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Title:

Mind through chick eyes: memory, cognition and anticipation.

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Abstract

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

(250 words)

1. Introduction to the issue of “animal mind”

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

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

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

2. Backgrounds: evolution and brain anatomy of birds

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

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

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

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

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

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

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

3. Imprinting

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

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table-1 around here

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

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

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

Recently, Nicol, Horn and their colleagues have been successful in analyzing single neuron activities in freely-behaving chicks both during and after the imprinting training (Nicol *et al.*, 1995, 1998; Horn, 1998; Horn *et al.*, 2001). Population of neural correlates of the imprinting object (such as coding of the color and the shape) in IMHV increased as the training proceeded, thus yielding direct evidence for the IMHV as a constituent of the memory system. For the system-level understanding of imprinting, however, we must specify what aspects of behavioral execution the IMHV is responsible for.

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

4. Passive avoidance learning

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

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

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

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

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

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

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

5. Spatial memory

Chicks move. Along the movements, visual images on the retinal surface move accordingly. But, it is not the world that moves, but the chick itself. The chick must reconstruct own location in space based on the changes in sensory signals. For the signal conversion, concurrent retinal images are referenced to the memorized images, so that place of the chick in a familiar space is determined. Internally represented reference for the localization is the *cognitive map*, which is supposed to be one of the universal mental toolkits shared by diverse animals with distinct evolutionary histories, such as desert ants, foraging honeybees, homing pigeons, and migrating salmons (Hauser, 2000).

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

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

Center of a place Further elegant experiments developed by the same group of Italian psychologists revealed that chicks adopt two distinct strategies in spatial localization (Tommasi *et al.*, 1997). In this paradigm, chicks were trained to find a food item hidden at the center of a training arena. The food was initially placed on the surface, and subsequently hidden in the sawdust on the floor. By simply observing the locations where the subject chick scratched the floor in a test arena, experimenters could study how the chick localized the center. The trick is that the test arena differed from the training arena in either the size (with the shape being identical) or the shape (with the size being identical). In order to localize the center, the chicks could utilize either the absolute distance from one wall (local absolute cue), or depend on the equal distance from both of the opposing walls (global relational cue) (Tommasi and Vallortigara, 2000). Surprisingly, the right and the left telencephalic hemispheres differed in localizing strategies; chicks with the operational right hemisphere (with its right eye covered by eye-patch) adopted the global cue, whereas chicks with the left hemisphere (with its left eye covered) searched for food based on the local cue (Tommasi and Vallortigara, 2001). Further unilateral lesion of hippocampus suggested that the global and local cues are separately stored in the right and left hippocampi, respectively (Andrew *et al.*, submitted).

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

6. Memory of colors and shapes

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

Color map With their tetra-chromatic nature of the retinal cone photoreceptor cells (ultra-violet, blue, green, and red; Bowmaker *et al.*, 1997), domestic chicks are supposed to be endowed with acute sense of colors. Visual discrimination task with food reinforcement actually demonstrated that domestic chicks have accurate color memory for foraging (Osorio *et al.*, 1999); the pattern proved much less significant. Basically identical conclusion was drawn in the quail chicks, in which visual memory was examined by selective habituation and passive avoidance task (Aoki *et al.*, 2000). It is to be emphasized that chicks have a context-independent representation of colors. Subjective distance of a green measured from memorized image of a yellow was identical to the distance of the yellow from the green image (Aoki *et al.*, 2000); quail chick could have an internal color map as reference.

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

Neural basis of color discrimination In parallel with the two distinct processes of color discrimination, two relevant brain regions have been pointed out; a telencephalic region (IMHV) and a subtelencephalic region (dorsomedial thalamus). In a series of lesion experiments in passive avoidance task in domestic chicks, it has been shown that a post-training lesion placed to bilateral IMHV failed to cause amnesia (Gilbert *et al.*, 1991), in contrast to the pre-training lesion experiment (Davies *et al.*, 1988); it was thus concluded that the IMHV is required for acquisition, but not for recall, reminiscent to the functional involvement of the right IMHV in the imprinting (see above; Cipolla-Neto *et al.*, 1982). Further examination of the post-lesion effects revealed, however, that the lesioned chicks avoided the bitter-tasting bead by some (yet unidentified) non-color cues (Patterson and Rose, 1992); memory-based color discrimination was selectively impaired. In contrast, lesion experiments on the innate color preference revealed that even total telencephaloectomy (the whole telencephalon aspirated on the hatching day) does not impair posture, sensori-motor coordination for pecking, locomotion, and selective approach to the genetically preferred color (Kovach and Kabai, 1993). Much smaller lesion localized in the dorsomedial thalamic complex proved to attenuate the genetically determined color preferences (Csillag *et al.*, 1995); lesions to an ascending visual pathway (nucleus rotundus) failed to have effects. Most probably, color is multiply represented in the chick brain, with distinct controls over the behavioral executions.

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

7. Neuronal representations

Brain is full of spikes. But, the neuronal spikes tell us nothing, so long as we are unaware of their codes. To break the codes, we must find the causal link between the sensory signals and the neuron under study, i.e., in a *peripheral-to-center* approach of the "sensory physiology." In this approach, we understand how the brain detects specific features of an external stimulus through a cascade of signal processing. We might also search for the causal link between the neural activity and the behavioral execution, i.e., in a *center-to-peripheral* approach of "motor control." In this approach, we understand how the brain organizes coordinated behaviors. As the third approach, we could directly penetrate into the mental process that may lie between the (sensory) recognition and the (motor) execution. In this approach, we understand how the brain makes decisions. We adopted the third approach, because it was important and new in the bird researches. In the following, we will describe the task together with some technical tips, and summarize the logical consequences of our recent findings (Yanagihara *et al.*, 2001; Izawa *et al.*, 2001, 2002, 2003).

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

Figure 1 around here

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

Memory correlates in IMHV. Neuronal “pin-hole images” of memory should meet at least the following criteria. First, changes in the neuronal spikes (excitatory or inhibitory) should occur in response to the presentation of associated stimuli in a specific manner. Second, the responses should emerge only after relevant training, showing a good parallelism with the memory retention. Neuronal spikes that meet these criteria have been found in the chick brain in several different regions including the IMHV. Using the imprinting paradigm, it has been established that IMHV contains neuronal correlates of the imprinting memory (Nicoll *et al.*, 1995, 1998; Horn *et al.*, 2001). Some IMHV neurons responded specifically to a combination of color and shape, whereas others showed generalized responses to color or shape. These authors argued that the IMHV neurons principally represent stored visual features of the imprinting object.

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

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

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

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

In concurrent choice task (Fig. 1B), post-training LPO lesion actually had an effect. In this task, chicks learned to peck one of two simultaneously presented beads, e.g., red and yellow. Red bead was associated with a large reward (6 pellets of millet grain), and yellow with a small reward (1 pellet). Naturally, chicks learned to peck the red bead to gain the large reward. The choice differed when the large reward was delivered with a delay of 1-3 sec. When the red bead was associated with a large but delayed reward (delay time of 3 sec), the chick learned to choose the yellow bead to gain the small reward. For a delay of 1-2 sec, chicks proved to be patient enough to wait for the large reward, just staring at the still empty food tray. Chemical lesion of LPO (particularly the posterior LPO) ablated the chick-sized patience, thus unmasking the underlying impulsiveness; no amnesia accompanied the lesion. With the *anticipation* code in LPO neurons, the future gain would be "guaranteed" so that the chick reasonably suppressed the impulsive action for immediate reward. In other words, past experiences yield an internal representation of the future reward in LPO, and the represented reward makes the chick behaviorally tolerant. At the neuronal level, we can further assume that the *anticipation*-coding neurons in LPO could be responsible specifically for *temporal proximity*, rather than *quantity* and *quality* of the reward; the *quantity* and *quality* of anticipated reward should be represented in somewhere else in the chick brain. Note that the system for the patient choice is highly adaptive, because the net gain (i.e., total amount of food obtained) could be optimized, thus serving for a rapid growth and a higher chance of survival (see table 1).

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

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

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

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

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

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

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

9. Scopes

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

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

Deviations from optimal foraging: "naïve curiosity," "contra-freeloading," "Concorde fallacy," and "altruism" Chicks might be wise enough to actively "earn" information at the expense of immediate material benefits. In our controlled laboratory condition, week-old chicks are trained and tested under a limited diet so that the chick's motive toward food reward is maximized. Consequently, chicks quickly learn the association between cue colors and reward quantity, so that chicks reliably choose a color associated with a larger reward (Izawa *et al.*, 2003). In this context, chicks behave in accordance with the most normative theory of the optimal foraging (Alcock, 2001) with a slight modification that anticipated reward in the future should weigh proportionately less than the immediate gain. Internal representation of anticipated reward in the future plays a critical role.

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

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

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

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

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

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

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Footnotes

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

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Figure legends

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

Figure 2 Biological implementation of the Analysis (A) – Recognition (R) – Execution (E) model proposed by Bateson and Horn (1994) with an emphasis on the execution of foraging behaviors. Direct connections between the Analysis layer and the Execution layer were omitted. Brain regions involved in the A-layer are responsible for coding elements of visual features (i.e., colors, movements, patterns and spatial relationships). Those involved in the R-layer act as an attention filter (IMHV) by which conspicuous novel / alerting object is separated, or as sites for memory-based anticipation of the future gain. It has been shown that the caudal LPO is specifically involved in the anticipated proximity, whereas the AIv could be responsible for other aspects (quantity and quality) of the anticipated outcome. Both of the AIv and the LPO exert actions onto the regions in the E-layer as suggested by Csillag (1999). Optic tectum and reticular formation are supposed to be responsible for the spatial localization of object, whereas the tegmental VTA/SN could be involved in characterizing the attributes such as appetitive or aversive reinforcements. See text for further explanations.

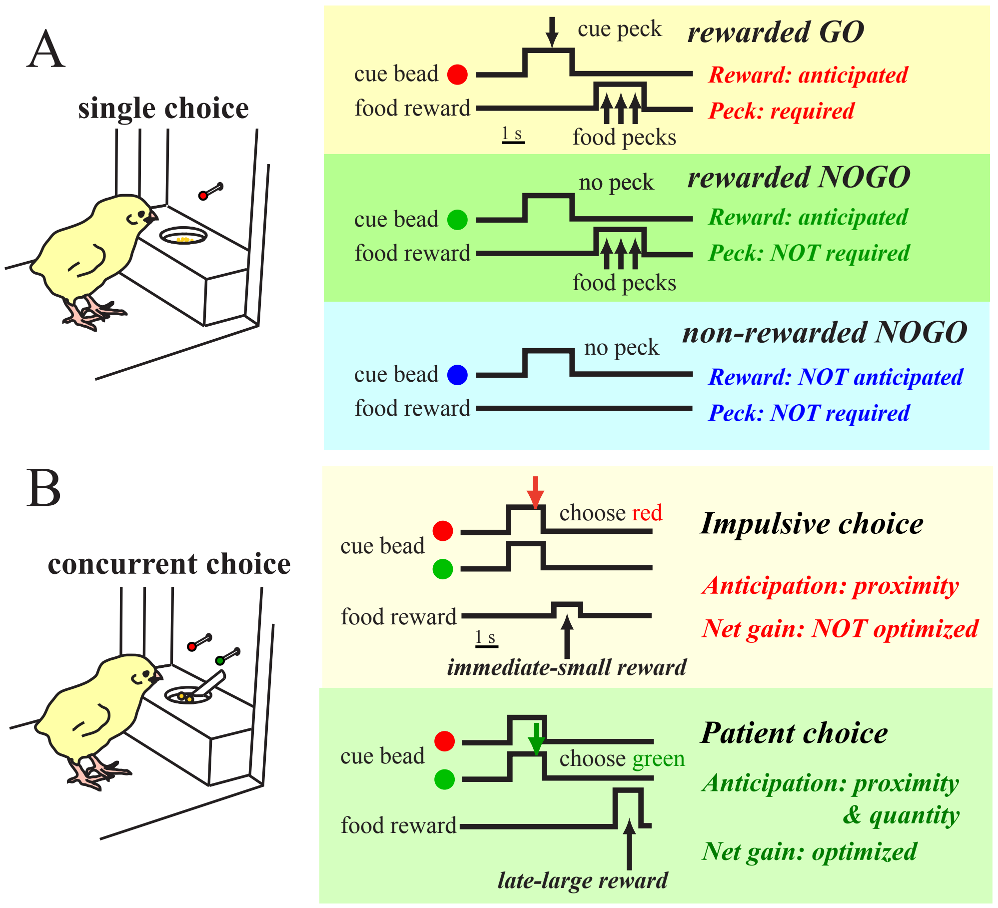
Table 1 Important features of filial imprinting, sexual imprinting, passive avoidance, and reinforcement learning in chicks of precocial birds.

	Filial imprinting	**Sexual imprinting**	**Passive avoidance**	**Reinforcement learning**
Sensitive period (development)	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).
Cues of the effective stimuli (functions: sensory aspects)	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.
Behavioral executions (functions: motor aspects)	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.
Fitness gain (evolutionary causes)	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.
Relevant brain regions (proximate mechanisms)	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.

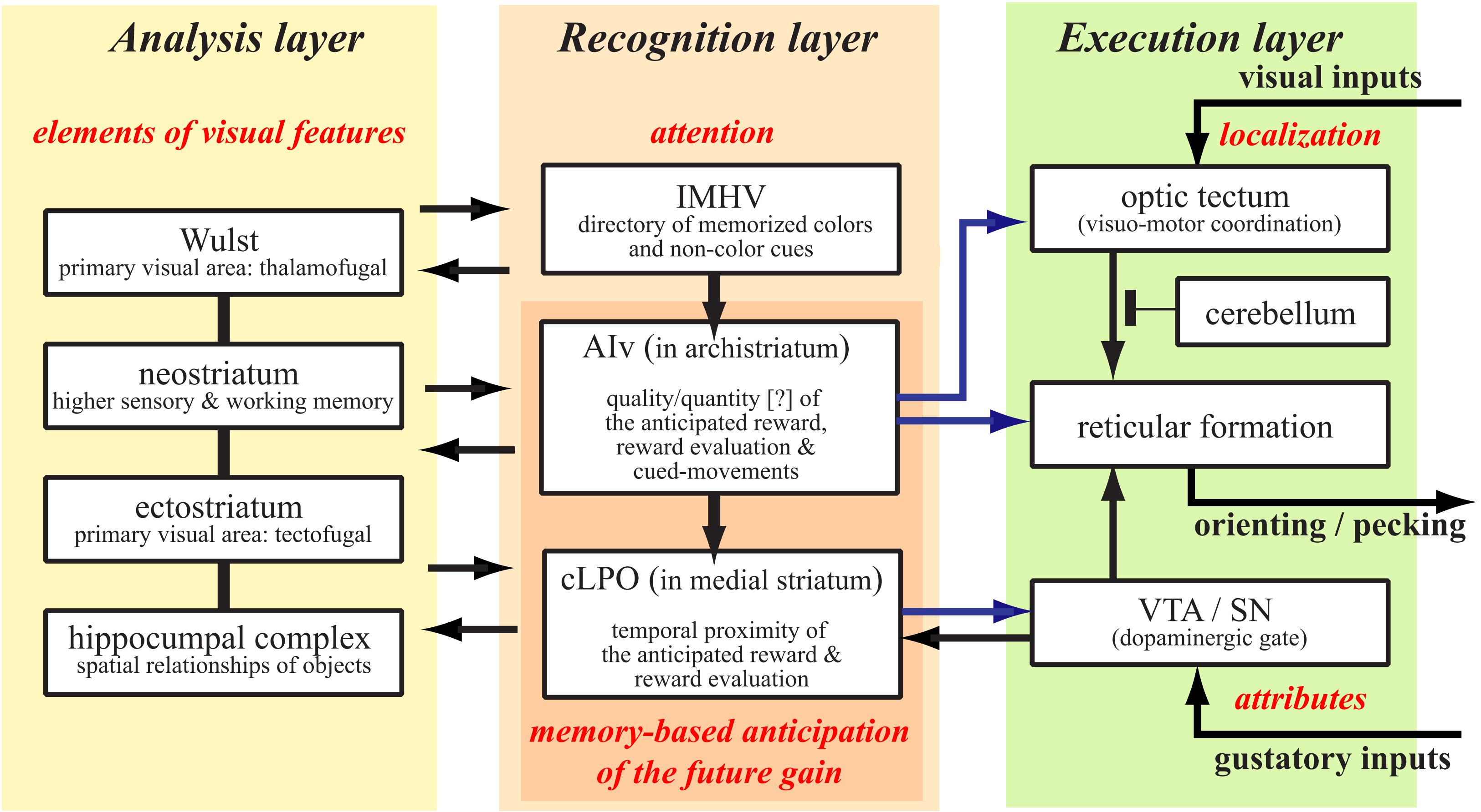
#1: The sensitive period of the filial imprinting is not necessarily fixed; see Bateson (1979) for further discussion. Furthermore, it is reported that the exposure to light during the late pre-hatch period significantly changes the learning performances in the post-hatch period (Cherfas, 1977), suggesting 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