How do nonhuman animals perceptually integrate figural fragments?\(^1\)

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Abstract: Visual information available from the environment is often fragmented in time and space. Integrating such fragmentary information is essential for animals to recognize meaningful objects surrounding them. It has been well-documented that humans perceptually organize visual inputs. In nonhumans, on the other hand, little has been known about their process of perceptual organization. This paper focuses amodal completion in nonhuman species as one of such processes. So far, several nonhuman species including primates, rodents, and birds have been tested for amodal completion of a variety of stimuli. Positive results have been obtained in most of the species tested. In particular, nonhuman primates have been suggested to share many characteristics of this process with humans; a notable exception is pigeons. They have been shown to fail to complete with a variety of stimuli in a variety of procedures. However, this may be understood as a nature of this species adapted to their ecology. Surprising differences in perception in species that share many cognitive characteristics such as memory, concept formation, figure recognition, and so on, advises us to pay more attention to the correlation of perceptual systems and the way the species live in.

Key words: perceptual organization, amodal completion, nonhuman primates, birds.

Visual information we receive through our eyes is in most cases fragmented. For instance, when we observe a house through shrubbery, all we can see is a collection of small irregular shapes. We experience, however, little difficulty to recognize a house behind the shrubbery. Our visual system quickly integrates such fragmentary information to form a meaningful whole.

In order for our visual system to do this job, an occluding relationship is sometimes critical. We perceive a whole of the occluded house by completing information occluded by the shrubbery only when we recognize it closer than the house. Figure 1a shows an example of this. When we recognize the bright parts closer, we would not integrate the four. But once we recognize them further, we quickly find a full moon behind the grid.

In other times such integration occurs without depth perception. For example, we perceive the stimuli in Figure 1b as a large H rather than the collection of O. Humans have a strong tendency to attend to the global form rather than the local stimuli. This is called the global precedence effect (Navon, 1977).

In the examples above all the visual fragments come at a time. In fact, we sometimes integrate information conveyed through time.

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A good example is perception of biological motion (Johansson, 1973). When we observe a human with spotlights on the major joints walking in the total darkness, we instantly recognize the collection of point lights as a human. We can tell even the age and the sex of the walker. However, we cannot recognize the stimuli as a human before the model starts to move or when the point lights are displaced. Thus, in this case, systematically changing the series of information is required for the stimulus fragments to be integrated.

How do other animals do? This question is critical to know the evolutionary history of perceptual organization of external inputs. This paper intends to discuss this point by showing what is known about this process in nonhuman animals. I will mainly focus on amodal completion and some related issues.

What is amodal completion

Completing lacking portions of stimuli in recognizing the stimuli is often referred to as perceptual completion. Kanizsa (1979) identified two types of this process. One is called “modal” completion and the other is called “amodal” completion.

For both types, something not actually there is perceived. For the former, the illusory percept is difficult to distinguish from that of what actually exists. For example, in the famous Kanizsa’s triangle figure (Figure 2), in which a subjective contour is perceived, it is difficult to have eyes keen enough to tell the absence of the contour at the first observation. Such perception is often compulsory. For the latter, on the other hand, perceivers know that there is no such reality. Thus, the percept is easily distinguished from the reality. Figure 1a is a good example. We can recognize a white disk but at the same time we know that this disk is not actually there. Although this process is demonstrated to be compulsory at the very early stage of visual information processing (Rauschenberger & Yantis, 2001) we can freely change this impression at later stages.

Suggestion for the perception of subjective contour is available for a variety of groups of animals including nonhuman primates (chimpanzees: Fagot & Tomonaga, 2001; squirrel monkeys: Nagasaka & Osada, 1996; rhesus monkeys: Osada & Schiller, 1996); carnivores (cats: Bravo, Blake, & Morrison, 1988; De Weerd, Vandenbussche, Bruyn, & Orban, 1990); birds (barn owls: Nieder & Wagner, 1999; chickens: Zanforlin, 1981); and even honeybees (Van Hateren, Srinivasan, & Wait, 1990) (see Nieder, 2002 for a review). Although not all of these studies are conclusive, at least one form of modal completion process may be widespread in the animal kingdom. In fact Von der Heydt, Peterhans, and Baumgartner (1984) detected the neurons in the V2 of rhesus monkeys responding to the illusory contours.
as well as the real contours. Thus, the modal completion may be realized at early stages of visual information processing.

Compared with modal completion, amodal completion could include a wider variety of perception from a simple computational outcome to completing lacking information using knowledge. The simplest case includes the example shown in Figure 3a, in which we perceive a disk behind a triangle. In this case, completion is done as a result of calculating the most likely contour of the occluded figure. This process seems mostly bottom-up. In Figure 3b, on the other hand, we perceive that the head of a German shepherd is hidden behind a rectangular plate because we know how German shepherds are like. This process requires top-down flow of lacking information.

It is noteworthy that amodal completion is simply one solution of the visual recognition system. We can accept the pattern in Figure 3a as being a pacman biting a triangle and the pattern in Figure 3b as being a lion-headed dog. Thus, amodal completion is a choice of many perceptual options, probably most appropriate to the necessary agendas for the species and the current context.

As a result, this type of completion should be one of the ideal materials to infer how perceptual systems have evolved to adapt to the environment.

One form of amodal completion is evident in very young human infants. When 4-month-old infants are habituated to two rods arranged to make a line moving in concert behind the belt occluding the gap between the two rods, the infants are dishabituated to the two rods rather than the one long rod without the occluder (see Figure 4). Thus, the infants are supposed to recognize the first rods as unitary (Kellman & Spelke, 1983). The same perception of object unity occurs without the common motion between the two rods when the infants get to be 6 months old.

In nonhumans, amodal completion has been tested in a variety of species including...
Amodal completion in mammals

Sato, Kanazawa, and Fujita (1997) trained a female chimpanzee on the identity matching-to-sample task with a unitary rod and a pair of separate rods in full view on the computer display. In the probe tests after the training, the chimpanzee matched the two rod-like figures moving in concert “behind” the occluding belt to one unitary rod. On the other hand, she matched the two rods moving out of concert to a pair of separate rods. The same chimpanzee maintained this performance for the rotating rods and the static rods aligned to make a line (see Figure 5). Similar perception of object unity has been reported in Japanese monkeys (Sugita, 1999) and tufted capuchin monkeys (Fujita, 2000).

In situations other than the object unity, three reports have shown positive results suggesting amodal completion. Fujita (2001b) tested rhesus monkeys whether they perceived continuation of a bar touching a rectangle behind it. When a small figure touches another we humans overestimate the length or the size of the former (Kanizsa, 1979) (Figure 6).
Kanizsa suggested that this illusion occurs because we perceive something occluded behind the latter figure and hence complete the occluded portion automatically. Rhesus monkeys were trained to classify bars of a variety of lengths placed next to a rectangle at a fixed distance into “long” and “short.” Then the monkeys were tested with the bars placed at varied distances from the rectangle. The monkeys’ classification was biased toward “long” only when the bar touched the rectangle (Figure 7). Thus, the same illusion suggesting amodal completion as humans was demonstrated in rhesus monkeys.

Deruelle, Barbet, Dépy, and Fagot (2000) also demonstrated that Guinea baboons completed partly occluded figures drawn on the cardboard. The baboons were trained in a simultaneous discrimination task to choose a complete disk over a pacman (or vice versa for the second group). In probe tests in which an occluded disk and a pacman having the occluder next to it with a small gap were presented, the baboons chose the occluded disk (or a pacman for the second group).

Nagasaka and Osada (2000) reported their unpublished studies on completion in rhesus and squirrel monkeys. They trained the monkeys to match four geometric figures behind cross hatches from intact figures (Figure 8). The monkeys’ matching accuracy changed as the width of the crosshatch changed, and this pattern was similar to humans who performed the same task. Such decrease could result from choosing the figures based on their local characteristics. However, in Nagasaka and Osada’s study in squirrel monkeys, the authors tested them with the stimuli having the portion occluded by the crosshatches simply deleted. In this condition the squirrel monkeys’ matching accuracy dropped drastically. Thus, the squirrel monkeys seemed to have completed the portions occluded by the crosshatches.

As these findings suggest, a variety of species of nonhuman primates have been repeatedly shown to complete occluded figures in a variety of procedures.

In a different taxum, Kanizsa, Renzi, Conte, Compostela, and Guerani (1993) reported that mice might complete two-dimensional figures. They trained mice to jump at complete geometric figures and avoid incomplete figures having their contour cut off (or vice versa) in the two-choice jumping stand. The mice trained to choose the complete figures jumped at partly occluded test figures and the animals trained to choose the incomplete figures avoided the same
test figures. These behaviors were consistent with completion. But the authors also noted that behavior based on some local characteristics of stimuli might be possible. Thus, the data on non-primate mammals are still inconclusive.

**Details of primate completion**

In human infants, at least three stages are distinguished in the developmental course of perception of object unity. At the first stage, as Kellman (1996) notes, common motion specifies unity. That is, even if the top portion and the bottom portion do not match, such as a rod and an irregular shape, 4-month-old infants recognize that the two portions are connected behind the occluder as long as there is common motion. This perception is simple recognition of connectedness. At the second stage, relatability of the edges of the two portions specifies unity. Thus, 6-month-old infants perceive the two stationary objects arranged so that they have nicely relatable contours as united.

However, at this second stage, infants’ completion of the occluded contour is not in a specified form. In fact, 6-month-old infants are not surprised if they see an irregular contour behind the occluder as long as they are connected, whereas 8-month-old infants are (Cronin, 1996). Thus, the smooth interpolation of contours requires two more months after the infants start to follow the relatability rules.

I systematically tested how tufted capuchin monkeys interpolate the occluded contours (Fujita & Giersch, submitted).

The first test was designed to test whether the monkeys’ perception of object unity was a simple recognition of connectedness of two portions. Two tufted capuchin monkeys were first trained to perform on the identity matching-to-sample with the four figures shown in Figure 9a at the accuracy higher than 85% correct. Note that the figures are different only at the middle portion. The top and the bottom portions are disconnected for the first figure but are connected for the latter three. Later they were tested in all-reinforced probe trials with the sample figures whose middle portion was occluded by a horizontal belt. When either the upper or lower middle portion was

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**Figure 9.** (a) The four stimulus patterns used to test how capuchin monkeys complete occluded contours in Fujita and Giersch (submitted). (b) Examples of three types of test stimuli having a belt occluding the part of the stimuli. The figures are identifiable for the top two but unidentifiable for the one at the bottom.
occluded, the sample figures were discriminable to each other, but when the central portion was occluded, they were not (Figure 9b). Comparison stimuli were always the intact figures.

The question was to which comparison the monkeys would match when the central portion was occluded. If the monkeys simply recognize connectedness of the two portions above and below the occluder, the monkeys’ choice among the three connected figures should be random, though they avoid the disconnected rods. The first test was done for the sample figures moving left and right. The second test was done for stationary sample figures. For both moving and stationary figures, both monkeys overwhelmingly chose the straight rod rather than the other two connected rods. This clearly suggested that the monkeys completed the boundary of the occluded portion into straight line. Thus, the perception of object unity by tufted capuchin monkeys reaches the last stage, smooth interpolation, in human development (Figure 10).

The second question was whether the monkeys would share the rules humans follow in connecting two edges. Kellman and Shipley (1991) suggested that for humans two edges are relatable by a monotonically curved line if their extensions make an obtuse angle. In this experiment two sets of figures were prepared. One was the figures shown in Figure 11a and the other was in Figure 11b. The top and the bottom portions of the figures of the former set were relatable and those of the latter were non-relatable according to Kellman and Shipley’s suggestion. When the central portion of the sample stimuli was occluded in test trials (Figure 11c), the same monkeys overwhelmingly chose the connected figure for the relatable sample figures while they chose the disconnected figure for the non-relatable sample figures. This was the case for both moving and stationary stimuli. Therefore, this relatability rule seems shared between humans and capuchin monkeys.

The third question was whether the monkeys follow the regularity rule. The zigzag figures shown in Figure 12a were used. When the central portion of the moving sample figures was occluded in the test trials (Figure 12b), the two monkeys matched them to the regular zigzag figures. Thus, as long as there was common motion

[Figure 10. The results of the completion test in capuchin monkeys (Fujita & Giersch, submitted). (a) The results of individual monkeys for the moving stimuli. The horizontal axis is the comparison stimuli and the vertical axis is the proportion of the selection of each comparison stimulus. (b) The results for the stationary stimuli.]
among the top and bottom portions of stimuli, capuchin monkeys completed the occluded part following the overall regularity rule. Without motion, however, one monkey still followed the regularity rule but the other monkey chose disconnected figure. Thus, in capuchin monkeys there is interaction between the regularity rule and common motion; some monkeys may follow regularity rule only if there is common motion between the visible fragments.

The fourth question was how the monkeys would complete if the local and global rules for completion contradicted. The four figures having many pins on the contour were used (Figure 13a,b). Unfortunately one monkey did not match these figures accurately. The other monkey performed at more than 85% correct. In later tests, this successful monkey matched the sample figures with central portion occluded to the figure with regularly distributed pins (Figure 14). Thus, the overall regularity overwhelmed the local connection rule that specifies the third figure in the Figure 13a.

This is in contrast with the local precedence effect demonstrated by Fagot and colleagues for baboons and chimpanzees in recognizing...
patterns consisting of small elements (Deruelle & Fagot, 1998; Fagot & Tomonaga, 1999). The difference may be attributable to either species difference or to the difference in the task; that is, in the present task, the monkeys discriminated (implicitly) connected figures. Whatever the cause may be, it is evident that nonhuman primates sometimes show something analogous to a global precedence effect.

Finally, adult humans were also tested as to how they complete all of the figures above. Humans were tested in a 10-choice matching-to-sample task with all theoretically “matchable” figures included as comparison stimuli in each trial. The result closely matched those obtained from capuchin monkeys. Much of the rules that govern the boundary completion process seems to be shared between humans and capuchin monkeys. We are still not sure if this similarity is homology or homoplasy. If it is homology, this means that at least one perceptual logic of recognizing boundary of objects can be traced back to the common ancestor of humans and platirhinni primates (i.e., New World monkeys). More species must be tested in order to make a complete sketch of the evolution of amodal completion in primate taxa.

**Birds and pigeon problem**

In birds, the results are mixed. Regolin and Vallortigara (1995) imprinted newly hatched chicks to a variety of cardboards. In later tests the chicks showed preference for the cardboard that was consistent with completion. For example, when the chicks were imprinted to a triangle with its central portion occluded followed a complete triangle rather than a triangle with its central portion cut out. Lea, Slater, and Ryan (1996) also imprinted chicks to the moving two rods behind the “occluder” on TV display. They later followed a unitary rod rather than two separate rods.

Okanoya and Takahashi (2000) also demonstrated that male Bengalese finches sang for courtship at the video of a conspecific female with the upper half of its body occluded (i.e., with its head occluded) by the cardboard while they did not at that of the same female with its upper half erased.

In contrast, pigeons have been repeatedly shown not to complete occluded portions of a variety of stimuli in a variety of different procedures. Cerella (1980) is the first to have tested this process in pigeons. He trained pigeons to discriminate a complete triangle from other figures in a go/no-go procedure. In subsequent tests, the pigeons consistently reported incomplete triangles touching a box (as if the box was hiding the triangles) as “no triangle.” More recently, Sekuler, Lee, and Shettleworth (1996) also reported that pigeons completed neither a circle nor a rectangle in a Yes/No discrimination of complete and incomplete figures.
Several newer reports have examined the generality of this finding in varied tasks and stimuli. Fujita (2001a) and Ushitani, Yamanaka, and Fujita (2001) asked whether pigeons would complete moving stimuli. This prediction is based on the fact that, as described earlier, human infants recognize the unity of moving stimuli two months earlier than that of stationary stimuli. Pigeons matched a single unitary rod and a pair of short disconnected rods moving in concert to corresponding stationary stimuli. Pigeons chose disconnected rods as a comparison when they were shown two moving rods behind the occluding belt (Figure 15). The results were always negative for a variety of differently shaped occluders.

Ushitani and Fujita (2002) tested another possibility that pigeons might complete more naturalistic stimuli. Pigeons were trained to peck at all the photos of food and not to peck at those of non-food presented on the monitor at a time. Pigeons were later tested with the stimulus display having occluded and truncated photos. It was hypothesized that the birds would peck at the intact, occluded, and possibly truncated photos of food in this order if they complete. However, they actually pecked at the truncated photos earlier than the occluded photos. Thus the data were again negative.

Similar failure was also reported in the go/no-go discrimination of a partly occluded pigeon and that of the occluder (Watanabe & Furuya, 1997). Pigeons’ responses did not vary as long as the visible part in the original training remained regardless of whether the part was presented alone (i.e., truncated pigeon) or the intact photo was presented.

Even a combination of motion and naturalistic stimuli do not seem to be enough for pigeons to complete. Shimizu (1998) tested male pigeons’ courtship display toward videotaped images of females. Pigeons made the display when the bottom half of the monitor was occluded by the cardboard. However, they showed very little display when the top half was occluded. Thus, the pigeons simply seem to have responded to the head of conspecific females. These results are in good contrast with those from Bengalese finches in Okanoya and Takahashi (2000).

In Fujita’s study (2001b) described earlier, pigeons were also tested for the perception of continuation of the target bar behind the large rectangle. In contrast to rhesus monkeys, pigeons showed no overestimation of the length of the bar touching the rectangle. Thus, pigeons do not even seem to recognize that one object continues behind another.

Figure 15. The result of three pigeons tested for their perception of object unity in Fujita (2001a) and Ushitani, Yamanaka, and Fujita (2001). The vertical axis is the proportion of choice for unitary rods. The horizontal axis is the stimuli and the subjects. The pigeons matched the stimuli that suggested unity of two rods because of the synchronized motion of portions above and below the occluding belt (labeled “sync”) to a pair of separate rods.
Pigeons might not simply maintain their trained performance in the test situation where occluding stimuli appears adjacent to the target. In fact when DiPietro, Wasserman, and Young (2002) trained pigeons to discriminate the stimuli on “top” of the occluder, their discrimination performance of the same stimuli “behind” it improved. Although the result does not necessarily warrant that pigeons completed the occluded portion, a more careful training procedure might reveal the ability for completion in pigeons.

Another possibility is of course that pigeons may complete only three-dimensional stimuli. This hypothesis has not been tested yet. However, even if they do so, pigeon data obtained so far seem peculiar in the literature. These results strongly suggest that pigeons may have evolved with a visual system that would not complete occluded portions of stimuli as other animals would do.

**What determines ability for completion**

Amodal completion is a process in which an organism has, in a sense, total freedom of how to accomplish because the results of completion are unlikely to be a simple sensory output of environmental inputs. Although some fundamental completion such as recognition of connectedness may be done in very early stages of information processing such as V1 (Sugita, 1999), completing more complicated stimuli by knowledge does not seem to be done there.

Perhaps amodal completion is the most adaptive if it incorporates the reality of the external world. Albert (2001) proposed the generic view principle (GVP). In GVP, visual system assumes that qualitative image structure is stable with respect to small changes of viewpoint. Thus, an observer rarely sees the pattern on Figure 3a as a pacman biting a triangle, because in this case subtle changes in the viewpoint alter the spatial relationship between the pacman and the triangle, which may result in a visible gap at somewhere between the two figures. Otherwise an observer often interprets the same pattern as a full circle on the triangle, because in this case subtle changes in viewpoints do not result in alteration of this overall impression.

Amodal completion assumingly requires the visual system to fulfill complicated calculation involving sensory inputs, knowledge, and environmental constraints. For animals having rich neural resources to complete routinely like humans, it is difficult to realize how an animal can recognize the environment without completion. However, repeated demonstration of failure of completion in pigeons suggests that it may be adaptive for some species with small brains not to do this job unless it is indispensable.

Pigeons live on grains. Grains are abundant and there seems little need for pigeons to collect partly or fully hidden seeds. In contrast, predators must hunt preys that may be partly or fully occluded by other objects such as leaves. Thus, the environmental pressure on completion is differentiated between grain eaters and predators. In fact pigeons have been shown not to follow the cart with food on it if it goes into the tunnel whereas mynahs go along the tunnel to wait for the cart to come out of the tunnel (Plowright, Reid, & Kilian, 1998). Similarly, a closely related species, ring doves have been shown not to go to pick up food behind an opaque screen if the food is occluded before they start to move forward to get the food (Dumans & Wilkie, 1995).

Another potentially important factor is the domain specificity in the ability for completion. Pigeons have been tested for completion in situations where they obtain food by some operant responses. On the other hand, the two species that were reported to complete were tested in social situations (i.e., imprinting and courtship). It is possible that pigeons also complete if they are tested in any of the non-feeding contexts. However, there may be considerable species differences even within the feeding domain. Forkman (1998) has demonstrated that adult hens recognize pictorial depth of the elements of combined figures in a feeding context. Recognition of pictorial depth from two-dimensional information develops early in human and nonhuman primates (Yonas, Cleaves, & Pettersen, 1978; Gunderson, Yonas, Sargent, & Grant-Webster, 1993). As described
before, Fujita (2001b) has shown that pigeons do not even recognize continuation of one figure behind another in two-dimensional display and this may suggest that this species may fail to recognize pictorial depth at all. Similar difficulty was also demonstrated in forming a concept of 2D representation of wire cubes (Cerella, 1990) and in pattern superiority effect for 3D-like figures (Blough, 1984). Chickens are much more omnivorous than pigeons and often hunt worms under the leaves.

In summary, we can draw a tentative conclusion that not to complete may be an adaptive strategy for pigeons. Pigeons can probably survive without inferring a whole object behind an occluder.

On the other hand, not only a variety of nonhuman primate species are consistently shown to complete occluded figures, but also one species, tufted capuchin monkeys, are shown to do so in almost the same manner as humans do. Thus, the completion process may be homological among simian primates.

**Related processes**

As the perceptual completion process involves integrating and organizing ambiguous figural fragments, it may be related to other perceptual organization processes such as recognition of faces and biological motions. In humans, both of these processes develop early in infancy as well as perceptual completion. For instance, newborns prefer to look at a very abstract stimulus consisting of three filled boxes arranged so that they make a “face” over the same stimulus presented upside down (Johnson, Dziurawiec, Ellis, & Morton, 1991) (see Figure 16).

The same preference has been demonstrated in one gibbon (Myowa-Yamakoshi, & Matsuzawa, 2001). Human infants of 2–4 months-old prefer more face-like stimuli with schematic facial parts arranged so that they make a face (e.g., the left most pattern in Figure 16) over those with the parts arranged randomly (Johnson & Morton, 1991). The same process is demonstrated in chimpanzees and macaque monkeys as well as the gibbon described above (Kuwahata, Ishikawa, & Fujita, 2002). Thus, at least human and nonhuman primates recognize a global aspect of facial stimuli at early developmental stages.

As to recognition of the biological motion, human infants are shown to distinguish upright and inverted motion when they are 5 months old (Bertenthal, 1993). We have found that chimpanzees come to prefer seeing the biological motion of a chimpanzee over the inverted one when the chimpanzee infants get to be 4 months old (Ishikawa, Fujita, & Kuwahata, 2003). Macaque monkeys raised in the outdoor enclosure also come to prefer the biological motion of a Japanese monkey over the inverted one after 4 weeks old. Interestingly, the monkeys raised in the indoor cages came to prefer the canonical biological motion of a human at 8–15 weeks old, a little later than the development of corresponding preference for monkey biological motion by enclosure-reared monkeys. The development of recognition of biological motion may be determined mainly by experience to observe real motion but there might be interaction with native predisposition to recognize species-specific locomotion pattern (Adachi, Fujita, Kuwahata, & Ishikawa, 2003).

These results for development of recognition of faces and biological motion by nonhuman primates share its characteristics with that by human infants. We have also shown that chimpanzees perceive spatio-temporal boundary (Fujita, Matsuzawa, & Tokuhisa, 2000). Shipley and Kellman (1994) first demonstrated this process in human adults. This is close to our perception of an occluded figure behind a randomly punched board (see Figure 17). It is difficult to identify the stationary figure but we immediately recognize the figure once it starts to move. Put in a different way, when a stimulus

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**Figure 16.** The four schematic faces used in Myowa-Yamakoshi and Matsuzawa (2001) to test an infant gibbon.
attribute such as color, orientation, and position of the elements in an imaginary figure placed in an array of randomly arranged element figures is different from the other elements, the ease of identifying the imaginary figure depends on motion of the figure. Thus, processes of integrating and organizing spatially and temporally fragmented visual information may be common among primates.

**Conclusion and future direction**

Interpreting environmental information as a meaningful entity is essential in recognizing the external world. In particular, when the information is fragmented and ambiguous, the visual system must integrate and organize such fragments. However, how the visual system does this job may differ between animal species.

Amodal completion is a case in point. Many species have been shown to complete occluded visual stimuli. In one primate species, tufted capuchin monkeys, the rules they follow in completing occluded contours and textures have been suggested to be common with humans. Pigeons are a notable exception in this literature. They have been tested in a variety of stimuli and procedures, but the data have been consistently negative. There is possibility that pigeons may complete three-dimensional objects. However, even so, there is still a big difference in the ability for completion of two-dimensional stimuli between pigeons and other species tested so far.

I suggest that pigeons may have evolved with a visual system that does not complete. Such information processing seems odd to humans but it may be adaptive for pigeons once their locomotive and feeding ecology is taken into account. The generality of this hypothesis must be tested in other avian species of which feeding ecology is similar to that of pigeons.

At the same time, we should examine whether this peculiarity of pigeons is restricted for completion. One interesting topic may be how they perceive facial stimuli. As described earlier, primates attend to global aspects of facial stimuli, though they tend to attend to local aspects of meaningless patterns (Deruelle & Fagot, 1998; Fagot & Tomonaga, 1999). So far pigeons have been shown to attend to local characteristics of line-drawn cartoon characters (Cerella, 1977; Watanabe, 2001). Pigeons may not recognize schematic faces as a representation of faces. In a related study, we trained pigeons to form a concept of human faces (Adachi & Fujita, submitted). We later analyzed what clues they used to discriminate the photos of faces from those of other body parts. The pigeons were found to use only two clues, color and hair. Other facial parts and contour were simply neglected. Such a tendency of pigeons to attend to local features may underlie both failure to complete occluded stimuli and failure to recognize faces as a whole.

Another point is whether pigeons integrate temporally fragmented information. This question has not been directly answered yet. One hint may be that in Jitsumori, Natori, and Okuyama (1999), pigeons trained to discriminate videos of behavior of other birds generalized their discrimination to the same videos played backwards. Thus, their pigeons do not seem to have...
used the motion as a clue for discrimination; they seem to have failed to integrate the temporal flow of visual information into organized motion.

Perception of biological motion requires organizing temporal flow of information as well as spatially fragmented stimuli. This perception has not been demonstrated in pigeons. We examined whether pigeons perceive a relative motion of two moving dots (Ushitani, Fujita, & Sato, 2004; this volume). This is a minimum requirement to perceive biological motion in which a complex set of relative motion among point lights are given to observers. The data were in fact negative. However, when the second dot was replaced with a rectangular frame, they perceived the motion of the first dot relative to the frame. Thus, they seem to have the ability to abstract relative motion only when there is a secure frame.

I have stressed the peculiarity of pigeons. However, in fact this peculiarity implies that perceptual processes may be diverse in the animal kingdom. It is difficult for us humans to imagine how other animals perceive the world because we tend to believe that our perceptual system is the best solution to recognize the external world. But in fact our perceptual system is likely to be one of the many solutions other animals have developed.

References


Shipley, T., & Kellman, P. J. (1994). Spatiotemporal boundary formation: boundary, form, and motion perception from transformations of surface...


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