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Amodal completion by baboons (*Papio papio*): contribution of background depth cues

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Abstract Four baboons (*Papio papio*) were tested in a computerized two-alternative forced choice task in which partially occluded graphic stimuli were shown either on linear perspective backgrounds depicting a corridor or on uniformly black backgrounds. The results indicated that baboons complete partly occluded stimuli and that amodal completion is facilitated by the display of pictorial background depth cues. Inter-individual differences emerged in the ability to extrapolate three-dimensional information from two-dimensional visual information.

Keywords Baboon · Amodal completion · Depth perception

Introduction

Humans do not have a great degree of difficulty in recognizing objects that are partly occluded by other objects. This ability implies a process of perceptual completion by which objects are perceived as complete even though some of their parts are invisible (Palmer 1999; Kanizsa 1979). Michotte (1963) coined this process “amodal completion (AC)” to emphasize the fact that completion occurs despite the fact that the observer does not actually see the “completed” part of the object. Several recent comparative studies have demonstrated that a variety of animals, including chimpanzees (Sato et al. 1997), baboons (Deruelle et al. 2000), macaques (Sugita 1999), mice (Kanizsa et al. 1993), pigeons

(Wasserman et al. 2001; Watanabe and Furuya 1997), hens (Forkman 1998; Forkman and Vallortigara, 1999) and even domestic chicks (Lea et al. 1996; Regolin and Vallortigara 1995) have this ability. The experimental demonstration of AC in such a wide variety of different species suggests that the ability to perceive occluded objects as complete ones has a high value with respect to survival. Most probably, AC permits well-adapted behaviors in response to predators or prey that are only partly visible. However, while the presence of AC seems to be irrefutable in animals, the factors influencing it remain to be verified. It is important to know if AC in animals obeys the same principles as in humans because such information (1) can provide insight into the phylogeny of the visual system, from animals to humans, and (2) can moreover indicate to what extent animals can serve as models of human perception and cognition. The current research was a first attempt towards this goal.

In real vision, occlusion is suggested by a combination of monocular (e.g., relative size) and binocular (e.g., stereopsis) depth cues, as well as motion cues (see Cutting and Vishton 1995 for a review). This information might combine to launch completion processes by suggesting a spatial ordering in the depth plan of the occluded object relative to the occluder (Palmer 1999). Particularly important in humans are the so-called T-junctions. This kind of junction arises when the contour of the occluding surface intersects with that of the occluded surface (Rubin 2001). To test the effect of junction cues in animals, Kanizsa et al. (1993) trained mice to discriminate two different shapes presented on a homogeneous background. After training, completion was demonstrated by a significant transfer of performance in probe trials, in which the positive stimulus was partly occluded by another shape. Because occlusion in this study was only indicated by the junctions between the objects, clearly the presence of such junctions may be sufficient to elicit completion (for a complementary finding for macaques, see Fujita 2001). Junction cues, however, do not always suffice for AC. Indeed, several

The procedure employed in this research was given the full approval of the regional “comité d'éthique pour l'expérimentation animale.”

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studies failed to reveal AC with junction cues as the sole indices of occlusion (Sekuler et al. 1996; Deruelle et al. 2000), suggesting that there is not a one-to-one mapping between the presence of junction occlusion cues in images and AC.

Unfortunately, little is known about the contribution of depth cues other than junctions to AC in animals. It is plausible however that, as in humans (Bruno et al. 1997), completion is facilitated when depth cues – such as stereopsis of motion depth cues – are added to junction cues. Hence, Sugita (1999) showed a selectivity of V1 cells of macaques to occluded contours in a situation of binocular disparity suggesting depth. Selectivity did not emerge in the absence of binocular disparity. This effect indicates that binocular depth cues also serve as input in completion processes. AC was also demonstrated in a chimpanzee when motion was used as an additional depth cue to junction cues (Fujita 2000, 2001; Sato et al. 1997). In addition, Forkman (1998) and Forkman and Vallortigara (1999) showed AC in hens using a test paradigm in which the visual display contained perspective lines providing an apparent three dimensional (3-D) context to the occluded and occluder objects (at least for human vision) in addition to junction cues. Unfortunately, neither Forkman (1998) nor Forkman and Vallortigara (1999) ran control trials to ascertain if AC in hens was facilitated by this apparent 3-D context.

The objective of the research on baboons presented here was to contribute to the identification of the factors supporting the ability of animals to AC and was inspired by two major findings. First, Deruelle et al. (2000) demonstrated that baboons failed to perceive occluded objects as complete when T-junctions were the unique depth cues available in two-dimensional (2-D) visual displays shown on a computer screen, but were able to complete the objects when the same the stimuli were shown on small cards directly manipulated by the experimenter. Second, it was found that the same animals experienced the corridor illusion – a size illusion induced by the perception of an in-depth corridor – both with realistic pictures of the corridors (Barbet and Fagot 2002) and with drawings of the same corridors made only with perspective lines (Barbet and Fagot 2005). This effect demonstrates that the baboons can use pictorial depth cues as an indicator of depth and that they can experience depth based on the presentation of converging perspective lines (Barbet and Fagot 2005). Our study took advantage of these findings to investigate amodal completion using occluded objects presented on perspective lines.

Methods

Participants

Two adult male (B03 and B07) and two adult female *Papio papio* baboons (B04 and B08) were studied; they were all maintained in the primate facility of the

C.N.R.S (Marseille). The baboons had already participated in a variety of experiments using the same apparatus. In particular, they had all served as subjects in the study of Deruelle et al. (2000), which allows the results of their study to be compared directly with the present results, and two of them (B08 and B07) had participated in Barbet and Fagot's (2005) study on the corridor illusion. The baboons were not food-deprived but received their food ration at the end of daily training and testing.

Apparatus

The experiment took place inside a 68×50×72 cm³ experimental cage comprising a view port and two hand ports that provided free access to an analog joystick and a starting panel located 25 cm in the front of the cage. Manipulation of the joystick controlled the displacements of a cursor on a 14-inch color monitor screen situated 49 cm from the view port.

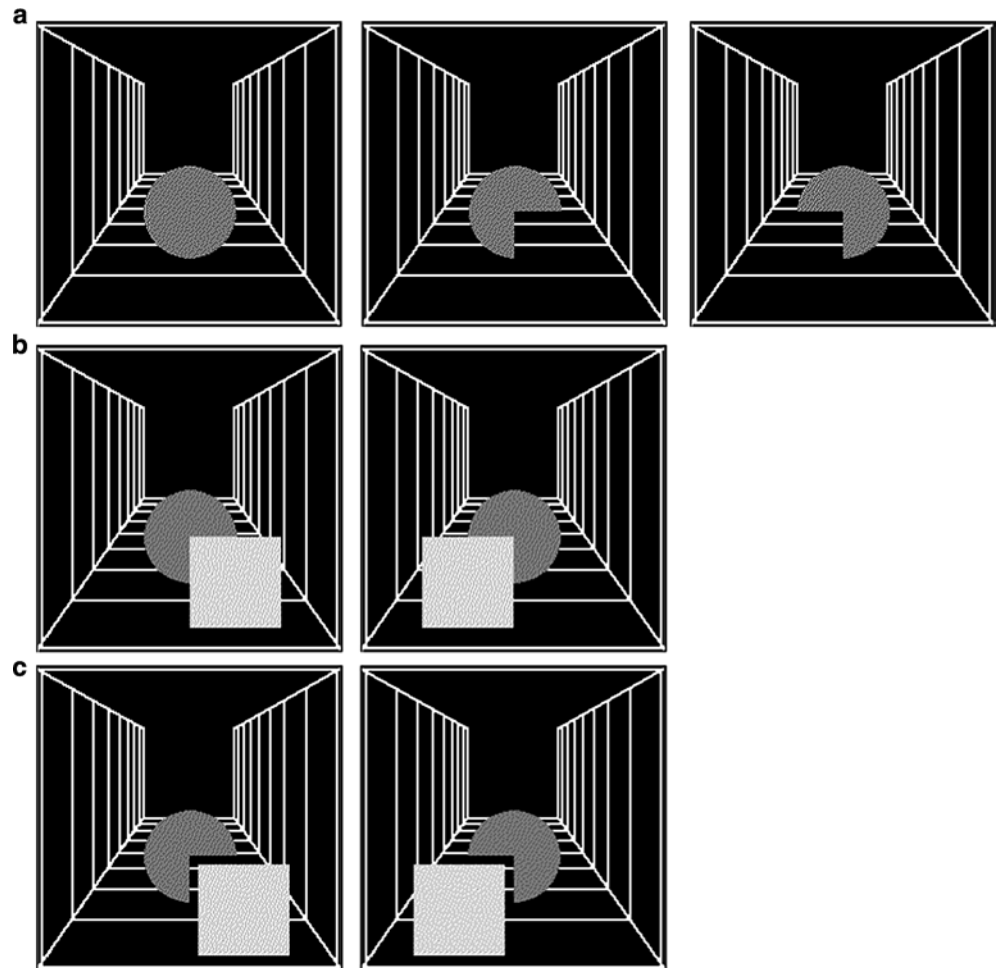
Stimuli

The training stimuli (Fig. 1a) were a 2° of visual angle blue circle and two pacman shapes made from the same circle from which the lower left or right quadrant had been removed (Fig. 1). Two types of stimuli were used for testing; these are referred to as the occluded and amputated stimuli, respectively, in subsequent text. The occluded stimuli were formed using a 2°×2° of visual angle square covering the lower left or right quadrant of the circle (see Fig. 1b). The amputated stimuli contained the same yellow square but now displayed 0.2° from the missing sector of the pacman shape (see Fig. 1c). All training and testing stimuli were pasted on a perspective line corridor background similar to the one described in Barbet and Fagot (2005). The yellow square was made brighter (149 cd/m²) than the blue pacman (39.5 cd/m²) in order to provide an additional cue favoring depth perception (Pratt 1979; Solso 1998).

General procedure

A trial was initiated when the baboon touched the starting panel. A cursor (a 0.5° of visual angle green circle) and a fixation (a 0.5×0.5° of visual angle white square) point then appeared in the center of the monitor screen. In response to this display, the baboon had to move the cursor using the joystick and place it on the fixation point for 35 ms. Two discriminative stimuli then appeared on the screen, one to the right and the other to the left of the fixation point. Three degrees of visual angle separated the fixation point from the innermost side of the left and right stimuli. By manipulating the joystick, the baboon had bring the cursor into contact with the discriminative stimulus

Fig. 1 Stimuli used in this research. **a** Training stimuli, **b** occluded probe stimuli, **c** amputated probe stimuli. Note: the actual stimuli were in color instead of black and white



that had been designed by the experimenter as positive (S+) and to avoid contacting the negative stimulus (S-). Three seconds were available for responding after the onset of the discriminative stimuli. Correct responses resulted in the delivery of a food pellet. The screen was refreshed immediately after the baboon had responded or after a 3-s period had elapsed. The inter-trial interval was set at 4 s.

Preliminary training

Baboons received repeated training sessions consisting of 80 randomly ordered trials. A training trial involved the simultaneous presentation of the circle stimulus, along with either the Pac-Man with the lower left quadrant missing (one-half of the trials) or the Pac-Man with the lower right quadrant missing (the other one-half). Location of the circle stimulus in the left or right hemiscreen was counterbalanced. All trials were differentially reinforced; that is, animals received a food reward whenever the correct stimulus was selected. Training sessions were repeated until the baboons performed correctly at 80% of the trials or more in two successive sessions. A total of 260 training trials (SD = 113) were needed on average to acquire the task.

Testing procedure

Each baboon received three test sessions of 100 trials each. Test sessions contained 80 baseline trials, the same as in training, involving the simultaneous presentation of a circle and the Pac-Man stimuli shown in Fig. 1a. They also included 20 probe trials involving the simultaneous presentation of an occluded and an amputated stimulus. The occluded and amputated quadrants were the same (lower left quadrant) for the two stimuli of each trial, and the left/right spatial location of the stimuli was balanced across trials. All baseline trials were differentially reinforced. Because there was no correct response for probe trials, these trials were randomly reinforced on a 50% basis, irrespective of a subject's response.

Results

Performance was 98.1% correct on average in the baseline trials, demonstrating that the baboons paid attention to the task. Table 1 presents data on an individual basis for the baseline and probe trials along with the results of the χ^2 tests ($p < 0.05$) indicating significant preferences for one or the other of the

Table 1 Number of selections of the circle, pacman, occluded and amputated stimuli in the test sessions, and results of two-tailed binomial tests for comparison of pacman versus circle, and occluded versus amputated (*NS* not significant)

Subject	Baseline trials			Probe trials		
	Pacman	Circle	<i>p</i>	Occluded	Amputated	<i>p</i>
B03	6	234	< 0.001	51	9	< 0.001
B04	6	234	< 0.001	40	20	< 0.03
B07	5	235	< 0.001	39	21	< 0.02
B08	1	239	< 0.001	33	27	0.6 NS
Mean	4.5	235.5	–	40.5	19.5	–

Bold characters indicate significant preferences

stimuli. Three baboons (B03, B04, B07) had a reliable preference for the occluded stimulus. The fourth (B08) showed a consistent but a non-significant bias in the same direction; a one-tailed binomial test showed a preference for the occluded sample at $p=0.06$. In brief, the results indicate that the circle shape was recognized from the occluded forms and thereby demonstrate that at least three of the four baboons perceived the occluded objects as complete.

These results were compared with those of Deruelle et al. (2000, Experiment 5), who tested the same baboons but with homogeneous instead of perspective line backgrounds. This comparison indicates that all of the baboons exhibited a higher percentage of occluded stimulus selection with the 3-D backgrounds (current experiment) than with the 2-D backgrounds (Deruelle et al. 2000; B03: 85 vs. 62.5%; B04: 66.7 vs. 37.5%; B07: 65.0 vs. 50%; B08: 55 vs. 50%, respectively). These intra-individual shifts as a function of background content correlate with the hypothesis that pictorial depth cues favored AC in the current study.

The current results have implications for the phylogeny of AC. To date, AC has been demonstrated with static visual displays in several animal species, including domestic hens and mice (Forkman 1998; Kanizsa et al. 1993). It has also repeatedly been demonstrated with moving stimuli in non-human primates (Fujita 2001; Sato et al. 1997), but little is known about the perception of static occluded objects in these animals. Interestingly, Deruelle et al.'s study (2000) using static stimuli has already reported AC in baboons, but AC was limited in that study to a test situation involving stimuli presented on small cards directly manipulated by the experimenter. The fact that AC has also been demonstrated in the current study when the display contained background depth cues suggests that these kind of cues, in addition to junction cues, contribute to AC. However, this suggestion has to be viewed with caution given that 2 years have elapsed between the two studies. Rather than being attributable only to depth cues, it is possible that completion emerged in the present study as a result of increased training, the mere passage of time, participation in other experiments, or some combination of these factors. To explore this possible causal relationship in

baboons between AC and background content in more depth, we ran a control experiment.

This control experiment combined the procedures used in Deruelle et al. (2000, Experiment 5) and that of our first experiment within a single experimental design. Baboons B03, B04 and B07 were tested again. B08 was omitted because it previously failed to show reliable completion. Two types of stimuli were presented within the same test session in the control experiment (Fig. 2). The first comprised the forms displayed on perspective line corridors that had been used earlier; the second comprised the same stimuli as previously used but now displayed on a uniform black background. This test condition was similar to that of Deruelle et al. (2000, Experiment 5). Each baboon received six 100-trial test sessions. Each 100-trial session contained 80 (40 with perspective and 40 uniform backgrounds) baseline trials

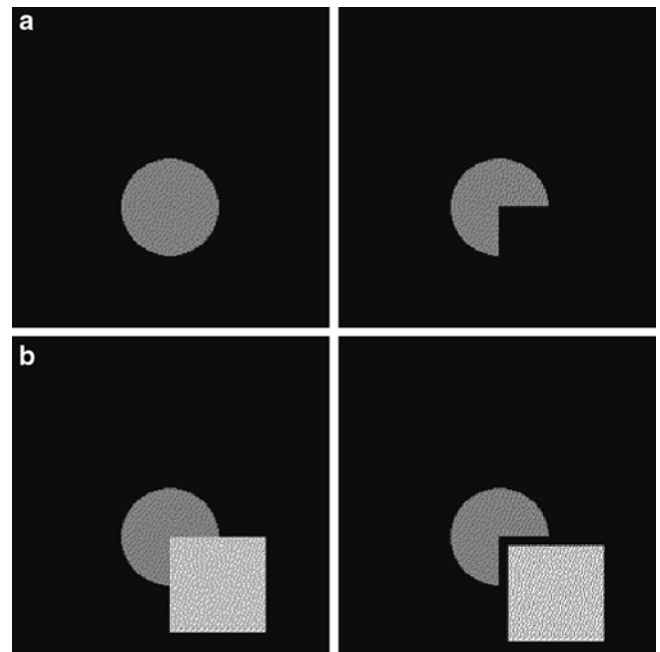


Fig. 2 Example of the stimuli employed in the control experiment. **a** training stimuli, **b** probe stimuli. Note that the actual stimuli were in color instead of being black and white

Table 2 Control experiment: number of selections of the circle, pacman, occluded and amputated stimuli and results of two-tailed binomial for pacman versus circle and occluded versus amputated comparisons for each baboon and type of background (*NS* not significant)

	Baseline trials			Probe trials		
	Pacman	Circle	<i>p</i>	Occluded	Amputated	<i>p</i>
2-D background						
B03	7	233	< 0.0001	49	11	< 0.001
B04	24	216	< 0.0001	30	30	NS
B07	17	223	< 0.0001	32	28	NS
3-D background						
B03	9	231	< 0.0001	55	5	< 0.001
B04	38	202	< 0.0001	41	19	< 0.001
B07	9	231	< 0.0001	31	29	NS

Bold characters indicate significant preferences

intermixed with 20 probe trials involving the amputated and occluded forms. Ten of the probe trials presented a perspective background; the other ten presented a uniform black background. Baboons received training sessions prior to the test using the plain circle and pacman stimuli. Training sessions intermixed 40 perspective background trials with 40 uniform black background trials. Two sessions were sufficient to achieve 80% correct performance under these conditions.

Results of the control experiment indicated that the three baboons performed well above chance in the baseline trials, regardless of the type of background (see Table 2). Consistent with the results of Deruelle et al. (2000), homogenous background probe trials provided no evidence for AC in either B04 or B07. Differences in performance between B03 and the two others suggest: (1) that junction cues may suffice to induce depth perception in some animals (as demonstrated by B03), but (2) that all individuals are not equally sensitive to junction cues as an indicator of depth.

Probe trials revealed that perspective line backgrounds did not induce AC in B07. Why B07 did not complete in this situation remains puzzling, considering that it had completed before. We suspect that disturbances due to the intermixing of the two types of test trials prevented generalization of the AC performance. More interestingly, however, both B03 and B04 showed AC during the probe trials of this second experiment. This result suggests that perspective backgrounds can serve as input for AC processes in baboons. In fact, the strongest evidence for an interaction between background content and AC comes from B04. Although the two test conditions were mixed within the same sessions, this baboon showed completion only when the backgrounds contained cues to depth. This baboon therefore exhibited a systematic shift from one mode of image processing, associated with AC, to a second mode in which the occluded objects were not completed. To our knowledge, this is the first time that this effect has been reported in a non-human species.

Discussion

One important aspect of this research is to confirm that baboons experience AC, although it appears restricted to some experimental contexts. Demonstration that AC is available to baboons is in line with other studies on non-human primates – for example, chimpanzees (Sato et al. 1997), macaques (Sugita 1999) – as well as non-primates, such as mice (Kaniza et al. 1993), hens (Forkman 1998; Forkman and Vallortigara 1999), and domestic chicks (Lea et al. 1996; Regolin and Vallortigara 1995). These findings indicate that AC processes in humans have a long evolutionary history and, presumably, a high adaptive value for a large number of species.

The results of this research also show that AC in baboons is partly under the control of contextual depth information. Two lines of evidence support this conclusion. First, none of the three baboons that completed objects in our first experiment had shown AC when previously tested with homogeneous backgrounds (Deruelle et al. 2000). Second, B04 showed a systematic shift from a completion to a non-completion mode of processing when background pictorial depth cues were removed. The current data therefore confirm that AC is a non-obligatory process that may appear (or disappear) as a function of type and/or quantity of occlusion indices that are present in the display. They further indicate, in line with Barbet and Fagot (2005), that presentation of perspective lines can induce a sensation of depth in baboons.

Like most 2-D images depicting depth, our stimuli were ambiguous. Thus, some of the cues provided by binocular vision, motion parallax, surface-texture of the screen, and light reflection indicated that the stimuli were indeed flat. However, our stimuli also contained salient cues suggesting depth. These included the junctions between the occluder and occluded shapes and, in the case of 3-D trials, linear perspective backgrounds.

The selection of a stimulus in probe trials thus presumably implied a decision process favoring either element of depth information. Relative to the response of the baboons in the homogenous background trials, none showed a reduced tendency for AC when a linear perspective was added to the display. In contrast, one of them (B04) showed AC only when contextual depth cues were added to junction cues. It thus seems that junction and perspective cues have cumulative effects favoring a 3-D encoding of the stimuli. This would explain why AC was readily observed in the studies by Forkman (1998) and Forkman and Vallortigara (1999), in which stimuli contained both junction and linear perspective cues.

As a last point, it is noteworthy that considerable inter-subject variability emerged in AC. These differences among individuals suggest that baboons are not equally sensitive to pictorial depth. The findings – (1) that pictorial background depth contributes to a 3-D encoding of the stimuli, and (2) that there are individual differences in the sensitivity to depth cues – are both reminiscent of human studies reported in the literature. The results of these human studies suggest that AC is more readily expressed when displays contain convergent depth cues than when they only contain junction cues (Bruno et al. 1997). Data in the literature also suggest individual differences in the processing of pictorial depth (Benson and Yonas 1973). When the results from these human studies are taken in consideration together with those reported here, it would appear that there are similarities in the processes underlying the perception of pictorial depth and AC in humans and monkeys.

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