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Accurate Visual Memory of Colors in Controlling the Pecking Behavior of Quail Chicks

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ABSTRACT—Animals are predisposed to memorize specific features of objects they encounter, and to link them with behavioral outputs in a selective manner. In this study, we examined whether chicks memorize objects by colors, and how they exploit the memorized color cues for selective pecking in 1- to 2-days-old quail chicks (*Coturnix japonica*). Ball-shaped beads painted in green (G), yellowish green (YG) and the intermediate color (YGG) were used. Repetitive presentation of a bead (interval: 4.5 min) resulted in gradually fewer pecks (*habituation*). Subsequent presentation of a different color caused proportionately more pecks (*dishabituation*); e.g., after habituation to the G bead, the YG bead caused a stronger dishabituation than the YGG bead did. The dishabituation appeared symmetric; e.g., the YG bead caused as strong dishabituation after the G-habituation, as was caused by the G bead after the YG-habituation. Number of pecks could thus reveal the memory-based color perception in chicks. Similar discrimination of beads by memorized color cues was found after one-trial passive avoidance training, where chicks learned to avoid a bitter-tasting object without any differential pre-training experiences. However, proportion of the chicks that discriminated between different colors became progressively smaller at test 15 min, 1 hr, and 24 hr post-training. On the other hand, proportion of chicks that distinguished beads by non-color cues remained unchanged. Chicks may primarily form an accurate memory of colors, but gradually change the link between the color memory and the pecking behavior.

INTRODUCTION

Animals are born to learn something. Most “hard-wired” instinctive behaviors do not properly function without memory. Similarly, most learning processes are not free from evolutionary backgrounds, and are deeply rooted in species-specific instinctive processes. Due to their unique characters, newly-hatched chicks of precocial birds (such as chicken, quails, ducks and geese) has presented a unique opportunity where visual memory can be studied in terms of cellular / molecular neurobiology, ethology, and cognitive neuroscience. First, chicks are born with functionally *matured* sensori-motor functions, and they quickly start to walk, run, call, peck and bite objects even on the day of hatch. Second, chicks are *curious*; they approach to, walk around and peck at a variety of objects upon their first encounter, if these objects are conspicuous enough and not too big to cause fear. Third, they are *naive*, and practically all experiences and environmental factors can be experimentally controlled. Finally, but most importantly, chicks are *high learner*.

A series of learning paradigms have been developed by exploiting these characters of chicks, including visual habituation, pebble floor task, one-trial passive avoidance task, filial imprinting, and sexual imprinting (for a comprehensive list of references, see the accompanying paper by Sakai *et al*.). Of these tasks, underlying neural mechanisms have been most intensively studied in the avoidance task (Cherkin, 1969; Ng and Gibbs, 1991; Rose, 1991 1995) and the imprinting (Horn, 1985, 1998). In both cases, specific telencephalic regions (IMHV and LPO) have been shown critical for the visual memory. Detailed neuroanatomical and neurochemical changes have been documented in these regions concerning the cellular basis of memory.

On the other hand, relatively few studies have been done to reveal the cognitive capabilities in chicks, except for recent findings by Vallortigara and his colleagues (Vallortigara *et al*., 1990, Regolin and Vallortigara, 1995). They have clearly revealed that chicks form internal representation on the generic visual image of objects they encounter. Nevertheless, it is yet unknown what aspects of objects do chicks memorize as the primary cue for recall, among a variety of possible visual cues such as color, shape, size, surface texture, shading patterns,

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three-dimensional features, movement, and so forth.

In this study, we analyzed how chicks memorize colors and link the memorized color cues to selective pecking behavior by using two forms of visually controlled pecking tasks. Habituation was examined by using dry beads of various colors, and passive avoidance learning by using same beads dipped in methylanthlanilate (MeA) as aversant. In contrast to the widely accepted protocols (Andrew, 1991), we trained chicks without any differential pre-training experience before the training using the MeA-coated bead. Under this condition, chicks were just confronted with a terrible experience of pecking at a bitter-tasting bead, and they could have associated any possible cues with selective avoidance. It was totally up to chicks as to which cues they learn and exploit for selective avoidance. The present results suggest that chicks are predisposed to form an accurate color memory as the primary cue for recall.

METHODS

Subjects and housing conditions

Newly hatched quail chicks (*Coturnix japonica*) were used. Breeding and housing conditions were identical to those reported previously (Yanagihara *et al*., 1998; Sakai *et al*., 2000,). Briefly, fertilized eggs were obtained from outbred wild-type colony, and incubated until hatch. On the next day (at 1 day old), chicks were paired randomly in small transparent plastic cages (12.5 x 8.5 cm^2, 8.2 cm high) and raised in a breeder. The breeder was illuminated by dim white light (12L:12D with the light period starting at 9:00), highly moisturized, and kept at a constant temperature of around 35°C. Chick pairs were transferred, trained, and tested in the same plastic cage so that the experimenter did not handle the chicks directly. Chicks were not fed but given a petri-dish of water-soaked cotton, so that they could drink freely.

General procedure of training and testing

Chicks were trained a few hr after they had been paired. Chick pairs in cages were placed in an experimental chamber, the inside of which was illuminated by a fluorescent light and kept at 31–35°C. Behavior was observed through a Plexiglass one-way window. Before each session of training and testing, chicks were equilibrated in the chamber for 5 min. Chicks were then presented with one object at a time for 30 sec, 1 min or 2 min, and number of pecks was recorded for each chick. In habituation task (Experiment 1 and 2), dry beads were used in all sessions. For the passive avoidance training (Experiment 3 and 4), bead was coated by a bitter-tasting substance (methylanthranilate: MeA) and presented to the chicks. Experiments were performed between 10:00 and 15:00.

Objects: colored beads

Plastic ball (2.5 mm diameter) was painted with an enamel paint either in yellow (Y; type X-8, Tamiya Co. Japan), green (G; type X-28), yellowish green (YG; type X-15), or an intermediate color between G and YG (YGG; a 1:2 mixture of type X-28 and type X-15), and glued to a transparent plastic rod (1.5 mm diameter). All of these beads were manipulated by experimenter's hand, and presented through a small hole in the cage located at 50 mm above the floor. Preliminary experiments showed that chicks have an innate preference for green and yellow beads over red and blue, and no significant difference was found between green and yellow. In our experimental condition, most of naive chicks pecked at green and yellow beads at their first encounter (95% and 90% for green and yellow, respectively). On the other hand, much less chicks pecked at red and blue beads (67% and 46%, respectively). It is possible that the fluorescent illumination used in our study might have caused this experimental bias. Anyhow, we used these G, YGG, YG, and Y beads for studying the color perception in chicks.

As the final step of test in Experiment 3 and 4, we observed chicks behavior to simultaneously presented twelve beads of various colors (green, yellow, blue and red); 3 beads for each color, all dry. These beads were painted by enamel paints (yellow: type X-8, green: type X-28, blue: type X-14, red: type X-7) and glued to white cotton surface of a cardboard (7 cm x 7 cm). This cardboard was put on the cage floor, thus was collectively referred to as 'floor beads.'

Habituation

In Experiment 1, chick pairs were given 5 successive presentation (30 sec each) of a dry green (G) bead at 4.5 min intervals, and number of pecks were recorded. Chick pairs were randomly assigned into 3 experimental groups, and each group was tested using the same G bead after a retention period of 15 min, 1 hr or 24 hr. During the retention period, chicks stayed in the breeder. Two more control groups of chick pairs were prepared, where chicks stayed in the breeder and examined by using the G bead only once. Number of pecks was compared between an experimental group and a naive control group of corresponding age: 15 min group vs. 1 day naive, 1 hr group vs. 1 day naive, and 24 hr group vs. 2 day naive, respectively. Number of chicks (n) used in each group is shown in parentheses (Fig.1). Mann-Whitney's U-test was adopted at the significance level of 0.05.

In Experiment 2, chick pairs were similarly given 6 successive presentation (30 sec) of a dry bead painted in either G, YG or YGG at 4.5 min intervals. The 1st–4th and the 6th presentations were done using the same color, and the 5th using a different color. Chick pairs were randomly assigned to 6 experimental groups, and these groups were tested as shown in Fig.2A; habituated to G and tested by YG, habituated to YG and tested by G, habituated to G and tested by YGG, habituated to YGG and tested by G, habituated by YG and tested by YGG, habituated by YGG and tested by YG. Number of

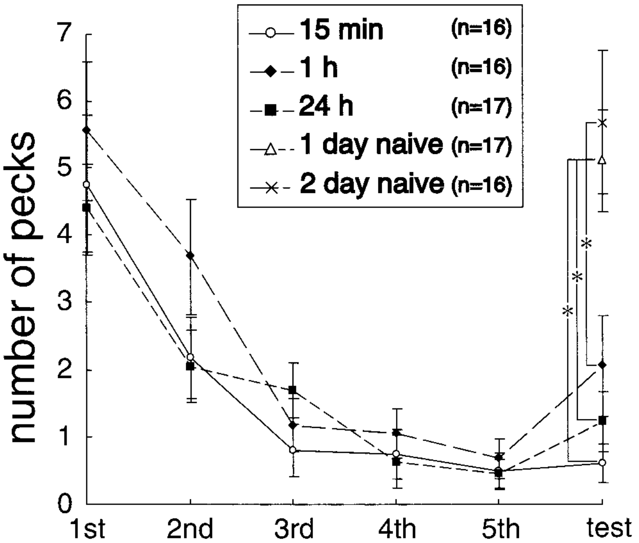

Fig. 1. Repeated presentations of a colored bead resulted in a lasting habituation in pecking. Chicks were trained by 5 successive presentations (each for 30 sec) of a water-coated G (green) bead at intervals of 4.5 min. At 15 min, 1 hr or 24 hrs after the 5th presentation, the trained chicks were tested with the same G bead; n denotes number of chicks in each group. The number of pecks (mean± S.E.M.) during each presentation is shown. At test, significant differences were found between the trained chicks and naive control chicks of corresponding ages (1 or 2 day naive, ∗: p<0.05; Mann-Whitney's U-test).

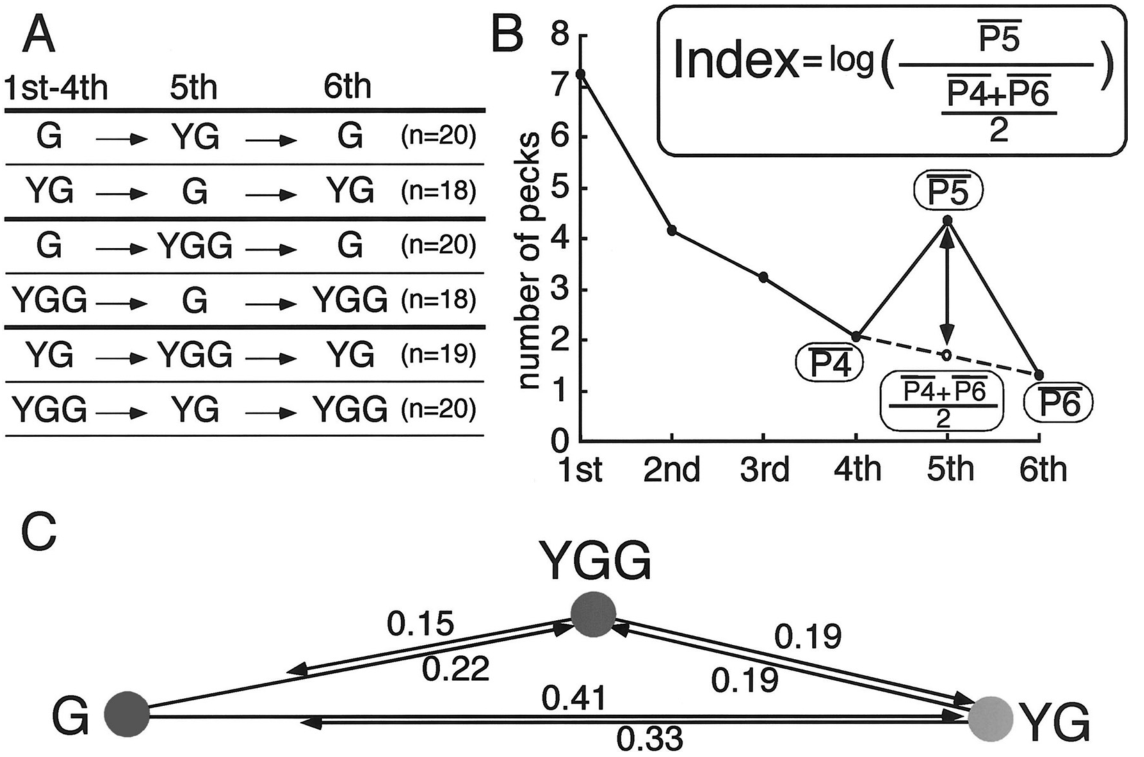

Fig. 2. The habituation was color specific. A: Six groups of chicks were trained and tested by different combinations of colors; *n* denotes number of chicks in each group. B: Mean numbers of pecks are shown for the (G-YG-G) group. Number of pecks decreased monotonically through the 1st to 4th presentations, and increased at the 5th. See text for definition of $\overline{P4}$, $\overline{P5}$, $\overline{P6}$ and index. C: The colors G, YGG and YG were graphically plotted based on the indices. Value above each vector denotes the corresponding index.

chicks (*n*) used in each group is shown in parentheses (Fig.2A). Number of pecks at the 4th, the 5th, and the 6th presentation was denoted as P4, P5 and P6, respectively, and averaged in each group. The ratio of the actual average pecks $(\overline{P5})$ was divided by the expected average pecks $(\overline{P4} + \overline{P6} / 2)$, and converted to an index by a common logarithm (see the formula shown in Fig.2B). For example, index values of 1.0, 0.3 or 0.0 mean that 10 times, 2 times more or the same number of pecks are elicited by the 5th presentation, respectively, than the number of pecks expected on the assumption that chicks do not discriminate between these two beads. No statistic comparison was made on this index.

Passive avoidance task

In Experiment 3, chick pairs were trained by a single presentation of G bead dipped in MeA (duration: 30 sec) without any pre-training experiences. Around 10% of chicks failed to peck at the bitter-tasting bead, or pecked but failed to show aversive responses (characteristic head-shaking and bill-wiping behaviors), and were discarded. Chick pairs were then randomly assigned to three groups, and each group was tested after retention period of 15 min, 1 hr or 24 hr. During the retention period, chicks were left in the breeder. Chick pairs were tested by Y bead (duration: 1 min), then by G bead (1 min), and finally by floor beads (2 min); intervals between tests were 4 min (Fig.3). We noted if chicks pecked or avoided the beads, and calculated the proportion of avoiding individuals out of all the chicks examined (% avoidance). For each step of tests using Y, G and floor beads, statistic comparisons were made between two of the three groups of different retention times by using chi-square test at the significance level of 0.05. Dry beads were used for all test sessions. Number of chicks (*n*) used in each group is shown in parentheses.

In Experiment 4, chick pairs were trained by single presentation of G or YG bead dipped in MeA (duration: 30 sec) with no pre-training. Chick pairs were then tested, after a retention period of 15 min, 1 hor or 24 hr, by three successive steps at 4 min intervals. The first step of the test (duration: 1 min) was performed by using a color different from that used for training; those chicks trained by the G bead

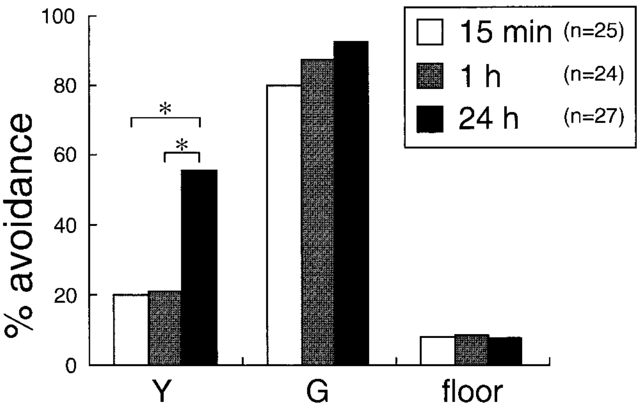

Fig. 3. Single experience of pecking a bitter-tasting bead resulted in a lasting avoidance. Values of % avoidance (percentage of chicks that avoided the bead out of all chicks examined) were compared between any two groups of chicks tested at 15 min, 1 hr, or 24 hrs post-training. In all groups, chicks were trained by using a G bead dipped in MeA. Significantly higher value of % avoidance was found in the 24 hr group at the tests using the Y bead (∗: $p<0.05$; chi-square test), in comparison to either of the 15 min and the 1 hour group. At the tests using the G bead and the floor beads, no significant difference was found between any pairs of the groups of different retention periods. The % avoidance for the floor beads denotes the percentage of chicks that did not peck any one of the 12 beads on the board.

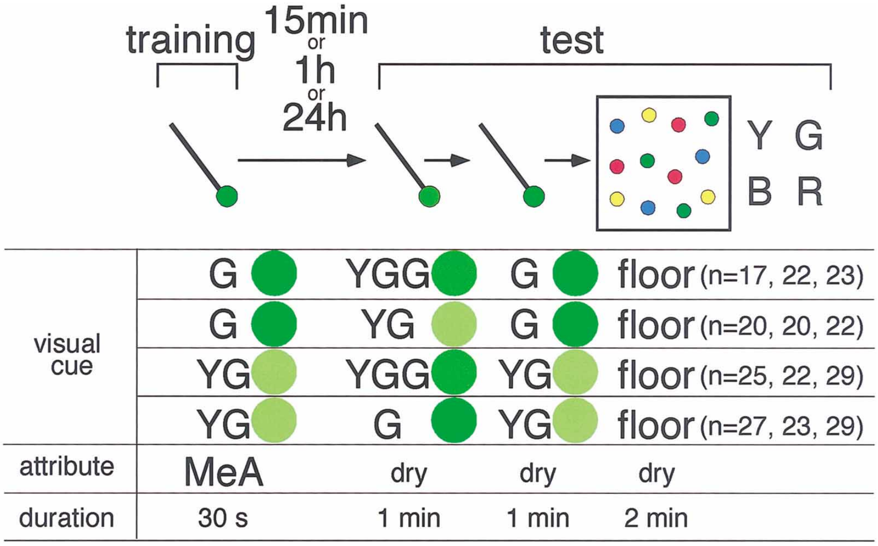

Fig. 4. Procedure of passive avoidance task using G, YG, and YGG beads. Note that the MeA-training was not preceded by any differential experiences. Chicks were just trained by a single presentation of either a G bead or a YG bead dipped in MeA. The chicks were tested at 15 min, 1 hour, or 24 hr after training using the beads shown in the figure. Sets of three numbers (*n*) in parentheses denote the number of chicks in each group tested at 15 min, 1 hr and 24 hr, respectively. Attributes (MeA or dry) and duration of the bead presentation are shown below.

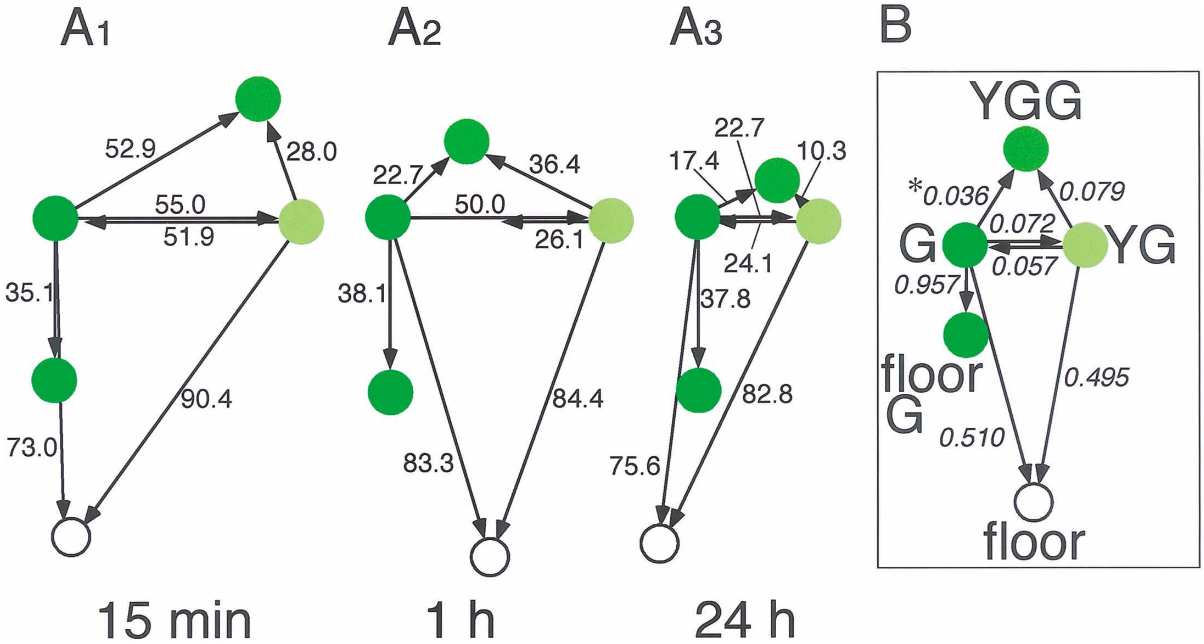

Fig. 5. Accurate memory of colors was formed after one-trial passive avoidance training even without a differential pre-training procedure. Chicks were trained and tested as shown in Fig. 4. The colors G, YGG and YG were graphically plotted based on the discrimination ratios between the 4 pairs of colors at tests; i.e., from G to YG, from G to YGG, from YG to G, and from YG and YGG. Discrimination ratios of the G bead on the floor bead (*floor G*) and 12 beads of the floor (*floor*) were also calculated for each group of the successful G- and YG-learners. See texts for further explanations. A_{1-3}: Graphs plotted for each of the different post-training retention periods (15 min, 1 hr and 24 hr for A_1, A_2 and A_3, respectively). B: Probabilities (*P*-values), where the differences among groups of 15 min, 1 hr, and 24 hr groups would be expected by chance, were calculated using chi-square test. The null hypothesis is that the discrimination ratio did not differ among three groups of different retention periods. The discrimination ratios between the 4 pairs of colors progressively shortened at 15 min, 1 hr and 24 hr. Statistical significance was obtained only from G to YGG ($*$: $P=0.036<0.05$); *P*-values in the other pairs ranged between 0.05 and 0.10. On the other hand, the discrimination ratios between beads of different contexts (from G to *floor G*, from G to *floor*, from YGG to *floor*) remained unchanged, and had much larger *P*-values.

were tested by the YGG or YG bead, whereas chicks trained by YG bead was tested by YGG or G bead. We therefore had 4 groups for each retention period, i.e., 12 groups in total as illustrated in Fig.4. Number of chicks (*n*) used in each group is shown in parentheses. Chick pairs were randomly allocated to either one of these groups. The second step of the test (duration: 1 min) was performed by using the training color, and the third step (duration: 2 min) the floor beads.

At tests, we noted if chicks pecked at the bead (the first and the second steps), and recorded which color chicks pecked at (the third step). Thereafter, we calculated the proportion of discriminating chicks (discrimination ratio), as percentage of chicks that pecked on the first step out of those chicks that did not peck on the second step. For example, a ratio of 40% means that 40 chicks discriminated and pecked at the bead of different color among a total of 100 learners that successfully avoided the bitter bead. Discrimination ratio was also defined for the floor beads as the percentage of chicks that pecked at the G bead in the floor beads (the third step). For example, a ratio of 40% means that 40 out of 100 successful learners discriminated the bead by the difference in bead presentation (contextual cues), but not by the difference in color, size and shape of the bead. We also calculated discrimination ratios for the floor beads; a ratio of 80%, for example, means that 80 out of 100 successful learners pecked at any one or more of the 12 beads on the board. For each of the 7 corresponding sets of discrimination ratios, statistic comparisons were made among 3 groups of different retention periods by using chi-square test at the significance level of 0.05. The null hypothesis was that discrimination ratios did not differ among groups of different retention periods, or that the pattern of discrimination did not show a temporal change.

RESULTS

Experiment 1 Habituation: the effects lasted long.

Effects of habituation lasted at least for 24 hr. In all of the 3 experimental groups with different retention periods (15 min, 1 hr, and 24 hr), number of pecks monotonically declined from the 1st to the 5th presentation (Fig.1). At test, chicks showed fewer pecks than the 1st irrespectively of the retention periods. Comparisons between each group and the corresponding naive control group revealed statistically significant difference in all cases (Mann-Whitney's U test); 15 min vs. 1 day naive (U=17, N_1=16, N_2=17, $p < 0.05$), 1 hr vs. 1 day naive (U =49, N_1=16, N_2=17, $p<0.05$), 24 hr vs. 2 day naive (U=44.5, N_1=17, N_2=16, $p<0.05$). We therefore conclude that, even without the aversive experience of MeA, repetitive presentation (and probably the experience of repetitive pecking *per se*) causes a lasting habituation on subsequent pecking behavior.

Experiment 2 Habituation: the effects were color specific.

The habituation depended on the memorized color cue. The colors G, YGG, and YG were graphically plotted as corner points of a triangle, and length of each line was made proportional to the corresponding index value defined by the formula (Fig.2B). When the index of color *X* after habituation to color *Y* differed from that of *Y* after *X*, the larger one of these two values was adopted. It is to be noted that physically closer colors were bound closer on this diagram. YGG was closer to G than YG was, and YGG was closer to YG than G was. The dishabituation appeared almost symmetric. The index measured from G to YGG (0.15) was not very different from the index measured from YGG to G (0.22), and similar symmetry was found also between YGG and YG, and between G and YG. Although statistic tests are not available for this index, we can reasonably assume that the index represents subjective distance between colors. In other words, chicks accurately memorize the color of bead at least for a short period of the habituation task, and quantitatively link it to pecking behavior.

Experiment 3 Passive avoidance task: the avoidance lasted, but the color specificity did not.

After passive avoidance training with MeA-coated G bead, chicks continued to avoid the G bead even at 24 hr, however, the specificity of avoidance for color did not last accordingly. Fig.3 shows the results. At 15 min or 1 hr post-training,% avoidance was low for the Y bead (ca. 20%) whereas it was high for the G bead (80% or higher). However, at 24 hr post-training, chicks showed much more generalized avoidance, and more than half of chicks actually avoided the Y bead. Proportion of chicks that did not peck any one of the floor beads (% avoidance for the floor beads) remained low for all groups of different retention periods, thus suggesting that general pecking activity did not change drastically. To examine if the decline in color specificity was due to a loss of the memorized color cue, we systematically analyzed the proportion of generalizing chicks by using G, YGG and YG beads.

Experiment 4 Passive avoidance task: the generalization was accompanied by progressively weaker discrimination among colors.

In Fig.5, the colors G, YGG and YG were graphically plotted on the basis of the discrimination ratios at test. At 15 min, the discrimination ratio of YG from G was 55.0%, while that of G from YG was 51.9%; more than half of the successful learners discriminated and pecked at the bead of different color. The discrimination ratio of YGG from G was 52.9%, while that of YGG from YG was 28.0%. The colors G, YG and YGG were thus plotted as three corner points of the upper triangle shown in Fig.5A_1 in a manner similar to Fig.2C. Discrimination ratio of the floor G bead (G beads on the floor beads) measured from the G bead was 35.1%; i.e., 35.1% of the successful G-learners pecked at the floor G. Out of the same group of successful G-learners, 73.0% individuals pecked at any one or more of the 12 beads on the floor beads. Similarly, 90.4% of the successful YG-learners pecked at the floor beads. The lower triangle in Fig.4A_1 was thus drawn. Note that the ratio of YG from G was almost the same as the ratio of G from YG. Also note that the distance of floor G from G is shorter than the distance between G and YG; chicks most probably recognized beads by color as the primary cue.

At 1 hour (Fig.5A_2), the diagram slightly changed and the area enclosed by the upper triangle became smaller, while the lower triangle remained almost unchanged. At 24 hr (Fig.5A_3), the upper triangle shrunk significantly and discrimination ratios among G, YG and YGG became smaller. Discrimination ratios for the floor beads remained high. The probability where the null hypothesis (i.e., the distinction ratio does not change) is valid (*P*-value) was calculated for each of discrimination ratios (Fig.5B). Statistically significant *P*-value below 0.05 was found only for the distinction ratio of YGG measured from G (0.036), whereas *P*-values for the other ratios among G, YG and YGG were only suggestive, ranging between 0.05 and 0.10. On the other hand, *P*-value for the discrimination ratio of floor G from G was much higher (0.957), as were *P*-values for floor beads from G and YG (0.510 and 0.495, respectively). It might be concluded that the memorized color cue faded away, and / or was gradually dissociated from the selective pecking behavior. On the other hand, the other non-color and non-shape cues (such as movement, location, or spatial arrangement of the bead) might have remained unchanged.

DISCUSSION

Chicks are predisposed to memorize colors as the primary cue for recall even without any differential pre-training experiences.

The present results confirm earlier findings that chicks memorize the bitter-tasting bead mainly in terms of its color, whereas other non-color cues are less significant (Gilbert *et al*., 1991; Patterson and Rose, 1992). Also in operant conditioning task, where chicks were trained to find hidden food in colored containers, Osorio and colleagues (1999) have shown that chicks have accurate memory of colors. Studies using the color imprinting paradigm (Kovach, 1980; Kabai *et al*., 1992; Kabai and Kovach, 1993) indicate that quail chicks have genetically pre-determined color preference, which can be re-oriented toward different color by simply exposing a batch of chicks to a flashing but non-moving light for 2–6 hr.

However, all of these studies were accomplished in a condition that could have favored the acquisition of color memory. Actually, experimental protocols of passive avoidance task have almost always recommended a differential experience of pre-training procedure as critical requisite (Andrew ,1991). Presentation of a bitter MeA-coated colored bead must be preceded by one or more trials of dry or water-coated beads of different colors. According to the procedure developed by Ng and colleagues (1991; the La Trobe procedure), for example, chicks are initially given two successive trials of pre-training with chrome beads, followed further by another couple of successive pre-training trials using blue and red beads, before the final training using a MeA-coated red bead. In this case, chicks have a good chance to “realize” that some beads of different colors are not aversive, and that color is the critical cue. Indeed, they also reported that the pre-training procedure promotes retention of the avoidance memory, and reduces variability of data among experimental groups. Furthermore, such a differential pre-training procedure is reported to facilitate memory retention under a weak avoidance learning paradigm using a diluted solution of MeA (Burne and Rose, 1997). Also in our recent study on the shape memory in chicks, differential experience proved to facilitate the proportion of chicks that distinguished beads by the shape cue (see the accompanying paper by Sakai *et al*., 2000).

In this study, on the other hand, chicks were not pre-trained at all; in both habituation and passive avoidance task, chicks were trained just by using a single bead, and then tested by beads of different colors. Without pre-training, chicks could have associated any aspects of their experience with selective avoidance. Instead of the color, chicks might have learned to avoid beads by other cues such as shape, surface texture, shading pattern, size, or movement (i.e., direct attributes of the bitter-tasting bead). Alternatively, the cues might also have been location of the bead, spatial arrangement of objects in the chamber, or even the experimenter’s hand or face that chicks could have watched (i.e., contextual cues of the aversive experience). The fact was that chicks memorized the color of bead as the primary cue for selective avoidance (*Experiments 3 and 4*). Results of the accompanying paper by Sakai *et al*. also support the idea that chicks are predisposed to memorize the color, rather than the shape of the bitter bead. Effects of specific pre-training procedures should be systematically analyzed on the possible significance of the other non-color, non-shape cues. The progressive generalization of avoidance towards beads of different colors (*Experiment 4*) could be examined in this respect; with differential pre-training, the color specificity might have lasted longer, or less chicks might have shown generalized pecking.

Formation of the color memory does not require reinforcement by aversive experience with MeA.

Given that chicks are predisposed to memorize colors as the primary cue, it is still to be asked if the aversive MeA or other reinforcing factors are really required for the formation of lasting memory of specific colors. In most studies of the passive avoidance paradigm, pecking at a water-coated bead, instead of the MeA-coated bitter bead, is supposed as the control condition where chicks do not learn. However, the results of *Experiment 1* showed that the effects of repetitive pecking lasted for at least 24 hr. Specificity of the habituation effect on the trained color was shown in *Experiment 2*, but only in its short-term form of the memory. It should be examined if the lasting habituation at 24 hr post-training is also color-specific.

It is also to be noted that appetitive, rather than aversive, conditions are also effective in forming specific color memory. Operant conditioning of approaching and pecking has been developed with radiant heat or food as reward (Wallhäuser and Scheich, 1987; Osorio *et al*., 1999). Yanagihara and Izawa (unpublished observations) have found that chicks show drastically high rate of pecking once they were rewarded by a drop of water. The reinforced pecking, however, was not strongly color specific, just favoring most of the beads presented in the same contexts. However, when followed by 2 more successive trials where a bead of different color was not rewarding, chicks turned out to show high pecking activity specifically for the rewarding color. Most probably, we can presume that chicks memorize colors as the primary cue, irrespectively of whether the bead was associated with reinforcing factors (such as aversive MeA or appetitive water) or not. Rather, it might be that these reinforcers simply determine the behavioral outputs with which the chicks should associate the learned visual cue(s). The cue(s) to be learned, on the other hand, are not determined solely by the very experience of pecking at the bitter or the rewarding bead. Instead, it depends on the differential experiences just preceding, and chicks “rationally” find out the critical cue(s) as has been discussed above. It remains, however, unknown if differential experience that follows (instead of the one that precedes) could also influence the cue(s) to be learned. With these ideas in mind, we may have to reconsider the research strategies that have so far been adopted in order to reveal neural representatives of memory, or the memory trace.

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