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A review article prepared for *Zoological Science*

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**Title:**

**Mind through chick eyes: memory, cognition and anticipation.**

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1 **Abstract**

2  
3 To understand the animal mind, we have to reconstruct how animals recognize the external world  
4 through their own eyes. For the reconstruction to be realistic, explanations must be made both  
5 in their proximate causes (brain mechanisms) as well as ultimate causes (evolutionary  
6 backgrounds). Here, we review recent advances in the behavioral, psychological, and  
7 system-neuroscience studies accomplished using the domestic chick as subjects. Diverse  
8 behavioral paradigms have been reviewed (such as filial imprinting, sexual imprinting, one-trial  
9 passive avoidance learning, and reinforcement operant conditioning) in their behavioral  
10 characterizations (ontogeny, sensory and motor aspects of functions, fitness gains) and relevant  
11 brain regions. We will stress that common brain processes are shared by these distinct  
12 paradigms, particularly those in the ventral telencephalic structures such as AIv (in the  
13 archistriatum) and LPO (in the medial striatum). Neuronal ensembles in these regions could  
14 code the chick's anticipation for forthcoming rewards, particularly the quality/quantity and the  
15 temporal proximity. Without the internal representation of the proximity codes in LPO,  
16 behavioral tolerance will be lost, and the chick shows impulsive choice for less optimized goals.  
17 Functional roles of these regions proved compatible with their anatomical counterparts in the  
18 mammalian brain, thus suggesting that the systems linking between the memorized past and the  
19 anticipated future have remained highly conservative through the evolution of the amniotic  
20 vertebrates during the last 300 million years. Future interesting research topics will also be  
21 discussed in terms of behavioral deviations from optimized foraging, such as "*naïve curiosity*,"  
22 "*contra-freeloading*," "*Concorde fallacy*," and "*altruism*" in bird behaviors.

23 (250 words)

24

1 **1. Introduction to the issue of “animal mind”**

2 Do animals have mind? Do non-mammalian vertebrates in particular have mental  
3 processes similar to humans? Recent advances in *evolutionary (or, comparative) cognitive*  
4 *neuroscience* have shown a variety of non-mammalian cases, which suggest common mental  
5 processes. Particular attention has been paid to the high cognitive capability of birds. A short  
6 list of such outstanding researches includes; visual recognition of subjective contour in barn owls  
7 (Nieder and Wagner, 1999), episodic-like memory in food-storing bird (scrub jays) (Clayton and  
8 Dickinson, 1998; also see Emery and Clayton, 2001), discrimination of paintings by *Picasso* and  
9 *Monet* in pigeons (Watanabe *et al.*, 1995; Watanabe, 2001), and verbal communication and  
10 Piagetian development of cognition in parrots (Pepperberg, 2002).

11 One of the possible ideas is that birds have mind similar to us, and the similarity is due to  
12 common selective pressures that are shared by birds and humans. The similarity therefore  
13 represents an *analogy* or a *homoplasy* (footnote 1) due to evolutionary convergence. In other  
14 words, they are similar but different from us. Alternative idea is that the physiological  
15 constraint is so strong and the brain-mind linkages cannot easily be dissociated. The similarity  
16 could therefore represent a *homology*, and the mental process is deeply rooted in the common  
17 Bauplan of our brains. We could therefore argue that they are basically identical to us.

18 To address this question in a scientifically realistic manner, we have accomplished a series  
19 of neuro-behavioral studies to unravel the brain-mind linkages using chicks of the domestic  
20 chicken and the Japanese quails. In this review article, we will synthesize our recent findings in  
21 close comparisons with their mammalian counterparts. We will focus mostly on the issue of  
22 cognitive processes in the domestic chicks, and would rather regret to miss the recent advances  
23 in songbird studies; please see reviews (Doupe and Kuhl, 1999; Carr, 2000; Okanoya, 2002).  
24 We would also encourage readers to refer to monographs by Vouclair (1996), Rogers (1997), and  
25 Hauser (2000) for extensive facts and discussions on the issues of “animal minds.”

26

27 **2. Backgrounds: evolution and brain anatomy of birds**

1        In this session, as an introductory note, we will briefly review some of the important issues  
2 that have long caught attentions of, or even annoyed, the avian neurobiologists; i.e, the evolution  
3 of birds and the nomenclatures of brain structures.

4  
5        ***Evolution of amniotes*** According to the current view of evolutionary relationships among  
6 jawed vertebrates, several lines of early amniotes derived from a common ancestor during the  
7 Carboniferous in the Paleozoic era, c.a. 320 million years ago (Carroll, 1988). Amniotes  
8 therefore constitute a monophyletic group composed of synapsids (leading to mammals),  
9 diapsids (leading to dinosaurs and birds), and anapsids (leading to extinct reptiles; the linkage to  
10 the present turtles is still questioned), the classification based on the patterns of temporal  
11 openings in the skull as the critical cue. Ancestors of mammals are supposed to date back to  
12 the amniotic origin, and showed a massive diversification during the whole period of the  
13 Permian. Most groups of the primitive mammals perished at the Permian mass extinction,  
14 however, some survived, giving rise to the Triassic cynodonts. Accordingly, all of the late  
15 Mesozoic and Cenozoic mammals are supposed to have stemmed from this group. During the  
16 era of great reptiles, or dinosaurs, the cynodonts stayed relatively small in their diversity. With  
17 their small size and high metabolic activities, shrews-like ancestors survived without major  
18 changes until the dawn of the Cenozoic era.

19        ***Origin of birds*** Origin of modern birds dates back to the Jurassic in the Mesozoic era,  
20 about 200 million years ago. The idea that the birds are rooted in the theropod dinosaurs has  
21 gained more and more supports from recent fossil records of common features shared by birds  
22 and theropods such as wishbone, breastbone, and feathers (Norell *et al.*, 1997; Qiang *et al.*, 1998).  
23 Although the intensive and earnest research activities have suffered from a fossil forgery (Zhou  
24 *et al.*, 2002), steady lines of evidence have been accumulated for the theropod origin of the  
25 modern bird. However, consensus has not yet been reached, and an alternative hypothesis of  
26 older origin of the modern birds is still holding.

27        ***Bird brain*** In accordance with the evolutionary relationships, brain of the amniotic

1 vertebrates share many features in common. Neural organizations of subtelencephalic  
2 structures such as spinal cord, medulla oblongata, cerebellum, pons, mesencephalic, and  
3 diencephalic structures (optic tectum, tegmentum, thalamic and hypothalamic nuclei) are  
4 basically comparable wide among different classes of amniotes (Butler and Hodos, 1996). On  
5 the other hand, correspondence of telencephalic structures is much more vague, and has long  
6 been debated, seeking for the genuine homological relationships.

7 ***Traditional nomenclature*** Traditional nomenclature has been used since it was  
8 summarized by Ariens-Kappers and his colleagues (1936), but now the presently used  
9 terminology has proved to be terribly misleading. For the brain atlases available to date, see  
10 Kuenzel and Masson (1988) for the domestic chick, and also see Karten and Hodos (1967) for  
11 the pigeon. According to the traditional view, most of the avian telencephalon was equated to  
12 sub-regions of the basal ganglia (or striatum) in the mammalian brain, and the nuclei were given  
13 names with “striatum” as post-fix; e.g., paleostriatum, archistriatum, neostriatum, and  
14 hyperstriatum. Actually, Golgi study (Tömböl *et al.*, 1988a, 1988b; Tömböl, 1995) shows that  
15 cytoarchitecture of these avian telencephalic nuclei are somewhat similar to the mammalian  
16 striatum.

17 ***Genuine homologies*** However, data obtained by analyses of embryonic gene expression  
18 patterns (Fernandez *et al.*, 1998; Puelles *et al.*, 2000), and detailed neurochemical examinations  
19 of transmitter and receptor types together with hodological data for neuronal connectivities  
20 (Reiner *et al.*, 1998; Durstewitz *et al.*, 1999), revealed that a considerable portion of these  
21 “striatal” structures have nothing to do with the mammalian striatum, or caudate-putamen in the  
22 primate telencephalon. Instead, structures in the dorsal telencephalon are actually homologous  
23 to the mammalian cortex (Shimizu, 2001; Medina and Reiner, 2000), even though they lack  
24 laminated (layered) architecture and pyramidal neurons characteristic of the mammalian cortex.  
25 The ventro-medial telencephalic (sub-pallial) structures, on the other hand, proved to be highly  
26 conservative in their neural characters (Reiner *et al.*, 1987; Reiner *et al.*, 1998), thus some of  
27 them could deserve the post-fix of “striatum.” It remains still controversial as to whether the

1 major evolutionary changes occurred at the transition from amphibians to the amniotes (Reiner *et*  
2 *al.*, 1998), or at the transition from finned anamniotes to tetrapods (i.e., at the origin of  
3 amphibians) (Marín *et al.*, 1998).

4 ***Nomenclature reform*** The traditional terminology is now under a reform in the  
5 contemporary view of the evolution of telencephalon. Organized by E.D. Jarvis (Duke  
6 University, USA) and H. Karten (University of California San Diego, USA), comparative  
7 neuroanatomists formed a platform called “Avian Brain Nomenclature Exchange” (refer to the  
8 website <http://jarvis.neuro.duke.edu/nomen/>). We will soon find the final form of the  
9 nomenclature report to be published, and most of the avian researchers will follow the proposal.  
10 The basic idea underlying the reform is that the inappropriate post-fix “striatum” should be  
11 removed, leaving many of the abbreviations unchanged. In this review, we will follow the  
12 traditional (and therefore incorrect) terminology, but state the homological relationships to the  
13 mammalian counterparts so far as reasonable consensus has been reached.

14

### 15 **3. Imprinting**

16 Chicks are born learners. When exposed to a conspicuous moving object for several hours,  
17 newly-hatched chicks of precocial birds selectively form a social attachment to that object; the  
18 process widely known as filial imprinting. Since it was documented by K. Lorenz, the  
19 imprinting has been assumed to be a simple but unique case of recognition learning (see review  
20 by Shettleworth, 1998) with many characteristic features; i.e., fixed nature of the sensitive period  
21 and irreversibility; for a critical examination of the fixed nature of sensitive period, see Bateson  
22 (1979). For comparisons with other forms of learning, see table 1. We should emphasize that  
23 the imprinting is not a passive process in which an exposure to the hen-like object is sufficient.  
24 Instead, a behavioral contingency must be established between actions of the subject chick and  
25 the imprinting object for an intense preference to be formed (ten Cate, 1986). Similar  
26 requirement of social interactions has been pointed out also in the sensory phase of song learning  
27 in zebra finches (Houx and ten Cate 1999).

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**ARE model** Attempts have been therefore accumulated toward finding common features of imprinting shared by other learning paradigms such as sexual imprinting, operant conditioning and Pavlovian conditioning (see Hollis *et al.* 1991 for review). Theoretical study using an abstract neural-net model (Analysis-Recognition-Execution model, or ARE model; Bateson and Horn, 1994) has been actually successful in unifying the learning paradigms in terms of common representations shared by distinct learning processes. Different learning paradigms could be understood in terms of distinct combination and distinct changes in connectivities among the presumed sub-processes of A, R, and E. However, biological implementation of the sub-processes (such as A, R, and E) into relevant brain structures remained totally untouched.

**Brain mechanisms** Due to the high tractability of ducklings, goslings or domestic chicks as experimental subjects and reproducibility of the learning, the underlying brain mechanisms have been intensively studied in terms of relevant brain regions involved, underlying neurochemical cascades, and accompanying morphometric changes in neural structures (see reviews by Horn, 1985, 1998; Bolhuis and Honey, 1998; Bolhuis, 1999). Research activities have been concentrated on a telencephalic region abbreviated as IMHV (or, intermediate medial hyperstriatum ventrale). Note that the IMHV has nothing to do with the mammalian striatum; readers are rather requested to regard the term “IMHV” as a label for a distinct brain region, instead of “a portion of ventral striatum” that is just incorrect. The IMHV was initially identified as a region where the training procedure of imprinting selectively enhanced the uptake of radio-active uracil (Horn *et al.*, 1979) and also of radioactive 2-Deoxyglucose (Kohsaka *et al.*, 1979). Hodological (tract-tracing) study (Bradley *et al.*, 1985) revealed that the IMHV have reciprocal connections wide with telencephalic structures that include hyperstriatum accessorium (area analogous to the primary visual cortex in mammals; not a “striatal” region) and archistriatum (a complex of structure analogous to the limbic and somato-motor cortices in



1 mammals; also see below), suggesting that the IMHV could function as a cite for association of  
2 signals issued from multimodal sensory inputs (see also Durstewitz *et al.*, 1999).

3 ***Acquisition and retention*** Localized lesions placed in the bilateral IMHV (i.e., IMHV  
4 regions in both right and left hemispheres) actually proved to prevent the chicks from successful  
5 learning in the imprinting paradigm (McCabe *et al.*, 1981); therefore, IMHV is necessary for  
6 acquisition. When the IMHV was lesioned soon (within 3 hours) after the imprinting training,  
7 on the other hand, the ablated chicks also showed significantly less selective approaches at test  
8 accomplished at 24 hours post-training (McCabe *et al.*, 1982a); the IMHV is also necessary for  
9 retention at least for several hours after the end of training. When the bilateral lesions were  
10 made much later (6 hours or afterwards), however, the ablated chicks showed selective  
11 approaches at test; the IMHV is no longer required for recall (McCabe *et al.*, 1982b).

12 ***Permanent and transient storages*** In a further series of sequential unilateral IMHV  
13 lesions (i.e., the right IMHV was ablated, and subsequently the left IMHV was lesioned, or *visè*  
14 *versa*), functional laterality has been shown in the involvements of the IMHV in memory  
15 formation (for detailed review, see McCabe, 1991). Briefly, the left IMHV is supposed to be a  
16 long-term storage site for the imprinting memory, whereas the right IMHV acts as a buffer  
17 storage (Cipolla-Neto *et al.*, 1982; also see Bolhuis and Honey 1998). The right IMHV is  
18 required for another memory trace to be formed outside of the bilateral IMHV with a  
19 considerable delay (6 hours or longer). In other words, the memory traces are supposed to be  
20 represented in multiple brain regions, and copies are subsequently delivered from the right  
21 IMHV to other regions. The memory trace stored outside of the IMHV is referred to as S'  
22 [S-dash], although its location has not been identified so far. Since the IMHV was assumed to  
23 be the major storage site of permanent memory, studies on the neural basis of imprinting have  
24 been concentrated on IMHV.

25 Recently, Nicol, Horn and their colleagues have been successful in analyzing single neuron  
26 activities in freely-behaving chicks both during and after the imprinting training (Nicol *et al.*,  
27 1995, 1998; Horn, 1998; Horn *et al.*, 2001). Population of neural correlates of the imprinting

1 object (such as coding of the color and the shape) in IMHV increased as the training proceeded,  
2 thus yielding direct evidence for the IMHV as a constituent of the memory system. For the  
3 system-level understanding of imprinting, however, we must specify what aspects of behavioral  
4 execution the IMHV is responsible for.

5 ***Recognition of occluded image and biological motion*** Imprinting has been useful also in  
6 revealing the cognitive capability of chicks. Selective approaches toward partly occluded  
7 imprinting object have suggested that the chicks can utilize the partial visual features for  
8 recognition (Regolin and Vallortigara, 1995). Further analysis of orienting behaviors toward a  
9 hidden imprinting object has successfully shown that the chicks can maintain the location of  
10 invisible (hidden) object for up to 3 min (Vallortigara *et al.*, 1998), similarly to the delayed  
11 matching-to-sample task. Object permanence and working memory have, however, not yet  
12 approved unequivocally in the chick. Chicks can also recognize the imprinting object by its  
13 biological motion, or point-light animation sequences depicting a walking hen (Johanson's  
14 biological motion; Regolin *et al.*, 2000). All these facts suggest a high degree of similarity in  
15 the capability in visual cognition between the newly-hatched chicks and the humans.

16

#### 17 **4. Passive avoidance learning**

18 Chicks also learn by association. Development of the one-trial passive avoidance task in  
19 the domestic chick is credited to Cherkin (1969). This task takes advantage of the innate  
20 tendency of chicks (up to 3-5 days post-hatch) to peck at visually conspicuous small objects in a  
21 non-selective manner. When a colored bead is presented, chicks repeatedly peck at the bead  
22 even when the pecking gives rise to no immediate consequences such as food delivery. Instead,  
23 when the bead was soaked in a strong bitter liquid, the chick would peck at the bead once, taste  
24 the solution, and show characteristic disgust responses such as head shaking and bill-wiping.  
25 Within a few to several tens of minutes, the chicks become somewhat depressed or inactivated,  
26 and even falling in sleep. Afterwards, the chicks recall the visual characteristics of the bead  
27 (mostly the color; Aoki *et al.*, 2000), and learn not to peck at the similar beads.

1        ***Taste aversion*** Passive avoidance learning has some features common with the taste  
2 aversion learning (Mazur, 2002); in both cases, the memory is formed only after one-trial  
3 experience of association, and the chick learns to avoid the object. However, these two  
4 paradigms can be clearly distinguished. In the taste aversion, the subject animal was given a  
5 food, and subsequently an intra-peritoneal injection of a LiCl solution that makes the animal feel  
6 ill several hours afterwards. The taste-aversion is assumed to represent a case of classical  
7 conditioning, with the food acting as a conditioned stimulus, and the illness as an unconditioned  
8 stimulus. However, the taste-aversion does not require a strict contingency of events to be  
9 associated; the induced illness causes the subject to recall the characteristics of food that was  
10 ingested several hours previously. In the passive avoidance, on the other hand, a strict temporal  
11 contingency is required between pecking the bead and tasting the bitter liquid; a delayed delivery  
12 of the bitter liquid by only 5 min, chicks failed to form the avoidance memory (M. Aoki and T.  
13 Matsushima, unpublished data).

14        Fitness gains of the chick's high performance in this task could be that the capable chicks  
15 have higher chance of survival because they can avoid bitter-tasting, therefore possibly  
16 poisonous objects. This argument is however questionable because of the following reasons.  
17 First, the bitter taste does not necessarily mean a poisonous food; the taste-aversion paradigm  
18 would be much more adaptive in this context. Second, the avoidance memory quickly  
19 generalizes within 24 hours after the training, so that the learned chicks would have a risk of  
20 avoiding even edible food items with slightly different colors (Aoki *et al.*, 2000).

21        ***Common brain mechanisms*** The underlying brain mechanisms for the formation of  
22 passive avoidance memory have been intensively studied in terms of neurochemical and  
23 morphological correlates (see reviews by Rose 1991, 1995; Rose and Stewart 1999). Rose's  
24 research strategy has been to identify specific changes at the molecular level, which have direct  
25 correspondence with the memory formation (Rose, 1993). Most importantly, time course of the  
26 changes must be compatible with development of the learning. The passive avoidance task is  
27 appropriate in this context, because the memory is established in single and short training trial.

1 Experimenters can thus identify the exact instance when the memory is formed; in the imprinting  
2 paradigm, on the other hand, chicks are exposed to the imprinting object for a couple of  
3 1-hour-long training sessions.

4 ***Neurochemical approaches*** Again, the IMHV proved to be involved in the passive  
5 avoidance (Rose and Csillag, 1985; Davies *et al.*, 1988). Learning-specific permanent changes  
6 were identified also in another brain region referred to as LPO (lobus parolfactorius) (Stewart *et*  
7 *al.*, 1987; Csillag, 1999). The LPO constitutes the medial part striatum, that is homologous to a  
8 complex of caudate-putamen / nucleus accumbens in mammals. In the IMHV, enhanced  
9 metabolic activities immediately after the training leads, through enhanced expression of  
10 immediate early genes (*c-fos*, but also see Yanagihara *et al.* (2001) for *ZENK* or *zif/268*) and  
11 expression of late response genes such as those coding cell adhesion molecules (NCAM and L1),  
12 to morphological changes in both pre- and post-synaptic structures. The permanent changes in  
13 LPO include; increase in the length of thickening of the post-synaptic density (indicative of the  
14 active zone) (Stewart and Rusakov, 1995), and enhanced neurogenesis in the post-hatch and  
15 post-training period (Dermon *et al.*, 2002). Although not all of these events have been fully  
16 understood in their functional roles, the cellular / molecular studies proved to be extraordinarily  
17 fruitful when applied to such a simple association learning as passive avoidance.

18 ***Underlying cognition.*** For system-level understanding, however, the passive avoidance  
19 task fails to give us few clues for elucidating the neural representations. First, chicks are  
20 trained once, and tested once for recall; any neuronal activities recorded in single trials cannot be  
21 a basis for reliable functional analyses. Second, memory contents of chicks are too much  
22 simplified; chick is either recalling (successfully avoiding the bead) or amnesic (pecking at the  
23 bead), without telling how the chick recognized the aversive bead.

24

## 25 **5. Spatial memory**

26 Chicks move. Along the movements, visual images on the retinal surface move  
27 accordingly. But, it is not the world that moves, but the chick itself. The chick must

1 reconstruct own location in space based on the changes in sensory signals. For the signal  
2 conversion, concurrent retinal images are referenced to the memorized images, so that place of  
3 the chick in a familiar space is determined. Internally represented reference for the localization  
4 is the *cognitive map*, which is supposed to be one of the universal mental toolkits shared by  
5 diverse animals with distinct evolutionary histories, such as desert ants, foraging honeybees,  
6 homing pigeons, and migrating salmon (Hauser, 2000).

7 ***Right or left*** Contemporary researches on the spatial memory in chicks emerged from a  
8 psychological study on the right-left asymmetry in position learning, indicative of a functional  
9 lateralization of telencephalic hemispheres (Vallortigara and Zanforlin, 1986; Vallortigara *et al.*,  
10 1988). Basically, the subject chicks (1-2 weeks post-hatch) are tested in a rectangular arena, the  
11 front wall of which is equipped with a pair of food container boxes. Chicks are introduced  
12 from the entrance on the other side of the arena, approach to the boxes, and are requested to peck  
13 either one of these two boxes; pecks at the correct box is immediately rewarded by an opening of  
14 the box for chicks to gain the food inside (Vallortigara *et al.*, 1996).

15 Taking an advantage of biased preferences for food items, it has been shown that the chicks  
16 memorize both of the content (“what” information) and the position (“where” information) of the  
17 boxes (Cozzutti and Vallortigara, 2001), reminiscent of the “episodic-like” memory in jays  
18 (Clayton & Dickinson, 1998). Briefly, under a control condition, chicks approaches to the box  
19 of their preferred food. When the chicks were fed sufficiently with the preferred food, the  
20 satiated chicks would re-orient to the other box, presumably due to the reduced attractiveness of  
21 the over-fed food; this process is referred to as “devaluation.”

22 ***Center of a place*** Further elegant experiments developed by the same group of Italian  
23 psychologists revealed that chicks adopt two distinct strategies in spatial localization (Tommasi  
24 *et al.*, 1997). In this paradigm, chicks were trained to find a food item hidden at the center of a  
25 training arena. The food was initially placed on the surface, and subsequently hidden in the  
26 sawdust on the floor. By simply observing the locations where the subject chick scratched the  
27 floor in a test arena, experimenters could study how the chick localized the center. The trick is

1 that the test arena differed from the training arena in either the size (with the shape being  
2 identical) or the shape (with the size being identical). In order to localize the center, the chicks  
3 could utilize either the absolute distance from one wall (local absolute cue), or depend on the  
4 equal distance from both of the opposing walls (global relational cue) (Tommasi and Vallortigara,  
5 2000). Surprisingly, the right and the left telencephalic hemispheres differed in localizing  
6 strategies; chicks with the operational right hemisphere (with its right eye covered by eye-patch)  
7 adopted the global cue, whereas chicks with the left hemisphere (with its left eye covered)  
8 searched for food based on the local cue (Tommasi and Vallortigara, 2001). Further unilateral  
9 lesion of hippocampus suggested that the global and local cues are separately stored in the right  
10 and left hippocampi, respectively (Andrew *et al.*, submitted).

11 ***Position as supplementary cue for association*** Position could serve an important cue for  
12 the chicks, which depend on seeds and grains scattered unevenly in their foraging ground. In a  
13 reinforced concurrent choice task, quail chicks proved to recognize beads primarily by color, and  
14 secondarily by position (N. Aoki and T. Matsushima, unpublished); the positional cue appeared  
15 operational only when the color cue was no longer available. It will be extremely interesting to  
16 see if the IMHV-lesioned chicks (therefore, possibly color-blind subjects; see below) could  
17 discriminate objects by the second supplementary positional cues. So far, on the other hand,  
18 color-cue dependent object discrimination proved to remain intact in the domestic chicks with  
19 bilateral hippocampal lesions (S. Nakajima and T. Matsushima, unpublished data), suggesting a  
20 possible double dissociation of neural representations of color and position.

21

## 22 **6. Memory of colors and shapes**

23 Chicks depend on vision. All of these paradigms depend on the chick's ability to  
24 recognize objects by visual cues. To examine the similarity and differences of visual world  
25 between chicks and us, systematic survey has been accomplished.

26 ***Color map*** With their tetra-chromatic nature of the retinal cone photoreceptor cells  
27 (ultra-violet, blue, green, and red; Bowmaker *et al.*, 1997), domestic chicks are supposed to be

1 endowed with acute sense of colors. Visual discrimination task with food reinforcement  
2 actually demonstrated that domestic chicks have accurate color memory for foraging (Osorio *et*  
3 *al.*, 1999); the pattern proved much less significant. Basically identical conclusion was drawn  
4 in the quail chicks, in which visual memory was examined by selective habituation and passive  
5 avoidance task (Aoki *et al.*, 2000). It is to be emphasized that chicks have a  
6 context-independent representation of colors. Subjective distance of a green measured from  
7 memorized image of a yellow was identical to the distance of the yellow from the green image  
8 (Aoki *et al.*, 2000); quail chick could have an internal color map as reference.

9 ***Genetic basis of color preference*** Experimental manipulations of color perception must  
10 be carefully accomplished, because the chicks have innate preference to specific colors and the  
11 preference is genetically determined (Kovach, 1980). With traditional inbreeding techniques,  
12 Kovach established several lines of quails with innate blue- and red-preference (blue- and  
13 red-line). Furthermore, quail chicks can be imprinted to the color opposite to their original  
14 preference by simply exposing the subject chicks to the color (Kovach, 1990). It is to be noted,  
15 however, that the genetically determined color preference reflects a selective choice for shorter  
16 (blue-line) or longer (red-line) wavelength, respectively. When confronted with a concurrent  
17 choice between yellow and green, chicks of the blue-line chose green over yellow; in the red-line,  
18 on the other hand, the same test revealed green preference over yellow. Innate color preference  
19 thus could represent a process, which is distinct from that involved in the color map based  
20 discrimination (Aoki *et al.*, 2000).

21 ***Neural basis of color discrimination*** In parallel with the two distinct processes of color  
22 discrimination, two relevant brain regions have been pointed out; a telencephalic region (IMHV)  
23 and a subtelencephalic region (dorsomedial thalamus). In a series of lesion experiments in  
24 passive avoidance task in domestic chicks, it has been shown that a post-training lesion placed to  
25 bilateral IMHV failed to cause amnesia (Gilbert *et al.*, 1991), in contrast to the pre-training  
26 lesion experiment (Davies *et al.*, 1988); it was thus concluded that the IMHV is required for  
27 acquisition, but not for recall, reminiscent to the functional involvement of the right IMHV in the

1 imprinting (see above; Cipolla-Neto *et al.*, 1982). Further examination of the post-lesion  
2 effects revealed, however, that the lesioned chicks avoided the bitter-tasting bead by some (yet  
3 unidentified) non-color cues (Patterson and Rose, 1992); memory-based color discrimination  
4 was selectively impaired. In contrast, lesion experiments on the innate color preference  
5 revealed that even total telencephaloectomy (the whole telencephalon aspirated on the hatching  
6 day) does not impair posture, sensori-motor coordination for pecking, locomotion, and selective  
7 approach to the genetically preferred color (Kovach and Kabai, 1993). Much smaller lesion  
8 localized in the dorsomedial thalamic complex proved to attenuate the genetically determined  
9 color preferences (Csillag *et al.*, 1995); lesions to an ascending visual pathway (nucleus  
10 rotundus) failed to have effects. Most probably, color is multiply represented in the chick brain,  
11 with distinct controls over the behavioral executions.

12 **Shapes** Objects might also be recognized by the shape cue. Actually, the domestic  
13 chicks with bilateral IMHV lesions were successful in avoiding the bitter bead by non-color  
14 cue(s) as has been described above (Patterson and Rose, 1992); the shape cue was supposed the  
15 most plausible candidate for discrimination. However, to date, even intensive examinations  
16 failed to reveal the chicks' ability to discriminate objects by shapes in quail chicks (Sakai *et al.*,  
17 2000; Ono *et al.*, 2002). Our inability to reveal the shape recognition might reflect the  
18 ecological situation of chicks, which do not depend on the food shape for selective foraging.  
19 Another study of visual behavior in the quail chicks (Hayashi *et al.*, 2001) suggested the chick's  
20 capability to discriminate conspecific hatchlings by fine plumage patterns; biological motion  
21 might be another cue as has been shown in imprinting (Regolin *et al.*, 2000).

22

## 23 **7. Neuronal representations**

24 Brain is full of spikes. But, the neuronal spikes tell us nothing, so long as we are unaware  
25 of their codes. To break the codes, we must find the causal link between the sensory signals  
26 and the neuron under study, i.e., in a *peripheral-to-center* approach of the "sensory physiology."  
27 In this approach, we understand how the brain detects specific features of an external stimulus



1 through a cascade of signal processing. We might also search for the causal link between the  
 2 neural activity and the behavioral execution, i.e., in a *center-to-peripheral* approach of “motor  
 3 control.” In this approach, we understand how the brain organizes coordinated behaviors. As  
 4 the third approach, we could directly penetrate into the mental process that may lie between the  
 5 (sensory) recognition and the (motor) execution. In this approach, we understand how the brain  
 6 makes decisions. We adopted the third approach, because it was important and new in the bird  
 7 researches. In the following, we will describe the task together with some technical tips, and  
 8 summarize the logical consequences of our recent findings (Yanagihara *et al.*, 2001; Izawa *et al.*,  
 9 2001, 2002, 2003).

10 ***Reinforced color discrimination task*** Housed in an experimental chamber, the subject  
 11 chick was presented with a bead (Fig. 1A). The bead was protruded from a hole on a wall for a  
 12 short period of time (2-4 sec cue-period). The bead was colored either in red, green or blue.  
 13 When a red bead was presented, chick was required to peck at the bead, and food reward was  
 14 subsequently delivered after a short delay (2-4 sec reward-period after a 1-sec delay). Red was  
 15 thus associated with a delayed reward via pecking as operant (*rewarded GO*). When a green  
 16 bead was presented, on the other hand, chick was required NOT to peck in order to be rewarded  
 17 (*rewarded NOGO*). When a blue bead was presented, chick learned not to peck, because  
 18 reward was not delivered irrespectively of whether the chick pecked or not (*non-rewarded*  
 19 *NOGO*). This is the basic configuration of the task designed and developed by Yanagihara *et al.*  
 20 (2001). In this task, we can clearly dissociate the overall procedure into distinct phases, i.e.,  
 21 perception of color, recall of association memory, execution of operant pecking, anticipation of  
 22 reward during the delay, recognition of food item, execution of food pecking, and finally  
 23 ingestion of food.

24 -----

25 Figure 1 around here

26 -----

27 ***Single neuron as a “pin-hole”*** By a miniature micro-drive mounted on the chick skull

1 together with FET-input buffer amplifiers, we obtained stable extracellular recording of action  
2 potentials (spikes) from single neurons continuously for up to 6-9 hours. But, what could a  
3 neuron tell us? What do we know by analyzing spiking behaviors of a single neuron, that is  
4 truly a “microscopic” entity among millions of similar cells in the whole brain? A simple  
5 rationale behind the single-unit analysis could be that we observe the whole brain system  
6 through the neuron as a “pin-hole.” Assume that a neuron is connected with a network. We  
7 search for positive correlation of the neuronal firing with various behavioral events, and  
8 fortunately find a link. For example, the neuron fires in response to a stimulus (light or buzzer)  
9 that is given in advance to delivery of reward (food or water). One interpretation is that the  
10 neuron codes the “memory-based anticipation of the forthcoming reward.” If we could dissect  
11 out the neuron under study and put it in a culture dish, however, the neuron might generate a  
12 regular pattern of spikes in isolation, but the spiking would tell us nothing about “anticipation”  
13 any longer. Without that neuron, on the other hand, rest of the whole brain would “anticipate”  
14 the reward by the associated stimuli, due to redundant organization of the brain. The link  
15 between spikes and the code is not an attribute to the neuron; instead, it is an attribute to the  
16 whole brain system. For the observer, the neuron operates as a “pin-hole,” and the projected  
17 “image” represents the whole relevant process viewed from that neuron. One recorded neuron  
18 produces one “image,” and thousand simultaneous neuronal recordings gives rise to thousand  
19 “images” of the single brain. Thus, our job is to synthesize the brain performance from these  
20 thousand of “images.”

21 ***Memory correlates in IMHV.*** Neuronal “pin-hole images” of memory should meet at  
22 least the following criteria. First, changes in the neuronal spikes (excitatory or inhibitory)  
23 should occur in response to the presentation of associated stimuli in a specific manner. Second,  
24 the responses should emerge only after relevant training, showing a good parallelism with the  
25 memory retention. Neuronal spikes that meet these criteria have been found in the chick brain  
26 in several different regions including the IMHV. Using the imprinting paradigm, it has been  
27 established that IMHV contains neuronal correlates of the imprinting memory (Nicoll *et al.*,

1 1995, 1998; Horn *et al.*, 2001). Some IMHV neurons responded specifically to a combination  
 2 of color and shape, whereas others showed generalized responses to color or shape. These  
 3 authors argued that the IMHV neurons principally represent stored visual features of the  
 4 imprinting object.

5 ***Code of attention in IMHV*** In our reinforcement learning paradigm, on the other hand,  
 6 IMHV neurons responded to wider range of objects, such as rewarding colors as well as novel  
 7 colors. When habituated, presentation of a familiar color failed to elicit any responses (E-I  
 8 Izawa, S Yanagihara, and T Matsushima, unpublished data). Most probably, these IMHV  
 9 neurons are related to the chick's subjective "attention," or what appears conspicuous to the  
 10 chick. Note that the "attentions" should be generated only after specific experience with the  
 11 rewarding colors. Similarly, the novelty responses should appear only after the chick had  
 12 experienced, memorized and recalled a finite number of colors. In this sense, these responses  
 13 represent the memory, and our interpretation of the IMHV as "attention-generator" fits the  
 14 memory trace hypothesis. A possibility is not excluded that the memory trace resides  
 15 somewhere outside of the IMHV, and the IMHV neurons responded secondarily. To localize  
 16 the memory trace, therefore, we should systematically survey the brain regions that are  
 17 interconnected with the IMHV; these candidate regions include, e.g., visual Wulst in the dorsal  
 18 pallium, Arc (archistriatum), and LPO.

19 ***Anticipation code and "paradox" in LPO*** Survey of the task-related neuronal activities in  
 20 the LPO revealed two important populations of neurons. One group of neurons fired  
 21 specifically to the visual cues associated with the reward, i.e., those responded in the cue- /  
 22 delay- periods in both of the *rewarded GO* and *rewarded NOGO* trials, but not in the  
 23 *non-rewarded NOGO* trials (Yanagihara et al. 2001; E-I Izawa and T Matsushima unpublished).  
 24 Most probably, these neurons coded the memory-based *anticipation* of the forthcoming food  
 25 reward. Another group of neurons fired when the chick actually gained a reward; a subset of  
 26 these neurons fired irrespective of whether food or water was gained. Neurons of the second  
 27 group might represent chicks' subjective *evaluation* of the gained reward.

1       What do these codes (*anticipation* and *evaluation*) do in the behavioral execution? The  
2 *evaluation* code could be responsible for the formation of novel cue-reward associations. If this  
3 were the case, localized LPO lesion should result in an acquisition failure (anterograde amnesia).  
4 Otherwise, the anticipation code could be responsible either for selective execution of  
5 color-selective pecking. If this were the case, LPO lesion should result in a recall error  
6 (retrograde amnesia). In a series of lesion experiments (Izawa *et al.*, 2001, 2002, 2003), we  
7 analyzed the effects of pre-training and post-training lesions on a variety of learning paradigms  
8 in the domestic chicks; i.e., filial imprinting, passive avoidance learning, water-reinforced color  
9 discrimination task, food-reinforced GO-NOGO task, and food-reinforced concurrent choice task.  
10 For the imprinting, both of pre- and post-training lesions caused no effects. For the  
11 reinforcement learning, similar LPO lesions caused severe deficiency in the acquisition, whereas  
12 the learned associates were recalled without difficulties. Therefore, the *evaluation* code in LPO  
13 could actually have a role. For the GO-NOGO color discrimination task, similarly, the LPO  
14 lesion caused anterograde amnesia, but no retrograde amnesia. Here arises a “paradox.” The  
15 *anticipation* code is formed in LPO after the training, however, the LPO does not seem to be  
16 required for execution of selective pecking. Without the memorized code, how could chicks  
17 execute the correct operant pecking?

18       ***Impulsiveness and behavioral tolerance*** One possible way to account for the “paradox”  
19 is to assume that the *anticipation* code in LPO is responsible for some other functions than  
20 behavioral execution *per se*. Alternative account for the “paradox,” though not exclusive, is  
21 that the *anticipation* code is multiply represented in various regions of the brain, and the lesion  
22 localized in LPO failed to interfere with the link between the color and pecking.

23       In concurrent choice task (Fig. 1B), post-training LPO lesion actually had an effect. In this  
24 task, chicks learned to peck one of two simultaneously presented beads, e.g., red and yellow.  
25 Red bead was associated with a large reward (6 pellets of millet grain), and yellow with a small  
26 reward (1 pellet). Naturally, chicks learned to peck the red bead to gain the large reward. The  
27 choice differed when the large reward was delivered with a delay of 1-3 sec. When the red

1 bead was associated with a large but delayed reward (delay time of 3 sec), the chick learned to  
 2 choose the yellow bead to gain the small reward. For a delay of 1-2 sec, chicks proved to be  
 3 patient enough to wait for the large reward, just staring at the still empty food tray. Chemical  
 4 lesion of LPO (particularly the posterior LPO) ablated the chick-sized patience, thus unmasking  
 5 the underlying impulsiveness; no amnesia accompanied the lesion. With the *anticipation* code  
 6 in LPO neurons, the future gain would be “guaranteed” so that the chick reasonably suppressed  
 7 the impulsive action for immediate reward. In other words, past experiences yield an internal  
 8 representation of the future reward in LPO, and the represented reward makes the chick  
 9 behaviorally tolerant. At the neuronal level, we can further assume that the *anticipation*-coding  
 10 neurons in LPO could be responsible specifically for *temporal proximity*, rather than *quantity*  
 11 and *quality* of the reward; the *quantity* and *quality* of anticipated reward should be represented in  
 12 somewhere else in the chick brain. Note that the system for the patient choice is highly  
 13 adaptive, because the net gain (i.e., total amount of food obtained) could be optimized, thus  
 14 serving for a rapid growth and a higher chance of survival (see table 1).

15 ***Alternative code of anticipation in AIv*** Archistriatum located in the ventro-lateral  
 16 telencephalon might be in charge. In particular, the AIv region (a ventral subdivision of  
 17 intermediate archistriatum) has reciprocal connections with IMHV, and a massive efferent  
 18 projection to LPO (Székely *et al.*, 1994), thus could play an important role as relay center for the  
 19 memory formation (Davies *et al.*, 1997; Csillag, 1999). Actually, localized lesions to the Arc  
 20 are reported to prevent memory formation in passive avoidance learning (Lownders and Davies,  
 21 1994) as well as in imprinting (Lownders *et al.*, 1994). The “paradox” of LPO functions (see  
 22 above) might thus be explained by assuming an alternative code of cue-reward association in the  
 23 Arc. Actually, single-unit recordings revealed a population of Arc neurons that responded  
 24 specifically to the cues associated with reward (Aoki *et al.*, 2002, submitted). We should  
 25 examine whether these Arc neurons code the aspects of the anticipation, i.e., *quality* and / or  
 26 *quantity* of the forthcoming reward, rather than *temporal proximity*.

27

## 1 **8. Toward a synthesis: a biological implementation of the ARE model**

2 With the present data available, we can reasonably formulate a working hypothesis on the  
3 functional network; block diagram shown in Fig. 2 show the basic organization of the model.  
4 This model recapitulates some important features of the ARE model proposed for the imprinting  
5 (Bateson and Horn, 1994), and the functional network proposed for passive avoidance learning  
6 (Csillag, 1999).

7 Basically, the system is composed of 3 layers; layer of *Analysis* modules (A-layer),  
8 *Recognition* modules (R-layer), and *Execution* modules (E-layer). The A-layer is composed of  
9 Wulst, neostriatum (particularly its caudo-lateral part), ectostriatum, and hippocampal complex;  
10 these regions are mutually interconnected. The R-layer is composed of IMHV, AIv, and LPO  
11 (particularly its caudal part, cLPO). The E-layer is composed of optic tectum, cerebellum,  
12 reticular formation, and dopaminergic system (accompanied by non-dopaminergic SN subregion).  
13 Similarly to the ARE model of Bateson and Horn, the A-layer send signals to the E-layer directly  
14 and indirectly with a relay of the R-layer. As another important feature, dopaminergic system is  
15 incorporated as supervisor for memory formation to be made in LPO, archistriatum (its dorsal  
16 part), and neostriatum (dorsolateral region, in particular).

17 For the filial imprinting, LPO and tegmental dopaminergic nuclei (VTA and SN) are not  
18 involved, and the memory formation is accomplished mainly by the Hebbian type synaptic  
19 plasticity within the IMHV (Matsushima and Aoki, 1995; Yanagihara *et al.*, 1998). The role of  
20 the IMHV could be to associate visual features of the imprinting object scattered wide in the  
21 modules of the A-layer. Reciprocal connectivities between IMHV and Arch (Csillag *et al.*,  
22 1994; Davies *et al.*, 1997; Csillag, 1999) could be responsible for the emotional control of  
23 imprinting (ten Cate, 1986), although the idea to equalize the whole Arch to the mammalian  
24 amygdala (Aoki *et al.*, 2002) remains highly questionable. Most probably, the selective  
25 attachment and approaching behaviors could be executed by way of the direct descending system  
26 from Arch; actually a population of the Arch neurons proved to selectively code the cued  
27 movements, particularly those cued by the auditory stimuli (Aoki *et al.*, submitted).

1 For the passive avoidance learning, the same set of modules in the A-layer and the R-layer  
2 are involved as in the imprinting. Additional process is that the gustatory inputs contribute to  
3 the memory formation, probably via the dopaminergic control from tegmental nuclei to LPO  
4 (Stewart *et al.*, 1996). The memory formation might be performed by either (or both) of the  
5 plastic processes in IMHV and in LPO (Matsushima *et al.*, 2001), though neither one of these  
6 regions could be the principal site for permanent storage of memory, as has been discussed above.  
7 Taste aversion (caused by delayed illness) might be performed in the same assembly of networks,  
8 however the relevant neural mechanisms are not yet evident. Execution of the passive  
9 avoidance should be accomplished by a selective suppression of visuo-motor responses within  
10 the optic tectum through the brainstem reticular formation.

11 For the reinforced GO/NOGO color discrimination task, the functional roles of LPO and the  
12 tegmental dopaminergic neurons could be most significant (Yanagihara *et al.*, 2001; Izawa *et al.*,  
13 2001, 2002, 2003). Actually, our preliminary exploration revealed a neural code of reward  
14 within the VTA (Izawa E-I, Matsushima T, unpublished); these VTA neurons started to fire upon  
15 the presentation of food reward, and then started to fire at a high rate immediately after the chick  
16 actually gained food. Most probably, AVT neurons signal the reward, and gate the dopamine  
17 D1-receptor dependent synaptic plasticity within the LPO (Matsushima *et al.*, 2001). As to the  
18 execution, however, the final motor regions are not yet identified in the telencephalon, except  
19 that some AIV neurons coded preparatory activities selectively for the cued turning movements  
20 toward the target. Despite our efforts, we are still unable to identify pecking-relevant command  
21 signals within archistriatum and striatum (Aoki *et al.*, 2002); lateral striatum (or, paleostriatum  
22 augmentatum; homologous to the mammalian caudate-putamen) together with the pallidum (or,  
23 paleostriatum primitivum) might be involved (not shown in Fig. 2). Sensori-motor  
24 coordination of targeted movements at the bead could be accomplished within the optic tectum.  
25 Definitely, we need further intensive studies for fully understanding how the system works as a  
26 whole.

27

## 1 9. Scopes

2 With these findings in the chick brain and behavior in hand, we can make a list of future  
3 research topics. To address these topics, we will have to find novel behavioral paradigms in  
4 novel bird models, other than the domestic chicks discussed in this review. Here, we will focus  
5 on the following three issues.

6 ***“Observation learning”: a social transmission*** Chicks could learn also by observation.  
7 In addition to the own experiences of pecking and tasting as described above, the pecking  
8 preference can be socially transmitted from hens to day-old chicks (Suboski and Bartashunas,  
9 1984). Even a motor-driven arrow-shaped paper model, that moved its taper pointing to a  
10 colored bead, could tell a chick which object to peck. The chick subsequently pecked at the  
11 “instructed” bead object, even after the arrow-operation was removed. Authors argued that  
12 “information about the visual characteristics of food objects” could be transmitted from hens to  
13 chicks by the same process. Similar transmission of pecking selectivity is reported in the  
14 one-trial passive avoidance (Johnston *et al.*, 1998). Just by observing another individual  
15 pecking at a bitter bead, and subsequently showing disgust responses, day-old subject chicks  
16 learned not to peck at the same bead when tested afterwards. This finding is reminiscent of the  
17 finding in monkeys, in which a lasting phobia of snakes developed by observing another  
18 individual’s fearful reactions to a snake (Mineka, Davidson, Cook and Carr, 1984; cited by  
19 Mazur, 2002). Beside the well-documented effects of social context (being observed by other  
20 individuals) on the re-caching behavior in scrub jays (Emery and Clayton, 2001), chicks might  
21 also be endowed with a high ability to actively learn by observations. Development of a novel  
22 paradigm tractable for system neuroscience will enable us to penetrate into many interesting  
23 issues, such as how chicks observe others, how chicks convert the observed events into own  
24 behavioral rules, and what neural mechanisms are responsible for the conversion.

25 ***Deviations from optimal foraging: “naïve curiosity,” “contra-freeloading,” “Concorde***  
26 ***fallacy,” and “altruism”*** Chicks might be wise enough to actively “earn” information at the  
27 expense of immediate material benefits. In our controlled laboratory condition, week-old



1 chicks are trained and tested under a limited diet so that the chick's motive toward food reward is  
2 maximized. Consequently, chicks quickly learn the association between cue colors and reward  
3 quantity, so that chicks reliably choose a color associated with a larger reward (Izawa *et al.*,  
4 2003). In this context, chicks behave in accordance with the most normative theory of the  
5 optimal foraging (Alcock, 2001) with a slight modification that anticipated reward in the future  
6 should weigh proportionately less than the immediate gain. Internal representation of  
7 anticipated reward in the future plays a critical role.

8 The situation somewhat differs in day-old chicks. They are much more *curious*, pecking  
9 non-selectively at a variety of conspicuous objects they encounter. During the initial 3-4 days  
10 post-hatch, chicks survive by the yolk reserve and do not depend on food. During this period,  
11 chicks have to make up an internal directory of edible foods and non-edible objects of similar but  
12 distinct appearance such as gravels or ground debris. "*Naïve curiosity*," or an eagerness for  
13 information in the limited post-hatch period could play a critical role as internal representation,  
14 thus serving a biological basis for the passive avoidance learning and reinforced pecking tasks.

15 Deviation from the optimal foraging can also be found in adult birds, which often work (i.e.,  
16 pay behavioral "cost") for food even when the same food items can be freely available; a process  
17 known as "*contra-freeloading*" (Inglis *et al.*, 1997). The "*contra-freeloading*" has been  
18 reported in a variety of vertebrate species, including fish (*Betta splendens*), pigeons, domestic  
19 chicks, crows, starlings, rats, monkeys, chimpanzee, and humans. In this context, it is argued  
20 that animals have "a hunger for information," and a more information gain could offset the extra  
21 cost to be paid, so long as the immediate need for food is not so great.

22 In European starlings, it is further reported that the cost that had been paid for gaining food  
23 reward increased the preference in choice condition (Kacelnik and Marsh, 2002), in a clear  
24 contrast to the consequence predicted by the optimization theory. The authors claim that they  
25 can relate their finding of the behavioral "perversity" in birds to a phenomenon known as  
26 "*Concorde fallacy*," in which a behavioral choice is biased toward a recipient of big efforts in  
27 previous history, just as the maladaptive investments by developers to the supersonic airplanes

1 Concorde that simply did not pay. Though it is difficult to separate the effects of investment in  
2 the past and the effects of anticipated gain in the future, a plausible explanation is that the past  
3 record of investment is a reliable measure for estimation of future gains in most of the  
4 ecologically realistic circumstances, and the fallacy could represent a maladaptive side effect.

5 Some cases of “*altruism*” could constitute still another example of deviation from the  
6 optimal foraging. When an indirect fitness gain is available, animals often invest material  
7 benefits to genetically related individuals as has been demonstrated in the Florida scrub jays  
8 (Woolenfenden 1974, cited by Wilson, 1975). The choice by helpers in this context is the one  
9 between giving food to others and ingesting it by oneself. We can assume a similar proximate  
10 mechanism for the “*altruistic*” choice, to the one found in the anticipation codes of chick LPO.  
11 The scrub jay helpers could suppress the option of own *ingesting*, probably after developing an  
12 internal representation of the benefits available by the alternative option of *giving*. Future  
13 researches by system neuroscience might be successful in revealing the internal representation, a  
14 mental representation comparable to our ethical self-control or the Freudian *super-ego*.

15 In summary, evolution of these behavioral variations such as “*naïve curiosity*,”  
16 “*contra-freeloading*,” “*Concorde fallacy*,” and “*altruism*” should be examined, in concert with  
17 the accounts by behavioral ecology, toward understanding the responsible brain mechanisms as  
18 targets of the selection pressures responsible. Definitely, the telencephalic structures (limbic  
19 system and striatal complex) involved in cognitive processes (evaluation, anticipation,  
20 preference and decision making) should be the sites for the future researches. These processes  
21 could be understood as deviations from the gain optimization, rather than assuming distinct  
22 centers of “instincts.” The issue of “animal mind” could be argued most fruitfully, if approaches  
23 of the system neuroscience are synthesized with the evolutionary perspectives.

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6

## 7 **Footnotes**

8 1. *Analogy* simply implies that animals with distinct phylogenetic histories share a similar trait.  
9 For example, wings of birds and insects are analogous; evolutionary origins are not relevant in  
10 this context. The similarity could either be functional or morphological in nature. *Homoplasy*  
11 implies, on the other hand, that similar traits emerged from a common ancestor, but the  
12 phylogenetic development occurred independently in these animals under comparison. For  
13 example, wings of birds and bats are homoplastic, since both organs have similar function as  
14 “flying organ”, but emerged independently from forelimbs of the tetrapoda. *Homology*  
15 indicates that a trait is shared because the trait occurred also in the common ancestor. For  
16 example, wings of birds and *Archeopteryx* (a Mesozoic bird-like reptile) are homologous  
17 because they derived from a group of extinct feathered theropod dinosaurs. The distinction  
18 between *homology* and *homoplasy* can be made only on the basis of cladistic analysis of related  
19 animals groups, which enables us to reconstruct features of the extinct ancestors. These basic  
20 concepts are perfectly applicable also for the structures and functions of brain and behaviors; for  
21 further discussions, see Shimizu (2000).

22

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- 19

1 **Figure legends**

2

3 **Figure 1** Behavioral paradigms developed for the study of cognitive processes underlying  
 4 foraging behaviors in the domestic chick. **A:** In the single choice task, the subject chick was  
 5 presented with a single cue bead, and required either to peck or to stay unpecking. The chick  
 6 must memorize the association between the color cue (red, green or blue) and the required  
 7 operant (peck or unpeck), as well as the association between the color and the consequence (i.e.,  
 8 whether a reward is delivered). In this manner, sub-processes (such as *cue recognition*, reward  
 9 *anticipation*, and *operant* behavior) could be experimentally dissociated (Yanagihara *et al.*,  
 10 2001). **B:** In the concurrent choice task, the subject chick was presented with a pair of cue  
 11 beads, and required to peck either one of them. The chick must memorize the associations as in  
 12 the case of the single choice task. At execution, on the other hand, the chick should recall the  
 13 associated rewards, thus forming the anticipated consequences for each option, compare them,  
 14 and finally make a choice. The anticipated rewards could differ in either the temporal  
 15 proximity and/or the quantity, depending on the choice. In this manner, anticipation of the  
 16 *temporal proximity* of the reward could be experimentally dissociated from that of the reward  
 17 *quality* (Izawa *et al.*, 2003).

18

19 **Figure 2** Biological implementation of the Analysis (A) – Recognition (R) – Execution (E)  
 20 model proposed by Bateson and Horn (1994) with an emphasis on the execution of foraging  
 21 behaviors. Direct connections between the Analysis layer and the Execution layer were omitted.  
 22 Brain regions involved in the A-layer are responsible for coding elements of visual features (i.e.,  
 23 colors, movements, patterns and spatial relationships). Those involved in the R-layer act as an  
 24 attention filter (IMHV) by which conspicuous novel / alerting object is separated, or as sites for  
 25 memory-based anticipation of the future gain. It has been shown that the caudal LPO is  
 26 specifically involved in the anticipated proximity, whereas the AIv could be responsible for other  
 27 aspects (quantity and quality) of the anticipated outcome. Both of the AIv and the LPO exert

1 actions onto the regions in the E-layer as suggested by Csillag (1999). Optic tectum and  
2 reticular formation are supposed to be responsible for the spatial localization of object, whereas  
3 the tegmental VTA/SN could be involved in characterizing the attributes such as appetitive or  
4 aversive reinforcements. See text for further explanations.

Table 1 Important features of filial imprinting, sexual imprinting, passive avoidance, and reinforcement learning in chicks of precocial birds.

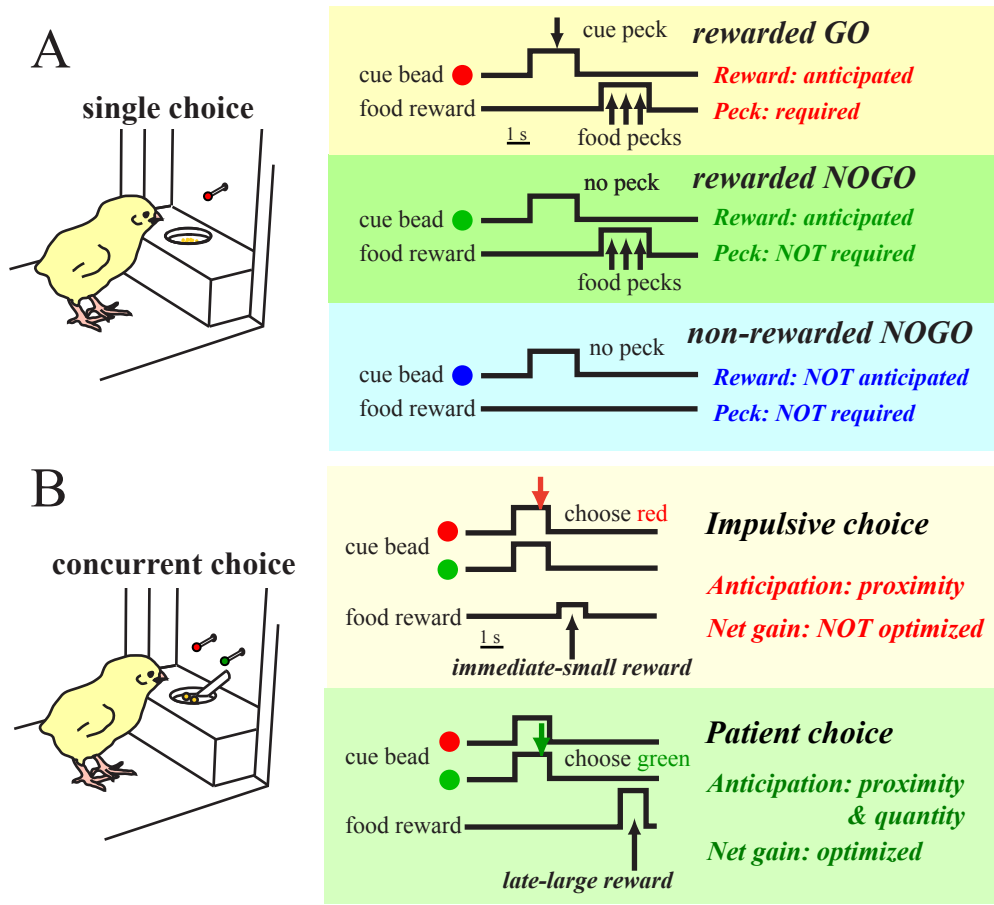
	<b>Filial imprinting</b>	<b>Sexual imprinting</b>	<b>Passive avoidance</b>	<b>Reinforcement learning</b>
<b>Sensitive period (development)</b>	In 24 hours post-hatch (#1).	Days to weeks post-hatch.	Up to 3-5 days post-hatch, until the “curiosity pecking” (i.e., tendency to non-selectively peck at novel conspicuous objects) perishes.	Particularly at 3-5 days post-hatch and later (i.e., after the yolk has been consumed).
<b>Cues of the effective stimuli (functions: sensory aspects)</b>	Conspicuous moving objects, with predisposition toward morphs of the conspecific adults. Contingent response to the distress calling of the subject is facilitatory.	Plumage coloration of the chicks that accompany the subject (#2).	Color is the primary cue, with location as a secondary supplementary cue. The shape serves as the least effective cue.	Color is the primary cue, with location as a secondary supplementary cue.
<b>Behavioral executions (functions: motor aspects)</b>	Selective social attachment and following behaviors.	Selective avoidance and choice of individuals as mate.	Selective avoidance of the aversive bead, with considerable generalization exclusively in the color cue.	Selective pecking at the cued pecking key. The cue object could be spatially displaced from the pecking target to some extent.
<b>Fitness gain (evolutionary causes)</b>	Higher chance of survival with better parental cares.	Better genetic conditions of the offsprings due to optimal out-breeding (#3).	Higher chance of survival with selective and optimized foraging (questionable: See text.)	Higher chance of survival with selective and optimized foraging.
<b>Relevant brain regions (proximate mechanisms)</b>	IMHV is required for acquisition and retention. Relocation of the memory trace outside of the right IMHV (S-dash) is suggested.	Data not available.	IMHV is required for acquisition, but not for retention. Memory flow occurs toward LPO, where the memory is stored permanently.	LPO is required for acquisition, but not for retention. Future gain is “guaranteed” in the caudal LPO, so that impulsive option can be suppressed.

#1: The sensitive period of the filial imprinting is not necessarily fixed; see Bateson (1979) for further discussion. Furthermore, it is reported that the exposure to light during the late pre-hatch period significantly changes the learning performances in the post-hatch period (Cherfas, 1977), suggesting that the chicks are sensitive to the pre-hatch experiences. Furthermore, termination of the sensitive period can also be modified by behavioral experiences. According to Peter Kabai (St Istvan University, Budapest, Hungary; personal communication), the color preference of quail chicks can be repeatedly imprinted or even reversed, if the subject had been initially hand-reared by the experimenters; development of social attachment could elongate the sensitive period.

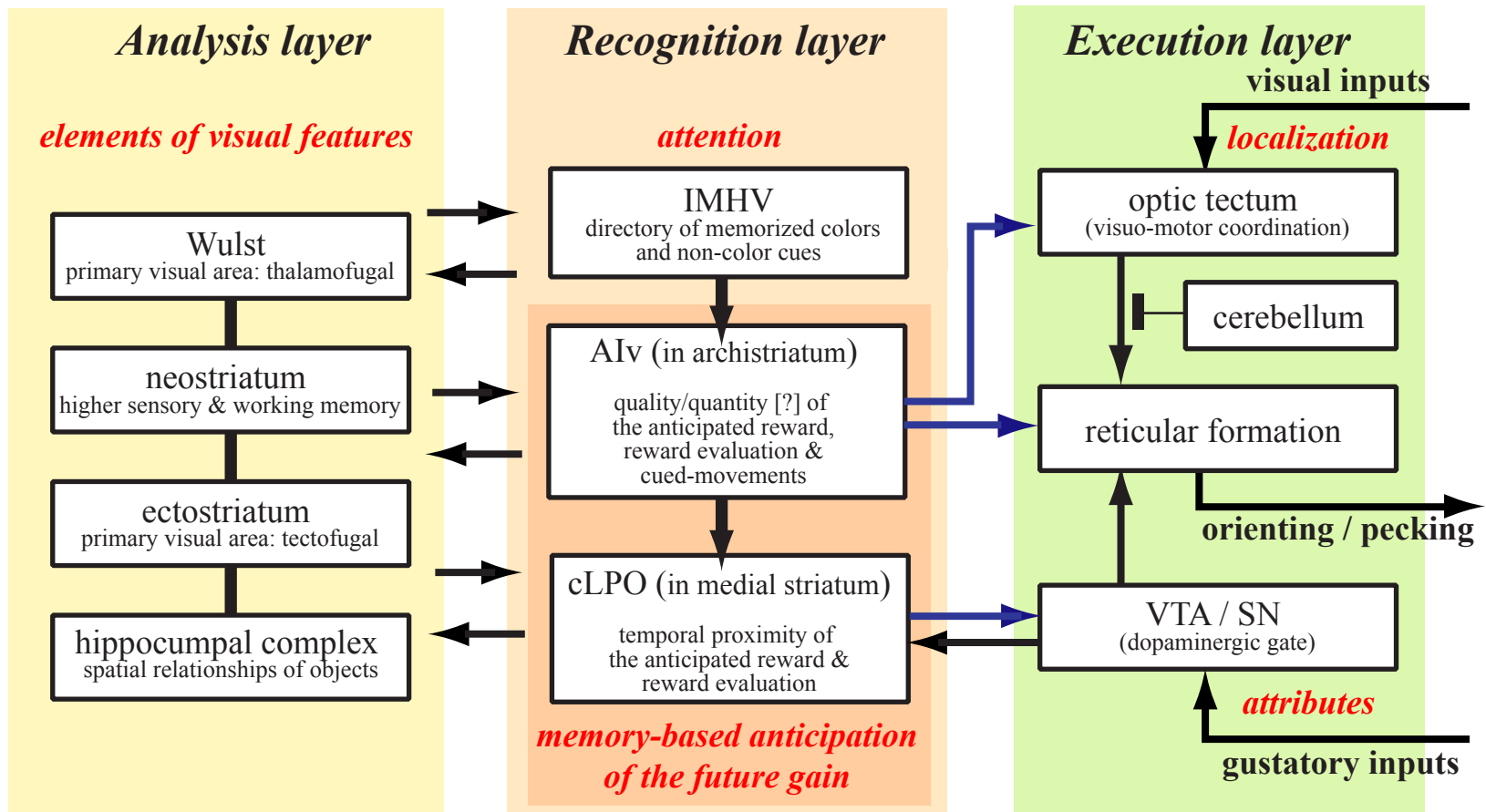
#2: A search for the effective cues involved in suppression of the distress call (Hayashi *et al.*, 2001) revealed, however that the plumage coloration is not significant. Behavioral functions of the distress calls are yet to be analyzed.

#3: Sexual imprinting causes the subjects to prefer individuals with slightly deviated morphs from the imprinted individuals (Bateson 1982). Moreover, individuals with “supernormal” features are preferred (ten Cate and Bateson 1989). This process is adaptive most probably through a behavioral suppression of in-breeding, which may reduce the immune activities and viability of offsprings.





Matsushima *et al.*, Figure 1



Matsushima *et al.*, Figure 2