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Authors: Hayashi, Isako, Ono, Yumiko, and Matsushima, Toshiya

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# Visual Cues for Suppressing Isolation-Induced Distress Calls in Quail Chicks

Isako Hayashi, Yumiko Ono and Toshiya Matsushima\*

Laboratory for Animal Information Biology, Graduate School of Bioagricultural Sciences,  
Nagoya University, Nagoya 464-8601, Japan

**ABSTRACT**—When socially isolated from siblings, newly hatched chicks emit distress calls at a high frequency. As a step toward identifying brain mechanisms responsible for recognition of conspecifics, we analyzed sensory cues critical for suppressing distress calls in socially isolated quail chicks at post-hatch day 2 to 4. Each subject of wild-type chicks was reared with another wild-type companion chick for 1–2 nights before tests. As the first step, we found that distress call was completely suppressed when accompanied by another wild-type chick, irrespective of whether the subject had previously been familiarized with the chick or not. When paired with an *albino* chick, on the other hand, the subject emitted significantly more calls, suggesting that the wild-type plumage is important. As the next step, in search of the critical sensory modality, we found that visual display of a conspecific chick suppressed the distress call even without accompanying acoustical stimuli. On the other hand, the acoustical stimuli alone were without effects. Olfactory as well as tactile sensations also proved irrelevant. As the final step, we tried to identify the significant sub-modalities in the visual images of conspecifics. Degraded visual image of a moving chick (degraded in fine details) caused a significant but incomplete suppression, whereas an anesthetized chick was without effects. On the other hand, distress calls were completely suppressed even without behavioral correspondence or exact plumage coloration. All of these data suggest that visual image of a moving chick should be given at a high spatial resolution, and wild-type plumage pattern might provide important visual cues.

**Key words:** imprinting, emotion, cognition, hyperstriatum ventrale, suppressor stimulus

## INTRODUCTION

Newly hatched chicks of precocial poultry birds emit two distinct types of call; distress calls and contentment calls. These two call types differ in their phonetic characteristics as well as in their behavioral contexts. The distress call is a type of loud and high-pitched vocalization that is accompanied by a typical upright posture (see Fig. 1B). The distress calls appear when a chick is isolated from its siblings or parents in a novel environment (social isolation stress), or when a chick suffers physically from a hypothermal environment, pain or restraints (physical stress) (Collias, 1952, Yazaki *et al.*, 1997). On the other hand, the contentment call is weaker, lacks distinct phonetic patterns, and is emitted without any specific postures. The contentment calls appear when a chick is in the company of other conspecifics or familiar objects, with which the chick was imprinted (Horn 1985). The call type can thus faithfully reveal the emotional state of the chick.

Neural substrates for controlling the distress calls have

been analyzed in a series of studies using quail chicks (Yazaki *et al.*, 1997a, b, 1998, 1999). Fos-immunostaining (Takeuchi *et al.*, 1996) revealed that social isolation caused an enhanced expression of an immediate early gene *c-fos* in several brain regions such as mesencephalic nuclei (mesencephalic lateralis pars dorsalis [MLd]: *auditory relay nucleus*, intercollicular nucleus [ICo]: *vocal relay nucleus*, and substantia grisea centralis [GCt]: *central gray*), thalamic nuclei (nucleus dorsolateralis anterior thalami pars medialis [DMA]: *limbic thalamus*), and various telencephalic regions (area parahippocampalis [APH]: *hippocampal-entorhinal cortex homologue*, archistriatum pars ventralis [Av]: *amygdaloid complex*, and hyperstriatum ventrale [HV]: *association cortex homologue*). These regions might be involved in production of distress calls (ICo), auditory processing of own calls (MLd), control of accompanying emotional states (GCt, Av, and DMA), and enhancement in the cognitive / mnemonic functions (APH and HV).

Actually, the distress call could have a direct functional link with the formation of visual memory in the form of filial imprinting (ten Cate 1986). When confronted with a motor-driven rotating stuffed fowl, chicks showed a stronger preference for the moving fowl if the movement was coherent with

\* Corresponding author: Tel. +81-52-789-4081;  
FAX. +81-52-789-4012.  
E-mail: matusima@agr.nagoya-u.ac.jp

the chick's own distress calls. Temporal coincidence between the calling-related emotional state (represented in the avian analogue of the amygdaloid complex, or Av; Csillag *et al.*, 1997; Durstewitz 1999) and the selective auditory / visual attention (represented in HV; Izawa *et al.*, 2000) might have caused the enhancement in imprinting. Actually, both of these telencephalic regions (Av and HV) have been shown to be involved in filial imprinting in a series of localized lesion experiments (Horn 1985, 1998). Furthermore, these neural nuclei are mutually interconnected (Csillag *et al.*, 1994, 1997; Davies *et al.*, 1997), suggesting a tight link between distress calls and cognitive functions.

The purpose of the present experiments is to identify sensory cues (significant modality and sub-modalities) responsible for suppressing distress calling in a condition of social isolation. Searching for the sensory signals that effectively suppress distress calling may thus lead to a description of the chicks' internal representation of conspecifics. We analyzed the number of distress calls in a variety of different conditions, and found that high-resolution visual stimuli of a moving chick are critical, and that the plumage pattern might be particularly important.

## MATERIALS AND METHODS

Total of 12 independent experimental groups (each composed of non-overlapping 6–46 subject chicks) were classified into 3 experiments according to each purpose.

In experiment-1, we tried to confirm that the distress call is consistently suppressed when accompanied by conspecific individual, or a chick of wild-type plumage. Responses of subjects to familiar / unfamiliar wild-type chicks, to subject's own mirror images, or to *albino* chicks without characteristic plumage patterns were analyzed.

In experiment-2, we tried to identify critical sensory modality by examining whether visual and/or non-visual (acoustic, olfactory, or tactile) stimuli are involved. Responses of subjects to video images were compared between groups with and without acoustic stimuli. Responses to acoustic stimuli alone, or effects of physical separation, were also analyzed.

In experiment-3, we further analyzed the critical sub-modalities involved in the visual images of conspecific chicks. Responses of subjects to chicks with unusual coloration (by staining in green), to immobilized chicks (by anesthesia), or to chicks with visual degradation (by using half-mirrors) were examined.

In the following, we will describe the subjects, general experimental procedures, and apparatuses used in each group.

### Subjects and housing condition

Quail chicks (*Coturnix japonica*) of wild-type plumage were incubated in our laboratory. Fertilized eggs were purchased from a commercial supplier, and incubated in a dark incubator at 37.7°C. Chicks were left in the incubator for about 24 hr after hatching. On day-2, chicks were randomly paired and housed in small plastic cages (13×9 cm<sup>2</sup>, 9 cm high; opaque surface with white adhesive tape). The cages were kept in a breeder without any sound barriers, so that the chicks could hear calls from neighboring cages. One of the paired chicks served as subject, and the other chick as companion. We labeled chicks by leg rings for identification; wild-type chicks had basically identical plumage coloration and patterning, so that experimenters could not identify individuals without the leg rings. The housing cages were maintained in a breeder that was illuminated by dim white light bulbs (80 lux, 12 L:12 D photoperiod), and the temperature

was kept constant at around 31–35°C. Water and quail mash food were freely available. Experiments were performed on post-hatch day-3 to 5, i.e., after the chicks had been reared with their companion chick for 1–2 nights in the breeder. The rearing time ranged from 19 to 47 hr, while the breeder was kept dark during the 12 hr night period starting from 9 pm. The total illumination period in the breeder thus ranged from 7 to 23 hr. The rearing and illumination periods were not correlated with the number of distress calls (data not shown).

### General experimental procedures

Chicks were placed in a transparent plastic cage, and housed in a thermo-controlled soundproof chamber (Fig. 1A). The inside of the chamber was illuminated (640 lux) and kept at 30.5–32.0°C. Behaviors were observed through a Plexiglas one-way window in the chamber. Part of the window was covered with white adhesive tape, so that chicks did not see their own reflected images on the inner surface of the window. We counted the number of distress calls emitted by the subject chicks in 5 consecutive sessions (8 min each) with different conditions. Calls emitted during the later 5 min of the session were counted, and data from the initial 3 min was discarded. Unless noted otherwise, each chick was paired with its own companion in the 1st, 3rd and 5th sessions (paired). In the 2nd session, the subject chick was left alone (single) by removing the companion chick from the cage. The effects of various conditions were examined in the 4th session. The number of calls in the 4th session was compared with the expected value, or the average of the 3rd and the 5th sessions. Data in the 4th session were also compared with the 2nd session, which had the single condition. In both cases, Wilcoxon's signed-ranks test of corresponding data was used for statistical tests at a significance level of 0.05 (\*) or 0.01 (\*\*). Numerical data are expressed in terms of mean±s.e.m., and *n* denotes the number of chicks used in each group. Direct statistical comparisons were not made among groups.

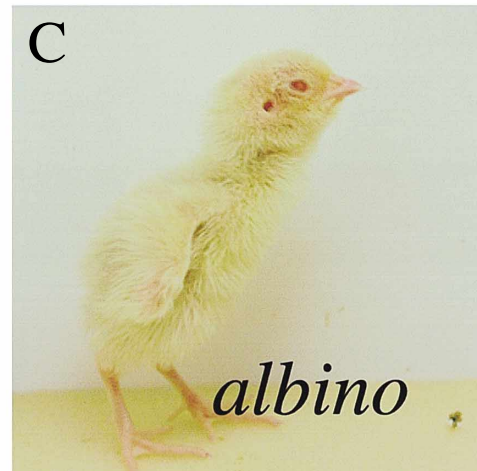
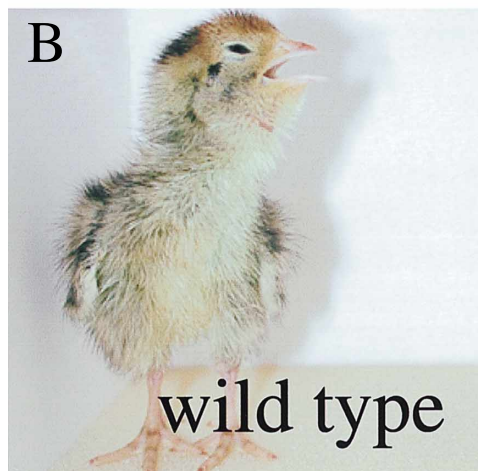
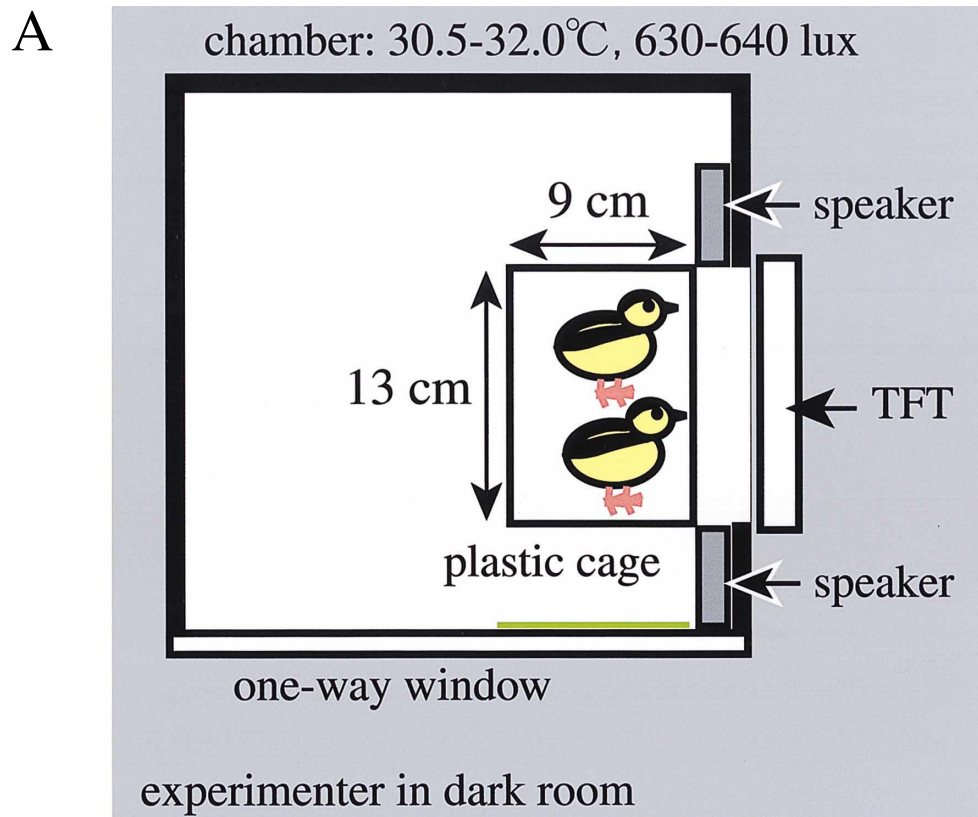
### Specific procedures and apparatuses

#### Experiment-1

In **group 1**, number of distress calls was compared in repeated sessions of *single* condition. In **group 2**, the companion chick was replaced by another wild-type *unfamiliar* chick, which the subject had never been reared together. In **group 3**, a mirror replaced the companion chick. A 9×9 cm<sup>2</sup> metal-plated glass mirror was placed upright in the experimental chamber. In **group 4** (Fig. 2D), an *albino* chick replaced the companion chick. As shown in Fig. 1C, *albino* chicks had yellow plumage and red eyes, but lacked the characteristic pattern of the wild-type plumage. Fertilized eggs of the *albino* line (*AWE* strain) were kindly supplied by the Nippon Institute for Biological Science (Yamanashi, Japan), and incubated in our laboratory until hatching. On post-hatch day-2, the *albino* chicks (5.81±0.14 g; *n*=16) weighed slightly, but significantly, less than the wild-type chicks (6.40±0.16 g, *n*=10) (mean±s.e.m.; Mann-Whitney's U-test, *p*=0.040). Furthermore, *albino* chicks seemed less active in the experimental chamber than the wild-type chicks in their spontaneous walking / pecking behaviors.

#### Experiment-2

In **group 5** and **group 6**, the companion chick was replaced by video images on a thin film transistor (TFT) liquid crystal color display (LC-84TV1, 640×480 pixels; Sharp Co.). The size of single pixel was 0.32 mm (width)×0.27 mm (height). It has been reported that TFT images are superior to CRT images in eliciting behavioral responses in finches, presumably because the visual system of birds has a high temporal resolution. For detailed information about the physical properties of the TFT, refer to the analysis in that previous study by Ikebuchi and Okanoya (1999). In **group 5** and **group 7**, we used a pair of *speakers* (SC-C37, Active Speaker System; Aiwa Co.) for reproduction of simultaneously recorded calls. For video replay, we selected a part of a recording (8 min long) of a non-subject wild-type chick, which emitted distress calls at a rate of 26 calls / min in social isolation. The



**Fig. 1.** A: Schematic illustration of the experimental chamber. For details, see text. B and C: Photographs of wild-type (B) and *albino* (C) chicks, just emitting distress calls.

size of the chick images on the TFT display was adjusted to be almost the same as that of a real chick. The sound pressure was roughly adjusted to the level of a live chick calling in the cage. In other groups where TFT display was not used, the surface of the display was covered with a Styrofoam plate. In **group 8**, instead of replacing the companion chick, the subject chick was *separated* from the companion by using a transparent Plexiglas plate (2 mm thick, 10 cm high). In this condition, the subject chick could recognize the companion by either visual or acoustic cues, although direct tactile stimuli were not available. Since the chamber was not separated into two airtight partitions, the subject could also have recognized the companion by olfactory cues, even if attenuated to some extent.

#### Experiment-3

In **group 9**, the companion chick was replaced by a wild-type chick stained in *green*. A green acrylic paint (type X-28, water-soluble acrylic paint; Tamiya Co., Japan) was used. The plumage of 2 wild-type chicks was carefully stained using a brush, then immediately dried in a moisturized incubator for 30 min at 37°C. These stained chicks walked, called, and pecked at food and water normally, without any behavioral signs of physical or mental stress. In **group 10**, an anesthetized chick of wild-type plumage replaced the companion chick. A wild-type chick was anesthetized by subcutaneous injection of Ketalar (0.15 ml; containing 11.5 mg ketamine per 1 ml of saline) immediately before test. The anesthetized chick lay down with its side

on the floor, and continued stable respiratory movements without any active movements until recovery (for 20–30 min). In **group 11** and **group 12**, we separated the subject from the companion with a half-mirror. The cage was divided into two by a Plexiglas plate (2 mm thick), on which half-mirror film was attached. One partition was illuminated as usual, while the other was not. In this condition, the subject chick in the dark partition could see the companion chick in the illuminated partition, while the companion could not see the subject. The companion chick faced its own mirror image, and then emitted distress calls to some extent. The number of calls emitted by the companion was not counted. In **group 11** and **group 12**, we used different half-mirror films; half-mirror 1 (type VM-S101, transmissivity: 22%; IKC Co.) in **group 11**, and half-mirror 2 (type WF-301, transmissivity: 19%; Wako Co.) in **group 12**. The illumination in the subject partition was turned off, so that the subject chick could see the companion chick in the illuminated partition. On the other hand, the companion chick faced its own mirror image, and did not see the subject. The half-mirror 1 degraded the fine details of the visual image, whereas the half-mirror 2 simply attenuated the luminance (see Fig. 4C, and D). Due to fine cross-stripe patterns (0.4 mm×0.4 mm), images viewed through half-mirror 1 were much more vague than those viewed through half-mirror 2.

## RESULTS

### Experiment-1

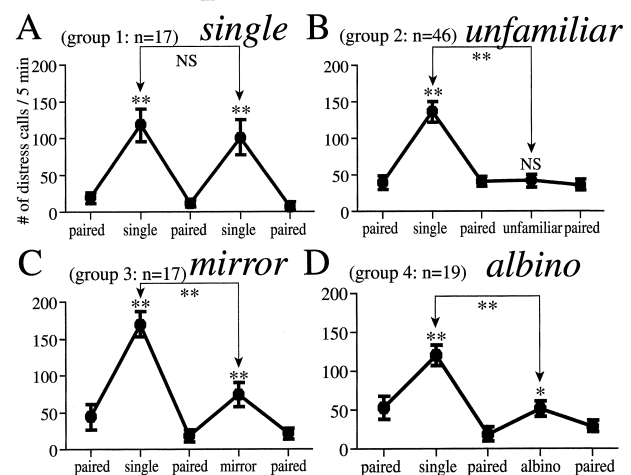
In 4 experimental groups with different conditions, we tried to confirm that distress call is consistently suppressed when accompanied by another conspecific chick with wild-type plumage.

In **group 1**, subject chicks emitted relatively few distress calls when paired with their companion, while they emitted distress calls at a high frequency when left alone (Fig. 2A). In both of the “single” sessions (2nd and 4th), subject chicks emitted significantly more calls than in the “paired” sessions (1st, 3rd, and 5th). No significant differences were found in a comparison of the 2nd and the 4th, indicating little habituation in the distress calling in repeated sessions of social isolation. In the following groups, therefore, subject chicks were exposed to a variety of different conditions in the 4th session, and the number of calls was compared with data from the single and paired sessions.

In **group 2**, even an unfamiliar chick was effective in completely suppressing the distress calls (Fig. 2B). With an unfamiliar chick, the number of calls by the subject chick did not significantly differ from the “paired” session. Slight differences in the individual cues, visual or non-visual if any, do not seem to matter.

In **group 3**, mirror image was effective in reducing the number of distress calls (Fig. 2C). When confronted with their own image on the mirror, chicks emitted significantly fewer calls than in the 2nd session of the “single” condition. However, the number of calls was still significantly greater than the average of the 3rd and the 5th sessions (paired). It is thus suggested that chicks recognized the mirror image similar, but not identical, to the companion chick. Taking into account the fact that the subjects did not concern the differences in individual appearance (**group 2**), the unusually coherent behavior of the mirror image might have impaired the suppressive effects.

## experiment-1



**Fig. 2.** Effects of different behavioral conditions on the distress calls in socially isolated quail chicks. A: Single condition. B: Unfamiliar chick. C: Mirror image. D: *albino* chick. The number of distress calls emitted during 5 min was plotted for 5 successive trials. Mean values  $\pm$  s.e.m. are shown, and *n* denotes the number of chicks in each group. The “paired” indicates that the subject chick was paired with the companion chick, while the “single” indicates that the subject chick was left alone in the chamber. Asterisks denote that chicks showed significantly more distress calls than in the paired conditions; \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , Wilcoxon signed rank test of corresponding data. Data from the 4th trial were also compared with data from the 2nd single trial using the same statistical test. NS indicates no significant difference above  $p > 0.05$ .

In **group 4**, similarly, an *albino* chick partially suppressed the distress call (Fig. 2D). This also demonstrates that subject chicks discriminate between the wild-type and the *albino* chicks. The incomplete suppression could have been due, either to the obvious difference in the external appearances, or to the slightly less active nature of the *albino* chicks in their behaviors.

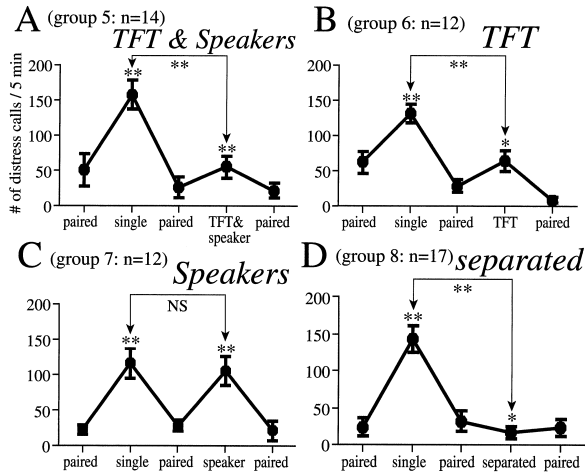
These results suggest that the appearance of conspecific wild-type individual is critical in suppressing the distress calls. What aspects of the conspecific individuals could be responsible for the effects? In the next set of experimental groups, we tried to identify critical modality of the conspecific chick as call suppressor.

### Experiment-2

Conspecific chicks may suppress the distress call by way of visual, acoustic, olfactory, tactile cue, or a combination of multiple cues. In the following 4 groups, we tried to identify the modality of the most critical cue. In **groups 5** and **6**, the companion chick was replaced by video images with or without replay of calling sound.

In **group 5**, video images and simultaneously recorded sound (mostly the distress calls) of another wild-type chick were replayed using a TFT display and a pair of speakers (Figs. 1A, 3A). In **group 6**, video images were given without the sound (Fig. 3B). In **group 7**, recorded sound was replayed without video images (Fig. 3C). In both **groups 5** and **6**, distress calls were suppressed, but not completely as in the

## experiment-2



**Fig. 3.** Effects of video images and sound replay on the distress calls. A: Video images of a single chick on a TFT monitor with sound via a couple of speakers. B: TFT monitor alone. C: Replay of call sound alone. D: Separation by a transparent Plexiglas. In D (physical separation), the subjects emitted significantly less calls than in the “single” condition (\*:  $p < 0.05$ ).

“paired” session. In **group 7**, on the other hand, the calling sound per se did not suppress the distress calls at all. As shown in **group 8**, distress call was suppressed even without physical contacts. We can therefore eliminate the possibility of calling sound and direct tactile stimuli as significant cues, and reasonably assume that visual stimuli gives some critical cues. Olfactory cues, if any, might not be relevant, since it

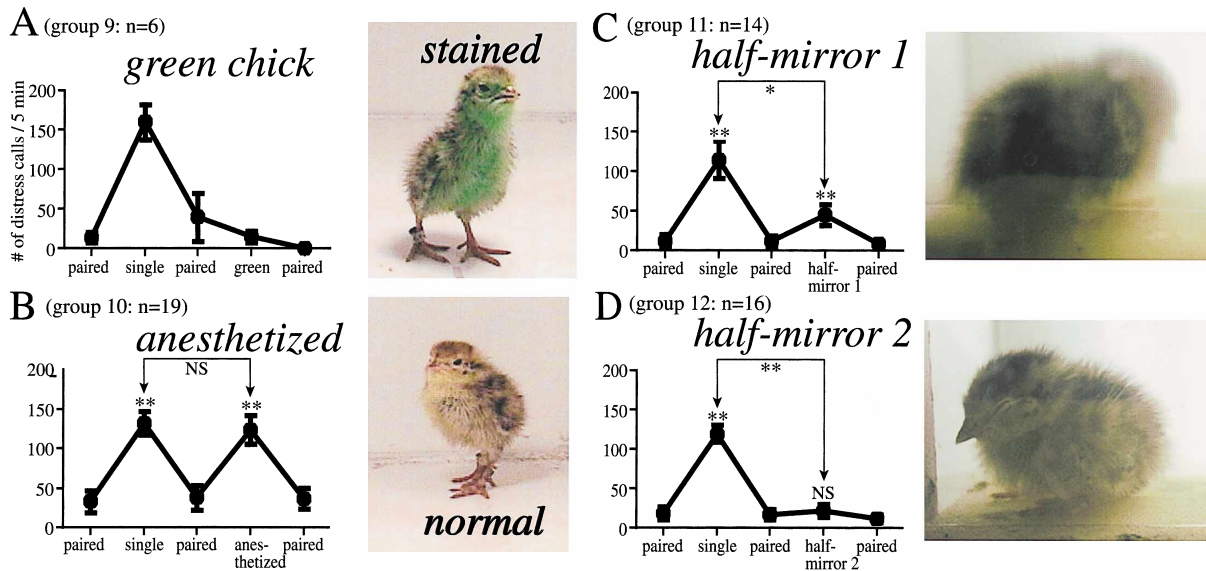
was absent in the *TFT* (**group 6**) and the *Speaker* (**group 7**) conditions and present in the *separated* (**group 8**) condition; no obvious correlations between the possible olfactory cues and the call suppression. Visual cues thus proved critical.

### Experiment-3

For suppressing the distress calls, visual TFT images were effective but not completely. What aspects of the TFT image caused the suppression, and why the suppression was incomplete? Several possibilities can be considered about critical sub-modalities of the visual cues which the wild-type companion chicks could give rise to. These are; exact coloration, natural movements, patterning of the plumage at a high spatial resolution, or behavioral correspondence between the subject and the companion. In other words, we can argue that the TFT image differs from the wild-type companion in coloration. Otherwise, the chick on the TFT seems to move in an unnatural way for the subject. Or, the TFT image does not have a sufficient spatial resolution, while chicks need fine details of the visual images. Or, chick on the TFT does not respond to the subject, thus fails to give some behavioral signals necessary for call suppression. The following 4 experimental groups were designed in order to examine these possibilities.

In **group 9**, experimentally altered coloration did not impair the ability of the wild-type chick to suppress the distress call (Fig. 4A). The green chick, however, perfectly suppressed the calls just as the companion chick of normal plumage. Exact coloration thus does not appear to be critical, though we did not try other colors, e.g., reddish or blue chicks. In **group 10**, where an anesthetized chick of wild-type plumage was presented, distress calls were not suppressed at all,

## experiment-3



**Fig. 4.** Effects of altered / degraded visual images on the suppression of distress calls. A: chick stained in green. B: anesthetized chick. C: obscured image of a wild-type chick through one-way half-mirror 1. D: clear image of a wild-type chick through half-mirror 2. Photographs on the right show a stained chick (A), a normal wild-type chick (B), and visual image of a wild-type chick viewed through the half-mirror 1 (C) and 2 (D), respectively.



and the subject behaved as if no chicks accompanied (Fig. 4B). Visual images of normally behaving chick are definitely needed.

Further experiments using half-mirrors suggested the importance of high spatial resolution in the visual images. In **group 11** (Fig. 4C), vague images viewed through the half-mirror 1 partially suppressed the calling, whereas clear images through the half-mirror 2 completely suppressed the calling in **group 12** (Fig. 4D). A high spatial resolution of the chick image is thus important. It should be emphasized again that the companion chick was placed in the illuminated partition. The subject was therefore paired with a companion chick that did not see the subject, similarly to the case with the TFT images. Mutual behavioral correspondence, if any, thus is not relevant.

## DISCUSSION

### Do distress calls really reveal the internal representation of conspecifics?

The following conclusion can be drawn from the present study. Visual image of an actively moving chick should be given for suppressing the distress calls in socially isolated chicks. Wild-type plumage patterns should be viewed at a high spatial resolution, while precise coloration and auditory / tactile / olfactory stimuli are not relevant. However, the sensory cues effective in suppressing the distress calls might not tell us directly about the internal representation of the conspecifics, which the subject chicks could have in mind.

Discrepancies between the present study and others might be suggestive. In this study, the chicks' own images on the mirror did not completely suppress their calls (**group 3**, Fig. 2C), and thus were presumed to provide insufficient cues as conspecifics. On the other hand, it has been reported that adult jungle crows perceive their own mirror images as representing other conspecific individuals (Kusayama *et al.*, 2000). These different conclusions could be ascribed to differences in age and species of subjects, or to different behavioral paradigms adopted.

A similar discrepancy occurs also on the issue of individuality. In this study using quail chicks, an unfamiliar chick was equally effective as the true companion with which the subject was reared (**group 2**, Fig. 2B). This means that subtle differences in individual external appearances do not matter. On the other hand, it is reported that domestic chicks show significantly more pecks at unfamiliar chicks than at familiar individuals, even after the subjects were exposed to the companion for only 16 hr (Zajonc *et al.*, 1975). Their study clearly showed that chicks have the ability to distinguish an unfamiliar individual from familiar ones. Similarly, it is reported that pigeons discriminate individuals visually under an operant conditioning (Watanabe and Ito, 1991). Quail chicks can distinguish individuals but may not care about individual differences, so long as critical cues are present for suppressing the distress calls. Otherwise, quail chicks may not have a capability to discriminate individuals. Further studies are needed on this

point.

### Critical cues for suppressing distress calls

Of the possible cues, we will discuss the issues of spatial resolution and coloration of visual images, olfactory cues, and behavioral correspondence in further details.

#### *Spatial resolution*

A high spatial resolution seems to be critical, as was shown in the series of experiments using the TFT monitor (**groups 5 and 6**) and the coarse half-mirror 1 (**group 11**). The size of single pixels on the TFT (0.27 mm×0.32 mm) was finer, but almost comparable to the size of cross-stripes of the half-mirror (0.4 mm×0.4 mm). Visual stimuli obtained through these apparatus should have been filtered, so that components of high spatial frequency above 3–4 cycles / mm were eliminated. In general, birds can see objects at a high spatial resolution despite their relatively small eyes. For example, pigeons can detect up to 18 cycles / degree (Hodos, 1993). The value of 18 cycles / degree corresponds to ca. 20 cycles / mm if viewed at a distance of 50 mm. Though comparable data are not available for quail chick vision, we can assume that the TFT display and half-mirror 1 did not have sufficiently high spatial resolution.

#### *Coloration*

Several studies have reported that chicks can precisely memorize and discriminate colors (Aoki *et al.*, 2000; Osorio *et al.*, 1999). Also, from a study of sexual imprinting, it was reported that mate choice in sexually mature quails is dependent on plumage coloration (Bateson, 1978, 1982). Male quails showed the highest preference for those females who had slightly different colors from the companions to which the subject males had been exposed as juveniles, a phenomenon known as optimal out-breeding. In this study, however, chicks stained a greenish color (**group 9**, Fig. 4) proved to be similarly effective to normal companions in suppressing the distress calls. It is therefore supposed that chicks might have recognized the green chick, but were not concerned with the strange coloration as far as distress calling was concerned.

#### *Olfactory cues*

It has been documented that chicks depend on olfaction for food selection (Turro *et al.*, 1994) and discrimination of familiar objects (Vallortigara and Andrew, 1994). Although we did not examine olfactory cues in this study, they would seem irrelevant for the suppression of distress calls. Separation by a transparent plate (**group 8**, Fig. 3D) or half mirror 2 (**group 12**, Fig. 4D) failed to increase, in fact decreased, the number of distress calls, and such separation if anything would have obscured the olfactory cues. Experiments using TFT display (**groups 5 and 6**, Fig. 3A and B) also support the idea that chicks do not depend on the smell of conspecifics.

#### *Behavioral correspondence*

Two-way behavioral correspondence, or social interactions, between chicks may not significantly influence the distress calls. In **group 12** where half-mirror 2 was used (Fig. 4D), the companion did not see the subject in the darker partition; visual interactions were one-way. Interactions by way

of vocalization and other auditory cues can also be disregarded, because the sound replay via speakers (group 7, Fig. 3 C) was not effective.

### Innate nature of visual cues

It remains to be answered as to whether the visual cues are innate or acquired post-hatch. It has been reported that male quail chicks memorize visual images of their companions when they were juveniles (Bateson, 1978, 1982). Also in the filial imprinting, domestic chicks can be trained to follow either a fowl (natural object) or a box (artificial object) (Horn, 1985, 1998). However, the preference in the box-exposed chicks gradually declines within a few days after imprinting. On the other hand, the preference in the fowl-exposed chicks is gradually strengthened (Johnson *et al.*, 1985). This means that, even in learning paradigms such as imprinting, the preference is innately biased in favor of natural objects. The visual cues revealed in this study might also be ascribed to the innate predisposition toward natural objects such as the wild-type plumage.

### Neural substrates for controlling distress calls

The neural substrates for distress calling may be linked with cognitive / mnemonic functions, as has been pointed out in the INTRODUCTION. Several research strategies should be pursued in the near future. By searching for brain regions where localized lesions cause disinhibition of the distress calls, or "prosopagnosia" in chicks, one might be able to localize the brain regions specifically involved in the recognition of conspecific chicks. Single unit recordings in freely behaving chicks (Yanagihara *et al.*, 2001) might also be adopted in these brain regions in the search for neurons coding visual images of chicks. The archistriatal complex (Davies *et al.*, 1997; Lowndes *et al.*, 1994) is one among the most plausible candidate regions where the emotional state meets the cognitive process, thus favoring the establishment of imprinting (ten Cate, 1986).

## ACKNOWLEDGEMENTS

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