *occluded* testing stimuli. For this reason, in experiments 3 and 4, we randomized the locations of the choice report keys. We also used a filled shape with distinctive surface properties as the focal visual object in experiment 4. Now in these two experiments, three of the four pigeons evidenced completion of partially occluded moving objects; these three birds reliably reported 'complete' when they were presented with an *occluded* moving stimulus. These data represent rare instances of amodal completion behavior in pigeons and suggest that motion may be an important factor in the process.

In an earlier study, Ushitani et al (2001, experiment 1) used a white rod moving behind a gray belt and found that pigeons did not exhibit amodal completion behavior. This finding is consistent with the results of our own experiment 1. But, when Ushitani et al (their experiments 2, 3, and 4) later used a red occluding belt, their pigeons still perceived the occluded moving rod to be multiple broken rods. What is responsible for the disparate results between their study and ours?

One possibility is the experimental apparatus that they used. Ushitani et al (2001) used a CRT monitor and we used an LCD display for stimulus presentation. Pigeons' visual temporal resolution is much higher than humans' and it reaches 145 Hz (Emmerton 1983). Hence, the pigeons may have detected the flickering of the CRT monitor, thereby changing their perception of the moving stimuli. Furthermore, Yamaguchi et al (2003) found that pigeons' discrimination of paintings on an LCD display worsened when the same paintings were presented on a CRT monitor. Finally, Ikebuchi and Okanoya (1999) reported that male zebra finches and Bengalese finches showed robust courtship displays to video images of conspecific females when the videos were presented on an LCD display, but not when they were presented on a CRT monitor. Therefore, the failure to find evidence of amodal completion behavior of pigeons by Ushitani et al (2001) may have been due to suboptimal experimental methods.

These considerations notwithstanding, if we focus on the behavior of each of our individual pigeons, then evidence of consistency is in short supply. Consider only the data from experiments 3 and 4, in which our experimental methods ought to have been the most sensitive and reliable. In experiment 3, only one bird (80Y) chose the 'complete' key when it viewed the *occluded* testing stimulus, suggesting that the pigeon

perceived a complete moving square behind the occluders. But the same bird chose the ‘incomplete’ key in experiment 4; this trend was statistically significant, suggesting that the pigeon did not see a complete square in this later experiment. Recall that, when we conducted experiment 4, we had hoped that providing the target shape with surface cues would help the birds to complete it; this was certainly not the case for this particular pigeon.

On the other hand, when the other three birds (6Y, 81Y, and 97W) were presented with the *occluded* testing stimulus in experiment 3, they chose the ‘incomplete’ key, suggesting that they perceived broken lines. Yet, in experiment 4, two out of these three birds (6Y and 81Y) appeared to complete the *occluded* testing stimulus; thus, surface cues might have affected these pigeons’ perception of the *occluded* testing stimulus. Finally, the results from the fourth bird (97W) never exceeded chance in experiments 3 or 4, suggesting that this bird never perceived a complete square in the *occluded* testing stimulus—with or without surface cues available.

At this time, we cannot explain these inconsistent results of our pigeons. The choice behaviors of birds 6Y, 81Y, and 97W in experiment 3 and bird 80Y in experiment 4 replicated previous results in pigeons (eg Sekuler et al 1996); that is, the pigeons appear to have discriminated the stimuli by using local features. Indeed, our *incomplete* stimuli showed the same portions of the shapes that were visible in *occluded* stimuli. If our birds had used these common features for discrimination of the task stimuli, then they should have treated the *occluded* stimuli as *incomplete*. On the other hand, the same birds (80Y in experiment 3, and 6Y and 81Y in experiment 4) showed the opposite choice tendency when the *occluded* and *incomplete* stimuli shared common features. Therefore, our pigeons seem to have solved the discrimination task by using other cues, quite possibly global interpolated shape formed by amodal completion. So, overall, our albeit inconsistent positive results do generally suggest that an object’s motion may play an important role in the amodal completion behavior of pigeons, especially in light of the numerous failures to obtain amodal completion behavior with static stimuli and in light of the fact that these same pigeons had failed to evidence amodal completion behavior with static visual stimuli in experiments that preceded the ones reported here.

It might be of relevance to note that the perception of the moving stimulus we used in the current study is actually bistable in humans; when we pay particular attention to local features of the stimulus, we can see broken rods or an ambiguous area moving behind the occluders although we see the complete object most of the time. Some prior studies (Sekuler et al 1996; experiments 1 and 3, Ushitani and Fujita 2005) as well as the current study showed that the pigeons classify occluded objects as incomplete. Thus, the pigeons might have a tendency to pay attention to the partial features even when those features are moving in unison. Perhaps the current inconsistent results are due to the unique perceptual behavior of pigeons.

Kellman et al (2001) suggested that object segregation is required in the early stages of amodal completion. These authors argued that motion information is more robust for object segregation than are luminance or chromatic discontinuities, because motion is more highly correlated with object boundaries. Furthermore, research has shown that 4-month-old infants and still older human children require common motion to support amodal completion behavior (for summaries, see Johnson 2003). Also, research in our own laboratory has disclosed that specific training experiences can enhance pigeons’ recognition of partially occluded objects (DiPietro et al 2002; Lazareva et al 2007). These studies suggest that the improvements obtained in pigeons’ recognizing partially occluded objects are due to training experiences which encouraged the birds to segregate the objects from the occluders. Perhaps the moving objects used in the current

study also encouraged the pigeons to segregate the target shapes from the occluders, thereby helping the birds to complete the partially occluded shapes.

This interesting possibility merits further experimental scrutiny. So, too, does the interaction of stimulus properties and past experience. Segregating object from background is surely basic to navigating in the visual world. Such successful navigation may need to be cultivated by active experience with relevant stimulus information.

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