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ORIGINAL PAPER

Recognition of partly occluded objects by fish

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Abstract The ability to visually complete partly occluded objects (so-called “amodal completion”) has been documented in mammals and birds. Here, we report the first evidence of such a perceptual ability in a fish species. Fish (*Xenotoca eiseni*) were trained to discriminate between a complete and an amputated disk. Thereafter, the fish performed test trials in which hexagonal polygons were either exactly juxtaposed or only placed close to the missing sectors of the disk in order to produce or not produce the impression (to a human observer) of an occlusion of the missing sectors of the disk by the polygon. In another experiment, fish were first trained to discriminate between hexagonal polygons that were either exactly juxtaposed or only placed close to the missing sectors of a disk, and then tested for choice between a complete and an amputated disk. In both experiments, fish behaved as if they were experiencing visual completion of the partly occluded stimuli. These findings suggest that the ability to visually complete partly occluded objects may be widespread among vertebrates, possibly inherited in mammals, birds and fish from early vertebrate ancestors.

Keywords Visual completion · Amodal completion · Occlusion · Visual recognition · Fish

Introduction

The human brain represents visual objects as continuous bounded units in space and time (Spelke 2000); such a continuity principle allows us to perceive partially occluded objects as whole objects. In fact, although in the environment, most objects are opaque and may overlap and partly hide each other, in our visual experience when an object is partially concealed by an obstacle, and cannot be seen in its entirety, we do not perceive the pieces or fragments of that object: the parts that are directly visible usually suffice for recognition of the whole object. Such a process has been dubbed “amodal completion” (Kanizsa 1979; Michotte et al. 1964). Psychophysical and neurophysiological evidence suggest that grouping mechanisms underlie the achievement of amodal completion (Grossberg and Mingolla 1985; Kellman et al. 2001, 2005; Sekuler and Palmer 1992; Sugita 1999; Palmer 1999). It seems worthwhile investigating to what extent humans share similar mechanisms with other organisms (see Spelke 2003; Vallortigara 2004, 2006).

Several comparative studies have shown that mammals can perceive amodal completion (mice: Kanizsa et al. 1993; squirrel monkeys: Nagasaka and Osada 2000; Japanese macaques: Sugita 1999; rhesus macaques: Bakin et al. 2000; Osada and Schiller 1994; Fujita 2001; baboons: Deruelle et al. 2000; chimpanzees: Sato et al. 1997). In birds, several studies using operant techniques have yielded no clear evidence that pigeons can perceive amodal completion (Aust and Huber 2006; Cerella 1980; Fujita 2001; Sekuler et al. 1996; Ushitani and Fujita 2005), whereas in other species of birds evidence for amodal completion has been obtained using both naturalistic techniques such as filial imprinting (domestic chicks: Regolin and Vallortigara 1995; Lea et al. 1996; Vallortigara and Regolin 2002;

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Regolin et al. 2004) and courtship behaviour (Bengalese finches: Okanoya and Takahashi 2000) as well as more traditional conditioning techniques (adult hens: Forkman 1998; Forkman and Vallortigara 1999; Vallortigara and Tommasi 2001). The possibility of differences among bird species has recently been dismissed by mounting evidence that pigeons can perceive partly occluded objects as complete under appropriate testing conditions (Cavoto and Cook 2007; DiPietro et al. 2002; Nagasaka et al. 2005; Lazareva et al. 2005; Nagasaka et al. 2007).

Thus, overall, the available evidence suggests that recognition of partly occluded objects may be quite common among mammals and birds. This could reflect convergent evolution in the two taxonomic groups. Alternatively, it could be that mechanisms of amodal completion are present in these two classes due to inheritance from a common ancestor and that this feature is widespread in the other vertebrate classes. The aim of this paper was to investigate whether an ability to complete partly occluded objects can be observed in a fish species.

Experiment 1

We used *Xenotoca eiseni* fish (Family Goodeidae), a livebearer fish, native of Mesa Central plateau of Mexico. These fish are omnivorous; males are only slightly smaller than females, but there is strong dimorphism in the coloration, with males more colorful than females (in males, but not females, the front part of the caudal peduncle is blue, and the area adjacent to the caudal fin is bright red). We chose to study this particular species because it lives in shallow, quiet, transparent water with pebbles and rich vegetation (though the fish rapidly adapt even to different environments), thus relying on visual features of the physical environment for orientation and of visual features of the social environment for mate selection and other social behaviours (see Meyer et al. 1985). This species has been widely used recently in cognitive tests, particularly those dealing with use of visual landmarks and geometric information for spatial reorientation (Sovrano et al. 2002, 2003, 2005, 2007).

Methods

Subjects

Subjects were nine male mature fish (ranging 3–5 cm in length) of the species *Xenotoca eiseni* from a stock maintained in our laboratory within vegetation rich (*Ceratophillum* sp.) large tanks (55–120 l) provided with artificial illumination, 16 h per day.

Apparatus

The apparatus (Fig. 1), which was placed in a darkened room, consisted of a square tank (15 cm long, 15 cm wide and 15 cm high), with uniform white walls covered with a one-way screen in order to eliminate extra-tank cues and lit centrally with a 75 W light bulb. The testing tank was inserted in a larger tank (60 × 36 × 25 cm) so as to create an annular region with vegetation and food where the test fish was located together with other five conspecifics (females not tested) that provided motivation for social reinstatement.

In two corners of the apparatus was inserted a small tunnel (2.5 cm in length, 2 cm in size, 3 cm in height, located

Fig. 1 The apparatus used in the experiment. On the *left*, overall view of the apparatus with the inner and outer tanks. On the right, details of the inner tank (*top*) with positions of the two doors with the stimuli (*bottom*)

4.5 cm from the floor of the tank), of white plastic material, allowing the fish to pass through it to rejoin conspecifics in the annular region in the outer tank (see Fig. 1). At the end of each tunnel was a door (2.5 × 3.5 cm) made of a sheet of an opaque plastic material on top and of a transparent very flexible plastic material on the bottom. The two doors were visually identical, but only one door could be opened, the other being blocked with an outside plastic transparent panel. Fish thus could open the correct door to rejoin conspecifics by pressing on it with the snout; choices for each door were clearly visible from videorecording, because of characteristic movements of the tail and the most caudal part of the body of the fish that remained visible outside the tunnel.

Below each door, the stimuli used for visual discrimination learning and test were attached on (disks: 7 mm distance, exagonal polygons: 3 mm distance; see Fig. 2). The stimuli were made of a special plastic cardboard designed to resist the aquatic environment. The orange disk was 2.4 cm in diameter and the hexagonal polygon was 1.8 cm in height and 2 cm in width.

Fish had to discriminate between a complete and an amputated orange disk. After fulfilling the learning criterion, fish were presented with two stimuli in which a dark green hexagon was either exactly juxtaposed (Fig. 2d) or only placed close (Fig. 2c) to the missing sectors of the orange disks in order to produce or not produce the impression (to a human observer) of an occlusion of the missing sectors by the hexagons.

Procedure

Before testing, fish underwent a shaping procedure in their home-tank (30 × 40 × 20 cm) for 10 days, using a partition that divided their home-tank in two halves, one ('enriched') with food and vegetation and the other ('unenriched') without any food and vegetation. Four tunnels with moveable doors identical to those subsequently used at test were positioned on the partition, two of which allowing the fish to move between the two compartments. In this way, fish were accustomed to the use of the moveable doors before testing.

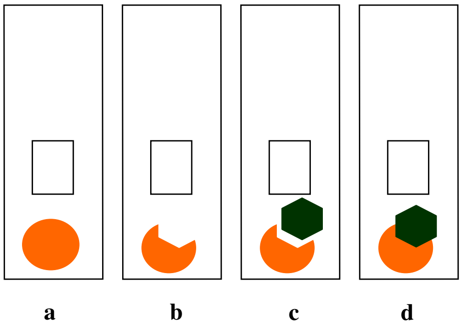

Fig. 2 Schematic representations of the stimuli to be discriminated, located below the two doors

The experiment comprised two parts: training and test.

During training, fish had to discriminate between a complete and an amputated orange disk. Five animals were trained with the complete disk as positive (reinforced), four with the amputated disk. Fish were given daily sessions of 10–12 trials (a 10–12 range was used because of differences in motivation among animals) until they reached the learning criterion (70% of correct choices in a single session—the time range needed for training to criterion was 6–13 days). In each trial the fish was brought to the inner tank by gently inserting it into a transparent plastic cylinder placed in the center. After 20 s, the cylinder was removed. In each trial, the number of choices for the two doors was video-recorded, until the fish were able to exit and rejoin conspecifics (the maximum time allowed was 15 min). A choice was considered correct when the fish were able to enter the tunnel at the correct door and exit from the inner tank to rejoin conspecifics in the annular region in the outer tank at first attempt. (Note that multiple choices for the correct door could occur, either because fish explored the door without actually exit or because no enough strength was exerted.) Inter-trial interval was 7 min, during which the fish were allowed to remain in the annular region (reinforcement time). Some food was given in the outer tank only after a correct choice. Every three trials, the tank was rotated 90° and the fish were tested again.

After reaching the learning criterion, fish performed test trials where they faced two stimuli in which a dark green hexagon (located randomly) was either exactly juxtaposed (Fig. 2d) or only placed close (Fig. 2c) to the missing sectors of the orange disks in order to produce or not produce the impression (to a human observer) of an occlusion of the missing sectors by the hexagons. The test consisted in a single session of ten trials (each trial lasting 2 min) with an extinction procedure (i.e., both doors were closed). If animals did not make a choice within 2 min they were allowed to stay longer, until they produced at least one choice, up to a maximum of 15 min. Trials with the same stimuli used during training were intermixed with the test trials (varying between animals within a range of 2–4 trials) in order to reinstate the motivation of the animals (these trials were of course not considered in the data analyses). The number of choices given to each of the two stimuli (fish were scored a choice when they entered with their bodies in one or other of the two tunnels, see section "Apparatus") during the 2-min test were recorded and entered an analysis of variance with type of choice during test as a within-subject factor and type of positive stimulus used during training as between-subject factor.

Results

There were no differences in the number of trials to the criterion between fish trained with the complete disk as positive (mean ± SEM: 118.6 ± 15.29) and those trained with the amputated disc as positive (135.5 ± 35.9) during training ($t_7 = 0.470$ $P = 0.29$ NS).

The results of test are shown in Fig. 3. The analysis of variance with type of positive stimulus used during training (complete disk vs. amputated disk) and choice during test (choice for amodally completed disk vs. choice for not completed disk) revealed a significant interaction between the two factors ($F_{1,7} = 43.175$, $P = 0.0001$; the main effects were not significant, respectively $F_{1,7} = 0.746$; $F_{1,7} = 0.098$).

Fish trained with the amputated disk as positive chose at test, the stimulus in which the non-occluding polygon was placed close to the missing sectors of the orange disks ($t_3 = 6.000$, $P = 0.009$), whereas those trained with the complete disk as positive chose at test the stimulus in which the polygon was exactly juxtaposed to the missing sectors of the orange disks, thus producing the impression of amodal completion ($t_4 = 4.390$, $P = 0.012$).

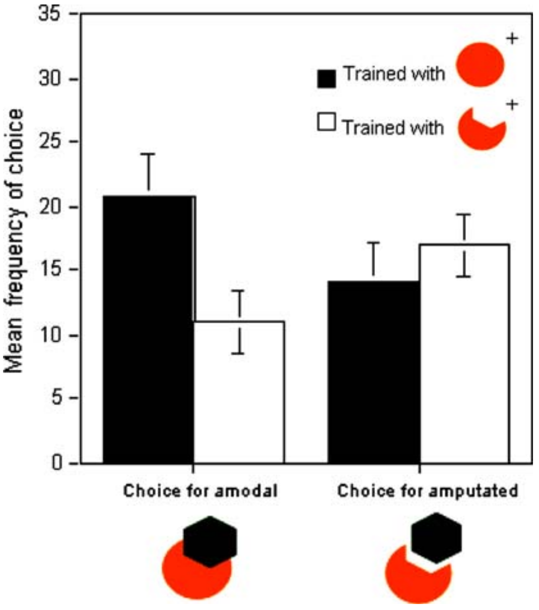

Fig. 3 Choice for the amodally completed disk and the amputated disk with the non-occluding stimulus located close in fish trained with the complete disk or with the amputated disk as positive (group means with SEM are shown)

Experiment 2

In Experiment 2, a reversed and complementary procedure was used. Rather than training fish to discriminate between a complete and an amputated stimulus and then check for their choices with partly occluded or not occluded stimuli, this time we trained fish to discriminate between a disk partly occluded by an hexagonal polygon and an amputated disk with the hexagonal polygon as a non-occluding stimulus placed close to the missing sectors of the disk; thereafter, the hexagonal polygon was removed and the fish were tested for choice with a complete and an amputated disk.

Subjects

Subjects were eight naive male mature fish (ranging 3–5 cm in length) of the species *Xenotoca eiseni*.

Apparatus and procedure

The apparatus was the same as in Experiment 1. The general procedure was also the same as in Experiment 1, with only a slight improvement in the procedure of shaping, in that we used this time only the positive stimuli (two doors) in the shaping tank, because pilot experiments had revealed that this could reduce the times needed to reach learning criterion during training. The test session consisted of 12 trials in extinction conditions (both doors were blocked) that could be spaced and intermixed with training trials (excluded from the subsequent analyses) in order to maintain the motivation of the animals.

Results

There were no differences in the number of trials to criterion between fish trained with the amodally completed disk as positive (mean ± SEM: 98.75 ± 23.69) and those trained with the amputated disc near to the hexagon as positive (55.5 ± 8.77) during training ($t_6 = 1.71$, $P = 0.14$ NS).

The results of test are shown in Fig. 4. The analysis of variance with type of positive stimulus used during training (amodally completed disk vs. amputated disk near to the hexagon) and choice during test (choice for complete disk vs. choice for not completed disk) revealed a significant interaction between the two factors ($F_{1,6} = 70.83$, $P = 0.0001$; the main effects were not significant, respectively $F_{1,6} = 5.39$, $P = 0.11$, $F_{1,6} = 0.22$).

As can be seen, fish trained with the amputated disk only near to the non-occluding hexagonal polygon as positive, thus giving the impression of two separate figures, chose at test, as expected, the amputated disk ($t_3 = -5.33$, $P = 0.01$), whereas those trained with the stimulus in which the hexagonal polygon was exactly juxtaposed to the missing sectors of the orange disks as positive, thus producing the impression of amodal completion, chose at test the complete disk ($t_3 = 6.67$, $P = 0.007$).

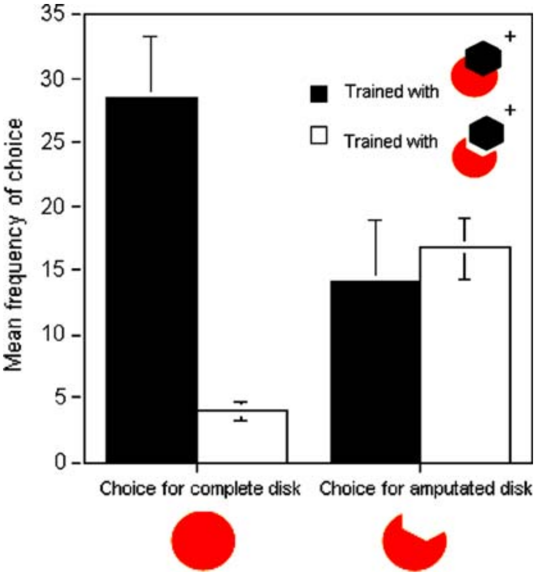

Fig. 4 Choice for the complete disk and the amputated disk in fish trained with the amodally completed disk or with the amputated disk with the non-occluding stimulus as positive (group means with SEM are shown)

Discussion

In Experiment 1, fish trained with the complete disk as positive chose at test the stimulus in which the positioning of the occluder generates (to human beings) the impression of a partially occluded complete disk. The choice cannot be due to a generic preference for the stimulus in which the occluder was exactly juxtaposed to the missing sectors of the disks, because in the reverse condition, when fish were trained with the amputated disk as positive, they chose the stimulus in which the non-occluding stimulus was only placed close to the missing sectors of the disks.

In Experiment 2, fish trained with the partly occluded disk chose at test the complete disk. The choice cannot be due to a preference for the complete stimulus because when trained with the stimulus in which the hexagon was only placed close to the missing sectors of the disk, without occluding anything, fish preferred the amputated disk. Fish, thus, behaved as if they could experience amodal completion.

Overall, the pattern of results shown here by fish parallels quite precisely the data obtained with mammals in similar experimental paradigms (e.g., Kanizsa et al. 1993).

This is the first evidence that amodal completion can be observed in a so-called "lower" vertebrate species. The fact that completion of partly occluded objects is so widespread among vertebrates—including mammals, birds and fish—may suggest basic homology (i.e., inheritance from a common ancestor) rather than independent convergent evolution in the three taxonomic groups. Neurophysiological evidence suggest that, in spite of certain differences in the general organization of the avian and mammalian brain (Jarvis et al. 2005), neural mechanisms for perceptual grouping can be very similar in the two classes (e.g., Vallortigara and Zanforlin 1989; Vallortigara and Regolin 2006; Vallortigara et al. 2005, 1990; Clara et al. 2006), giving rise for example to visual illusions such as subjective contours (review in Nieder 2002) that, like amodal completion, rely heavily on computations associated with occlusion phenomena (Kellman and Shipley 1991). Little is known in this regard to fish (see, however, Orger et al. 2000; Bshary et al. 2002 Braithwaite 2006, for a general review on cognition in fish), but the availability of behavioral evidence for amodal completion in these organisms may open the door to comparative neural investigations.

Acknowledgments All the experiments reported comply with the guidelines for the ethical treatment of animals in behavioral research and teaching (Animal Behaviour 2003) and with current European Community and Italian laws.
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