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Review

Innate visual object recognition in vertebrates: some proposed pathways and mechanisms

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Abstract

Almost all vertebrates are capable of recognizing biologically relevant stimuli at or shortly after birth, and in some phylogenetically ancient species visual object recognition is exclusively innate. Extensive and detailed studies of the anuran visual system have resulted in the determination of the neural structures and pathways involved in innate prey and predator recognition in these species [Behav. Brain Sci. 10 (1987) 337; Comp. Biochem. Physiol. A 128 (2001) 417]. The structures involved include the optic tectum, pretectal nuclei and an area within the mesencephalic tegmentum. Here we investigate the structures and pathways involved in innate stimulus recognition in avian, rodent and primate species. We discuss innate stimulus preferences in maternal imprinting in chicks and argue that these preferences are due to innate visual recognition of conspecifics, entirely mediated by subtelencephalic structures. In rodent species, brainstem structures largely homologous to the components of the anuran subcortical visual system mediate innate visual object recognition. The primary components of the mammalian subcortical visual system are the superior colliculus, nucleus of the optic tract, anterior and posterior pretectal nuclei, nucleus of the posterior commissure, and an area within the mesopontine reticular formation that includes parts of the cuneiform, subcuneiform and pedunculopontine nuclei. We argue that in rodent species the innate sensory recognition systems function throughout ontogeny, acting in parallel with cortical sensory and recognition systems. In primates the structures involved in innate stimulus recognition are essentially the same as those in rodents, but overt innate recognition is only present in very early ontogeny, and after a transition period gives way to learned object recognition mediated by cortical structures. After the transition period, primate subcortical sensory systems still function to provide implicit innate stimulus recognition, and this recognition can still generate orienting, neuroendocrine and emotional responses to biologically relevant stimuli. © 2002 Elsevier Science Inc. All rights reserved.

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1. Introduction

A considerable amount of evidence has been accumulated in the last century which suggests that all vertebrates, from primitive fishes to primates, are able to recognize important classes of stimuli, including visual objects, sounds and pheromones, with no previous experience of those types of stimuli. In animals and humans, innate recognition is inferred from behavioral responses

Abbreviations: CRS, command releasing system; LCC, large-celled column of the anuran mesencephalic tegmentum; mMRF, medial medullary reticular formation; MpRF, mesopontine reticular formation (cuneiform, subcuneiform and pedunculopontine nuclei of mammalian species); SGS, stratum griseum superficiale of the superior colliculus; SGI, stratum griseum intermediale; SGP, stratum griseum profundum; SO, stratum opticum.

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of infants or naive individuals to biologically relevant stimuli. For example, individuals of many species respond with freezing or flight behaviors when they encounter a natural predator, even when they have had no previous experience of that type of predator (Blanchard and Blanchard, 1971; Bronstein and Hirsch, 1976; Rager et al., 1986; Moriarty, 1995; Gargaglioni et al., 2001). The behavioral responses are also presumably innate, since no previous training has occurred. The adaptational benefits of the ability to recognize and respond to classes of stimuli at birth, or prior to any experience of those classes of stimuli, are fairly obvious. Infants that do not depend on nursing must be able to recognize food items and perform the necessary operations to consume them, and the ability to recognize and avoid predators at birth is of obvious importance to the survival of most animals. Phylogenetically ancient vertebrates, whose capacity for learned stimulus recognition may be quite limited, must rely on innate recognition and innate behavior patterns in most situations (Ewert, 1987). More recently evolved species, whose capacity to learn is greater, will only require innate recognition and behavior patterns in early ontogeny, and it is to be expected that innate stimulus recognition will eventually be replaced by recognition systems that are capable of learning to recognize individual objects. In these species, innate behavior patterns will be replaced in early ontogeny by learned behaviors, which furnish the individual with a much greater repertoire of responses in any given situation. In some species innate visual recognition is present at birth, while the cortical visual system does not become functional until several weeks have passed (Atkinson, 1984; Braddick et al., 1986). In these species innate visual object recognition is presumably mediated by subcortical visual structures.

The ethologists N. Tinbergen and K. Lorenz called the sensory (recognition) component of innate response mechanisms the 'innate releasing mechanism' (Tinbergen and Lorenz, 1938). These authors studied the characteristics of visual objects that elicited innate behavioral responses in newborn animals or animals that were raised in isolation. In general, they found that innate visual recognition usually depends on certain key features of objects ('key stimuli'), and that the probability that an object will 'release' a behavioral response is proportional to the number and strength of the key stimuli present in the stimulus object. They

also found that the criteria necessary for recognition are fairly broad, and animals will respond to a range of shapes and sizes in an object as long as the overall configuration and movement have a certain degree of similarity to those of biologically relevant objects. For example, naive turkey chicks respond with escape behaviors to the overhead presentation of moving birdlike silhouettes (Tinbergen, 1948).

Learned recognition of sensory stimuli is achieved through sequential (hierarchical) and parallel processing in several structures devoted to a particular sensory modality. In the cortical visual system, for example, learned object recognition is mediated by the dorsal processing stream, commencing in striate cortex and including several visual areas in the occipito-temporal cortex. The signals that signify that recognition of a particular object has taken place could, in principle, be represented by the activities of neurons in any one or all of the components of the cortical visual system (i.e. V1, V2, V3, V4 and inferior temporal cortex), or by the activities of a group of neurons in one particular structure (Steckler et al., 1998). It has been demonstrated that sufficient information for the recognition of familiar objects (faces, toys) is provided by the activity of a small group of neurons in macaque inferior temporal cortex (Rolls and Tovee, 1995; Rolls et al., 1997; Booth and Rolls, 1998). Thus, the neural 'engram' for which activation signifies that a particular object has been recognized is most probably represented by the activity of a relatively small group of neurons (i.e. the engram is a sparse distributed representation, meaning that, when each neuron in the group fires in a particular manner, the object in question has been recognized computationally), located in the highest order component(s) of the sensory system involved. Innate recognition of object classes is presumably also achieved by parallel/hierarchical processing of sensory inputs, and thus will also require processing in more than one structure to achieve recognition. Furthermore, engrams that represent the recognition of classes of objects are also required. We assume here that these engrams are also sparse distributed representations.

The concept of computational 'engrams' is similar to what Ewert (1980, 1987) has referred to as the 'command releasing system' (CRS) that activates motor programs in anuran species. A CRS is composed of specialized neurons—command

elements—that form an interface between sensory and motor systems, and is activated by the recognition of a particular class of objects. Thus, they are the neurophysiological equivalent of the innate releasing mechanisms originally described by Lorenz (1935). The ‘command neuron’ notion originally developed in invertebrate neuroethology (Wiersma and Ikeda, 1964), and refers to single neurons that trigger the motor programs for certain fixed action patterns (Davis and Kovac, 1981). The ‘command system’ concept, originally proposed by Kupfermann and Weiss (1978), is an extension of the command neuron concept, in which the concurrent activation of a group of neurons (rather than a single neuron) serves to activate the action patterns. Finally, Ewert (1980, 1987) incorporated ‘sensorimotor codes’ into the ‘command system’, thus allowing a group of neurons to represent the recognition of more than one class of objects. The principal difference between the engram and CRS concepts lies in the fact that a CRS signals, in addition to recognition of a stimulus object class, the location of the stimulus in space (e.g. ‘stimulus recognized as prey, n degrees outside of the fixation area’, Ewert, 1987), whereas here the engram is envisioned as exclusively representing recognition, and the information necessary to describe the location and movement of the object is computed and represented separately. One reason for believing that the computations required for object recognition and those necessary for stimulus location and movement (and physical relationships to other stimuli) are computed separately is the fact that in the mammalian cortical visual system these computations are effected (in part) separately, with object recognition processed in the ventral (occipitotemporal) stream, and spatial information in the parietal stream (Ungerleider and Mishkin, 1982; Gattass et al., 1990). However, in the early stages of the mammalian cortical visual analyzer (such as V1, V2 and V3 of the macaque), neurons must process information necessary for object recognition and for the determination of location and movement, and it is only in the latter stages that a segregation occurs between the two processing streams. In addition, it should be noted that Jeanerod et al. (1995) have argued that segregation between the ventral and parietal streams is not complete, and that neurons in parietal visual area AIP, for example, also process information about the shape of visual objects.

In this article, the term ‘innate’ when referred to stimulus recognition or behaviors means (1) that the neural mechanisms and pathways necessary for these functions are either present at birth, or genetically determined such that they will become functional shortly after birth, and (2) that the functions are unlearned (Ewert, 1987).

2. Innate visual prey and predator recognition in anurans

Toads can recognize prey stimuli—worm-like objects—immediately after metamorphosis (Ewert and Burghagen, 1974a,b). Although the accuracy of this recognition improves during ontogeny, it does not require repeated experience with the objects, and this indicates that the recognition is innate. There are no reports of overt visual recognition of objects such as abstract geometric patterns in anuran species, but stimulus-specific habituation of prey-catching responses has been demonstrated in toads (Ewert and Kehl, 1978). In this study triangular objects were used as prey stimuli, and responses were habituated when the triangle moved with its apex pointing in the direction of movement, but not when it pointed in the opposite direction. Thus, it would appear that individual objects belonging to a class of objects recognized by the innate visual recognition system may be discriminated, and this discrimination is due to specific configurational characteristics of the objects. Ewert et al. (2001) have speculated that the stimulus specificity of the habituation in this experiment may be mediated by activities in the anuran anterior thalamic nucleus, which receives retinal and tectal inputs, and projects to the ventral medial pallium (homologous to the mammalian hippocampus). In addition, toads can learn to associate a stimulus that is innately recognized as threatening (the moving hand of the experimenter which presents a worm to the toad, presumably recognized as a potential predator) with prey stimuli (the worm) (Brzoska and Schneider, 1978). In this case, the association is made between two innately recognized objects.

On the other hand, frogs can learn to recognize odors of substances, such as orange and citral, which are evidently not innately recognized, and this ability is present even before birth (Hepper and Waldman, 1992). All the neural apparatus necessary for recognition and discrimination of particular odors is present in amphibians, including

an olfactory 'cortex' and a primordial hippocampal formation (Duchamp-Viret et al., 1996; Roth and Westhoff, 1999). However, anurans have no visual cortex as such (Straube et al., 1987), and visually guided behavior is presumably primarily mediated by neuronal activity in medullary, pontine, mesencephalic and thalamic structures.

Although visual recognition of classes of objects is innate in anurans, and often the behavioral responses that occur in response to visual stimuli are species-specific motor sequences triggered by tectal, pretectal and tegmental structures, and generated by motor pattern generator circuits located in the medial medullary reticular formation (mMRF) and spinal cord (Matsushima et al., 1989; Ewert et al., 1990), responses to these objects can be modified through conditioning, but reappear in their original form after telencephalic lesions (Ewert et al., 1994).

2.1. Visual pathways involved in innate prey recognition in anurans

The neural basis of innate visual recognition of prey and predator objects in frogs and toads has been studied in great detail by Ewert and colleagues (for comprehensive reviews, see Ewert, 1987, 1997; Ewert et al., 2001), and by other authors (Ingle, 1973, 1977; Patton and Grobstein, 1998a,b). Lesion studies have elucidated the principal structures that are involved in visual prey recognition in toads. Ewert found that after bilateral ablation of both telencephalic hemispheres and removal of the dorsal thalamus, lesioned toads readily responded to moving visual stimuli with prey orienting and snapping (Ewert, 1968, 1987, 1997; Ewert et al., 2001). The lesions spared the retinotectal pathway, preoptic/hypothalamic structures and ventral thalamus, as well as all brainstem structures caudal to the thalamus. However, pretectal structures, including the lateral posterodorsal and posterior pretectal nuclei, were damaged and configurational prey stimuli were not adequately discriminated (i.e. the toads would orient to and snap at almost any moving object). In a subsequent study, it was shown that lesions restricted to the pretectal nuclei led to significant deficits in visual pattern discrimination, and the lesioned toads respond to moving stimuli in much the same fashion as did those with ablations to both telencephalic hemispheres (Ewert et al., 1996). Ewert and co-workers concluded that the deficits in

stimulus discrimination observed in the animals with telencephalic plus pretectal nuclei lesions were due to the damage to the pretectal nuclei.

Lesions to the optic tectum of frogs, which destroyed all the layers of that structure, cause a total loss of responses to moving predator and prey objects (Ingle, 1973, 1977; Kostyk and Grobstein, 1982). Thus, both the optic tectum and pretectal nuclei are necessary for accurate prey stimulus recognition. Electrical stimulation of the toad optic tectum elicits snapping, which is the final consummatory action of the prey-catching sequence in anurans (Matsushima et al., 1985).

The output pathways from the optic tectum and pretectal nuclei that mediate components of the prey-catching behavioral sequence in anurans, which is elicited by visual presentation of prey objects or electrical stimulation of the optic tectum, have recently been characterized (Kostyk and Grobstein, 1982, 1987a,b; Masino and Grobstein, 1989a,b, 1990). Two major pathways are involved, a crossed tecto-reticulo-spinal projection, and an ipsilateral projection from the optic tectum to the mesencephalic tegmentum (Masino and Grobstein, 1989a,b). The crossed projection terminates in the mMRF, where premotor structures for innate behaviors, including locomotion, orienting and snapping, reside (Matsushima et al., 1989; Ewert et al., 1990), and in the spinal cord. The ipsilateral tegmental projection terminates in a longitudinal structure that has been termed the large-celled column (LCC, Fig. 1), which includes parts of the nucleus of the medial longitudinal fasciculus, and the anterodorsal, anteroventral and posteroventral tegmental nuclei (Masino and Grobstein, 1989b, 1990).

The amphibian LCC receives afferent projections from layers 4 and 6 of the optic tectum (Lázár et al., 1983; Antal et al., 1986), and from the lateral posterodorsal and posterior pretectal nuclei (Trachtenberg and Ingle, 1974; Hall and Feng, 1987), and projects to the premotor area in the mMRF (Naujoks-Manteuffel and Manteuffel, 1988; Masino and Grobstein, 1989b). Orientation to prey objects is mediated by projections from both the optic tectum and LCC to the mMRF (Masino and Grobstein, 1989b). Lesions to the white matter tracts that project from the LCC to these areas result in a complete loss of orienting to visual stimuli, and when retrograde tracers are applied to the lesions, cells in the LCC are labeled (Kostyk and Grobstein, 1987b; Masino and Grob-

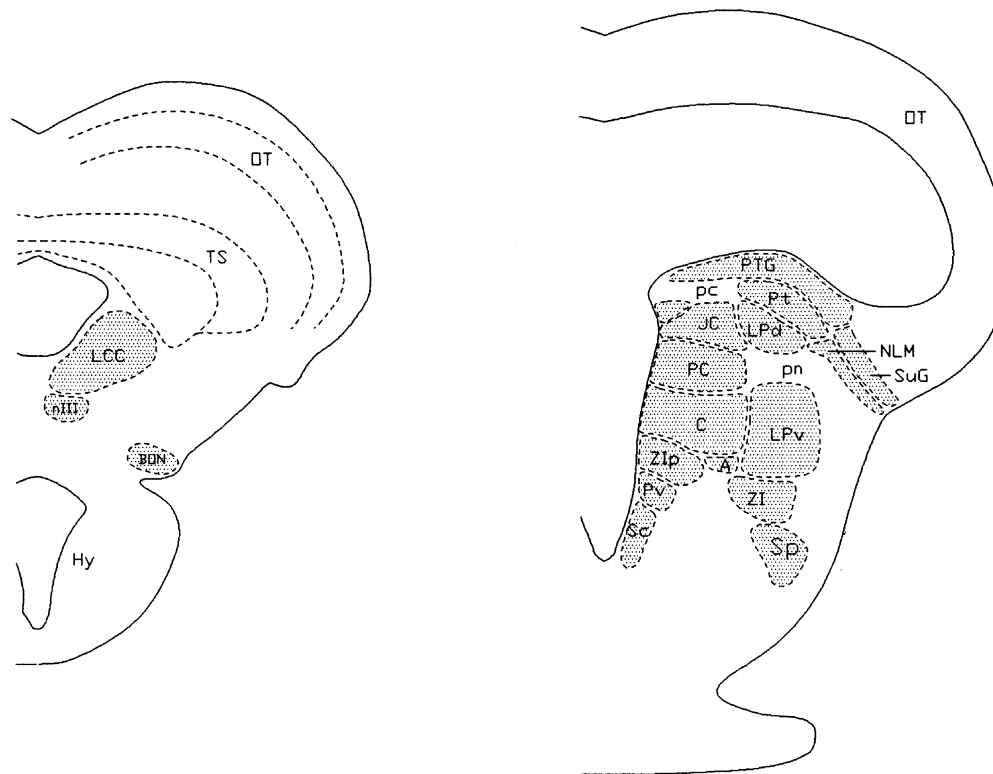


Fig. 1. Horizontal sections showing the location of tectal, pretectal, and reticular structures involved in innate visual prey and predator recognition in anuran species. Modified from Puelles et al. (1996). Note that the posterior pretectal nucleus (*P*) of Neary and Northcutt (1983) comprises the juxtacommissural and precommissural nuclei, and the nucleus of the posterior commissure (not shown). *Abbreviations*: A, anterior thalamic nucleus; BON, basal optic nucleus; C, central nucleus; cp, posterior commissure; Hy, hypothalamus; JC, juxtacommissural nucleus; LCC, large celled column; LPd, lateral posterodorsal pretectal nucleus; LPv, lateral posteroventral pretectal nucleus; nIII, oculomotor nucleus; NLM, mesencephalic lentiform nucleus; OT, optic tectum; PC, precommissural nucleus; pn, precommissural neuropil; Pt, pretectal nucleus; Pv, periventricular hypothalamic nucleus; PvG, periventricular tectal gray; Sc, suprachiasmatic nucleus; Sp, suprapeduncular nucleus; SuG, superficial tectal gray; TS, torus semicircularis; ZI, nucleus of the zona incerta; ZIp, periventricular zona incerta.

stein, 1989b). Aspiration lesions to the LCC, which damaged parts of the nucleus of the medial longitudinal fasciculus, anteroventral, anterodorsal and posteroventral tegmental nuclei, caused varying degrees of deficits in orientations to prey stimuli (Masino and Grobstein, 1989b). These lesions were bilateral, but extended more on one side than the other, and the deficits in orientations were more severe to stimuli presented on the same side as that which sustained the greater damage. In some animals, orientation to stimuli presented on the side ipsilateral to the major damage was completely abolished.

The results of these studies indicate that the optic tectum, pretectal nuclei and LCC are all structures necessary for behaviors in response to innate prey object recognition in anuran species

(Ewert, 1987; Ewert et al., 2001). It is possible that an additional structure located in ventral thalamus, which was spared in the lesion study by Ewert (1968), might also be necessary for this function.

Neurons located in the superficial layers (layer 9) of the frog optic tectum have extremely small ($2-3^\circ$) receptive fields (Grüsser and Grüsser-Cornehls, 1976). These neurons respond to small moving objects, even when the angular velocity is very small ($<0.01^\circ/\text{s}$), and the responses increase with increasing velocity. The responses are constant as the object moves through the receptive field. Small receptive field neurons, located in the upper part of layer 8 of the frog optic tectum, respond with tonic discharges to squares or discs with diameters of $2-15^\circ$ moving through the recep-

tive field (Gaillard, 1985). These responses rapidly habituate to repetitive stimulation. Neurons located in the lower part of layer 8 have relatively small receptive fields ($10\text{--}30^\circ$), and can be briefly activated by off–on moving-point source stimulation (Gaillard, 1985). Most of these units were driven by the contralateral eye and seemed to be more responsive to stimuli moving in an upward direction. Gaillard (1985) also described neurons in layer 6 with larger receptive fields, covering approximately one-quarter of the frog's frontal visual field, which were mainly activated by the leading edge of targets moving through the visual field, independently of the direction of movement. Four classes of frog tectal neurons that respond differentially to moving configurational visual stimuli have been described (Ewert and von Wiersheim, 1974; Schürg-Pfeiffer and Ewert, 1981; Matsumoto et al., 1986). Neurons classified as T5(1), T5(3) and T5(4) were located primarily in layer 8, and had receptive fields ranging from 20 to 33° . They all responded to the presentation of squares, and to horizontal (worm-like) and vertical (antiworm-like) rectangles moving through their receptive fields. The responses of T5(1) neurons were strongest for squares, and weakest for antiworm-like rectangles. T5(3) responded preferentially to squares, and their weakest activation was induced by worm-like stimuli. T5(4) neurons also responded most strongly to squares, and responses to worm- and antiworm-like objects were near zero. Neurons located in layer 6, designated T5(2), with average receptive fields of approximately 30° , responded most strongly to worm-like moving rectangles and least strongly to antiworm-like rectangles. Another class of layer-6 neurons, designated T1(1), with receptive fields of $30\text{--}40^\circ$, preferentially responded to square objects, with weaker and approximately equal responses to worm- and antiworm-like objects. Gaillard (1985) reported finding 'total-field' neurons, most probably located in layer 4 of the frog optic tectum, which have receptive fields that are approximately equal to the visual field of the corresponding eye, and respond vigorously to large ($6\text{--}30^\circ$) moving objects with no directional selectivity. These responses rapidly habituated to repetitive stimulation, and ceased after the second or third presentation.

Two principal types of visually responsive neurons in the toad pretectum have been characterized, designated TH3 and TH4 (Ewert, 1971, 1987).

TH3 neurons are primarily located in the lateral posterodorsal pretectal nucleus (LPd), and have relatively small receptive fields ($15\text{--}30^\circ$) that are best activated by moving dark objects of 10° or more in size. When responses to configurational features were tested (squares, and worm- and antiworm-like rectangles), it was observed that they responded most strongly to squares, and most weakly to worm-like rectangles (Ewert, 1987). TH4 neurons were primarily located in the posterior pretectal nucleus, and have larger ($90\text{--}180^\circ$) receptive fields, often covering the entire contralateral visual field. Most respond to each new kind of object motion, and rapidly adapt to repeated stimulation within a particular region of the receptive field.

Within the frog LCC there is a region in which neurons are spontaneously active, and respond with increasing discharges to the presentation of moving visual objects, such as a black disc attached to a lucite rod, or a human hand or body traversing the visual field (Smeraski, 1995). This region extends from the rostral border of the mesencephalon to at least the caudal aspect of the oculomotor nucleus. Responses could be obtained by presenting moving objects at disparate regions within the visual field on either side of the animal, indicating that the receptive fields of neurons in this area are bilateral, and probably cover the entire visual field. The responses immediately cease after the visual stimulus passes from the visual field, and rapidly habituate upon repeated presentation. The responses of these neurons are similar to those of optic tectum layer-4 'total-field' neurons described by Gaillard (1985), with the exception that their receptive fields cover the entire visual field, while layer-4 neurons only respond to objects in the monocular visual field. Many visual neurons in the LCC also respond to tactile inputs. Typically, a single unit in the LCC can be activated by electrical microstimulation of numerous sites within the ipsilateral and contralateral deep layers of the tectum (Smeraski, 1995). Although stimulus form and movement selectivity of the visual responses of LCC neurons were not examined in this study, the fact that they responded to whole moving objects, but not to simple punctate stimuli, and receive monosynaptic inputs from the deep tectal layers, where responses of neurons are stimulus-specific (Ewert, 1987), suggests that it is likely that differential responses to different classes of objects might be obtained.

Since the orienting and snapping responses of toads to visual objects only occur when these objects have a fairly specific geometric configuration and move in a particular manner (Ewert and Burghagen, 1974b; Wachowitz and Ewert, 1996), it is apparent that the ensemble of structures that participate in prey recognition in toads (and presumably also in the recognition of other classes of visual objects) must constitute a visual analyzer, comparable to the cortical visual analyzer of higher vertebrates (Felleman and Van Essen, 1991), but restricted to the recognition of certain innately determined objects. Ewert (1987) has argued that the anuran visual recognition system takes advantage of both parallel and hierarchical processing, much the same as the mammalian cortical visual analyzer (DeYoe and Van Essen, 1994).

2.1.1. Organization and hierarchy of the anuran innate visual recognition system

The structures involved in innate visual recognition in toads are shown in the diagram of Fig. 2, which is based on the studies of Ewert and co-workers (Ewert, 1987; Ewert et al., 1992, 2001). In this diagram, two of the structures included, the optic tectum and the posterior thalamic nucleus, are composite structures, in that they can be subdivided into anatomically discrete components. Here we wish to construct a more detailed schematic of the system, with the subdivisions of the optic tectum and individual pretectal nuclei considered as separate entities, and in which the hierarchical organization is detailed. The frog optic tectum can be divided into nine different layers, of which the lowest (layer 1) lies adjacent to the ventricle, and the topmost (layer 9) is subdivided into seven sublayers (Lázár et al., 1983). Only layers 1, 2, 4, 6, 7 and 8 are dense in cells; the remaining layers mostly contain fibers. It has been proposed that the periventricular layers (1 and 2) are homologous to the mammalian periaqueductal gray matter (Wilczynski and Northcutt, 1977), and we thus exclude them, since the periaqueductal gray is not a visual (sensory) structure. Layers 7 and 8 are not separated by a layer of fibers, so we consider them to be a single entity. Each of the remaining cell-dense layers (layers 4, 6 and 7/8) are regarded here as a separate component of the anuran visual system.

In order to determine the hierarchical organization of the anuran visual system, it is necessary to form criteria that allow the determination of the

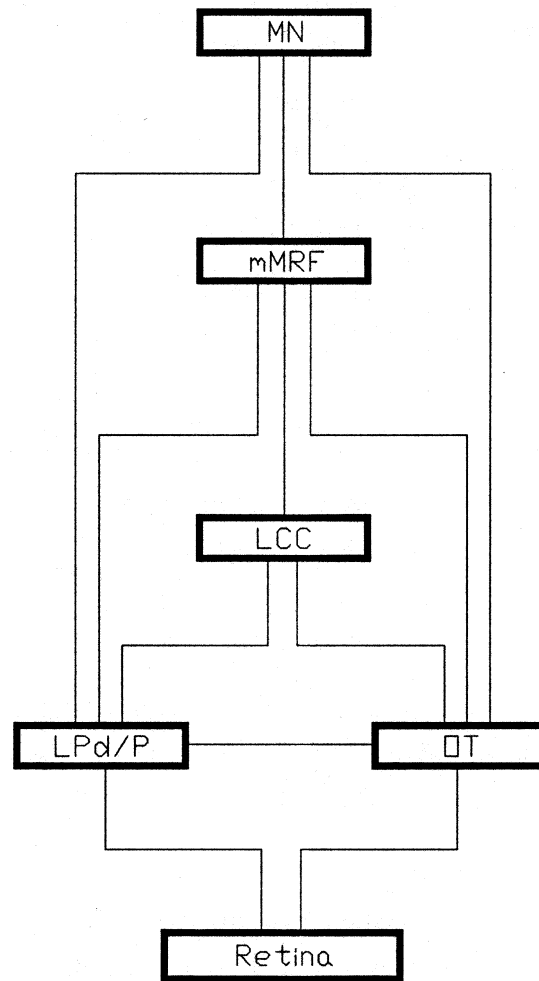


Fig. 2. Schematic diagram of neural network in anuran species mediating innate object recognition and output to the medullary premotor and spinal motor systems. Modified from Ewert et al. (1992). *Abbreviations:* LCC, large-celled column; LPd, pretectal lateral posterodorsal nucleus; mMRF, medial medullary reticular formation (premotor area); MN, motoneuron pools of the spinal cord ventral horn and brainstem motor nuclei, and associated circuitry; OT, optic tectum; P, posterior pretectal nucleus.

relative rank of different components. In the mammalian cortical visual system, all the connections between different components (such as V1, V2, V3 and V4 of the primate visual system) are reciprocal. The hierarchical organization of cortical visual systems has been determined using information on the laminar pattern of origin and termination of reciprocal projections (Rockland and Pandya, 1979; Felleman and Van Essen, 1991). In subcortical structures layering is rarely present, so establishing the hierarchical organization of com-

Table 1

Receptive field diameters for visual neurons in the anuran optic tectum, posterior thalamus and LCC

Designation	Species	Location	Mean RF (°)	Reference
T7	<i>R. esculenta</i>	TO, layer 9	2–3	Grüsser and Grüsser-Cornehls, 1976
Small RF	<i>R. pipiens</i>	TO, layer 9	5	Finch and Collet, 1983
Group 5	<i>R. esculenta</i>	TO, layer 8	4–6	Gaillard, 1985
Group 4	<i>R. esculenta</i>	TO, layer 8	10–30	Gaillard, 1985
T5(4)	<i>R. temporaria</i>	TO, layer 8	24	Matsumoto et al., 1986
T5(3)	<i>R. temporaria</i>	OT, layer 8	29	Schürg-Pfeiffer and Ewert, 1981
T5(1)	<i>R. temporaria</i>	OT, lyr 8 (6/7)	33	Ewert and von Wiersheim, 1974
T5(2)	<i>R. temporaria</i>	OT, layer 6	33	Ewert and von Wiersheim, 1974
T1(1)	<i>R. temporaria</i>	OT, layer 6	30–40	Matsumoto et al., 1986
Group 3	<i>R. esculenta</i>	OT, layer 6	1/4 VF	Gaillard, 1985
Group 2	<i>R. esculenta</i>	OT, layer 4	1/2 VF	Gaillard, 1985
Type 3 (TH3)	<i>B. americanus</i>	LPd	10–30	Ewert, 1971
Type 4 (TH4)	<i>B. americanus</i>	P	90–180	Ewert, 1971
LCC	<i>R. pipiens</i>	LCC	EVF	Smeraski, 1995

Abbreviations: LCC, large-celled column; LPd, pretectal lateral posterodorsal nucleus; OT, optic tectum; P, posterior pretectal nucleus; RF, receptive field.

ponents of the subcortical visual system of anurans is not as straightforward. However, an approximate hierarchy can be determined using electrophysiological and hodological data. In mammalian cortical visual systems, the receptive field diameters of visually responsive neurons in the lower-order areas of the system (V1, V2) are quite small, while those in higher-order areas (V4, TE) are considerably larger. In general, there is a progression within the system from small receptive fields in lower-order areas to larger receptive fields as the hierarchy of the system is ascended. Thus, the receptive field diameter can be used to determine the approximate position of a component of the visual system in the hierarchy. Areas that receive substantial direct retinal inputs are presumably 'primary' areas, comparable to V1 in the primate visual cortex. Using the receptive field data presented in Table 1 (Grüsser and Grüsser-Cornehls, 1976; von Wiersheim and Ewert, 1978; Ewert, 1987, 1997; Ewert et al., 1992), we have constructed the schematic of Fig. 3, in which the hierarchy of the components is detailed.

The receptive field data discussed in the previous paragraph indicate that the LCC is the highest-order component of the anuran visual system, since it appears that nearly all neurons in this structure respond to objects in the entire visual field. Although total-field neurons also occur in particular layers of the optic tectum and in the pretectal nuclei, these are intermingled with other neurons for which receptive fields are limited. Therefore,

according to the argument presented above, it may be expected that the neural engrams that represent the recognition of classes of objects will occur in the LCC. It should be pointed out, however, that direct evidence for the involvement of cells in the LCC in object recognition is scant. The fact that cells in LCC respond to the presentation of whole moving objects, but not to simple punctate stimuli (Smeraski, 1995), is suggestive. In the study of Masino and Grobstein (1989b) cited above, it was observed that partially bilateral aspiration lesions to the LCC caused deficits in orientations to prey objects presented in both hemifields. In general, the degree of deficit was dependent on the site and extent of the lesions, which might suggest that object localization (rather than recognition) was compromised, thus supporting the concept that recognition is represented by command neurons located in the optic tectum and pretectum, as proposed by Ewert (1987). However, in some of the animals the damage completely abolished orientation to stimuli presented on the side with greater damage. This suggests loss of recognition, rather than loss of localization, since it may be expected that if recognition still occurred, the animals would make some kind of response, even if inaccurate. The fact that orientation to stimuli presented on the side that sustained less damage was preserved to varying degrees suggests that the engrams are duplicated in the contralateral and ipsilateral LCC. Studies in which lesions were placed caudal to the LCC, which damaged the

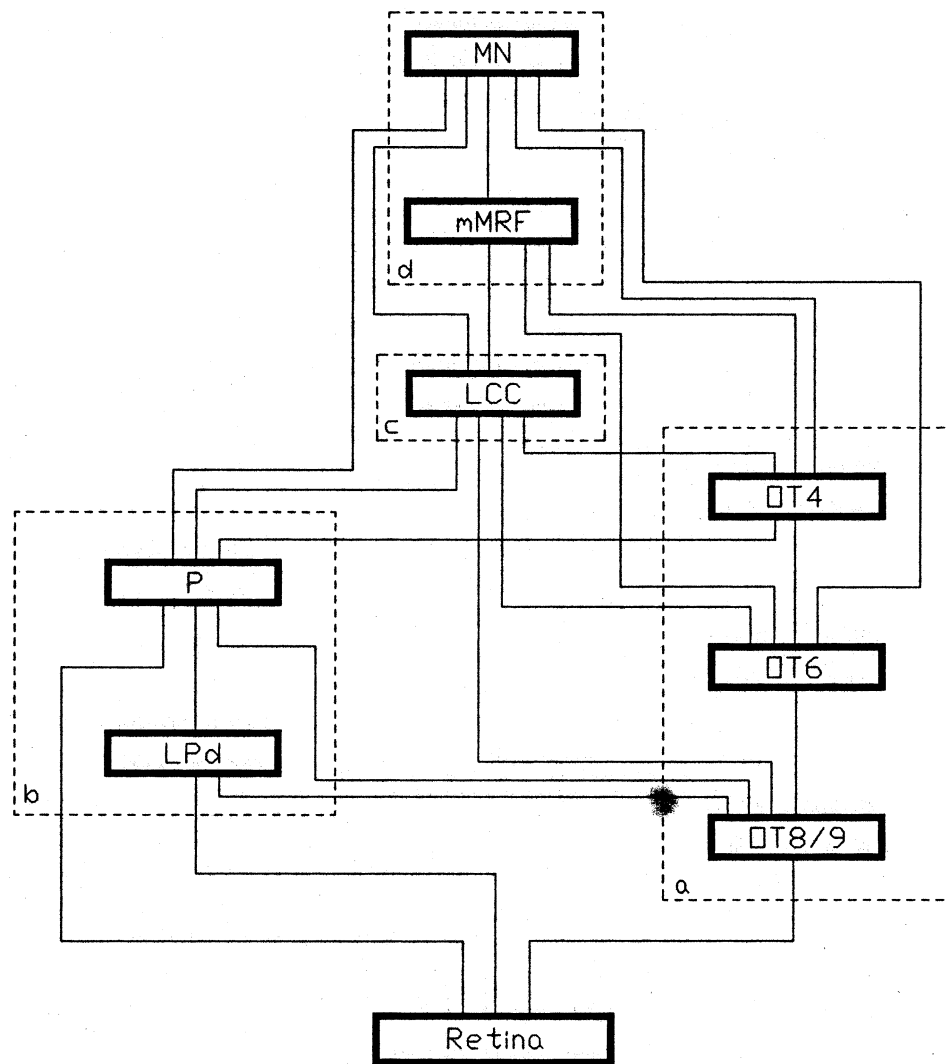


Fig. 3. Detailed schematic diagram of hierarchical organization of neural structures and pathways of the anuran subcortical visual system, and its output to medullary-spinal motor systems: (a) optic tectum; (b) pretectal nuclei; (c) large celled column in mesencephalic reticular formation; (d) medullary premotor area, motoneuronal pools and associated circuitry, which generate fixed action patterns. *Abbreviations:* LCC, large celled column; LPd, pretectal lateral posterodorsal nucleus; mMRF, medial medullary reticular formation; MN, motoneuronal pools of the ventral horn of the spinal cord, brainstem motor nuclei, and associated circuitry; OT4, OT6, OT7 and OT8, cell dense layers of optic tectum.

tracts linking the optic tectum and LCC with the premotor circuits of the mMRF, also demonstrated varying degrees of deficits, depending on the location and extent of the lesions (Kostyk and Grobstein, 1982, 1987a; Roche King and Comer, 1996), but it seems likely that the lesions damaged parts of both tracts, so the interpretation of these results is difficult at best. We propose below that in mammalian species the engrams for innate visual object recognition may be located in the more medial parts of the midbrain tectum, and

activity in the lateral tectum contributes to stimulus localization. Thus, an additional possibility is that the deficits in orientation due to the lesions in the study of Masino and Grobstein (1989b) may have been due to combined damage to tectal engram representations and tectal neurons that process stimulus localization and movement information.

In support of the 'command neuron' concept, Ewert and colleagues (Ewert, 1987, 1997; Ewert et al., 1992) have observed that tectal T5.1, T5.2,

T5.3 and T5.4 neurons can be backfired from the mMRF (Ewert et al., 1990), and that the response properties of some mMRF cells resemble those of T-type tectal and TH-type pretectal feature-sensitive neurons (Schwippert et al., 1990), which suggests that information related to stimulus configuration is conveyed directly to the mMRF by the direct tecto-bulbar and pretecto-bulbar projections. Hence, comparison of the responses of LCC, tectal, pretectal and mMRF cells may help to establish the localization of recognition representations in the anuran mesencephalon. More importantly, the stimulus specificity of responses of LCC neurons to prey, predator and other types of stimuli need to be investigated. Indirect support for the concept that engrams are located in the LCC is given below, where we note that electrical stimulation of sites within the mammalian medial mesencephalic tegmentum, which is homologous to the anuran LCC, evokes behaviors such as freezing, running, darting and mastication. Such behavioral responses are unlikely to be triggered by the activity of neurons that represent stimulus localization and movement.

2.1.2. Motor output

As mentioned above, premotor structures for innate behaviors that occur in response to prey and predator recognition are located in the mMRF (Ewert et al., 1984, 1990; Matsushima et al., 1989). This area of the medulla receives afferent projections from the optic tectum and LCC (Masino and Grobstein, 1989b), and projects to motoneuronal pools in the spinal cord and to the brainstem motor nuclei (Matesz and Székely, 1978; ten Donkelaar, 1982). Information about object recognition, spatial location, movement and relationships to other objects is transferred from the optic tectum, pretectal nuclei and LCC to the premotor area, and this information serves to initiate behavioral responses.

3. Innate visual stimulus recognition in avian species

Newly hatched chicks will peck at small objects shortly after birth and show definite preferences for certain types, colors and shapes of objects, even when these objects produce no reward (Hess, 1956; Fantz, 1957; Goodwin and Hess, 1969). When presented with flat shapes, chicks prefer small, horizontal, oval objects over all other

shapes, closely followed by small circular objects, while rectangles and other shapes with sharp corners are least preferred. It has been shown that telencephalated pigeons can locate and peck at food objects (seeds), and that this ability is not significantly different from that of intact animals (Silva and Ferrari, 1991). This result suggests that seed recognition is intact in pigeons lacking telencephalic visual structures. Since the behavioral data indicate that seed recognition is at least initially innate, it can be inferred from the results of Silva and Ferrari (1991) that innate recognition of food objects in birds is mediated by subtelencephalic structures.

Soon after hatching, visually naive chicks will approach a wide range of conspicuous objects and will follow those objects that move. These chicks exhibit a predisposition to follow certain types of objects, and the nature of this predisposition has been examined in several studies (Gray et al., 1980; Kovach, 1983; Kovach and Wilson, 1983; Bolhuis et al., 1985; Bolhuis and Honey, 1998; Bolhuis, 1999). For example, white leghorn chicks raised in isolation prefer moving painted silhouettes of ducks and other birds to static objects or moving objects that lack bird-like characteristics (Gray et al., 1980). Chicks show a tendency to approach a stuffed jungle fowl in preference to a red box (Bolhuis et al., 1985). In general, the predisposition—presumably innate—is to approach stimuli that resemble conspecifics, both in their shape and color, and in the way they move (Bolhuis and Honey, 1998). The process of imprinting involves the learned recognition of a particular stimulus object, which becomes ‘mother’ for the chicks. Thus, the innate recognition component of the process causes the chicks to preferentially follow adult conspecifics that could potentially act as mothers, and the (learned) selection of a particular conspecific presumably depends on the responses of that particular object (i.e. on whether the responses are reinforcing or not).

Complete bilateral hemispherectomy performed in early life spares many behaviors that require stimulus discrimination, such as pecking at food objects, flying and preening (Rogers, 1922; Kovach and Kabai, 1993). Martin and Rich (1918) observed that decerebrated domestic chicks ran toward moving objects, and their description suggests that the behavior was essentially the same as that of the approach of unlesioned chicks to poten-

tial mother objects. More recently, it has been demonstrated that bilateral removal of the telencephalic hemispheres at the junction between the telencephalon and the diencephalon prevents Japanese quail chicks from imprinting to colored stimuli, but spares the innate preference for particular colors and patterns (Kabai and Kovach, 1993, 1997; Kovach and Kabai, 1993). Post-imprinting telencephalic ablation on the third post-hatch day erased the imprinted memory. These results indicate that the innate preference for conspecifics (or objects that resemble conspecifics) is mediated by structures caudal to the telencephalic hemispheres. When deeper lesions were made, and various diencephalic structures were damaged, but the mesencephalon, including the optic tectum, were spared, this caused substantial impairments in the following response (Kabai and Kovach, 1993). It is apparent that a diencephalic structure must participate in mediating the following response, and in order to determine which structure(s) might be involved, Csillag et al. (1995) examined the effects of various diencephalic lesions on the following response in Japanese quail chicks. They found that extensive radio-frequency lesions in medial diencephalic structures diminished approach tendencies and greatly attenuated the innate preference for red objects. The deficits in the following responses due to lesions of medial hypothalamic structures is almost certainly largely due to the loss of motivational inputs to premotor and motor structures, since neuronal activity in the hypothalamus/preoptic area represents motivational processes (Valenstein et al., 1970; Simonov, 1997), and in mammalian species, lesions to homologous structures also cause severe deficits in behavioral responses to external stimuli (Panksepp and Dickinson, 1972; Paredes et al., 1993; Edwards et al., 1996; Canteras et al., 1997).

Csillag et al. (1995) also examined the effects of lesions to the pretectal area, including the pretectal nucleus, lateral spiriform nucleus, mesencephalic nucleus lentiformis, subpretectal nucleus and triangular nucleus, and found that these lesions did not affect the approach responses of chicks. However, in this study the effects of the lesions on pretectal nuclei on stimulus discrimination were not examined. As mentioned above, Ewert et al. (1996) found that after lesions to the pretectum, toads failed to discriminate between 'prey-like' and 'predator-like' stimuli, and oriented and snapped at any moving stimulus, so it is

possible that the following response of quail chicks with pretectal lesions could be affected in a similar manner (i.e. they would follow almost any moving object, irrespective of its geometric configuration).

The effects of lesions to the optic tectum and mesencephalic reticular areas, which might be homologous to the anuran LCC on the following response, have not been determined. However, since telencephalic lesions do not affect the responses, it is clear that the visual pathways involved must include either the retinotectal or retinopretectal projections. As discussed above, the latter projection probably contributes to stimulus discrimination, but the pathway through the optic tectum and midbrain reticular area are probably essential, given the effects of tectal and LCC lesions on anuran responses to visual stimuli (Ingle, 1973, 1977; Kostyk and Grobstein, 1982; Masino and Grobstein, 1989b). The locomotor component of the response can be elicited in decerebrate geese and ducks by electrical microstimulation of sites within the mesencephalic reticular formation (Sholomenko et al., 1991). We may therefore speculate that brainstem structures and pathways homologous to those involved in prey and predator recognition in amphibians (i.e. the optic tectum, pretectal nuclei and mesencephalic tegmentum) are involved in visual recognition of conspecifics in avian species.

Lesions to particular portions of the telencephalon have revealed that a restricted part of the chick forebrain, the intermediate region of the hyperstriatum ventrale, is necessary for imprinting to particular objects (McCabe et al., 1981; Horn, 1986, 1990; Bolhuis and Honey, 1998). Lesions to this area abolish learned object preferences as effectively as do complete ablations of the telencephalon, confirming the fact that the recognition of individual objects, including individual conspecifics, requires the participation of telencephalic structures.

4. Innate visual stimulus recognition in rodents

Rodents are capable of recognizing visual objects, such as predators, with no previous experience of those objects (Blanchard and Blanchard, 1971; Hirsch and Bolles, 1980), and respond to these objects with behaviors such as immobility (freezing) or flight. For example, naive (laboratory born and raised) rats exposed to a cat respond with freezing behavior, and wild running and

jumping (Blanchard and Blanchard, 1971; Canteras et al., 1997). Recognition of terrestrial predators in a natural environment is probably mediated by pheromonal as well as visual cues, since Fos induced in naive rats by exposure to a cat is elevated in the principal components of the vomeronasal pathway, the MeA and medial BNST, as well as in the principal brainstem visual structure, the superior colliculus (Canteras et al., 1997). In this section, we only address innate visual prey and predator recognition.

4.1. Structures and pathways

The data on the effect of lesions to telencephalic structures of anuran and avian species indicate that innate object recognition in these species is mediated by brainstem and diencephalic structures. Lesions to telencephalic structures have only minor effects on behaviors that occur in response to innate stimulus recognition (Kabai and Kovach, 1993, 1997; Kovach and Kabai, 1993; Patton and Grobstein, 1998a,b; Ewert et al., 2001). Given the conservative nature of subtelencephalic function, it may be expected that innate recognition in mammalian species might be similarly affected by telencephalic lesions. Rats with complete bilateral lesions of visual cortex, which cause retrograde degeneration throughout the dorsal lateral geniculate nucleus, cannot be distinguished by casual observation of their behaviors from normal rats, and are evidently not blind (Dean, 1978). Ferrier and Cooper (1976) observed that visually decorticate rats orient to luminous targets with the same accuracy as normal rats. Decorticate rats are unable to locate an invisible platform submerged within a tank of water made opaque with milk, but are able to swim directly to the platform if it is made visible using clear rather than opaque water (Whishaw and Kolb, 1984). Adult hamsters with extensive lesions to the visual cortex are still able to orient to, approach and consume seeds (Schneider, 1969), which are an important component of their natural diet. However, rodents with lesions to the visual cortex are unable to learn to recognize abstract, geometric visual objects (Schneider, 1969, 1970; McDaniel et al., 1982). It is clear that cortical visual structures are necessary for learned object recognition, but the abilities of visually decorticate animals suggest that not only are they not blind (Sowards and Sowards, 2000), but also

that some form of visual object recognition survives the lesions.

Ingle (1981, 1982) observed that normal gerbils orient to and approach or pursue animate objects, principally conspecifics and prey. These animals will often pursue females, other males or insects at high speeds. It was also observed that the gerbils would pursue and catch white disks when they emerged from behind opaque barriers, and moved at 30–40°/s around the rim of a semicircular arena, and this pursuit response did not need special training. After bilateral removal of areas 17 and 18 of the visual cortex, the animals still oriented to and pursued the moving disks, but the accuracy of their pursuit was deficient when compared to that of unlesioned animals. Ingle concluded that, while the cortically damaged gerbils were deficient in stimulus localization, they showed no deficits on the object identification task. It is clear that, as in the case of prey recognition in anurans, the precise shape of the stimulus object is not overly important, and recognition is primarily based on the characteristics of the movement of the object, and probably also its size. The visual recognition of the disks cannot be due to learning (Schneider, 1969, 1970; McDaniel et al., 1982), so the moving disks must be innately recognized as either prey or conspecifics. This form of recognition is evidently exclusively mediated by brainstem and diencephalic visual structures, since the disks were odorless.

The major visual structure that survives after visual decortication is the superior colliculus, since visual thalamic nuclei undergo severe degeneration after cortical lesions (Dean, 1978). This structure receives a major retinal projection, while lesser retinal inputs reach the pretectal nuclei, principally the nucleus of the optic tract. The involvement of the superior colliculus in visual function in rodents has been extensively investigated. Most of the behaviors that can be elicited from rodents by naturally threatening stimuli, including orienting, freezing, rapid running and darting (Blanchard and Blanchard, 1971; Blanchard et al., 1986), can also be produced by electrical or chemical stimulation of the superior colliculus (Redgrave et al., 1981; Sahibzada et al., 1986; Dean et al., 1988). The pathways that mediate the behavioral output elicited by stimulation of the superior colliculus have been determined (Redgrave et al., 1987, 1988, 1990, 1993; Keay et al., 1990). There are two major pathways, one contralateral and the other

Table 2

Receptive field diameters for visual neurons in the superior colliculus of mammalian species (rabbit, rat, hamster, cat)

Species	Location	RF (°)		Reference
		Mean	Range	
Hamster	SC: SGS	10	3–30	Tiao and Blakemore, 1976
Hamster	SC: SO	14	3–34	Tiao and Blakemore, 1976
Hamster	SC: SGI	25	3–54	Tiao and Blakemore, 1976
Hamster	SC: SGP	45	18–64	Tiao and Blakemore, 1976
Rabbit	SC: SGSu	2.86	1–11	Graham et al., 1982
Rabbit	SC: SGSI	8.63	1–23	Graham et al., 1982
Rabbit	SC: SO	12.73	7–14	Graham et al., 1982
Rabbit	SC: SGI	19.86	2–54	Graham et al., 1982
Rabbit	SC: SGP	*	29–100	Graham et al., 1982
Rabbit	NOT	20 × 30	*	Collewijn, 1975
Cat	NOT	14	5–50	Hoffmann and Schoppmann, 1981
Cat	NOT	*	2–56	Straschill and Hoffmann, 1969
Rat	Apt	28	18–35	Siminoff et al., 1967
Rat	Ppt	30	20–50	Siminoff et al., 1967
Cat	NPC	*	24–120	Straschill and Hoffmann, 1969
Cat	MpRF	*	20–EVF	Bell et al., 1964

Abbreviations: Apt, anterior pretectal nucleus; MpRF, mesopontine reticular formation; NOT, nucleus of the optic tract; NPC, nucleus of the posterior commissure; Ppt, posterior pretectal nucleus; SC, superior colliculus; SGSI, lower layer of the stratum griseum superficiale of the SC; SGSu, upper layer of the stratum griseum superficiale; SO, stratum opticum; SGI, stratum griseum intermediale; SGP, stratum griseum profundum. (* = no data available).

ipsilateral, which originate from different populations of cells in the superior colliculus. The major contralateral projection, termed the tectospinal or tectoreticulospinal projection, runs the length of the brainstem and innervates structures in the medial pons and medulla, including the area in the medullary gigantocellular and magnocellular reticular fields (the mammalian mMRF), in which premotor circuits for innate responses such as locomotion and other essential motor acts are located (Garcia-Rill and Skinner, 1987; Kinjo et al., 1990; Cowie et al., 1994). The major ipsilateral projection originates in the intermediate (SGI) and deep (SGP) layers of the superior colliculus and terminates in the cuneiform nucleus and some adjacent areas of the mesopontine reticular formation.

The responses of rodent collicular neurons to simple stationary and moving stimuli have been examined in numerous studies (Michael, 1972; Tiao and Blakemore, 1976; Mooney et al., 1985, 1993; Meredith and Stein, 1990; Gonzalez et al., 1992), and these results are not detailed here, although the receptive field diameters in the various tectal layers are summarized in Table 2. More importantly, Manteuffel and Fiseifis (1990) investigated the responses of mouse collicular cells to the same types of configurational stimuli used in

studies of amphibian prey and predator recognition. These stimuli consisted of a large square, a horizontal (worm-like) rectangle, and a vertical (antiworm-like) rectangle, all of which moved at various velocities. Approximately 40% of the neurons sampled preferentially responded to the square moving at medium and high velocities, while 10% preferred the horizontal bar at the same velocities. Most of these neurons were located in the intermediate and deep gray layers (SGI and SGP), and had receptive field diameters that ranged from 4 to 40°. The responses to configurational stimuli were similar to those of anuran optic tectum neurons described by Ewert and co-workers (Ewert and von Wiersheim, 1974; Ewert, 1987; Matsu-moto et al., 1986), and Manteuffel and Fiseifis (1990) concluded that certain aspects of tectal neuronal circuitry are conserved over phylogeny. Hence, the observations of Ingle (1981, 1982) that visual decorticate gerbils pursue objects that move in a naturalistic fashion is explained by their presumptive recognition as prey or conspecifics, and this recognition is mediated, at least in part, by activities in the superior colliculus, as is prey recognition in anurans by activities in the optic tectum.

In the anuran optic tectum, the periventricular layers (1 and 2) are most probably homologous to

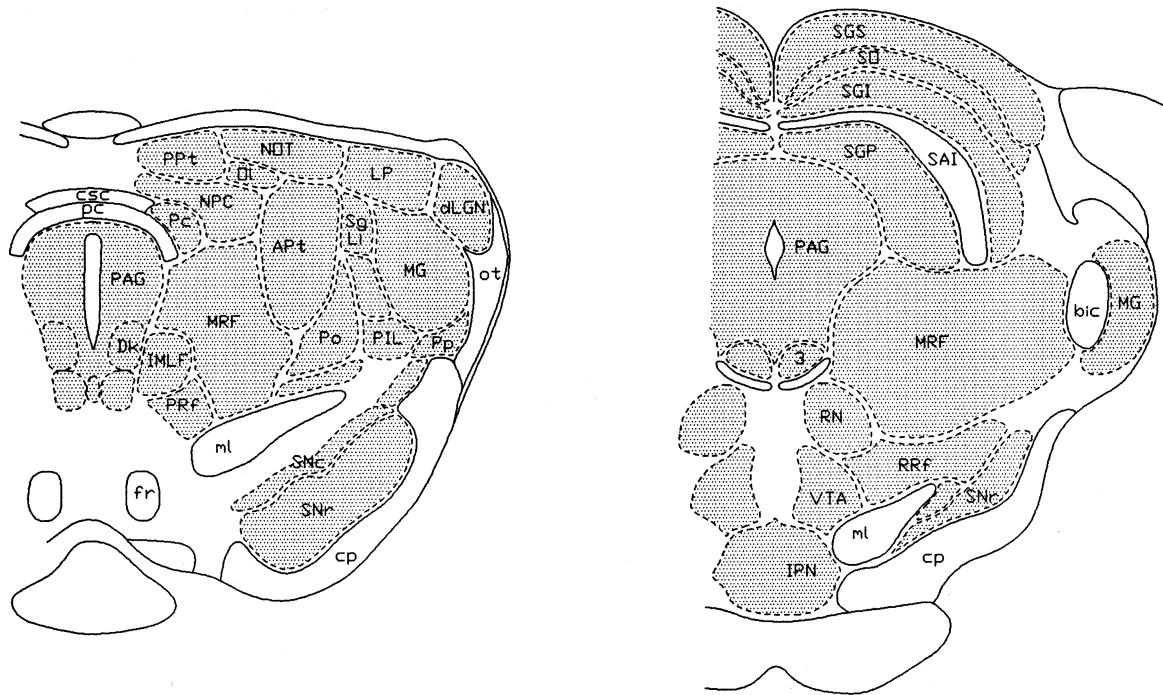


Fig. 4. Location of tectal and pretectal structures involved in innate visual object recognition in rodents. *Abbreviations:* APt, anterior pretectal nucleus; Dk, nucleus of Darkewitsch; dLGN, dorsal lateral geniculate nucleus; IMLF, interstitial nucleus of the medial longitudinal fasciculus; LP, lateral posterior thalamic nucleus; MG, medial geniculate nucleus; MpRF, mesopontine reticular formation; NOT, nucleus of the optic tract; NPC, nucleus of the posterior commissure; Ol, olivary pretectal nucleus; PAG, periaqueductal gray matter; Pc, precommissural nucleus; PIL, posterior intralaminar thalamic nucleus; Po, posterior thalamic nucleus; Pp, peripeduncular nucleus; PPt, posterior pretectal nucleus; RN, red nucleus; RRf, retrorubral field; SC, superior colliculus; SGS, SO, SGI, SAI, SGP, superficial, optic, intermediate, white, and deep layers of the SC; SG/Li, suprageniculate-limitans complex; SNc, substantia nigra compacta; SNr, substantia nigra reticulata; VTA, ventral tegmental area.

the mammalian periaqueductal gray matter (Wilczynski and Northcutt, 1977), so it is likely that the wide anuran optic tectum layer 6 is homologous to the mammalian SGI layer, which would make layer 4 homologous to the mammalian SGP. Layers 8 and 7 should then correspond to the mammalian stratum griseum superficiale (SGS) and stratum opticum (SO), respectively.

In the mammalian pretectum, three nuclei lie medial to the nucleus of the optic tract: the anterior and posterior pretectal nuclei, and the nucleus of the posterior commissure (Fig. 4), which is contiguous with the periaqueductal gray matter (Hutchins and Weber, 1985). In the anuran pretectum, only the posterior pretectal nucleus lies medial to the lateral posterodorsal nucleus (Ewert, 1987; Montgomery and Fite, 1991). Based on hodological and histochemical data, the anuran posterior pretectal nucleus has been subdivided into three separate entities, the precommissural and juxtacommissural nuclei and the nucleus of the posterior commissure

(Fig. 1) (Puelles et al., 1996). The precommissural nucleus is almost certainly homologous to the mammalian anterior pretectal nucleus. Other data suggest that the juxtacommissural nucleus is homologous to the mammalian posterior pretectal nucleus, and the anuran nucleus of the posterior commissure corresponds to the homonymous structure in mammals (Puelles et al., 1996). The nuclei of the pretectal area are all reciprocally interconnected, and connected with the different gray layers of the superior colliculus (Figs. 4 and 5).

From the above discussions, it is evident that four pretectal structures, the nucleus of the optic tract, anterior and posterior pretectal nuclei, and nucleus of the posterior commissure, are probably constituents of the rodent subcortical visual recognition system, since they are homologous to corresponding entities in anurans which mediate prey recognition. In addition, the three divisions of the superior colliculus (SGS/SO, SGI and SGP) are necessary components. The output pathways

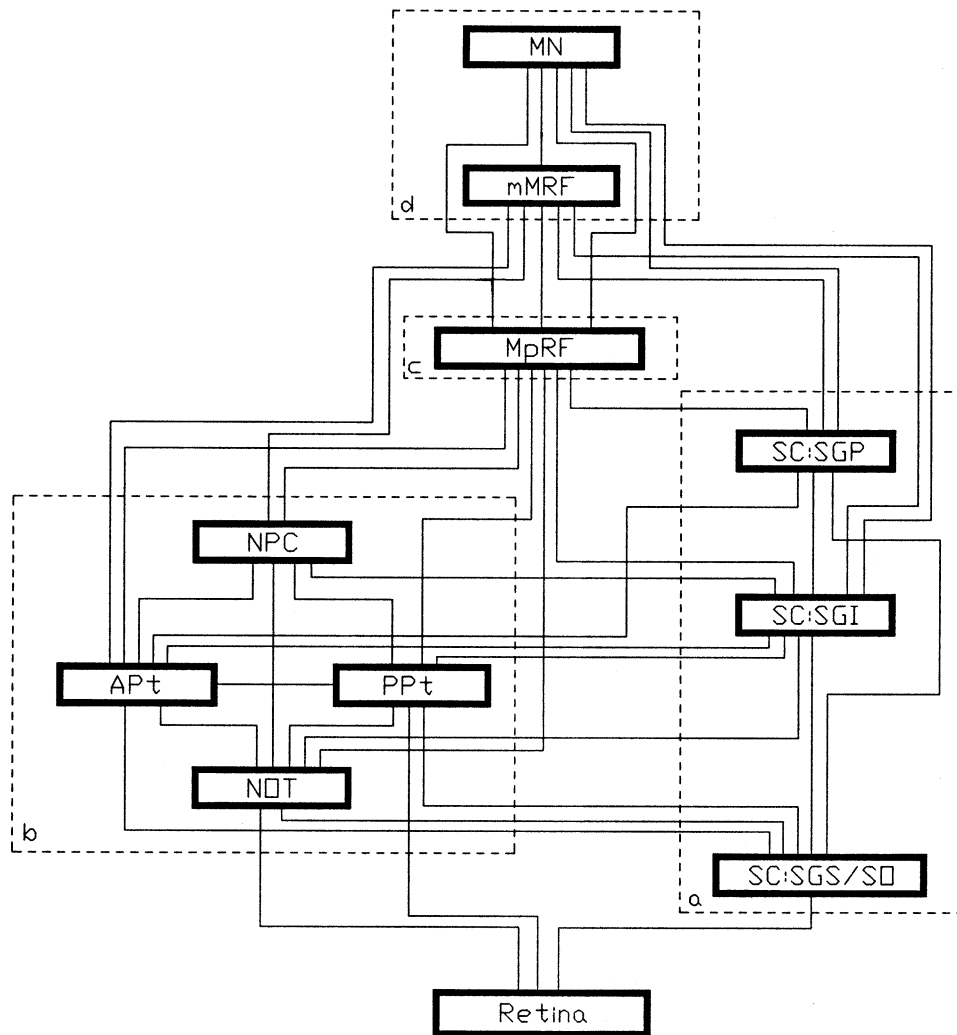


Fig. 5. Schematic diagram of the neural structures, pathways and hierarchical organization of the mammalian subcortical visual system: (a) superior colliculus; (b) pretectum; (c) mesencephalic locomotor region; (d) medullary premotor area and spinal cord motor columns. *Abbreviations:* APT, anterior pretectal nucleus; mMRF, premotor area of the medial medullary reticular formation, including the nuclei reticularis gigantocellularis and magnocellularis; MN, motoneuronal pools of the ventral horn of the spinal cord, brainstem motor nuclei and associated circuitry; MpRF, mesopontine reticular formation, which includes the cuneiform and subcuneiform nuclei; NOT, nucleus of the optic tract; NPC, nucleus of the posterior commissure; PPT, posterior pretectal nucleus; SC: superior colliculus; SGS, SO, SGI, SGP, superficial, optic, intermediate and deep layers of the SC.

from the rodent superior colliculus to the midbrain, medulla and spinal cord described above are clearly very similar to the output pathways from the anuran optic tectum (Masino and Grobstein, 1989a,b). In particular, the projections from the superior colliculus to the mesopontine tegmentum strongly resemble the projections from the anuran optic tectum to the LCC, so it is reasonable to conclude that the mammalian cuneiform nucleus and adjacent areas are homologous to the LCC. The total area within the midbrain and pons that

corresponds to the anuran LCC can be approximately determined by examining the projections from the rodent superior colliculus to the reticular areas in the midbrain and rostral pons. These projections terminate in the cuneiform nucleus, part of the subcuneiform nucleus and part of the pedunculopontine nucleus (Cohen and Büttner-Ennever, 1984; Redgrave et al., 1988; Semba and Fibiger, 1992; Steininger et al., 1992). For the sake of simplicity, we refer to this area as the mesopontine reticular formation (MpRF). The pro-

jections from the superior colliculus to the cuneiform nucleus and other parts of the MpRF primarily originate in the SGI and SGP layers (Cohen and Büttner-Ennever, 1984; Redgrave et al., 1988). The pretectal nuclei, including the nucleus of the optic tract, anterior and posterior nuclei, and nucleus of the posterior commissure, also project to the MpRF (Fig. 5) (Simpson et al., 1988).

The terminal field of superior colliculus projections within the MpRF coincides in part with the area that has been termed the 'mesencephalic locomotor region' (Shik et al., 1969; Grillner and Shik, 1973; Grillner and Dubuc, 1988; Garcia-Rill and Skinner, 1988). The mammalian mesencephalic locomotor region includes parts of the cuneiform and pedunculopontine nuclei, and electrical and chemical stimulation of the area produces locomotion at various velocities, depending on the intensity and location of the stimulation (Shik et al., 1969). The locomotion induced by this type of stimulation is probably a component of behavioral responses due to recognition of food and fear-inducing objects, among others, and it is thus likely that stimulation at different sites elicits locomotion for different purposes (Jordan, 1998). Stimulation of particular locations within the MpRF also evokes other types of behaviors, such as freezing, running and darting, and mastication (Garcia-Rill and Skinner, 1988; Mitchell et al., 1988). The MLR and adjacent parts of the subcuneiform nucleus project to the premotor structures for locomotion and other behaviors located in the mammalian mMRF, which includes parts of the gigantocellular and magnocellular reticular nuclei (Steeves and Jordan, 1984; Kinjo et al., 1990; Hermann et al., 1997; Lai et al., 1999) and to the spinal cord (Fig. 5).

We have previously proposed that the visual awareness that is evident in decorticate rodents (Ferrier and Cooper, 1976; Dean, 1978; Whishaw and Kolb, 1984) is due to neuronal activity in components of the subcortical visual system (Sowards and Sowards, 2000). Activity in these components must also contribute to the computational processes required for innate visual recognition of prey, predators and other biologically relevant objects, as they do in homologous structures of the anuran visual system.

4.2. Hierarchy

The same criteria that were employed for establishing the hierarchy of the anuran subcortical visual system can be used for the rodent system. The hierarchy is based on published data on the average receptive field diameters for neurons in the various components of the system, including the three principal layers of the superior colliculus, the anterior and posterior pretectal nuclei, and the NPC (Table 2). The connections between the various components are similar to those of the anuran system, and are shown in Fig. 5, together with the pathways that mediate behavioral output. Given the position of the MpRF as the highest-order component of the brainstem visual analyzer and its homology to the anuran LCC, we suggest that the neurons for which activity constitutes the engrams that represent the recognition of visual objects are located within the MpRF.

4.3. Motor output

Innate behavioral responses which occur as a result of the innate visual recognition of prey and predator stimuli are mediated by premotor structures located in the mMRF, and by the motoneuronal pools of the ventral horn of the spinal cord. Information that signifies that a particular class of stimulus object has been recognized presumably reaches the premotor structures via projections from the cuneiform nucleus. Motivational input may be mediated by projections from the periaqueductal gray matter (Graeff, 1981). The premotor circuits in the mMRF also receive inputs from the superior colliculus, and these inputs may supply information about the location and movement of the stimuli involved (Fig. 5).

5. Innate visual stimulus recognition in primates

5.1. Face recognition in human neonates

Human neonates, at an average of only 9 min from birth, tracked a slowly moving schematic face stimulus with their head and eyes significantly further than they follow scrambled faces or blank stimuli (Goren et al., 1975). This result was replicated by Morton and Johnson (1991) using the same stimuli used by Goren et al. (1975), and other experimenters have obtained similar results (Slater et al., 1985; Johnson et al., 1991; Valenza

et al., 1996). Morton and Johnson (1991) argue that the results of these studies indicate the existence of an innate face-recognizing device they call 'Conspec' (conspicuous), which serves to direct the newborn infant's visual attention to faces. The tendency to orient to face-like stimuli continues into the second month, and thereafter decays to be replaced by learned recognition of individual faces ('Conlearn'), starting at approximately 3 months of age (Dodwell, 1983; Morton and Johnson, 1991). It has also been observed that several newborn sensory-motor reflexes decline in the second or third month of life (Johnson, 1990). For example, orientation to sound sources declines after the first 2 months, with a subsequent re-emergence at the end of the fourth month (Muir et al., 1979, 1989; Field et al., 1980). Dodwell (1983) suggested that the 'built-in' (innate) tendency to orient toward external sources of stimulation might be mediated by subcortical structures, and that these responses may be inhibited at approximately the second or third month of life by the emergence of cortical activity.

There is strong evidence that the human retino-tectal visual pathway develops well in advance of the retino-geniculo-cortical pathway, and the latter is probably not functional until approximately 2 months after birth (Atkinson, 1984; Braddick et al., 1986). In the normal neonatal development of the flash visual-evoked potential, a short-latency (60–70 ms) negativity response emerges at 4–6 weeks of postnatal life, when the infants begin to display responsive smiling and show raised visual interest (Kraemer and Sjoström, 1998). The development of the specific evoked response represents the gradual onset of cortical activity mediated via the retino-geniculo-cortical pathway, so when the short-latency complex of the visual evoked potentials cannot be identified, visual function is presumably mediated by subcortical structures (Kraemer and Sjoström, 1998). Hence, the preferential tracking of face-like objects observed by Goren et al. (1975), Johnson et al. (1991) and Morton and Johnson (1991) in neonates is presumably mediated by subcortical structures, since the cortical visual system is almost certainly non-functional during the first few weeks after birth. It has been proposed that the subcortical structure most probably involved in the recognition of face-like stimuli is the superior colliculus (Johnson, 1990; Johnson et al., 1991). These authors have further suggested that two separate visual systems,

subcortical and cortical, mediate the sensory processing of faces in early infancy: one (subcortical) system that is functional at or very shortly after birth, which ensures that the infant orients toward face-like objects, and a second (cortical) system that develops or matures later, which is ultimately responsible for the sophisticated face-recognition abilities of the adult (Morton and Johnson, 1989; Johnson et al., 1991). These observations suggest that in humans innate object recognition is present in very early life, but gives way to learned recognition after approximately the second month.

According to the original concept of the Conspec and Conlearn mechanisms, the primary function of Conspec is to generate orientations toward face-like objects presented in the periphery (Morton and Johnson, 1991). Therefore, Conspec should not be involved in attention holding (i.e. duration of fixation), which Johnson (1990) argued involves a cortical mechanism. However, Valenza et al. (1996) and Macchi Cassia et al. (2001) found that, while measures of orientations were approximate indicators of face preference, measures of fixation duration were much more reliable. In light of the organization and proposed functions of the subcortical visual system presented above (i.e. it is a complete visual system, not just an orienting 'mechanism'), we would argue that this system mediates both orientation to, and fixation of, face-like objects in neonates, and that cortical activities do not contribute to either function until approximately the second month.

The maturation of the cortical visual system in human infants in terms of object recognition is reflected by the ability to remember individual faces. Recognition memory for individual faces has been demonstrated in 3-month-old infants (Pascalis et al., 1998). Similarly, it has been shown that infant monkeys develop visual recognition memory, as determined by the delayed non-matching to sample test, as early as 4 months of age (Bachevalier and Mishkin, 1984).

It should be mentioned here that some authors argue that there is a general neural substrate for face recognition, present at birth, which also mediates face recognition in adulthood, and that all face recognition is learned (Gauthier and Nelson, 2001; Nelson, 2001). However, this proposal appears to be at variance with the neurophysiological data on the onset of cortical visual responsiveness presented above. In addition, it has been reported that 4-day-old neonates look for longer at

their mother's face than at a stranger's face (Field et al., 1984; Bushnell et al., 1989; Pascalis et al., 1995), so some degree of visual discrimination learning appears to be possible before the cortical visual system becomes functional. This result brings to mind the experiment of Ewert and Kehl (1978), in which it was demonstrated that toads (who lack visual cortex) can learn to discriminate between individual objects within a class of object which is innately recognized. We have argued above that the brainstem components of the visual system mediate innate object recognition, and are thus presumably not involved in learned stimulus discrimination. In this regard, it is interesting that Armony et al. (1997) have reported that rats lacking auditory cortex can learn to discriminate between pure auditory tones of different frequencies. After the cortical lesions have been effected, the behavioral responses to these auditory signals are mediated by the subcortical auditory pathway originating in the cochlear nucleus, and extending through the inferior colliculus and auditory thalamus (medial geniculate body) to the lateral amygdala. The authors of this study suggested that crude auditory stimulus discriminations can be made through this pathway, and if the brainstem components are not involved, it seems likely that activity in the medial geniculate body may mediate this form of discrimination. By analogy, it may be speculated that visual stimulus discrimination in animals lacking visual cortex is mediated by activities in visual thalamic structures (probably in the lateral posterior/pulvinar thalamic complex of mammalian species).

5.2. *Conspecific and predator fear in monkeys*

Sackett (1966) examined the responses of monkeys reared in isolation from birth to 9 months, whose entire visual input (other than their cages) was due to colored pictures of threatening, playing, fearful, withdrawing and exploring monkeys, as well as pictures of mother and infant monkeys, and other monkeys not engaged in any activity. The infant monkeys responded to the pictures of threatening monkeys with alarm vocalizations at 2 weeks of age, and these vocalizations decreased and essentially disappeared at 1.5 months. However, the vocalizations reappeared at approximately 2 months, and increased dramatically to peak at 3 months, and thereafter decrease and stabilize at levels just below those present at 2 weeks. Com-

paring these results with those of Johnson and colleagues (Morton and Johnson, 1989; Johnson et al., 1991), it is reasonable to conclude that the alarm vocalizations that occur at 2 weeks of age are due to innate recognition of the threatening faces of adult conspecifics shown in the pictures, and that this form of recognition is replaced by learned recognition, mediated by the cortical visual system, at approximately 2 months of age.

Joslin et al. (1964) compared the responses of adult laboratory-raised (snake-naïve) and feral rhesus monkeys to the presentation of a live bullsnake, and a lifelike model of a bullsnake. They found that wild-reared monkeys responded with overt emotional behaviors, such as cage shaking or climbing, moving to the back of their cage, attack postures or fear grimaces and screeching, to the presentation of both the live snake and the model. It is clear that the recognition of the predator model is mediated at least primarily by visual structures, since the bullsnake model is odorless. Laboratory-reared monkeys reacted to the snakes with much milder avoidance responses. Similar results for wild- and laboratory-reared squirrel monkeys were also obtained by Murray and King (1973). In a more detailed study, the responses to the presentation of a live snake (a 122-cm live rainbow boa constrictor, a natural predator of the squirrel monkey) of juvenile male squirrel monkeys born to feral mothers that were (a) exposed to a live snake during infancy, or (b) snake-naïve, were tested (Levine et al., 1993). Several behavioral responses were observed, including orientations, vocalizations (peeps, screeches, clucks and alarm calls) and approaches. Plasma cortisol levels were determined after the exposure. Both the experienced and snake-naïve juveniles displayed changes in behavior in the presence of the snake. All of them emitted more vocalizations in the presence of the snake, but the increase in vocalizations was considerably higher in the experienced subjects. For example, of the juveniles that had been exposed to snakes as infants, six out of seven emitted alarm calls, while only one out of seven inexperienced subjects emitted an alarm call. No monkeys approached the snake, but almost all of them oriented to it. Plasma cortisol levels were elevated both in the experienced juveniles and in the snake-naïve juveniles, but the elevation was twice as high in the experienced juveniles. In order to determine whether the responses of the snake-naïve monkeys to the presentation of the boa

constrictor were specific to the snake, and not a generalized response to a moving animate object, the authors of this study exposed adult (presumably fish-naïve) squirrel monkeys to a large (25 cm) tropical fish. One group of monkeys was feral-born, the other laboratory-reared. Behaviors in response to the presentation of the fish were recorded and plasma cortisol levels were determined after exposure. In contrast to the numerous alterations in behavior in the presence of the snake, there were very few discernible changes following exposure to the fish. None of the distinct calls that were emitted in the presence of the snake were observed, and plasma cortisol levels remained normal in all subjects (Levine et al., 1993). These results indicate that the behavioral responses and elevation in plasma cortisol are specific to the presentation of the snake, and not just any live animal. Since these responses occur in both the snake-naïve and experienced animals, and are specific to snakes and not other animate objects, the authors of this study concluded that for the squirrel monkey there is an innate component in the responses. Furthermore, since the responses in the snake-experienced subjects were considerably more pronounced, they argue that there is a potent effect of prior experience during infancy on the responses. These findings are particularly suggestive, since not only were behavioral responses recorded, but a direct measure of the fear state—the cortisol response—was also measured.

Wiener and Levine (1992) observed that laboratory-born infant squirrel monkeys (evidently snake-naïve) exhibited strong avoidance responses to the presentation of the rainbow boa constrictor. These responses were comparable to those of their feral-born mothers, who were in the cage with them. Plasma cortisol levels were determined, and the increases over basal levels were nearly equal in infants and their mothers. It had previously been proposed that adolescent and young adult rhesus snake-naïve monkeys can acquire an intense and persistent fear of snakes as a result of observing their wild-reared parents' behavior when a live snake was presented simultaneously to both parent and offspring (Mineka et al., 1984). Wiener and Levine (1992) concluded that the infants' plasma cortisol and behavioral responses to the presentation of the boa constrictor was also due to observational conditioning. However, the observational conditioning in the adolescent and young adult monkeys observed by Mineka et al. (1984) was

induced by repetitive exposure (six conditioning sessions performed over 3 weeks), while the infant monkeys' responses (behavioral and plasma cortisol) occurred upon the first exposure. While the observational conditioning explanation of infants' responses may be correct, it appears to us that they are more likely to have been due to innate recognition of the boa constrictor.

While the behavior of the feral monkeys in the presence of snakes is overtly fearful and evidently directed at the predator, since they actively avoid the snakes, the behavior of the snake-naïve juvenile and adult monkeys in the presence of snakes or snake models is quite different. The plasma cortisol responses in these animals indicate that some form of recognition has probably occurred; the absence of alarm calls and other overt responses in the majority of snake-naïve monkeys suggests that this recognition may not be conscious. If this is the case, then the differences in the responses of laboratory- and wild-reared monkeys to snakes indicate that conscious recognition of a predator elicits a significantly higher degree of fear than implicit recognition. The strong avoidance responses and elevations in plasma cortisol in the infant monkeys, which are comparable to those of feral monkeys, suggest that innate predator recognition in infant monkeys may be overt (conscious). Comparing the responses of infant monkeys to predator stimuli to those of human infants to faces of conspecifics, we speculate that conscious innate predator recognition in primate species is only present in the first few weeks of life, and thereafter gives way to learned stimulus recognition mediated by cortical structures. If a predator object is encountered during the period in which innate recognition is overt and the cortical visual system is functional, then the fear responses will be transferred to stimuli within the class of object recognized by the cortical system. If no such object is encountered, then implicit recognition will replace overt recognition, and fear responses of the naïve individual to a natural predator will be much diminished.

We have previously argued that visual awareness in primate neonates is mediated by neuronal activities in subcortical structures, including the superior colliculus, and that there is a gradual transfer of this function to the visual cortex during early infancy (Sowards and Sowards, 2000). The arguments above suggest that, in addition to visual awareness, the primate neonate subcortical visual

system mediates innate object recognition. After a transition period during which both systems operate, visual awareness is entirely transferred to cortical structures, and innate object recognition becomes implicit.

5.3. Structures and pathways

Individual brainstem structures, such as the optic tectum and pretectal nuclei, and the connections between them tend to be conserved over phylogeny. In particular, the connections between the cell-dense layers of the superior colliculus and pretectal nuclei of rodents and primates are very similar. Hence, it can be expected that the components and pathways of the monkey subcortical visual system involved in innate stimulus object recognition will be essentially identical to those of the rodent system (Fig. 5). The area that corresponds to the LCC of the anuran system (the MpRF) probably includes the same areas in primates as it does in rodents (i.e. the cuneiform, subcuneiform and pedunculopontine nuclei), since the projections of the superior colliculus to the mesopontine reticular formation are very similar in rodents and primates (Harting, 1977; Redgrave et al., 1988).

Rizzolatti (1978) and Rizzolatti et al. (1980) have described two functional classes of neurons in the macaque superior colliculus with very different responses to visual stimuli. The first class, primarily located in the SGS layer, responds to simple stationary and moving stimuli such, as spots, bars or slits of light, has relatively small (mean 4°) receptive field diameters, and the responses do not habituate to repetitive stimulation. Neurons of the second type, primarily located in the stratum opticum, have larger (mean 6.5°) receptive field diameters and respond very poorly to simple visual stimuli. Their activation requires real objects or certain two-dimensional patterns, such as cubes, rectangles, cylinders and other geometric solids. However, many complex stimuli were able to drive a given unit, although some of them produce stronger responses than others. Usually, objects rich in detail elicited stronger responses than simpler stimuli. These responses rapidly habituate after repeated stimulus presentations. Arendes (1994) found a similar functional differentiation of macaque collicular neurons located in the SGI and SGP layers. Approximately 50% of neurons tested responded to simple stimuli, whereas the other neurons only responded to spe-

cific objects, such as human faces, a snake model and food items. Evidently the neurons in the SGI and SGP described by Arendes (1994) require more specific stimuli for their activation than the configuration-sensitive SO neurons reported by Rizzolatti et al. (1980), confirming that the receptive field complexity increases with increasing depth within the superior colliculus. The responses to the snake stimuli in particular lend credence to the proposal made above that innate visual recognition of predators is mediated by the subcortical visual system.

6. Relationships between cortical and subcortical visual systems

In rodents, carnivores and primates there are substantial inputs from visual cortical areas to the superior colliculus and pretectal nuclei via the corticotectal and corticopretectal projections (Rhoades and Chalupa, 1978; Graham et al., 1979; Harvey and Worthington, 1990; Lui et al., 1994), and it is apparent that cortical activity can influence neural processing in the subcortical system through these non-reciprocal projections. One function these projections must accomplish is the alignment of the topographic maps in the components of the two systems that are visuotopically organized (McIlwain, 1977). This is necessary so that when visual awareness is due to activities both in cortex and tectal and pretectal structures (as in rodents), there is a single coherent visual image. In addition to this function, several studies have demonstrated that cortical visual input to collicular cells exerts substantial influence on the cells. Ostrach et al. (1982) have reported that electrical stimulation of rabbit visual cortex excited approximately 29% of tectal cells examined, preferentially those that were responsive to moving visual stimuli. In the hamster, stimulation of primary visual cortex activated approximately 31% of cells examined, and a larger proportion of these were found in the deep layers (Rhoades and Chalupa, 1978). In rabbits, it has been reported that cryoblockade of visual cortex causes a substantial decrease in the responsiveness of collicular cells to light stimuli (Molotchnikoff et al., 1986). In rabbits, hamsters and cats, lesions to visual cortex cause the loss of directional selectivity and/or binocularity in a substantial proportion of neurons in both the superficial (SGS, SO) and intermediate (SGI) layers (Berman and Cynader,

1976; Mize and Murphy, 1976; Graham et al., 1982). As a result of these lesions, more neurons in SGS respond to stationary stimuli and RF diameters increase (Graham et al., 1982). It has been reported that, in primates, the activities in cells in the deep layers (SGI and SGP) of the superior colliculus are strongly dependent on input from visual cortex via the corticotectal projection (Schiller et al., 1974). After ablation or reversible inactivation of the visual cortex using lidocaine, cells in the deeper layers could no longer be driven by visual stimuli. Similar results for SGI and SGP cells after visual cortical ablation had been obtained earlier for ground squirrels (Michael, 1972) and cats (Wickelgren and Sterling, 1969). However, in another study using longer periods between surgery and the recording procedure, very different results were obtained (Rizzolatti et al., 1970). In this study, SGI and SGP cells in the cat superior colliculus regained their visually responsiveness after the extended recovery period, and these responses were very similar to those in intact cats, although the proportion of directionally selective units in the superficial layers was reduced to approximately half of that in intact cats. Thus, it appears likely that the results of the studies in which cells in the deeper layers became unresponsive after cortical cooling or ablation were due to the short recovery times used (in animals with surgical lesions) and to some other effect in the cryoblockade experiments. These studies suggest that, for rabbits, rats and cats, neuronal activities in visual cortex certainly influence the responses of collicular neurons to visual stimuli, but this influence is not a controlling one, and neurons in the subcortical structure still respond adequately to visual stimuli without cortical input. They also suggest that one of the functions of the corticotectal and corticopretectal projections could be to sharpen and otherwise improve the responses of collicular neurons.

7. Summary and discussion

In amphibian species, sensory awareness and object recognition in the visual modality are mediated by brainstem and diencephalic structures, and there are no telencephalic components that correspond to the visual cortex of mammalian species (Straube et al., 1987). It is likely that auditory awareness and stimulus recognition are also mediated by brainstem and diencephalic structures (Hall

and Feng, 1987; Kicliter, 1979). Thus, visual and auditory object recognition in these species is limited to classes of objects that are genetically predetermined, and they are unable to learn to recognize individual objects through these two modalities. However, the study of Ewert and Kehl (1978) indicates that individual objects within a class of objects that is innately recognized may be discriminated. The only modality through which amphibians are able to recognize (rather than discriminate) abstract objects not belonging to an innately recognized class is olfaction (Hepper and Waldman, 1992). In avian and rodent species, visual awareness is due to neuronal activities in both the subcortical and cortical visual systems, and lesions to either system of adult animals do not produce blindness (Sowards and Sowards, 2000). The arguments provided above suggest that, in rodent species, innate visual-stimulus object recognition is also mediated by the subcortical visual system and learned stimulus recognition by the cortical visual system, and that this dual function continues throughout ontogeny. This means that any object visually recognized may be simultaneously recognized by the subcortical system as belonging to a class of objects, and by the cortical visual system as a particular object. Presumably, only biologically relevant classes of objects will be recognized by the subcortical system. However, the observations by Ingle (1981, 1982) that visually decorticate rodents will pursue moving disks indicates that recognition mediated by the subcortical system is fairly crude, so even 'unnatural' objects may elicit behavioral responses. It is possible that visual recognition mediated by cortical structures in rodents is also fairly crude, since rodents are primarily olfactory animals, and rely to a large degree on the cortical olfactory system for the recognition of individual objects and places. Behavioral responses due to this dual recognition probably depend on the nature of the stimulus, but innate freezing and flight responses to stimuli recognized in the visual modality such as predators, are probably mediated by the subcortical, rather than cortical, systems.

In primates, subcortical visual awareness and object recognition are present at birth, but visual awareness is transferred entirely to the cortical system sometime during the first few months of life. During the transition period, if an individual experiences items belonging to a class of objects that is innately recognized, this recognition will be

transferred to the cortical system, so that when the innate system no longer functions there will be no loss in recognition ability, and the individual will continue to respond appropriately to objects within that class. If an individual fails to experience any items belonging to a particular class of objects during the period in infancy when the innate system is functional, he will not overtly recognize such an object after that period. Thus, adult snake-naïve laboratory monkeys show very mild behavioral responses when exposed to live snakes (Levine et al., 1993) because the recognition of these predators, mediated by the subcortical visual system, is implicit. In primate adulthood, while visual object recognition is mediated for the most part by the cortical system, the subcortical innate recognition systems continue to operate implicitly, and may still contribute to the generation of emotions such as fear and anger, and these emotions can therefore influence behavioral responses. The function of this preserved, implicit, innate visual-object recognition in primates, after the transition period, may be to guarantee that, should an individual not encounter any objects in a given class that is innately recognized prior or during the transition period, when such an object is eventually encountered, some emotion (fear, anger, etc.) will be generated. This emotion may then motivate behaviors that are at least minimally adaptive in the presence of the overtly unrecognized object.

During the transition period, when both subcortical and cortical sensory systems are operational, an individual primate will normally learn to recognize particular objects within an object class that is innately recognized. In addition, the recognition of the class or category of individual stimulus objects is accomplished by neuronal processing in limbic and prefrontal cortical structures (Dalla Barba et al., 1998; Mesulam, 1998). Since after the transition period is over, conscious recognition will be mediated exclusively by the cortical system, the emotion(s) generated by the class of stimuli as a result of innate recognition must be transferred to individual stimuli recognized by the cortical sensory systems, and/or to the category that the individual stimulus object belongs to. For example, learned recognition of predators mediated by cortical structures must evoke fear and aversion, just as innate recognition does, or else the animal will only experience low levels of fear as a consequence of implicit innate

recognition of the stimulus. It is natural to speculate that the transfer of this function from the subcortical to the cortical systems is accomplished by a process similar to classical fear conditioning, in which the unconditioned stimulus is the activation of the engram for the innately recognized object class, and the conditioned stimulus is the individual object (and/or object category) recognized by a cortical sensory system. In fear conditioning using unconditioned nociceptive stimuli, the association between the conditioned and unconditioned stimuli is made in the basolateral complex of the amygdala (Rogan et al., 1997). Signals related to auditory or visually conditioned stimuli processed in cortical sensory areas reach the basolateral amygdala primarily from the perirhinal cortex (Campeau and Davis, 1995). Components of the subcortical visual system, including the superior colliculus and pretectal nuclei, reach the basolateral amygdala via a relay in the nuclei of the posterior thalamus (Benevento and Fallon, 1975; Hicks et al., 1986; Linke et al., 2000), so the associational process could easily take place in the amygdala, and this association would ensure that the correct emotion and consequent behavioral responses occur.

The studies of Redgrave et al. (1988) and Mitchell et al. (1988) suggest that the cuneiform nucleus might serve as an 'output station' relaying signals arising in the superior colliculus to the spinal cord and medulla, for the purpose of controlling approach and avoidance behavior to prey and predators. Korte et al. (1992) have made a similar proposal for the function of the cuneiform nucleus, and have described a brain circuit that generates orientations, freezing behavior and autonomic responses to threatening stimuli in which the cuneiform nucleus has a central position. The concept of the MpRF as a 'mesencephalic locomotor region' is in accord with the tectal output station function, since stimulation of the superior colliculus or cuneiform nucleus should evoke behaviors such as locomotion. The idea presented here is that the 'engrams' for innate object recognition reside in the MpRF, and this proposal should not conflict with the concept of the reticular activating system originating in the MpRF, nor with the tectal output station concept. Certainly the latter concept is consistent with the position of the MpRF within the hierarchy of the subcortical sensory systems, and since behavioral output mediated by these sensory systems must be dependent

on stimulus recognition, the neural structure containing the 'engrams' should project directly to the premotor circuits in the mMPRF, and this is indeed the case. Early studies of the effects of stimulation of the MpRF suggested that it formed part of an unspecific ascending activating system (Moruzzi and Magoun, 1995; Steriade, 1995). This system originates in the MpRF, and through relays in the intralaminar thalamic nuclei activates large parts of the neocortex via projections from these nuclei to layer I of cortex. The 'reticular activating system' originating in the MpRF responds to external sensory stimuli, and presumably the pathways involved in providing sensory inputs to the MpRF include the subcortical sensory systems. In addition to inputs from the MpRF, the intralaminar thalamic nuclei receive projections from the superior and inferior colliculi and pretectal nuclei (Edwards and de Olmos, 1976; Weber and Harting, 1980; Krout et al., 2001). Although some of the information transferred from these structures to the intralaminar nuclei is nociceptive (Krauthamer et al., 1992), a large percentage of neurons in the central medial-parafascicular complex, for example, respond to visual and auditory stimulation (Matsumoto et al., 2001). Hence, it can be speculated that cortical activation occurs in response to innate stimulus recognition, mediated by the activation of engrams in the MpRF, and also to other stimuli that do not require recognition, such as somatic and visceral pain. In other words, when a biologically relevant stimulus object is recognized by one of the subcortical innate sensory-recognition systems, the corresponding engram in MpRF is activated and cortical arousal ensues. This should be true both in rodents and primates, even though in the latter species the subcortical recognition systems do not contribute to conscious awareness.

In mammals, the generation of involuntary saccades to suddenly appearing or moving objects presented in the periphery of the visual field is known to be primarily mediated by neuronal activities in the superior colliculus and MpRF (Cohen et al., 1985; Waitzman et al., 1996; Chen and May, 2000; Yoshida et al., 2001). Neurons in these structures project to the nucleus raphe interpositus, which contains the omnipause neurons that are pivotal in the generation of saccades (Langer and Kaneko, 1984, 1990; Büttner-Ennever et al., 1999). In view of the arguments presented above about the function of the mammalian superior colliculus

and MpRF in innate object recognition, it is natural to speculate that at least some involuntary saccades occur in response to the recognition of biologically relevant visual stimuli, and that this recognition is mediated by the subcortical visual system. For example, 'looming' stimuli are probably recognized as potential predators by all vertebrate species (King et al., 1992, 1999), and these stimuli elicit saccades and defensive responses, even in monkeys with unilateral striate cortex ablations (King and Cowey, 1992). Thus, the activation of an engram in the MpRF will generate a saccade if the class of object is recognized as being (for example) potentially dangerous. Signals reaching omnipause neurons from the superior colliculus may convey information about the location of the object in the visual map (Langer and Kaneko, 1984). However, it has been observed that neurons within a subregion of the primate MpRF, the central part of the subcuneiform nucleus, discharge before and during saccadic eye movements, and some of these discharges are correlated with saccade parameters, such as direction and amplitude (Waitzman et al., 1996). Thus, it is possible that at least part of the computations that result in codes for stimulus location and spatial relationships to other stimuli is represented in this subdivision of the MpRF, and projections from both the deep layers of the superior colliculus and the central subcuneiform nucleus are necessary for the initiation of saccades. If this is the case, then the area within the MpRF where the engrams that represent innate recognition of visual stimuli are located may be restricted to the more medial parts of the MpRF.

We propose above that the computational engrams which signify the innate recognition of classes of stimuli probably occur in the mesopontine tegmentum (anuran LCC or mammalian MpRF). As discussed above, these engrams correspond approximately to what Ewert (1980, 1987) terms CRSs, with the distinction that engrams only represent recognition, while activation of a CRS represents both recognition and stimulus location. As a result of detailed studies of the responses of tectal and pretectal neurons, Ewert (1987, 1997) and Ewert et al. (1992) have concluded that the CRSs are formed by certain specialized classes of neurons in the optic tectum and pretectum. The principal reason for proposing that engrams occur in the LCC/MpRF rather than in the tectum and/or pretectal nuclei is that the LCC/MpRF lies

downstream from the two complexes in the processing pathway (Figs. 3 and 5), and it is reasonable to suppose that the engrams will occur in the highest-order structure rather than in lower-order components, given that multi-level parallel/hierarchical processing is necessary for visual object recognition (Riesenhuber and Poggio, 1999; Rolls and Stringer, 2001). However, as discussed above, at the present time there is no compelling evidence that representations for object recognition occur in the LCC/MpRF rather than in the tectum/pretectum.

The generation of conscious emotion as a consequence of implicit visual stimulus recognition may mediate a particularly remarkable ability of a blindsight patient (G.Y.), who has a right hemifield blindness due to cortical damage. G.Y. was presented with video fragments of a female face pronouncing the same sentence with four different facial expressions. He was required to label the videos as happy, sad, angry or fearful. When the videos were presented in his intact left hemifield, G.Y. was flawless in identifying the affect on the face. When they were presented in his blind hemifield, G.Y. chose the correct affect 66% of the time (de Gelder et al., 1999). It had previously been demonstrated that in normal individuals, a masked (unseen) stimulus—an angry face classically conditioned to a loud burst of white noise—caused differential activation of the right amygdala, while unmasked presentations of the same face produced activation of the left amygdala (Morris et al., 1998). A subsequent study demonstrated increased connectivity between the amygdala, posterior visual thalamus and superior colliculus during the presentation of the masked angry face (Morris et al., 1999). It was hypothesized that the ability of G.Y. to discriminate emotional faces might also be due to this pathway (de Gelder et al., 1999), and this proposal was tested using functional magnetic resonance imaging (Morris et al., 2001). Presentation of unconditioned pictures of fearful or happy faces in the blind hemifield activated the superior colliculus, lateral posterior/pulvinar thalamic complex and amygdala, but not the spared areas of visual cortex. It was found that the emotional content of the faces presented in the blind hemifield influenced the covariation of the response between the amygdala (bilaterally) and the superior colliculus. A positive covariation was found during presentation of unseen fearful faces, whereas a negative cov-

ariation occurred when happy faces were presented. A similar pattern of covariation was observed between the amygdala and the lateral posterior/pulvinar thalamic complex. The brain activation data strongly suggest that the ability of patient G.Y. to discriminate fearful from happy faces is mediated entirely by subcortical structures. It is possible that separate innate recognition engrams exist for different facial expressions, and this implies that neonates should be able to respond differentially to sad, happy, angry and fearful faces. Most studies of the discrimination of facial expressions in human infants suggest that this ability is learned and appears at approximately 5–7 months of age (Walker-Andrews, 1997, 1998). However, Everhart and Henry (1992) have reported that infants 23–93-h-old could, by sucking on a pacifier, replace a digitized image of one expression for another, and that these neonates sucked more often to generate a happy expression. While the operant response is obviously learned, the preference for the happy face may well be innate. However, the involvement of the amygdala in the discriminations made by G.Y. made apparent by the brain activation study suggests some form of associative learning, and it is likely that the emotion generated by the recognition of the different facial expressions is gradually modified by learning.

In primate species, visual object recognition in early infancy is innate and entirely mediated by subcortical structures, and cortical visual areas are essentially non-functional. During the transition period, both the subcortical and cortical systems function, and thereafter only the cortical (learned) visual system operates overtly. This ontogenetic sequence mirrors the phylogenetic progression from the all-innate visual system of anurans to the dual system of birds and rodents, and ending in the all-cortical system of primates. Hence, for visual object recognition the principle of ontogenetic recapitulation of phylogenetic progression (von Baer, 1928) holds.

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