

# Tits use amodal completion in predator recognition: a field experiment

Kateřina Tvardíková · Roman Fuchs

Received: 16 November 2009 / Revised: 9 January 2010 / Accepted: 14 January 2010 / Published online: 4 February 2010  
© Springer-Verlag 2010

**Abstract** Amodal completion enables an animal to perceive partly concealed objects as an entirety, and to interact with them appropriately. Several studies, based upon either operant conditioning or filial imprinting techniques, have shown that various animals (both mammals and birds) can perform amodal completion. Before this study, the use of amodal completion by untrained animals in the recognition of objects had not been considered. Using two feeders, we observed in a field experiment the reaction of tits to the torso of a sparrowhawk (partly occluded or an ‘amputated’ dummy) in two different treatments (sparrowhawk torso vs. complete dummy pigeon; and torso vs. complete dummy sparrowhawk). It is clear that the birds considered the two torso variants as predators and kept away from both of them when the second feeder offered a ‘pigeon’ instead. On the other hand, when a ‘complete sparrowhawk’ was present on the second feeder, the number of visits to the occluded torso remained low; while the number of visits to the amputated one increased threefold. Birds risked perching near what was clearly an amputated torso; while the fear of a “hiding” (occluded) torso remained unchanged, when the second feeder did not provide a safe alternative. Such discrimination between torsos requires the ability for amodal completion. Our results demonstrate that in their recognition process, the birds not only use simple sign stimuli, but also complex cognitive functions.

**Keywords** Occluded predator · Amputated predator · Amodal completion · Sign stimuli · Pair-wise experiments ·

Feeders · Winter · Sparrowhawk · *Accipiter nisus* · Tit species

## Introduction

In the three-dimensional natural environment, objects frequently occlude portions of themselves, as well as other objects. Humans seem to have little difficulty recognizing a person who is sitting in a car or standing behind a counter, and casual observations suggest that animals can do the same (Vallortigara 2006). For example, a chick can recognize the mother hen even if it is partially hidden in the grass (Vallortigara 2004).

This adaptive ability is the phenomenon called amodal completion: the cognitive completion of an object that remains partially hidden behind another (Kanizsa et al. 1993). However, it is possible to recognize a partially occluded object without perceiving it as complete (Lazareva et al. 2007). Several studies have shown that mammals (mice: Kanizsa et al. 1993; rhesus macaques: Bakin et al. 2000; Fujita 2001; baboons: Deruelle et al. 2000, Fagot et al. 2006; squirrel monkeys: Nagasaka and Osada 2000; Japanese macaques: Sugita 1999; and chimpanzees: Sato et al. 1997) all can perform amodal completion.

Evidence for amodal completion has also been obtained in some species of birds. Chicks clearly recognized a triangle when faced with a partly occluded triangle, but could not recognize an amputated one (Regolin and Vallortigara 1995; Lea et al. 1996). This confirmed that chicks perceive object uniformity soon after hatching. Similarly, adult hens had the ability for recognition of overlapping squares and circles (Forkman 1998) or chromatically homogenous overlapping figures (Vallortigara and Tommasi 2001).

K. Tvardíková (✉) · R. Fuchs  
Department of Zoology, Faculty of Biological Science,  
University of South Bohemia, Branišovská 31,  
370 05 České Budějovice, Czech Republic  
e-mail: katerinatvardikova@seznam.cz

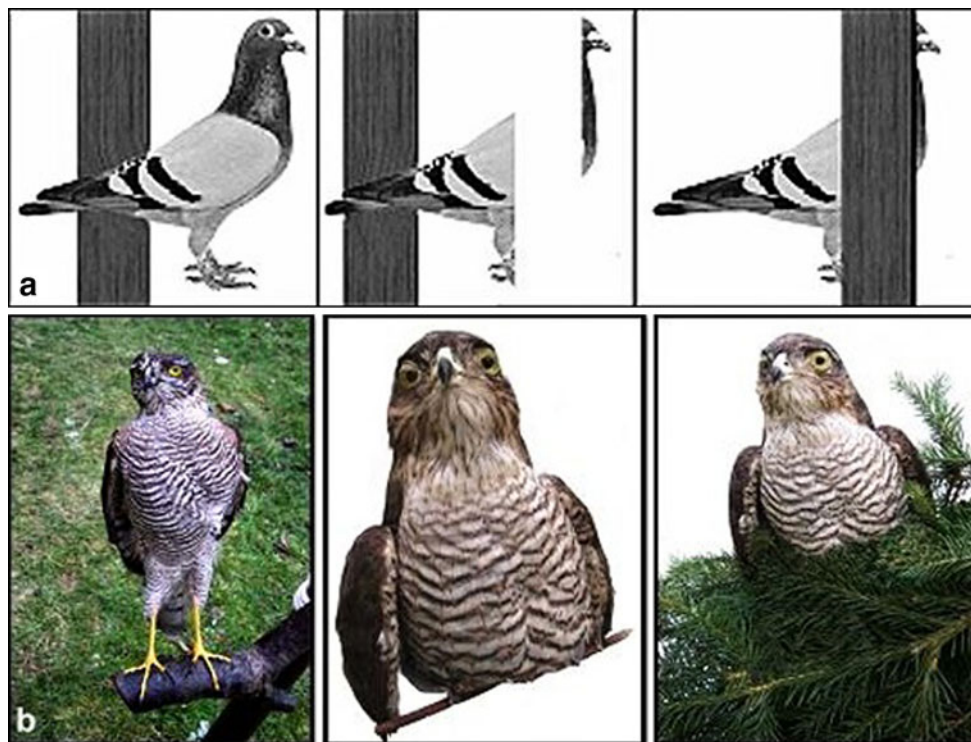
The evidence surrounding amodal completion in pigeons (the most studied species) is equivocal. Some findings seem to indicate that pigeons can compensate for an incomplete image (Watanabe 1999; Aust and Huber 2006). However, there are many other experiments suggesting that they are not able to perceive the unity and coherence of partly occluded objects. Watanabe and Furuya (1997) concluded that birds did not see the hidden figure in a video image. This finding was supported by the work of Fujita (2001) and Sekuler et al. (1996). By contrast, Lazareva et al. (2007) and DiPietro et al. (2002) suggest that pigeons can recognize partially occluded objects without amodal completion if they are given sufficient training.

Inappropriate stimuli may cause those biases. More ecologically valid objects and setting might better trigger the bird's ability to perceptually complete occluded items, as shows the work on courtship displays of Bengalese finches (Okanoya and Takahashi 2000). Most prior studies dealing with amodal completion in animals have been based upon operant techniques (Vallortigara 2006). The animals were trained to respond to a complete object (typically a geometric shape) (Vallortigara 2006), and then were tested as to whether they recognized the object in its amputated and occluded versions (Fig. 1). If the animal's responses suggested that only partially occluded objects looked to them like a complete object, it was considered that they were aware of the continuance of the object behind the obstruction.

Prior to this study, the possible use of amodal completion by untrained animals in their recognition of natural objects (e.g. animals) had been studied only exceptionally (Okanoya and Takahashi 2000). We designed an experiment in which an unambiguous recognition reaction of the experimental animals could be measured. The recognition of predators was one possibility. The ability of birds to recognize and discriminate predator dummies has been shown in many studies (for review, see Caro 2005); therefore these stimuli could be used for the amodal completion research. Experiments at a feeder have proven to be an effective tool to test a bird's ability in the discrimination of predator dummies in the field (Gentle and Gosler 2001; Desrochers et al. 2002; MacLeod et al. 2005). If a predator is recognized in the surroundings adjacent to the feeder, birds do not come near and prefer to stay within the cover provided in the environs without food intake. The more dangerous the predator, the stronger is this response.

In this paper, we report on the ability of tits (Paridae) for the visual completion of the upper half of an avian predator (*Accipiter nisus*). We observed the numbers of arrivals to a pair of feeders. On one of the pair, either an occluded or amputated sparrowhawk dummy was installed; the other paired experimental feeder was provided with either a dummy of a sparrowhawk or a harmless pigeon.

We set out to test two hypotheses: (1) If the number of arrivals between the amputated or occluded sparrowhawk



**Fig. 1** **a** Complete, amputated, and occluded pigeon (according to Aust and Huber 2006). **b** Dummies used in this experiment: complete, amputated, and occluded sparrowhawk

would likely differ, when a pigeon was presented on the alternate feeder. Ethologists have long assumed that sign stimuli, alone, functioned for the recognition of both predators and sexual partners (e.g. Tinbergen 1951; Chantrey and Workman 1984; Carbaugh et al. 1962; Schein and Hale 1957; Shoettle and Schein 1959). Therefore, we assumed that the birds would recognize a sparrowhawk with both torso alternatives (occluded and amputated); yet give priority to the perceived safer alternate feeder. (2) If the number of arrivals to an amputated sparrowhawk would be higher than to an occluded sparrowhawk, when a complete sparrowhawk was present on the alternate feeder. We assumed that the birds attempt and prefer to avoid any alternative feeder that is perceived as dangerous. Nevertheless, they will risk arrivals near an amputated (incomplete) sparrowhawk on the experimental feeder, in preference to one with an occluded sparrowhawk (thus perceived as continuing behind the obstruction, and perceived as being as/almost as dangerous as a complete sparrowhawk).

## Methods

### Experimental site and species

The experiment was done during the winter of 2007/2008 in an area of broad-leaved trees growing near the village of Chodská Lhota (49°21'15", 30°47'25"), Czech Republic. The site is 640 m above sea level and is located in a comparatively cold portion of Bohemia. The winter of 2007/2008 was quite a severe one. We studied three species of tits that predominated on the feeders: the great tit (*Parus major*), the blue tit (*Cyanistes caeruleus*), and the "marsh" tit. The "marsh" tits were represented by two species: the marsh tit (*Poecile palustris*) and the willow tit (*Poecile montanus*). As these two species are indistinguishable on videotape, they were lumped together as one species.

### Experimental design

The feeders were established in a small clearing, surrounded by mixed deciduous woodland and scrubland. The shortest distance from feeder to cover was ca. 4 m. The two feeders were 25 m apart, and the space between the feeders was free of trees. The feeders were surrounded by shrubs and trees on three sides. These served as both a shelter and surveillance position for the birds. The feeders were boards (45 cm by 45 cm) lying upon the ground, with raised edges to avoid food scattering. Between the experiments, the feeders were covered with a roof. Sunflower seeds were used as the food. To attract the birds, before the first experimental series the feeders were filled with sunflower seeds

for 4 weeks. Any remaining sunflower seeds were attentively removed and replaced with grated walnuts just before the trials. The grated walnuts were used because they required the birds to remain longer at the feeder (Desrochers et al. 2002). As the tits were not able to carry the grated walnuts away to consume them in the surrounding cover, they had to stay on the feeder longer in order to obtain a sufficient food intake.

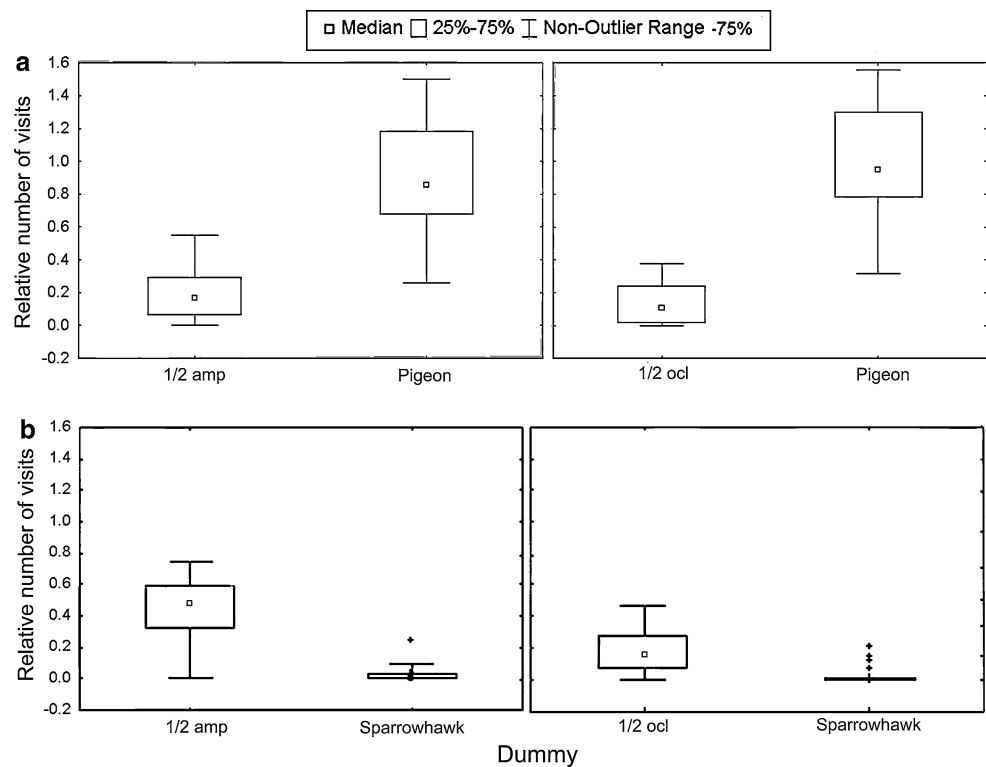
Stuffed models were used as both the test sparrowhawk and pigeon. They were placed on a 75-cm-high stake on the outer right corner of the feeder (as seen from the camera), and always faced toward the center of the feeder. Throughout the paper, we have used the terms occluded (for the upper torso hidden in the shrubs) and amputated (for only the upper torso on the perch) sparrowhawks. Either an amputated or occluded sparrowhawk model was tested on the experimental feeder, juxtaposed to a complete pigeon or a sparrowhawk on the alternate feeder. Two empty feeders were used in the last tested trial (as a reference control) and it always preceded two experimental trials. This amounted to four different trials in one series: two experimental (amputated/occluded sparrowhawk vs. sparrowhawk, amputated/occluded sparrowhawk vs. pigeon) and two reference controls. The reference control trials had fixed positions within the series (the 1st and 4th trials). The sequence of the dummy pairs (experimental trials) within each series was randomly arranged. Additionally, the placement of a dummy (on the left or the right feeder) was randomly arranged within a trial.

Each experimental day started 1 h after daybreak. Individual trials lasted 30 min, and the experimental feeders were videotaped continuously throughout the duration of the experiments. The camera was set up in a fixed position, facing the experimental feeder, at a distance of 8 m. Snow cover and temperature were noted for each experimental day. Between each series, there was usually a 6 or 7 days pause. Thirteen series were conducted during the winter of 2007/2008, amounting to a total of 78 half-hours of trials, from which a total of 14,672 tit visits were analyzed.

In this study, the birds additionally were trapped using mist-nests, in order to reveal the rate of pseudo replications. The experiment was designed so that the trapping level was constant (about 50 birds were ringed per day) throughout the study. Mist-nets were used 1 day before each series. A total of 568 birds were ringed during the winter. Each trapped individual bird was fitted with a standard metal leg-ring with a unique number. Additionally, an individual combination of color-rings was then fitted under license (Czech Bird Ring Association, #1062). Each bird was thus uniquely identifiable on the videotape.

Statistical calculations showed that of those birds which were ringed during individual mist-nettings (approximately 50 birds)  $51.23 \pm 2.55\%$  ( $X \pm SD$ ) returned to the feeder

**Fig. 2 a** Relative number (compared to the reference control) of visits to an amputated (1/2 amp) or occluded (1/2 ocl) sparrowhawk in the trials with a pigeon on the alternate feeder. **b** Relative number (compared to the reference control) of visits to an amputated (1/2 amp) or occluded (1/2 ocl) sparrowhawk in the trials with a sparrowhawk (sp. hawk) on the alternate feeder



1 day after ringing. Only  $37.33 \pm 2.09\%$  ( $X \pm SD$ ) of these stayed onto be in the next experiment (8 days later), and  $18.51 \pm 5.2\%$  ( $X \pm SD$ ) stayed through the third experiment (15 days later). Less than  $1.61 \pm 0.7\%$  ( $X \pm SD$ ) of the ringed birds appeared 4 weeks later. The average individual bird usually visited the feeder in  $1.26 \pm 0.51$  ( $X \pm SD$ ) trials (3 trials, at most) during one series. Once a bird appearing for the first time in the trial, on average they arrived at the feeder  $1.93 \pm 1.08$  ( $X \pm SD$ ) times.

### Statistical analysis

During the trials, the numbers of individual visits of tit species to the experimental feeders with the sparrowhawk torsos were analyzed. To remove the effects of a fluctuating pool of tits in the study area during the winter, we calculated the relative number of visits (the number of visits at the experimental feeder; the mean number of visits at one control feeder). The arithmetic means of the visits at both control feeders were used, because the number of arrivals to left and right feeders did not differ (One-way Anova:  $F_{1,12} = 0.14$ ,  $P = 0.713$ ).

The following explanatory variables were used: dummy combination (amputated sparrowhawk vs. complete pigeon, occluded sparrowhawk vs. pigeon, amputated sparrowhawk vs. complete sparrowhawk, and occluded sparrowhawk vs. complete sparrowhawk); the sequence of the series (1–13); tit species (only interactions between dummy and species

were important); temperature ( $^{\circ}\text{C}$ ); and snow cover (cm). GLMM was constructed; the data had a normal distribution, and the link function identity was used. The Tukey post hoc test in R (Hothorn et al. 2008) was performed in multcomp package of R software (R Development Core Team 2008), for the variable dummy combination.

Non parametric tests (Wilcoxon) were used when the data did not reach normality, and when appropriate. These statistical calculations (and all graphs) were made using STATISTICA 8 for Windows (Statsoft Inc. 2007).

### Results

Both sparrowhawk torso variants decreased the number of visits, when compared to the pigeon being present on the alternate feeder. (Wilcoxon test, relative number of visits; occluded:  $T = 75$ ,  $N = 36$ ,  $P < 0.001$ , amputated:  $T = 107$ ,  $N = 36$ ,  $P = 0.001$ , Fig. 2a). On the other hand, both sparrowhawk torso variants had less of an effect on the number of visits than did a complete sparrowhawk presented on the alternate feeder (Wilcoxon test, relative number of visits; occluded:  $T = 4$ ,  $N = 36$ ,  $P < 0.001$ , amputated:  $T = 0$ ,  $N = 36$ ,  $P < 0.001$ , Fig. 2b).

The combination of which dummies were presented on the two feeders significantly affected the relative number of arrivals to the feeder. No significant effects were found for snow layer, temperature, series sequence, or the interaction between dummy and the tit species (Table 1).

**Table 1** Effects of the dummies, weather, and experimental design on the relative changes in the number of visits to a feeder

	<i>Df</i>	<i>F</i>	<i>P</i>
Dummy comb.	1	13.18	<0.001
Temperature	1	2.42	0.102
Snow layer	1	0.95	0.332
Series	1	0.09	0.758
Dummy: species	2	0.37	0.693

Error *Df* = 135

The results of GLM show *Df*, *F* and *P* values for each predictor and some interactions (see “Methods”)

The Tukey post hoc test shows that the difference between the two torsos was only significant in those treatments when a complete sparrowhawk was on the alternate feeder (sparrowhawk as alternate dummy:  $P < 0.001$ ; pigeon as alternate dummy:  $P = 0.849$ ). The relative number of visits to the occluded torso did not differ between treatments with a sparrowhawk, and a pigeon as the alternate dummy ( $P = 0.850$ ); whereas the relative number of visits to the amputated torso was higher in those treatments with a sparrowhawk vs. one with a pigeon ( $P < 0.001$ ) on the alternate feeder (Fig. 3).

## Discussion

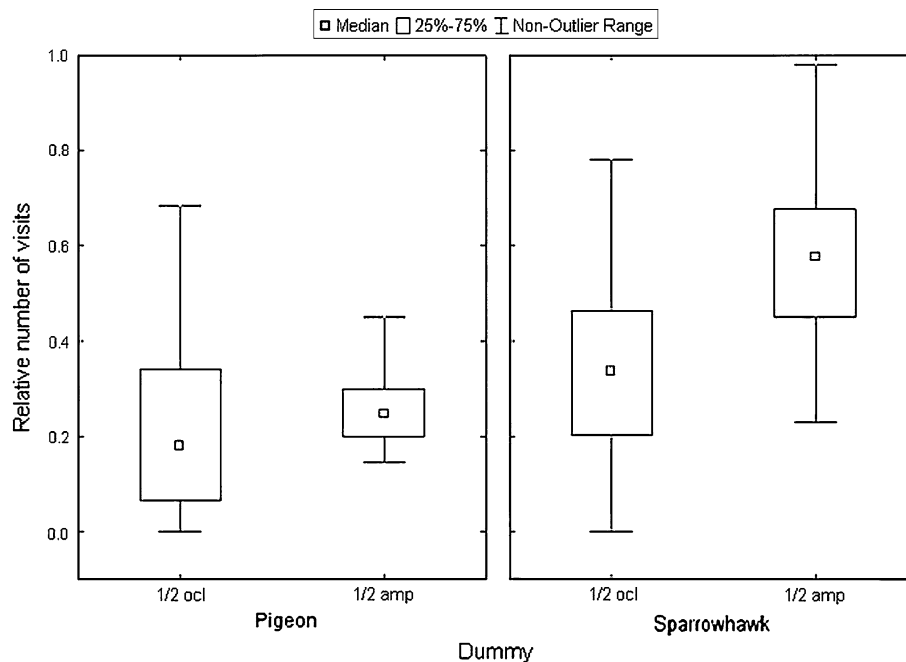
The tits recognized both of the sparrowhawk torsos (amputated, as well as occluded), as the decrease in the number of visits did not differ for either of the torso treatments with a pigeon on the alternate feeder. This could well be

interpreted as the tits not using amodal completion, but that instead they recognize a predator according to sign stimuli (i.e. on the head region it could be eyebrow stripe, hooked bill, and yellow eye), and thus keep away. However, in those treatments with a complete sparrowhawk on the alternate feeder, the relative numbers of visits to an amputated sparrowhawk increased intensively; up to nearly 100% of the reference controls in some trials.

This should be interpreted as the tits recognizing a predator in both torso variants; however, only the occluded one is perceived as “fully-featured”. On the other hand, the amputated torso is perceived as “partly-featured”. The birds keep away from both torsos when a safe choice (pigeon) at the alternate feeder exists. Nonetheless, when the alternate feeder offers only a dangerous complete sparrowhawk, they risked visiting the “partly-featured” amputated torso; while the fear of a “full-featured” occluded one remained unchanged. This kind of discrimination requires the ability for amodal completion. The birds seem to be sentient that the occluded sparrowhawk continues behind the branches, while an amputated sparrowhawk is clearly recognized as being incomplete.

The interesting result of our study was that the birds arrived near the occluded sparrowhawk dummy more often than to the complete sparrowhawk dummy. There may be some birds that do not recognize an occluded torso as a predator. This could be due to either limited experience (e.g. of young birds) or a lack of attentiveness. Sometimes when a bird landed at the feeder and was pecking at the food, it suddenly looked as if horrified and emitted an alarm call, as though it had seen the predator too late. A possible alternative explanation could be that a bird is more likely to approach a

**Fig. 3** Relative change in the number of visits (compared to control trial) to a feeder with the occluded (1/2 ocl) and amputated (1/2 amp) sparrowhawk when a pigeon or sparrowhawk are present on the alternate feeder



predator which has some occluding obstacle in front of it, in preference to a predator which has no obstacle blocking it, which could attack straight toward the potential prey.

Study of the occlusion phenomena has been extended from infants onto nonhuman species, and has become a popular topic in the last few decades. All of these groups of animals were trained to discriminate between various occluded and amputated objects (see reviews Vallortigara 2006 and Vallortigara 2006). Only occasionally, courtship behaviour to amputated or occluded con-specific female was studied (e.g. Okanoya and Takahashi 2000). The results of our study demonstrate, for the first time, that amodal completion is used as a part of object recognition in the natural discrimination and categorization processes of birds.

In particular, several comparative studies, using operant techniques, on amodal completion with birds have yielded inconsistent results. These operant technique studies have shown that domestic fowl can perceive amodal completion (Regolin and Vallortigara 1995; Lea et al. 1996; Forkman 1998; Forkman and Vallortigara 1999; Vallortigara and Tommasi 2001; Regolin et al. 2004). Conversely, other studies have not yielded any clear evidence that the pigeons can perceive amodal completion to distinguish between occluded and amputated objects (Cerella 1980; Fujita 2001; Sekuler et al. 1996; Ushitani and Fujita 2005; Aust and Huber 2006). In spite of this, previous results have been dismissed by the mounting evidence that pigeons can perceive partly occluded objects as complete, under the appropriate testing conditions (Nagasaka et al. 2005; Nagasaka et al. 2007), especially if the stimuli looks more natural (DiPietro et al. 2002; Nagasaka and Wasserman 2008). Generally, pigeons appear to be able respond to amodal completion or to subjective contours (closely linked to amodal completion) but only if they are strongly encouraged to do it so (Vallortigara 2006).

The results of our study show that field experiments, in which the predicted reactions (e.g. escape) of birds to real objects (e.g. predators) can be used as a suitable alternative for conditioning techniques. At the same time, our results show that discrimination and categorization in nature are not a simple process, and that amodal completion is only a part of that process. Birds recognize predators according to sign stimuli. Therefore, both occluded and amputated torsos of a predator are judged as dangerous; and incompleteness (with concomitant lesser danger sensed) of an amputated torso only appears in the situation where it is compared with a complete predator by the bird. Such complexity in the recognition processes should be taken into account even in conditioning experiments.

**Acknowledgments** The study was supported by grants of the Academy of Sciences of the Czech Republic (IAA601410803), and the Ministry of Education, Youth, and Sports (MSM6007665801).

## References

- Aust U, Huber L (2006) Does the use of natural stimuli facilitate amodal completion in pigeons? *Perception* 35:333–349. doi:10.1068/p5233
- Bakin JS, Nakayama K, Gilbert CD (2000) Visual responses in monkey areas V1 and V2 to three-dimensional surface configurations. *J Neurosci* 1(20–21):8188–8198
- Carbaugh BT, Schein MW, Hale EB (1962) Effects of morphological variations of chicken models on sexual responses of cocks. *Anim Behav* 10(3–4):235–238. doi:10.1016/0003-3472(62)90046-5
- Caro TM (2005) Antipredator defences in birds and mammals. The University of Chicago Press, London, p 591
- Cerella J (1980) The pigeon's analysis of pictures. *Pattern Recogn* 12:1–6. doi:10.1016/0031-3203(80)90048-5
- Chantrey DF, Workman L (1984) Song and plumage affects on aggressive display by the European Robin *Erithacus rubecula*. *Ibis* 126:366–371
- Deruelle C, Barbet I, Dépy D, Fagot J (2000) Perception of partly occluded figures by baboons (*Papio papio*). *Perception* 39:1483–1497
- Desrochers A, Belisle M, Bourque J (2002) Do mobbing calls affect the perception of predation risk by forest birds? *Anim Behav* 64:709–714. doi:10.1006/anbe.2002.4013
- DiPietro NT, Wasserman EA, Young ME (2002) Effects of occlusion on pigeon's visual object recognition. *Perception* 31:1299–1312
- Fagot J, Barbet I, Parron C, Deruelle C (2006) Amodal completion by baboons (*Papio papio*): contribution of background depth cues. *Primates* 47(2):145–150. doi:10.1007/s10329-005-0165-5
- Forkman B (1998) Hens use occlusion to judge depth in two-dimensional picture. *Perception* 27:861–867. doi:10.1068/p270861
- Forkman B, Vallortigara G (1999) Minimization of modal contours: an essential cross-species strategy in disambiguating relative depth. *Anim Cogn* 2:181–185. doi:10.1007/s100710050038
- Fujita K (2001) Perceptual completion in rhesus monkeys (*Macaca mulatta*) and pigeons (*Columba livia*). *Percept Psychophys* 63:115–125
- Gentle LK, Gosler AG (2001) Fat reserves and perceived predation risk in the great tit, *Parus major*. *P Roy Soc Edinb B* 268(1466):487–491. doi:10.1098/rspb.2000.1405
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical J* 50(3):346–363
- Kanizsa G, Renzi P, Conte S, Compostela C, Guerani L (1993) Amodal completion in mouse vision? *Perception* 22:713–721
- Lazareva FO, Wasserman AE, Biederman I (2007) Pigeons' recognition of partially occluded objects depends on specific training experience. *Perception* 36:33–48. doi:10.1068/p5583
- Lea SEG, Slater AM, Ryan CME (1996) Comparison of object unity in chicks: a comparison with the human infant. *Infant Behav Dev* 19:501–504. doi:10.1016/S0163-6383(96)90010-7
- MacLeod R, Gosler AG, Cresswell W (2005) Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. *J Anim Ecol* 74(5):956–964. doi:10.1111/j.1365-2656.2005.00993.x
- Nagasaka Y, Osada Y (2000) Subjective contours, amodal completion and transparency in animals. *JPN J Anim Psychol* 50:61–73
- Nagasaka Y, Wasserman EA (2008) Amodal completion of moving objects by pigeons. *Perception* 37(4):557–570
- Nagasaka Y, Hori K, Osada Y (2005) Perceptual grouping in pigeons. *Perception* 34:625–632. doi:10.1068/p5402
- Nagasaka Y, Lazareva OF, Wasserman EA (2007) Prior experience affects amodal completion in pigeons. *Percept Psychophys* 69(4):596–605
- Okanoya K, Takahashi M (2000) “Shikaku-teki hokan e no seitaigaku-teki apuroochi” [Ecological approach to visual completion]

- Kokoro no Hattatsu: Ninchi-teki Seicho no Kikoo 1999 (Reports of the Grant-in-aid for Scientific Research for Priority Areas)
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Regolin L, Vallortigara G (1995) Perception of partly occluded objects by young chicks. *Percept Psychophys* 57(7):971–976
- Regolin L, Marconato F, Vallortigara G (2004) Hemispheric differences in the recognition of partly occluded objects by newly hatched domestic chicks (*Gallus gallus*). *Anim Cogn* 7:162–170. doi:10.1007/s10071-004-0208-0
- Sato A, Kanazawa S, Fujita K (1997) Perception of object unity in chimpanzee (*Pan troglodytes*). *JPN Psychol Res* 39:191–199
- Schein MV, Hale EB (1957) The head as a stimulus of orientation and arousal of sexual behaviour in male turkeys. *Anat Rec* 128:617–618
- Sekuler AB, Lee JAJ, Shettleworth SJ (1996) Pigeons do not complete partly occluded figures. *Perception* 25:1109–1120. doi:10.1068/p251109
- Shoettle HET, Schein MW (1959) Sexual reaction of male turkeys to deviations from a normal female head model. *Anat Rec* 134:635
- StatSoft Inc (2007) STATISTICA, version 8.0. [www.statsoft.com](http://www.statsoft.com)
- Sugita Y (1999) Grouping of image fragments in primary visual cortex. *Nature* 401:269–272
- Tinbergen N (1951) *The study of instinct*. Oxford University Press, London
- Ushitani T, Fujita K (2005) Pigeons do not perceptually complete partially occluded photos of food: an ecological approach to the “pigeon problem”. *Behav Process* 69:67–78. doi:10.1016/j.beproc.2005.01.002
- Vallortigara G (2004) Visual cognition and representation in birds and primates. In: Lesley JR, Kaplan G (eds) *Comparative vertebrate cognition*. Chap 2, Kluwer/Plenum publishers, New York
- Vallortigara G (2006) The cognitive chicken: visual and spatial cognition in a nonmammalian brain. In: Wasserman EA, Zentall TR (eds) *Comparative cognition: experimental explorations of animal intelligence*. Oxford University Press, Oxford, pp 41–58
- Vallortigara G, Tommasi L (2001) Minimization of modal contours: an instance of an evolutionary internalized geometric regularity? *Brain Behav Sci* 24:706–707. doi:10.1017/S0140525X01670080
- Watanabe S (1999) Effects of hippocampal lesion on spatial discrimination in pigeons. *Behav Brain Res* 103(1):77–84. doi:10.1016/S0166-4328(00)00358-2
- Watanabe S, Furuya I (1997) Video display for study of avian cognition: from psychophysics to sign language. *Int J Comp Psychol* 10:111–127