Predisposed Visual Memory of Shapes in Quail Chicks

Authors: Sakai, Sayaka, Yanagihara, Shin, Kabai, Peter, Koga, Kiyoko, and Matsushima, Toshiya

Source: Zoological Science, 17(8) : 1045-1051

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.17.1045

ZOOLOGICAL SCIENCE **17**: 1045–1051 (2000)

Predisposed Visual Memory of Shapes in Quail Chicks

Sayaka Sakai, Shin Yanagihara, Peter Kabai[†],
Kiyoko Koga and Toshiya Matsushima*

Graduate School of Bioagricultural Sciences, Nagoya University
Nagoya, 464-8601, JAPAN

ABSTRACT—Newly hatched chicks will spontaneously peck at conspicuous objects in their field of view, and soon learn to distinguish between edible food particles and unpleasant tasting objects. To examine whether the selective pecking is based on the ability to memorize shapes, we analyzed pecking behavior of 1- to 2-days-old quail chicks (*Coturnix japonica*) by using ball- and triangle-shaped beads both painted in green. Repeated presentation of dry bead (either ball or triangle) resulted in a progressively fewer number of pecks (*habituation*). When chicks were tested by triangle after repeated presentation of ball, chicks showed a significant increase in the number of pecks at the triangle (*dishabituation*). On the other hand, when tested by ball after a series of triangle presentations, pecking frequency did not increase (*no dishabituation*). Chicks thus distinguished the triangle as a novel object after being habituated to ball, but did not respond to the ball after triangle. A similar asymmetry was found in one-trial passive avoidance task. Chicks were pre-trained by water-coated (neutral) triangle and then trained by methylanthranilate-coated (aversive) ball. In this case, most chicks learned to avoid the ball, and half of these successful learners pecked at the triangle; they distinguished triangle from ball. When chicks were pre-trained by neutral ball and trained by aversive triangle, on the other hand, most chicks did not distinguish the ball from triangle, and showed a generalized avoidance for both beads. Chicks may be innately predisposed to memorize a limited category of shapes such as ball, and associate them with selective avoidance.

INTRODUCTION

Newly hatched chicks of precocial birds have an innate tendency to peck at small conspicuous objects such as colored beads. Novel and unfamiliar objects that abruptly come into chick's field of view are particularly alerting, and effectively release pecking unless the object is too big to cause fear. When the object is edible or positively rewarding (e.g., with a few drops of water), chicks will show enhanced pecking that is often followed by active drinking and swallowing. When the object proves to be neutral and not accompanied by any reinforces, pecking frequency will gradually decline and the object will be ignored in a few trials. However, when the object tastes bitter, chicks will subsequently learn to passively avoid similar beads even after a single experience. In this manner, chicks quickly make up a directory about edible, neutral, and aversive objects encountered within days after hatching.

Such behavioral plasticity at early age, that is confined to neonatal period of life, contributes to survival of high learners through quickly maximizing the dietary intake per foraging investment and minimizing the risk of digesting possibly poisonous food items. Similar strategy is apparent also in their imprinting-related approaching response. Chicks quickly learn visual features of their mother which they will be selectively attached to (Lorenz 1965); the survival value is to maximize parental care and to minimize risk of social isolation. In both cases of food learning and imprinting, rapid development of target selectivity has been documented. Rapid learners could have a better chance to survive the neonatal period, when excess number of chicks compete with others for limited resources of diet and parental care, and only a fraction of them actually survive to more independent juvenile age. This is the basis for a variety of experimental tasks developed for studying memory formation in chicks, such as visual habituation (Andrew and Brennan 1985), pebble floor task (Andrew and Rogers 1972), one-trial passive avoidance task (Cherkin 1969; also see Ng and Gibbs 1991; Rose 1991, 1995), color imprinting (Kovach 1980, Kabai *et al.*, 1992), auditory imprinting (Wallhäuser and Scheich 1987), filial imprinting (Hess 1959; Horn 1985, 1998), and sexual imprinting (Bateson 1978, 1982).

Of this wide variety, one-trial passive avoidance paradigm is especially suitable for studying the time course of memory formation. Biochemical, pharmacological and morphological studies revealed a cascade of characteristic

---

* Corresponding author: Tel. +81-(0)52-789-4081;
FAX. +81-(0)52-789-4081.
E-mail: matusima@agr.nagoya-u.ac.jp

[†] Department of Ecology, Center for Zoology, Szent Istvan University H-1400 Budapest, HUNGARY

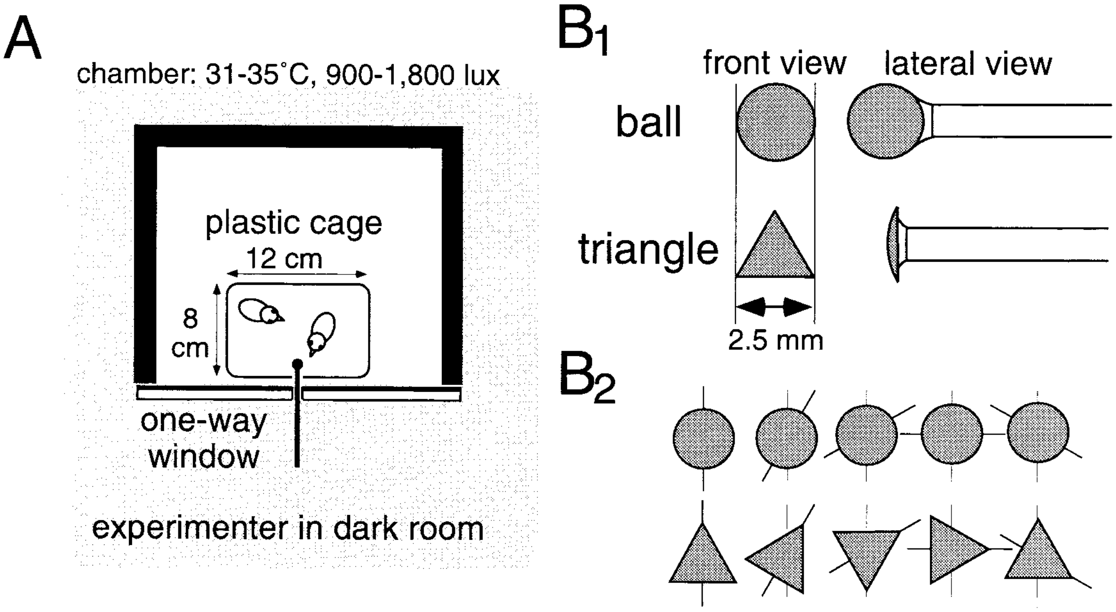

Fig. 1. **A:** Schematic illustration of the experimental set-up. A pair of chicks in cage was placed in a chamber, inside of which was illuminated (900–1,800 lux) and kept at 31–35°C. Object was presented through a small hall on a Plexiglass one-way window, and was manipulated by experimenter in dark room. **B$_1$:** Front and lateral views of the objects (ball and triangle) used in this study, which were glued at the tip of transparent rods. Note that the ball could gives rise to a constant retinal image of circle, while the triangle variant viewpoint-dependent images. **B$_2$:** Front view of ball and triangle at different orientation, showing that possible retinal image of the triangle is also variable depending on its orientation.

changes in distinct telencephalic areas that are involved in formation of long-term memory (for reviews see Rose 1991, Ng and Gibbs 1991). Intermediate medial hyperstriatum ventrale (IMHV; functionally analogous to associative area in mammalian neocortex; Shimizu and Karten 1993, Butler 1999) is critical for the initial process of memory formation, while lobus parolfactorius (LPO; anatomically homologous to caudate-putamen in mammalian basal ganglia; Csillag 1999) for the permanent storage of memory. However, relatively few studies have been done to reveal contents of the memory, so that we are left with a mass of detailed information about *how the memory is formed* without knowing *what is memorized.*

In the present experiment, we studied the significance of shapes for visual memory. We have recently found that quail chicks precisely memorize color of a bead even after a single experience of pecking, and distinguish beads of different color (Aoki and Matsushima 1997, see the accompanying paper). In case of the passive avoidance task, memorized color cue is most significant at 15 min after training, while chicks progressively show generalized avoidance for beads of more distant color. At 24 hr after training, chicks can recall the aversive bead, but on the basis of other yet unidentified cue(s). Shape of the beads is one among the most plausible candidates.

Generalization of the color cue in avoidance learning has been studied in some details (Andrew 1991b), however, not much is known about whether information provided by the shape might be exploited by chicks. Experimental protocols of passive avoidance task recommend the use of a spherical ball (Andrew 1991a), which could yield an invariant circular retinal image irrespectively of viewing angle (Fig.1B$_1$) and orientation (Fig.1B$_2$). However, in their natural habitat, chicks may peck at objects of a variety of shapes such as grains, droppings, worms, or small insects, all of which should give rise to variant retinal images depending on viewing angle and orientation. With a massive information available from different viewpoints, chicks may reconstruct a detailed three-dimensional image of the object from a pile of two-dimensional retinal images. Alternatively, in the case of passive avoidance training where chick watches bead only for a very short period of time (for several tens of seconds), chicks may fail to form distinct memory of its shape. In this study, therefore as the first step of analysis, we examined whether chicks would memorize shape of the aversive stimulus by using a pair of extremities: a sphere (ball) and a spiny plate (triangle).

MATERIALS AND METHODS

Subjects and housing conditions

Quail chicks (*Coturnix japonica*) were used. Fertilized eggs were obtained from outbred lines of a wild-type plumage in our colony, and incubated in our hatchery. For around 24 hr after hatching, chicks were left in a dark incubator kept at 37.7°C. One day after hatching, healthy individuals were randomly paired and housed in small transparent plastic cages. Each chick of every pair was labeled by leg ring for identification. The housing cages were then maintained in a breeder that was illuminated by dim white lights (12L:12D, with the light period starting at 9:00 am) and kept at a controlled temperature between 31–35°C. Chick pairs were transferred, trained, and tested in the same plastic cage until the end of experiment so that the experimenter did not directly handle the subjects. Chicks were not fed but given a petri-dish of cotton soaked with water, and chicks could drink *ad libitum.*

Objects: ball and triangle

In this study, we used ball and triangle as two extremities of shapes (Fig.1B). Object was presented through a small hole (10 mm) located at 50 mm above floor, and manually protruded up to around 3 cm from the cage wall toward chicks (Fig.1A). We never presented two objects simultaneously. Ball: plastic ball (2.5 mm diameter) was glued to a transparent plastic rod (1.5 mm thick). Triangle: a thin plastic film was cut in a triangle with an edge of 2.5 mm, and glued to a rod. Both of these objects were painted in green (type X-28 enamel paint; Tamiya Co., Japan). Front surface of the triangle was painted thick, and had a shiny curved texture and shading pattern similar to the ball. However, visual images of the ball and the triangle are basically incompatible in this study, since we did not hold these objects at fixed visual angle nor at a definite orientation in reference to the chick's eyes. While a ball should give rise to an invariant circular image on retina irrespectively of viewing angle, the image of a triangle should vary drastically (Fig.1B_1). Through axial rotation of the object, similarly, the ball image remains invariant, whereas image of a triangle should vary (Fig.1B_2).

General procedure of training and testing

Pairs of chicks in cages were placed in an experimental chamber, illuminated by a fluorescent light (900–1,800 lux) and kept at 31–35°C (Fig.1A). Behavior of the illuminated chicks was observed through a Plexiglas one-way window of the chamber. Before each session of training and testing, chicks were left in the chamber for 5 min for equilibration. Chicks were then presented with an object for 30 sec, and number of pecks were recorded from both chicks. In case of habituation studies (Experiments 1 and 2), dry beads were used in every session. For passive avoidance training (Experiments 3, 4 and 5), beads coated with a bitter-tasting substance (methylanthranilate: MeA) were presented for the trained groups, whereas water-coated beads were used for control groups. Dry beads were used at all test sessions. Around 5% of chicks failed to peck the bead at the first presentation, and were discarded from experiments. In this study, data were thus obtained from a total of 382 chicks.

The following notations were introduced to represent the nature and sequence of presentations. Objects: *T* for triangle and *B* for ball presented for 30 sec. MeA or water coating was indicated in parenthesis (*MeA* or *Wat*, respectively). Interval between presentations was indicated between dashes. Thus, the sequence of *T* (*Wat*)*–4 min –B* (*MeA*)*–1* hr*–T –4 min–B* presents, for example, pre-training by water-coated triangle, aversive training by MeA-coated ball, and tests by dry triangle and dry ball 60 min later.

Mann-Whitney's U-test or chi-square test of median values was used for comparing two independent sets of data at the significance level of 0.05. For paired sets of data, sign test was used at the significance level of 0.05. Experiments were performed between 10:00 am and 3:00 pm.

RESULTS

Experiment 1 Habituation; single training session

Chicks distinguished triangle after pecking at ball, while they did not distinguish ball as novel after repeatedly pecking at triangle. Naive chicks were randomly assigned into 4 groups, and each group was presented with either a triangle or a ball for 30 sec (1st trial); both of these objects were dry. Four min later, chicks were tested by a second presentation of the same or the other bead for 30 sec, and number of pecks was recorded (2nd trial; Fig.2A, B). These 4 groups were thus noted as *T–4 min–T*, *B–4 min–T*, *T–4 min–B*, and *B–4 min–B*, respectively.

When tested by the same bead, pecks during the 2nd trial were significantly fewer than the 1st, suggesting that habituation occurred (signed test, *T–4 min–T*: $p<0.02$, *B–4 min–B* : $p<0.001$). When exposed first to a ball and then tested by a triangle (*B–4 min–T*), pecking frequency did not diminish (NS, $p=0.114$) suggesting dishabituation. However, when first exposed to a triangle and then to a ball (*T–4 min –B*), chicks pecked significantly less at the 2nd trial than the 1st ($p<0.001$); dishabituation did not occur. It is also to be noted that, although naive chicks at the first trial tended to peck at the triangle more often than at the ball, such differences were not statistically significant (Mann-Whitney's U-test; $U=1{,}520$, $n_1=63$, $n_2=56$, $p=0.0968>0.05$). Therefore, we can hardly conclude that the differential response to the two shapes at the second trial was a result of unlearned predisposition for pecking preference for the triangle over the ball.

Experiment 2 Habituation; repetitive presentation

A similar bias in dishabituation was found after repetitive presentations (Fig.2C). Naive chicks were randomly assigned to two groups. The "ball habituation group" received 6 successive presentations:

4 times (B-4 min)–T –4 min –B,

whereas the "triangle habituation group" received a series of

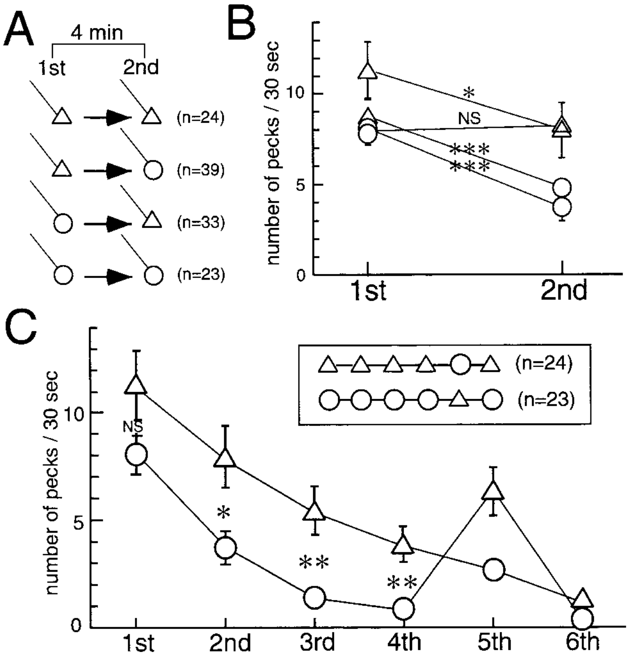

Fig. 2. Asymmetry in the habituation between ball and triangle. **A:** Two successive presentations of ball- or triangle-shaped beads at an interval of 4 min. **B:** Number of pecks per 30 sec was averaged over chicks (mean ± S.E.M.); number of chicks are shown in parentheses in A. Asterisks denote significant differences between the 1st and the 2nd trials; *: $p\leq0.05$, ***: $p\leq0.001$; NS: $p>0.05$. **C:** Number of pecks for 6 successive presentations of ball- or triangle-shaped beads at intervals of 4 min; averaged over chicks (mean ± S.E.M.); number of chicks are shown in the inlet. Asterisks denote significant difference between two groups of chicks for corresponding 1st to 4th trials; *: $p\leq0.05$, **: $p\leq0.01$; NS: $p>0.05$. Direct comparison was not made for the 5th and the 6th trial.

4 times (T–4 min)–B–4 min–T.

Although naive chicks at the first presentation in the "triangle habituation group" tended to peck more than chicks in the "ball habituation group," the difference was not significant (Mann-Whitney's U-test, [U=206, n_1 =23, n_2=24, p=0.068 > 0.05]). Differences in pecking rate at following presentations, however, were statistically significant with more pecks at the triangle than at the ball (Mann-Whitney's U-test, 2nd [U=184.5, p<0.05], 3rd [U=145, p<0.005], 4th [U=153.5, p<0.005]). Expected (habituated) response at the 5th trial was estimated as the mean pecking rate of the 4th and the 6th trials. Actual number of pecks at 5th trial (novel object) was significantly higher than the expected response in the "ball habituation group" (signed test, p=1.9×10^{-6}), but not in the "triangle habituation group" (signed test, p=0.33). Therefore, the ball did not seem to be distinguised as a novel object after repetitive presentation of a triangle.

Experiment 3 Passive avoidance task; effects of pre-training

Naive chicks were randomly assigned into 3 groups, and each group was trained by a single presentation of a ball coated with water (group *1*) or MeA (group *2* and *3*) (Fig.3). Twenty-four hours later, chicks were tested by successive presentations of a ball followed by a triangle (group *1* and *2*) or a triangle followed by a ball (group *3*) at an interval of 4 min; all the objects used at test were dry. These 3 groups are thus noted as,

group *1*: *B (Wat)–24 hr –B –4 min –T*
group *2*: *B (MeA)–24 hr –B –4 min –T*
group *3*: *B (MeA)–24 hr –T –4 min –B*

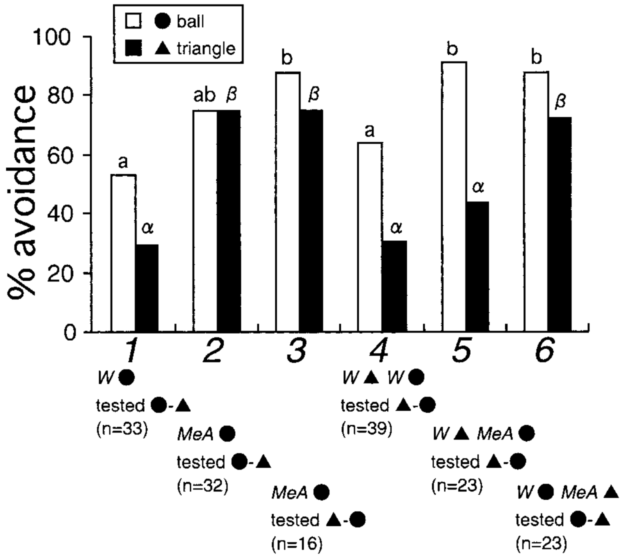

Fig. 3. Asymmetry in the association formed after one-trial passive avoidance task. Ratio of chicks that avoided the bead at test was expressed as % avoidance. Open and filled columns denote responses to ball and triangle at test, respectively. Test was performed at 24 hr post-training. See text for explanation on the training procedures in the groups *1* to *6*. Different letters denote statistic difference at p< 0.05 (chi-square test), and n denote number of chicks in each group. W and MeA denote training using a bead coated with water and MeA, respectively.

We recorded whether chicks pecked or not at test, and analyzed the ratio of avoiding chicks among a total of chicks that were successfully trained (% avoidance).

Single experience of pecking at a MeA-coated ball resulted in a generalized avoidance for both ball and triangle when tested at 24 hr post-training (group *2*). When compared with the control where chicks were trained by a water-coated ball (group *1*), MeA-trained chicks showed a higher ratio of avoidance for the dry ball at test, although the difference was not significant (chi-square test; *chi-square* =3.398, *d.o.f.* =1, $0.05 < p < 0.10$). On the other hand, % avoidance for triangle was much higher in MeA-trained chicks (group *2*) than control (group *1*) with a statistical significance (*chi-square* =13.66, *d.o.f.* =1, $p< 0.001$). It was not due to the sequence of objects at test, because similarly generalized avoidance was found in reversed presentation (group *3*).

To see if chicks could learn to distinguish the aversive object by its shape, we examined effects of pre-training. Before the MeA-training, chicks had experienced that an object of a different shape was not aversive. Naive chicks were randomly assigned to 3 groups, and chicks of each group were pre-trained by a water-coated triangle (group *4* and *5*) or ball (group *6*). Four min afterwards, chicks were presented with a water-coated ball (group *4*), MeA-coated ball (group *5*), or MeA-coated triangle (group *6*), respectively. Twenty-four hr later, chicks were tested by sequential presentation of triangle-and-ball (group *4* and *5*) or ball-and-triangle (group *6*) at an interval of 4 min; all the objects used at tests were dry. These groups are noted as,

group *4*: *T (Wat)–4 min–B (Wat)–24hr–T–4 min–B*
group *5*: *T (Wat)–4 min–B (MeA)–24hr–T–4 min–B*
group *6*: *B (Wat)–4 min–T (MeA)–24hr–B–4 min–T*

Pecking at a MeA-coated ball after pre-training with a water-coated triangle (group *5*) resulted in a significantly higher ratio of avoidance only for ball at test (chi-square test; *chi-square* =5.449, *d.o.f.*=1, $0.01 <p < 0.02$), when compared with its water-control (group *4*). The % avoidance for triangle was slightly higher than control, although the difference was not statistically significant (*chi-square* =0.977, *d.o.f.*=1, $0.3<p$). When compared with group *3* where chicks were trained without pre-training, the % avoidance for dry triangle in group *5* was significantly lower (*chi-square* =3.97, *d.o.f.*=1, $0.02 <p< 0.05$), indicating that pre-training caused a higher rate of chicks that distinguished. With pre-training by a neutral triangle, half of the chicks could thus memorize the shape of an aversive ball, and explicitly linked the shape memory to selective avoidance. It is to be noted that chicks might have failed to distinguish the MeA-coated ball as novel after a triangle (*Experiment-1*, Fig.2A).

In group *6*, where chicks were pre-trained by a water-coated ball and trained by a MeA-coated triangle, a generalized avoidance occurred for both ball and triangle. As the results of *Experiment-1* suggest, chicks must have distinguished the MeA-coated triangle from the ball (Fig.2A). However, when tested 24 hr later, chicks avoided both objects.

In a good contrast with a progressive generalization found in the memory of color (Aoki and Matsushima 1997), distinct changes were not found in the extent of generalization in the shape memory. Naive chicks were randomly assigned into two groups, and both of them were similarly trained by a water-coated triangle and, 4 minutes later, by a MeA-coated ball. These groups are noted as,

group *7*: *T (Wat)– 4 min–B (MeA)–15 min–T –4 min –B*
group *8*: *T (Wat)– 4 min–B (MeA)–1 hour –T –4 min –B*

In group *7* (15 min retention), 8 chicks out of a total of 24 chicks discriminated between triangle and ball. In group 8 (1 hr retention), 7 chicks out of 23 recall individuals showed discrimination. Data from these two groups were compared with group *5* (24 hour retention; 11 out of 21 recall individuals), and no significant difference was found (*chi-square* =2.17, *d.o.f.*=1, $0.1 < p < 0.2$).

DISCUSSIONS

Predisposed memory in chicks

The present study shows that chicks can learn to associate shapes with pecking / avoidance, but in a limited and predisposed manner. In *Experiment 1* and *2* (Fig.2B and C), chicks pecked at a triangle as if it were novel after habituation to a ball. However, chicks did not respond to a ball after habituation to a triangle. Furthermore, chicks showed more pecks at a triangle than at a ball after habituation (Fig.2C). Similar bias was found in *Experiment 3*, where the object was associated with bitter taste (Fig.3). A single experience of pecking at a MeA-coated ball, if immediately followed by pre-training using a water-coated triangle, resulted in a higher rate of distinguishing chicks at test 24 hr later (group *5*). However, after pre-training with a water-coated ball, a single experience of pecking at a MeA-coated triangle resulted in a generalized avoidance for both ball and triangle (group *6*). Even with strong reinforcement by MeA and with differential pre-training, chicks did not selectively associate the triangle with passive avoidance.

The “inability to memorize” such a simple shape as the triangle seems embarrassing, when taking into account the fact that chicks can actually memorize shapes such as box and cylinder in filial imprinting (Horn 1985). Study using operant conditioning (Vallortigara *et al*. 1990), where chicks were trained to find hidden foods in boxes with various two-dimensional geometric patterns, also revealed a high ability to discriminate various patterns. Furthermore, highly developed cognitive capacity has been shown in pigeons, which can learn to discriminate between individual pigeons by head shape (Watanabe and Ito 1991). It has also been shown that pigeons could develop a viewpoint consistent image of familiar objects (Watanabe 1997).

The present results might be ascribed to the difference in geometry of the two objects used in this study. A ball gives rise to an invariant retinal image of circle, while a triangle highly variant viewpoint- and orientation-dependent images (Fig.1B). Consequently, chicks might fail to form a distinct memory of the triangle due to its ambiguous retinal images, but were able to memorize the ball much easier.

It is also possible to argue that the difference could simply reflect an innately biased preference for particular shapes. As shown in the 1st presentations (Fig.2B and C), chicks tended to show more pecks in average at the triangle than at the ball, although the difference was not statistically significant. In the 2nd to the 4th presentations, significantly more pecks were elicited for the triangle (Fig.2C), suggesting a slight unconditional preference for the triangle over the ball. At the 5th presentation after the repetitive triangle, chicks might have recognized the ball as a distinct object, but failed to peck more, simply because the ball was much less attractive.

Alternatively to these interpretations, the cognitive function in chicks may be associated with a particular set of behavioral outputs in a selective and biased manner. In other words, chicks can memorize the ball, and are just biased to associate it with avoidance. Chicks can similarly memorize the triangle, but are biased NOT to associate it with avoidance. It is to be tested whether chicks can learn the shapes equally in appetitive paradigms such as pebble-floor task or water-reinforcement pecking task, instead of the present aversive task using MeA.

Separate processing of color and shape

In contrast to the complicated association between shapes and pecking behavior, the color cues are learnt in a simple and straightforward manner. Using ball-shaped beads, we found that the degree of habituation faithfully parallels the difference between colors (Aoki and Matsushima 1997). For example, after training by repetitive presentation of a green bead, chicks showed more pecks for a yellow bead than for a greenish-yellow bead at test. If trained by yellow bead, on the other hand, chicks showed more pecks for green than for greenish-yellow. Similar symmetry between colors was evident also in passive avoidance task (Aoki and Matsushima 1997); the subjective distance between colors, which was measured in terms of the rate of discriminating chicks at test, showed similar parallelism with difference in colors. It is to be noted that the genetic predisposition for red over blue (or, blue over red) preference were generalized as preference for long (or, short) wavelength, even after complete decerebration (Kabai and Kovach 1993). The fidelity of color memory in chicks has also been documented in operant conditioning experiment, where chicks were trained and tested by patterned stimuli with different color and contrast (Osorio *et al*., 1999). They have clearly shown that chicks developed a preference to the trained color, while they preferred patterns of higher contrast to the familiar ones. Taken all these results together, we could conclude that chicks are also biased to primarily memorize color of objects as significant cue for recall at pecking, and that other features such as shape and patterns are memorized secondarily. Although to our knowledge, there are no reports on the variety of harmful objects a quail chick might encounter in natural conditions, most of bitter tasting seeds and insects could have conspicuous warning coloration. It remains totally unknown, however, whether and how the color and shape cues are combined for chicks to recognize an object.

Brain mechanisms for processing and storing the visual memory

Extensive biochemical, pharmacological and morphological studies revealed a cascade of characteristic changes involved in formation of long-term memory in distinct brain regions (IMHV and LPO; for reviews see Rose 1991, 1995). Starting from increased glucose uptake (Rose and Csillag, 1985), enhanced expression of immediate early genes (Anokhin *et al*., 1991, Freeman and Rose 1995 for c-*fos* and c-*jun*; but see also Yanagihara *et al*., 1998) is followed by an increased synthesis of glycoprotein (Scholey *et al*., 1993), leading to lasting changes in ultrastructures (Stewart 1991). Trying to identify the loci where the memory for passive avoidance task is processed and stored permanently, Rose and his colleagues made a systematic survey for brain regions where pre- or post-training lesion caused amnesia. They found that the pre-training lesion of bilateral IMHV caused amnesia (Davies *et al*., 1988), while comparable lesion made 1–6 hr post-training was without effect, and suggested that the memory could relocate to some other brain region after it was once registered in the IMHV (Patterson *et al*., 1990, Gilbert *et al*., 1991). Passive avoidance training should thus lead to a cascade of memory correlates in IMHV, which however is not necessary for subsequent recall and performance of selective avoidance.

These results suggest that lasting changes continue to occur in the IMHV, even after this region is no more critical in passive avoidance task. To circumvent this paradox, Patterson and Rose (1992) have hypothesized that the avoidance memory is composed of distinct classificatory cues of objects, such as color, shape, size and so forth, and these cues are processed and stored in distinct brain regions. Actually, they found that post-training lesion of IMHV strongly impaired chicks' ability to discriminate objects by the color cues, and suggested that the IMHV is specialized for object recognition by colors. Accordingly, our recent single-unit study also revealed IMHV is involved in the association between aversive bitter taste and the color cues, though within a limited time window after training (Yanagihara *et al*., 1999). Further studies are required to identify the brain mechanisms involved in memorizing color and shape, as well as those for binding these cues.

ACKNOWLEDGEMENTS

We would like to express our sincere gratitude to Prof. Dr. T. Namikawa (Nagoya University) for supplying us with breeding facilities. This study was supported by Grant-in-Aid for Scientific Research (C) (No. 11680785) and Grant-in-Aid for International Scientific Research (Joint Research) (No. 10044202) from Japanese Ministry of Education, Science, Sports and Culture to TM.

REFERENCES

Andrew RJ (1991a) Aversive bead; a one-trial passive avoidance task. In: "Neural and Behavioural Plasticity: the Use of the Domestic Chick as a Model" Ed by RJ Andrew, Oxford University Press, Oxford, pp 17–18

Andrew RJ (1991b) The nature of behavioural lateralization in the chick. In: "Neural and Behavioural Plasticity: the Use of the Domestic Chick as a Model" Ed by RJ Andrew, Oxford University Press, Oxford, pp 536–554

Andrew RJ, Brennan A (1985) Sharply timed and lateralized events at time of establishment of long-term memory. Physiol Behav 34: 547–556

Andrew RJ, Rogers LJ (1972) Testosterone, search behaviour and persistence. Nature 237: 343–346

Anokhin KV, Mileusnic R, Shamakina IY, Rose SPR (1991) Effects of early experience on c-*fos* gene expression in the chick forebrain. Brain Res 544: 101–107

Aoki M, Matsushima T (1997) Passive avoidance learning in quail chicks: innate preference, habituation and reinforced learning. Neurosci Res 21: S260 (abstract in English)

Bateson P (1978) Sexual imprinting and optimal outbreeding. Nature 273: 659–660

Bateson P (1982) Preference for cousins in Japanese quail. Nature 295: 236–237

Bock J, Schnabel R, Braun K (1997) Role of the dorso-caudal neostriatum in filial imprinting of the domestic chick: a pharmacological and autoradiographical approach focused on the involvement of NMDA-receptors. Eur J Neurosci 9: 1262–1272

Butler AB (1999) Whence and whither cortex? Trends Neurosci 22: 332–334

Cherkin A (1969) Kinetics of memory consolidation: role of amnesic treatment parameters. Proc NAS 63: 1094–1101

Csillag A (1999) Striato-telencephalic and striato-tegmental circuits: relevance to learning in domestic chicks. Behav Brain Res 98: 227–236

Davies DC, Taylor DA, Johnson MH (1988) The effects of hyperstriatal lesions on one-trial passive-avoidance learning in the chick. J Neurosci 8: 4662–4666

Freeman FM, Rose SPR (1995) MK-801 blockade of Fos and Jun expression following passive avoidance training in the chick. Eur J Neurosci 7: 563–569

Gilbert DB, Patterson TA, Rose SPR (1991) Dissociation of brain sites necessary for registration and storage of memory for a one-trial passive avoidance task in the chick. Behav Neurosci 105: 553–561

Hess EH (1959) Imprinting. Science 130: 133–141

Horn G (1985) Memory, Imprinting and the Brain: an inquiry into mechanisms. Clarendon Press, Oxford

Horn G (1998) Visual imprinting and the neural mechanisms of recognition memory. Trends Neurosci 21: 300–305

Kabai P, Kovach JK, Vadasz C (1992) Neural correlates of genetically determined and acquired color preferences in quail chicks. Brain Res 573: 260–266

Kabai P, Kovach JK (1993) Subtelencephalic visual discrimination in selected lines of Japanese quail. NeuroReport 4: 255–258

Kovach JK (1980) Mendelian units of inheritance control visual preferences in quail chicks (*C. coturnix japonica*). Science 207: 549–551

Lorenz K (1965) Über tierisches und menschliches Verhalten: aus dem Werdegang der Verhaltendslehre. R. Piper & Co. Verlag, München

Ng KT, Gibbs ME (1991) Stages in memory formation: a review. In "Neural and Behavioural Plasticity: the Use of the Domestic Chick as a Model" Ed by RJ Andrew, Oxford University Press, Oxford, pp 351–369

Osorio D, Jones CD, Vorobyev M (1999) Accurate memory for color but not pattern contrast in chicks. Curr Biol 9: 199–202

Patterson TA, Gilbert DB, Rose SPR (1990) Pre- and post-training lesions of the intermediate medial hyperstriatum ventrale and passive avoidance learning in the chick. Exp Brain Res 80: 189–195

Patterson TA, Rose SPR (1992) Memory in the chick: multiple cues, distinct brain locations. Behav Neurosci 106: 465–470

Rose SPR (1991) How chicks make memories: the cellular cascade from c-*fos* to dendritic remodelling. Trends Neurosci 14: 390–397

Rose SPR (1995) Cell-adhesion molecules, glucocorticoids and long-term-memory formation. Trends Neurosci 18: 502–506

Rose SPR, Csillag A (1985) Passive avoidance training results in lasting changes in deoxyglucose metabolism in left hemisphere regions of chick brain. Behav Neur Biol 44: 315–324

Scholey AB, Rose SPR, Zamani MR, Bock E, Schachner M (1993) A role for the neural cell adhesion molecule in a late, consolidating phase of glycoprotein synthesis six hours following passive avoidance training of the young chick. Neuroscience 55: 499–509

Shimizu T, Karten HJ (1993) The avian visual system and the evolution of the neocortex. In "Vision, Brain, and Behavior in Birds" Ed by HP Zeigler, H-J Bischof, MIT Press, Cambridge, pp 103–114

Stewart MG (1991) Changes in dendritic and synaptic structure in chick forebrain consequent on passive avoidance learning. In "Neural and behavioral plasticity: the use of the domestic chick as a model" Ed by AJ Andrew, Oxford University Press, Oxford, pp 305–328

Vallortigara G, Zanforlin M, Compostella S (1990) Perceptual organization in animal learning: cues or objects? Ethology 85: 89–102

Wallhäusser E, Scheich H (1987) Auditory imprinting leads o differential 2-deoxyglucose uptake and dendritic spine loss in the chick rostral forebrain. Dev Brain Res 31: 29–44

Watanabe S, Ito Y (1991) Discrimination of individuals in pigeons. Bird Behaviour 9: 20–29

Watanabe S (1997) An instance of viewpoint consistency in pigeon object recognition. Behav Proc 39: 257–261

Yanagihara S, Yagi T, Matsushima T (1998) Distinct mechanisms for expression of Fos-like immunoreactivity and synaptic potentiation in telencephalic hyperstriatum of the quail chick. Brain Res 779: 240–253

Yanagihara S, Izawa E-I, Matsushima T (1999) Single unit activity in lobus parolfactorius (LPO: basal ganglion) of freely-behaving 2-day old domestic chicks during and immediately after one-trial passive avoidance training. Society for Neuroscience (Abstract), 25 (861.11, p.2158)

(Received April 18, 2000 / Accepted June 5, 2000)