Neural correlates of key stimulus and releasing mechanism: a case study and two concepts

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Major themes in neuroethology concern the specificity of key stimuli, neurones tuned to such stimuli, and the release of corresponding behaviour. Neurobiological data from the analysis of visuomotor functions of prey-catching and avoiding in amphibians support the view that retinal outflow in different combinations is pooled for further computation in interacting processing streams, rather than segregated into distinct retinal channels. The keys by which the visual system gets access to perceptual-motor categories are shown to derive from specific computational strategies that evaluate significant configurational features of objects. Rapid behavioural responses are assured by visuomotor pathways which, monitoring different aspects of visual objects, collectively select appropriate motor patterns. Responses can be adapted to varying environmental and internal conditions via modulating and modifying loops. This requires parallel distributed processing and integration at various levels in a macro-network.

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AS UNDERSTOOD from ethology[1], key stimuli elicit corresponding patterns of behaviour consistently, given that the animal's motivation is appropriate. The sensorimotor interfaces are provided by releasing mechanisms which refer to predispositions operating within the context of ontogenetic experience[2]. Searching for neural correlates, studies of visually released prey-catching and avoidance behaviours in amphibians focus on stimulus recognition and behaviour releasing processes. The detector concept of prey recognition in frogs was advocated in the 1950s by Barlow[3] and Lettvin[4] who suggested, from single neurone recording, that a type of retinal ganglion cell acts as a fly- or bug-detector. Their investigations stimulated comparable research in many laboratories: Grüsser[5] showed that no retinal ganglion-cell type in frogs or toads fulfils the criterion of a detector specific to prey, however, the retinal ganglion cells do say something perceptually important to the brain. Maturana[6] proposed that combinations of retinal ganglion cell outputs and further computations define categories of objects, thus addressing questions of category formation and sensorimotor interfacing.

Two competing concepts

Visual information leaving the retina is parcelled by different types of retinal ganglion cells (R) as regards their different sensitivities to object size, contrast between stimulus and background, object motion, stationary edges and colour (Table 1; reviewed in Refs 5,7). Tectal (T) and pretectal thalamic (TH) neurones organized in retinotopic maps receive this visual information (Fig. 1).

Concept A suggests that owing to convergence and divergence of retinal and postretinal processing streams, the parcelling of visual information can be different from one processing stage to the next ('interacting processing streams'). Consequently, there are T and TH cells that differ with respect to size and shape of (monocular or binocular) receptive fields, reflecting various key computational strategies for deriving perceptual categories from appropriate visual input[7–9] (Table 1). At these processing stages there is redundant representation of basic features shared by visual objects, such as area, motion, contrast and colour. Tectal and tegmental processes are involved in matching the retinal map and body position in order to derive information for object localization[10]. The network is sensitive to influences mediated by modulatory loops involving various forebrain structures[11]. The outputs of the tectal, pretectal and tegmental processing streams – representing sensorimotor interfaces – are used at the levels of the medulla oblongata and the spinal cord in the selection of the appropriate motor response[7].

Concept B differs from concept A (Table 2) in that it assumes[12] that the response property of each type of R cell determines the response characteristics of a distinct type of T cell: one T type monitoring object size and contrast between stimulus and background; another type monitoring object motion; and a third type monitoring changes in general illumination. It is proposed that these tectal neurones project to the medullary–spinal premotor and motor systems in three separate pathways ('segregated retinal channels'). The following data provide the main arguments[12] in support of concept B: (1) intracellular recordings in response to electrical stimulation of the optic nerve and biocytin labellings show three morphologically distinct types of tectal neurones; (2) the axons of these neurones descend in a crossed and two uncrossed routes to medullary–spinal structures; and (3) the dendritic trees of these three tectal neurone types arborize in three tectal layers of retinal afferent terminals assigned to three types of retinal ganglion cells. It

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is thus postulated that each type of retinal ganglion cell corresponds to a certain type of tecto–medullary–spinal projection cell. Concept B emphasizes that there is no convergence of the different streams of retinal information inside the tectum; regardless of the degree of interaction between these functional pathways inside the tectum, these descending tecto–medullary–spinal pathways form separate information channels to premotor and motor systems[12]. Convergence of information regarding three stimulus attributes – size and contrast, movement and ambient illumination – should therefore take place in the medulla oblongata. It has been argued[12] that this concept, derived from data obtained in salamanders, applies to amphibians generally.

The idea of selective retino–tectal correspondences is attractive. However, the available data, provide no evidence of such specific separate assignments. On the one hand, it is known from recording studies that termination fields of 'adjacent' different types of R cells show some overlap across the tectal laminae. On the other hand, there are tectal interneurones and projection neurones whose dendritic arborizations extend into various tectal laminae and layers enabling them to obtain inputs from different R cells as well as, for example, from tectal and pretectal cells[7,13–15] (Fig. 2A; concepts of functional units of cell assemblies are reviewed in Refs 7,8,13,14). If a tectal projection neurone obtains these different inputs, whereby the proportion is only a matter of degree, then the data[12] can be accommodated within concept A. In fact, neurophysiological recordings from toad tecto–medullary projection neurones[7] show that the responses of all these neurones contain information about object size, contrast between stimulus and background, and object motion (see Table 1). Further properties result from intratectal and pretecto–tectal interactions. The main issues requiring revision of concept B are discussed below.

TABLE 1. Response properties of various retinal ganglion cells (R), tectal neurones (T) and pretectal thalamic neurones (TH) in anuran amphibians

Type	Response property
R1	Excitatory receptive field (ERF) of 2–3° diameter; very sensitive to movement of contrast stimuli; optimal object size 2–3°; minimal detectable stimulus velocity 0.02°/sec; after stopping of the stimulus in the ERF, there are sustained responses that are erasable after darkening and brightening the field of vision; responses to chromatic stimuli
R2	ERF = 4–6°; similar to R1 except: optimal object size 4–6°, no erasability; strong neuronal adaptation
R3	ERF = 8–10°; very responsive to changes in stimulus contrast; minimal detectable stimulus velocity ~0.1°/sec; optimal object size 8–10°; responses to chromatic stimuli
R4	ERF = 12–16°; responses to moving dark objects, optimal size bigger than 16°; overall dimming is essential
T1.3	Nasal binocular ERF = 15–30°; responsive to objects moving at a narrow distance; involving properties of T5.1 neurones
T3	Nasal monocular ERF = 20–30°; sensitive to approaching small objects; involving properties of R3 and R4
T4	ERF encompassing the visual field of one or both eyes; sensitivity like T5.1 or T5.2; involving some properties of R2 and R3
T5.1	Monocular ERF = 20–30°; sensitive to moving objects of small or intermediate sizes; configurationally, preferring object extension in the direction of movement; no responses to moving large textures; involving some properties of R2 and R3
T5.2	Monocular ERF = 20–30°; sensitive to small objects with selective preference of objects elongated in the direction of their movement; involving some properties of R2, R3 and T5.1
T5.3	Monocular ERF = 20–30°; sensitive to moving large objects; configurationally, preferring object extension across the direction of movement; involving some properties of R3, R4 and TH3
T5.4	Monocular ERF ~35°; sensitive to moving big compact objects; involving some properties of R3 and R4
T6	Monocular dorsal wide ERF; sensitive to moving large objects; involving properties of R4
TH3	Monocular ERF = 40–50°; sensitive to moving large objects; configurationally, preferring object extension across the direction of movement; strong responses to moving large textures; involving properties of R3 and R4
TH4	ERF encompassing the visual field of one or both eyes; sensitive to moving large objects; there are neurones also showing sensitivity to cutaneous stimuli; involving visual properties of R3, R4 and TH3
TH6	Monocular wide ERF; sensitive to approaching big objects; involving some properties of T3
TH10	Frontal ERF = 30–90°; sensitive or specifically responsive to large stationary objects; there are neurones also showing sensitivity to cutaneous stimuli; involving some visual properties of R1, R3 or R4
TH11	ERF encompassing the visual field of the contralateral eye; response property similar to TH3 or TH4; unlike TH3 and TH4, object movement only from temporal to nasal positions is effective

Modified from Refs 5,7; see also Figs 2,3,5.

Stimulus–response relationships

Concept B seems to ignore the fact that during evolution of the visual system of terrestrial amphibians a sensory processing structure emerged[7] that allows individuals to discriminate moving objects in terms of configurational features: for example, by monitoring object extensions parallel to (ep) and across (ea) the direction of movement, taking into account stimulus area ep×ea. This requires a linkage between the stimulus attributes shape and movement. An efficient way of categorizing objects is evaluating the features ep and ea and relating them to each other. The computational strategy of a features-relating algorithm[11,19] provides the key instruction by which a toad's visual system derives the signal value of potential prey from visual input. We have shown this in experiments using dummies of cardboard and measuring the prey-catching activity in response to changes in ep or ea, or both[7,19]. Extension of a bar along ep, within limits, signals prey (Fig. 3A); extension along ea reduces the prey value (Fig. 3B); and in response to square objects of different sizes, the influences of ep and ea interact (Fig. 3C). The algorithm is invariant regarding the direction in which an object traverses the toad's visual field. From the visual input, different features-relating algorithms can derive other perceptual categories, such as predator, resembled by moving large compact objects. To discriminate between prey and nonprey, the feature ea is most decisive (Fig. 3B), suggesting inhibitory influences tuned to ea.

The prey features-relating algorithm is common to the individuals of a given amphibian species[7,19]; its principle displays species-specific variation across other amphibians[19,20]; it is present after metamorphosis to terrestrial predatory life[7]; it is subject to maturation during ontogeny[7]; and it can be modified by learning[7,11]. The prey-catching behaviour of toads also considers other visual stimulus qualities such as colour[21] and other sensory modalities, such as touch[22], that will contribute to rather than detract

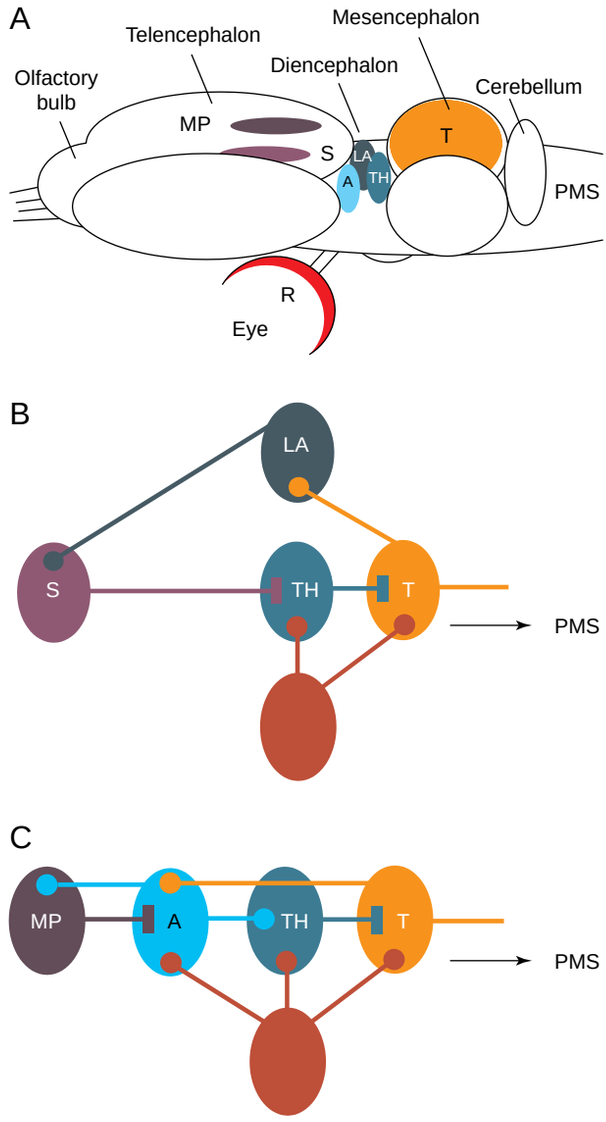

Fig. 1. ***Structures of the anuran brain involved in the release of visual behaviours.*** **(A)** *Various forebrain structures participate in the modulation and modification of visual output. In prey-catching and avoidance, the primary stimulus response pathways involve retinal ganglion cells (R), tectal (T) and pretectal thalamic (TH) neurones, and premotor–motor structures (PMS) in the medulla oblongata and spinal cord. The TH includes the lateral posterodorsal nucleus and the posterior nucleus. The medullary PMS includes medial reticular premotor structures and cranial nerve motor nuclei. There are also direct pretectal and tegmental projections to PMS (not indicated here). Two important telencephalic visual projections exist, one to the striatum (S) (R→T→LA→S), for example, suitable for response gating, and another to the medial pallium (MP) [R→(→T→)A→MP] involved in learning. Abbreviations: A, anterior thalamic nucleus; LA, lateral anterior thalamic nucleus; MP, posterior ventromedial pallium; S, caudal ventral striatum.* **(B)** *Gating loop*[11]*: the striatum obtains tectal visual information mediated by the LA. Inhibitory projections from S to TH*[49] *and from TH to tectum*[7,35] *are suitable for a disinhibitory gating of tectal responses.* **(C)** *Learning loop*[11]*: a hypothesis suggests that the posterior ventromedial pallium is involved in modifying tectal prey selectivity after hand-feeding conditioning*[51,53]*. It is assumed that during repetitive spatiotemporally contingent presentation of a mealworm with the experimenter's hand, the information related both to prey (worm) and large object (hand) coincide in the medial pallium. This sensitizes pallial neurones which, becoming responsive to large objects, alter tectal filter properties by a disinhibitory pathway via anterior thalamus (A) and pretectal thalamus. The inhibitory influence of MP on A emerges in the course of conditioning; as a result, prey-selectivity is impaired and the prey category generalized to include large moving objects, such as the experimenter's hand. The connections in* (B) *and* (C) *are from anatomical studies*[40,43–48,50]*, their putative functions are derived from neurophysiological investigations*[7,11,35,36,41,49,51]*. Oval symbols represent neuronal populations; the symbol ●— indicates excitatory projections; and the symbol —⊣ indicates inhibitory projections.*

TABLE 2. Major issues of concept A and concept B as applied to visually released motivated behaviours in amphibians

Issue	Concept A	Concept B
Visual information is parcelled by different types of retinal ganglion cells	yes	yes
The visual response property of each type of tecto–medullary projection neurone is dominated by an appropriate type of retinal ganglion cell	no	yes
Pooled retinal outflow contributes to the characteristics of a processing stream	yes	no
Retinal output is processed in a parallel-distributed manner by interacting tectal pretectal/tectal and tectal/tegmental structures	yes	no
Perceptual categories ('key stimuli') are derived from retinal output by specific tectal or pretectal/tectal computational strategies	yes	no
Sensorimotor interfaces ('releasing mechanisms') involve pretecto/tecto/tegmento–medullary processing streams	yes	not determined
Release of motor patterns takes advantage of sensorimotor codes	yes	not determined
Various forebrain structures (involved in modulatory loops) are responsible for the translation of perception into action	yes	not determined

from the visual configuration paradigm that is in focus here.

Evaluating ep and ea is clearly not the only way of characterizing visual objects in amphibians. There are other examples and these, too, account for the advantage of concept A vs B. These include the efficacy of looming patterns in releasing avoidance[23,24] and of stationary obstacles in inducing detour behaviour[25–27]. In addition, frogs exhibit different capture strategies to visually distinguishable types of prey[28–31], where ep vs ea provides only part of the necessary pattern recognition. Furthermore, as a result of individual experience (habituation and dishabituation), a variety of discrete visual cues of moving wormlike objects can be discriminated[7,32], such as the shapes of a leading edge vs a trailing edge, isolated dots and striped patterns.

Nevertheless, the ep–ea paradigm provides a simple and efficient tool in order to experimentally trace and to compare some behavioural and neuronal response properties. Figure 3A–C illustrates the activity patterns of R cells, and T and TH neurones in response to changes in ep or ea, or both. Different types of R cells (R2, R3 and R4) are responsive to various ranges of stimulus area based on the different strengths in receptive field center–surround antagonism[5] (see Table 1). Configurationally, the responses of these neurones reflect aspects of ea; this property[5,7] emerges in similar response profiles to moving bars of variable edge ea (Fig. 3B) and to squares of a comparable extension (Fig. 3C).

The stimulus configuration, shape in relation to the direction of movement, is evaluated differently at tectal and pretectal levels. The feature ea and the area are coded on a broad scale in T5.3, TH3 and TH4 neurones[7], due

to a pooling of information parcelled in R3 and R4 cells. Furthermore, there are tectal neurones[7], T5.1, that code for ep. This property emerges in the response profiles to moving bars of variable edge ep (Fig. 3A) and to squares of a comparable extension (Fig. 3C); it can be explained by a pooling of R2 and R3 outflow in connection with intratectal lateral excitation[7,8,13]. In addition, tectal T5.2 neurones[7,33,34] differentiate between ep (Fig. 3A) and ea (Fig. 3B; and see Fig. 4A,B). Their responses to moving square stimuli of varying sizes (Fig. 3C) result from a non-linear interaction of influences tuned to ep and ea, respectively. Contradictory to concept B, there is ample evidence[7,9,21,34–36] that this differentiating property is achieved by inhibitory pretectal influences from neurones, for example, TH3, responsive to ea (for a simulation model, see Ref. 8). This computation approximates characteristics of the prey features-relating algorithm. Further computational strategies link features differently to describe other perceptual categories. For example, T5.4 neurones respond selectively to large extensions both in ep and ea, thus resembling the principle of a predator features-relating algorithm.

Pretectal sharpening of tectal responses

The presence of lateral excitation in the tectum[8,13] calls for an inhibitory mechanism to check its unlimited spread. Therefore, Székely and Lázár[13] suggested a tectal intrinsic inhibition and an extrinsic pretectal inhibition, assuming that in the pretecto–tectal projection[38,39] retinal topography[40] is preserved. In fact, TH3 neurones of the retinotopic map and TH4 wide-field neurones project to the ipsilateral tectum as shown by antidromic stimulation–recording techniques[41]. One set of pretecto–tectal projections, suitable for controlling retino–tectal input, is mediated by neuropeptide Y (NPY). Kozicz and Lázár[17] showed that NPY immunoreactive fibres in the frog superficial tectum originate from ipsilateral pretectal thalamic areas that are congruent with the recording sites of toad TH3 and TH4 pretecto–tectal projection cells[41]. Administration of NPY to the tectal surface, or electrostimulation of the pretectum, attenuates the initial excitatory wave of the tectal surface field potential evoked by optic nerve stimulation[42].

Interrupting the pretectal–tectal connections unilaterally, or lesioning the pretectum by the axon sparing excitotoxin, kainic acid, induced the following syndrome for stimuli presented to the contralateral eye[7,34,35]: (1) a strong increase in visual responses of tectal neurones of the tectal lobe ipsilaterally to the lesioned pretectum; (2) impairment of configurational selectivity both in T5.2 neurones and prey-catching (Fig. 4A–C); (3) increased sensitivity of tectal T5.1 and T5.2 neurones to moving large objects and textures that were ineffective in these neurones prior to the lesion; (4) prey-catching in response to self-induced moving retinal images; and (5) inability to estimate object distance. It is thus suggested that inhibitory interactions of retino–pretectal processing streams with retino–tectal processing streams have various effects: limiting the spread of tectal excitation (modulating)[7,8,13]; and sharpening visual responses (specifying)[7,8,21,35,36] involving ep/ea discrimination, distinction between moving and self-induced moving retinal images, object–background interaction, and estimation of absolute object size.

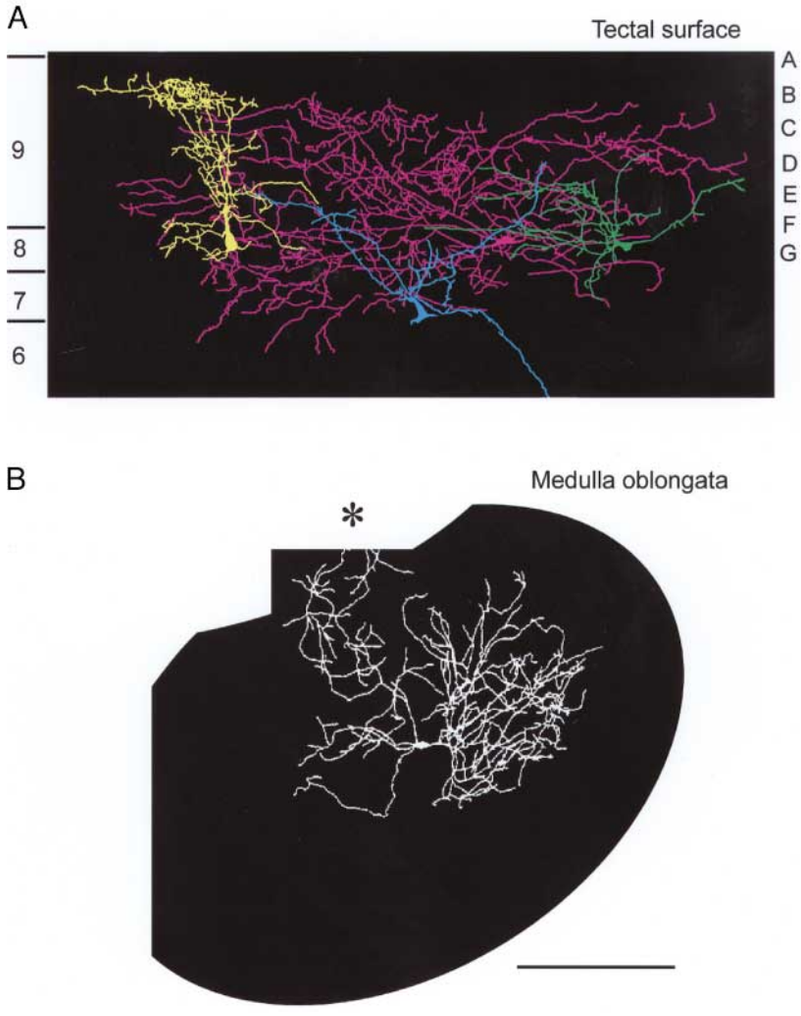

Fig. 2. ***Examples of dendritic arborization patterns of tectal neurones and a medullary neurone suitable for convergence of visual information at different processing levels in anurans.*** *Camera-lucida reconstructions of neurones recorded intracellularly in response to moving visual stimuli and labelled with cobalt-lysine (see Table 1). Fibres of retinal ganglion cells terminate in the contralateral tectum in lamina B and C (type R2), C to F (type R3), and F and G (type R4)[13]. A subtype of tectal T5.1 pear-shaped cell[14] of layer 8 (yellow) shows arborization fields that enable retinal inputs provided by lamina B through G to integrate (mainly from B and D–F). In addition, pretecto–tectal projections[17] mediated by neuropeptide Y terminate mainly in laminae B and C. A further subtype of T5.1 (green) shows an arborization pattern suitable for intratectal lateral interactions. The huge dendritic tree of another type of tectal cell (violet), responsive to any moving stimulus, provides the background of general integrative processes. The T5.2 pyramidal cell (blue), at the boundary between layers 6 and 7, integrates inputs from layers 8 and 9 and projects its axon along layer 7 towards the medulla oblongata (the axonal projection is distorted in this illustration). In the medullary motor nucleus of the trigeminal nerve, for example, there are neurones[16] responding best to prey-like stimuli. The richly arborized dendritic tree of the neurone shown here extends into the lateral and the medial reticular formation as well as into the vestibular and spino–cerebellar complexes; a branch extending toward the cerebellum, indicated by the asterisk, is rostral to the level of the transverse section half-segment. Neurophysiological data in toads suggest di(poly-)synaptic connections between neurones of the tectal 'snapping evoking area'[7] and medullary motor neurones involved in snapping (reviewed in Ref. 7). Scale bar, 250 μm.*

Another instance of pretectal–tectal interaction concerns the perceptual integration of a fence-like stationary barrier and a prey moving behind this semitransparent obstacle[26]. The barrier modifies the toad's approach towards prey, and leads to a detour movement around the obstacle. Ingle[26] suggests that pretectal TH10 'barrier-detecting neurones'[7] inhibit T5.2 'prey-selective neurones'[7] in the part of the tectal visual map corresponding to the barrier image, so that tectal neurones just lateral to the inhibited zone initiate a turning movement towards prey beyond the edge of the barrier. The

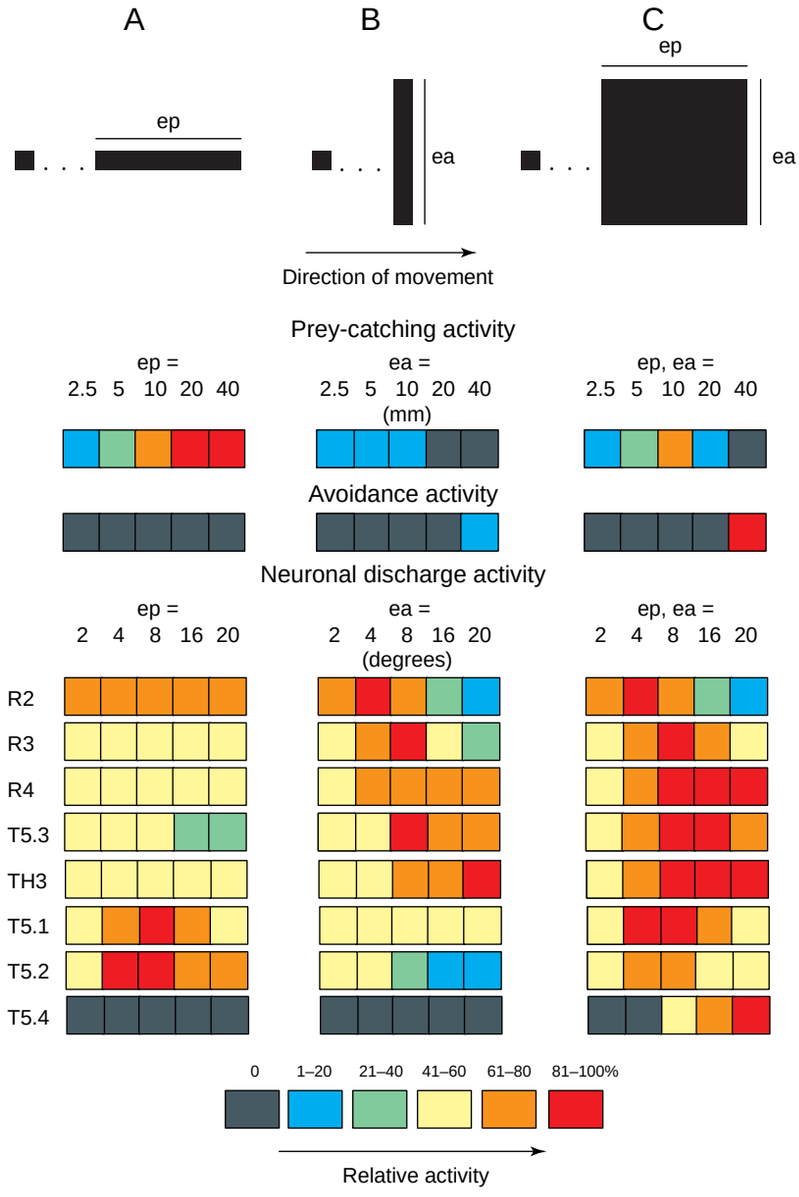

Fig. 3. ***In the analysis of key stimuli, the responses to changes of configurational stimulus features are of critical importance.*** *By means of an experimental setup, black rectangular objects are mechanically driven at constant velocity in front of a toad[7]; ep is the extension of an object parallel to the direction of its movement and ea is the extension across the direction of its movement. Starting with a small square, in series* **(A)** *ep is altered (ea is constant), yielding bars of different lengths parallel to the direction of movement; in series* **(B)** *feature ea is altered (ep is constant), yielding bars of different lengths across the direction of movement; and in series* **(C)** *both ep and ea (ep = ea) are altered, yielding squares of different sizes. The relative behavioural activities (prey-catching or avoidance responses per 30 s) and neuronal activities (discharges per s) are expressed as a percent (colour-coded) of the response to the optimal stimulus* (adapted from Refs 7,33). *The R, T and TH neurones from Table 1 considered in this survey have monocular, approximately radially symmetrical, excitatory receptive fields of different diameters: 4–6° (R2), 8–10° (R3), 12–16° (R4), 20–35° (T5.1, T5.2, T5.3 and T5.4), and 40–50° (TH3). During prey-catching, monocular toads judge the absolute size of moving objects; in toads immobilized with succinylcholine, both R- and T-type neurones with monocular receptive fields are sensitive to the angular size; in freely moving toads, however, the T neurones are sensitive to the absolute size, while the R neurones are sensitive to the angular size[37]. In this instance, it is suggested that monocular estimation of object distance – required for the evaluation of the absolute size at tectal level – takes advantage of motion parallax information (for comments on size constancy in visual perception in toads and frogs, see Ref. 26). Abbreviations: R, retinal; T, tectal; TH, pretectal thalamic.*

tectum is necessary for approaching the prey, but not for detouring the barrier[26]. After pretectal lesions, the 'detour-approach' in this complex stimulus situation fails and the animal collides with the barrier.

Concept B disregards computational strategies for visual perception mediated by interactions between retina-fed tectal and pretectal processing streams.

Telencephalic control of pretectum

Various thalamic nuclei[43,44] mediate and regulate information flow between tectum and telencephalon[45–48] (Fig. 1). However, concept B does not explicitly focus on the critical role of forebrain influences in the translation of perception into action. The following two examples illustrate such functions.

The caudal striatum plays a role in response gating by controlling pretectal nuclei through an inhibitory striato–pretectal connection[11,49] mediated by the lateral forebrain bundle (Fig. 1B). This bundle contains enkephalinergic fibres[50]. After striatal lesions[51], visual prey-catching fails to occur suggesting that pretecto–tectal inhibition overrides tectal responses. In the intact toad, such inhibition allows a cautious approach towards potential prey. Striatal activity in response to internal forebrain influences and to tectal visual influences mediated by the lateral anterior thalamic nucleus can reduce the pretecto–tectal inhibition, resulting in the release of prey-catching.

The ventromedial pallium ('primordium hippocampi'[52]) has been shown to participate in associative learning in toads. Indirect evidence from ^{14}C-2-deoxyglucose experiments[51] suggests that in the course of conditioning in a hand-feeding paradigm[7,51,53] the pretecto–tectal tuning, and thus the prey features-relating algorithm, can be chronically modified by medial pallial influences (Fig. 1C). In fact, following lesions to the posterior ventromedial pallium[51], endogeneous prey preference properties re-emerged. There are other examples of prey feature learning[11,54,55] involving other structures.

Sensorimotor codes of releasing systems

Prey-catching in amphibians consists of directed appetitive behaviour: 'turning', 'approaching', 'fixating' and the consummatory act 'snapping'. The release of each ballistic response requires prey categorization, whereas the selection of the response type depends on prey localization. How are objects categorized? Considering the response characteristics of neurone types to changing configurational features ep and ea (Fig. 3A–C), it is conceivable that ensembles of feature-selective neurones determine object categories, for example, prey (by T5.2 subtypes or T5.1 and T5.2), predator (by T5.4 subtypes or T5.3, TH3 and T5.4) or mate (T5.1 subtypes). These neurones express specific key computational strategies for deriving perceptual categories from appropriate visual input.

In addition, there is various 'action-related' visual processing with regard to different prey-catching strategies[28–31]: jaw grasping with a partially extended tongue in response to elongated wormlike objects vs striking with a fully extended tongue in response to small compact objects; the predator and barrier avoidance behaviours[23–27] (jumping away from a looming object vs side-stepping in front of a stationary obstacle); and the different dynamics of turning to escape vs turning to reach prey[56]. Further processing streams are responsible for monitoring other stimulus

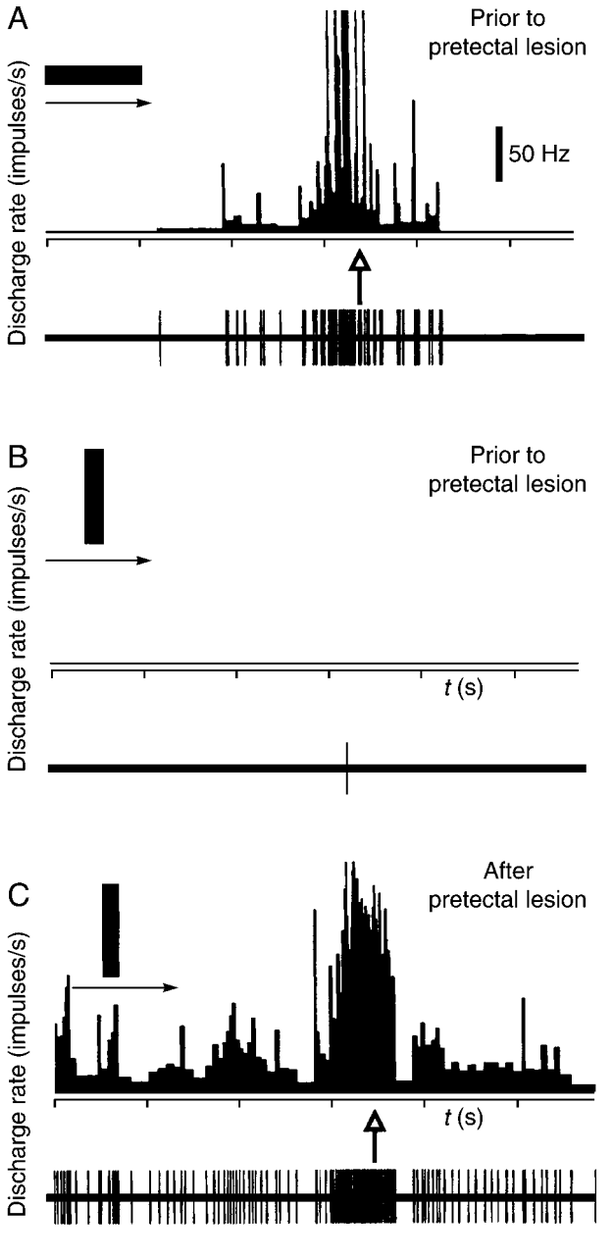

Fig. 4. ***Records of tectal neurones in freely moving toads allow correlations among stimulus features, tectal neurone activity and behaviour.*** *A bar of 2.5 mm × 20 mm in size and moving in prey configuration* **(A)** *traversed the receptive field of a T5.2 neurone: a strong burst of spikes preceded and 'predicted' the onset of the toad's orienting movement (see vertical arrow) towards the prey stimulus (top, frequency–time histogram; bottom, spike pattern). If the same moving bar was presented in nonprey configuration* **(B)**, *the T5.2 neurone showed very weak activity and prey-catching failed to occur. Shortly after an electrolytic pretectal lesion delivered (ipsilaterally to the tectal recording site) with a second implanted electrode* **(C)**, *this T5.2 neurone discharged strongly in response to the nonprey stimulus, whereby a strong burst of spikes preceded the onset of the prey-catching orienting movement towards that stimulus. The pretectal lesion impaired the neurone's and the behavioural ability to distinguish between prey and nonprey; furthermore, the receptive field of the neurone was enlarged and a resting discharge activity emerged.* Adapted from Refs 34,35.

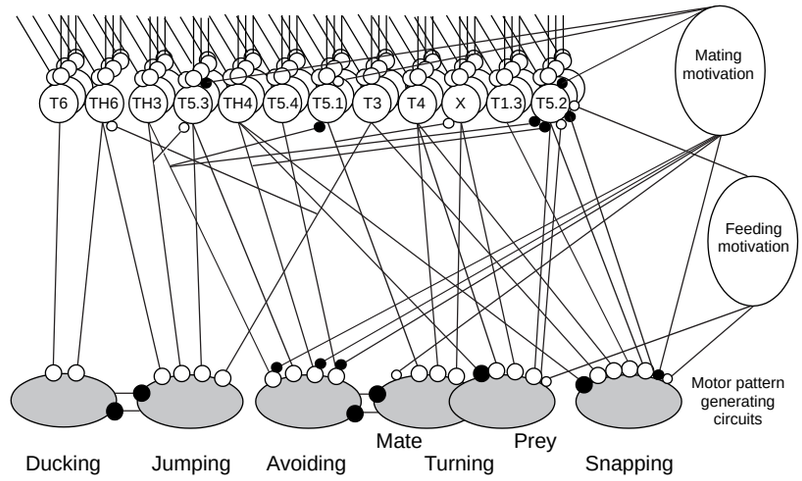

Fig. 5. ***The concept of sensorimotor codes suggests that combinations of distributed processing streams collectively activate a motor pattern.*** *Owing to convergence of inputs to T- and TH-type neurones, different visual response properties emerge in tectal and pretectal processing streams (see Table 1). One property can be represented in different processing streams (divergence) and one stream can contain information on many properties (convergence). The release of motor responses also involves convergence (different streams monitoring a releasing condition) and divergence (one stream contributing to monitoring different releasing conditions). Furthermore, motivation must be appropriate: during the feeding season, escape dominates prey-catching given that predator and prey are present simultaneously; in the mating season, escape and prey-catching are suppressed in favour of approaching (male) the sexual partner (female). Hierarchies and patterning in species-specific behaviour are reviewed in Refs 28,62,63. In many neurones (T1.3, T3, T4, T5.1, T5.2, T5.3, T5.4, TH3 and TH4), the projecting axons were determined by means of the antidromic stimulation/recording technique[41,57,58]; X refers to hypothetic tegmental neurones computing retinal topography and body segment orientation. The indicated connections to motivation systems are suggested from indirect data. As regards access to tectal cells, for example, it was shown that the stimulus responses of T5.2 neurones were extremely weak in fed, satiated toads during the hunting season or in unfed toads during the mating season[7]. Large circles refer to populations of neurones of a given type. Lines with open circles denote putative excitatory connections; lines with filled circles indicate inhibitory connections; large oval symbols refer to neuronal circuits.*

aspects including object location[10,56]. In toads, at least seven physiologically distinct types of tectal neurones project to medullary motor systems[57,58] (Fig. 5). Probably additional types descending from the pretectal–tectal–tegmental sensorimotor interface[10,59–61] will be characterized physiologically. Concept B, offering three types of retina-dominated, tectal, descending neurones cannot satisfy the rich repertoire of visually released behaviour.

We suggest that concurrent activity in combinations of distributed processing streams (Table 1; Fig. 5) provide the sensorimotor codes[7] of releasing mechanisms addressed to objects and to their location in space. Taking into account inputs from systems monitoring the motivational state[7,11,28,62], these large groups collectively select the appropriate behavioural response. Its variability might depend on the composition of the sensorimotor codes in connection with feedback[28,31]. How such codes are decoded by motor pattern generating systems is as yet unknown in amphibians (for a treatment in terms of schema theory, see Ref. 64). The huge dendritic arborization patterns seen in many medullary neurones[16,65,66] (see Fig. 2B) are suitable for converging inputs[16,18]. A precise temporal structure of the afferent activity[18,57,58,67] could play a decisive role in coincidence detection[68]; this is regarded as an economic way of binding distributed neurones into functionally coherent assemblies and to rapidly select subsequent response patterns.

Retinal ganglion cell dominated pathways might exist for particular functions that require a minimum of postretinal computation. For example, retinal R4 dimming detectors[4] (Table 1) directly influencing the responses of specific medullary neurones[58] suggest a fast channel suitable for startle behaviour.

Concluding remarks

The available evidence suggests that neuronal mechanisms responsible for perceptual category formation, localization and release of behaviour in toads and frogs take advantage of distributed processing and convergence at various levels. Such processes range from very basic in the retina to complex ones at tectal and the premotor or motoneuronal levels. The differentiated processes in the tectum can be sharpened and modulated by pretectum and regulated and modified by telencephalic nuclei. Specification of an appropriate choice from a large repertoire of motor programmes takes place in medullary and spinal premotor/motor systems which also receive modulatory inputs.

Regarding the notion 'processing stream', concept B suggests segregated 'visual streams' (retinal channels), each one determined by one type of R cell. By contrast, concept A deals with multiple 'behavioural streams': tectal processing streams, for example, are involved in approaching and acquiring prey or mate and in avoiding predators; pretectal processing streams are involved in avoiding predators or barriers. Here, retinal outflow can be pooled for the subsequent processing; furthermore, certain processing streams need to interact (Figs 4 and 5). Nonetheless, some segregation of streams might be useful for the animal to react quickly in 'extreme' situations. However, those streams are not the ones postulated by concept B, and the separation might be a matter of degree rather than total isolation.

Processing streams are presently discussed for various brain functions. A well known example is the concept of the two 'what' and 'where and how' cortical systems in primate vision[69] (reviewed in Ref. 70). One system is responsible for perceptual representations of visual objects. It originates from a subdivision of R cells projecting to the parvocellular layer of the lateral geniculate nucleus; this 'ventral stream' travels to the striate visual cortex and terminates in the inferotemporal lobe. The other one is responsible for visually guided actions directed at such objects. It originates from another subdivision of R cells that project to the magnocellular geniculate layer; this 'dorsal stream', travelling to striate visual cortex, terminates in the posterior parietal lobe. Current data suggest independence, but also important interaction between the perceptual system and the action system[71].

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Schizophrenia as failure of hemispheric dominance for language

T.J. Crow

Schizophrenic illnesses occur with approximately the same incidence in all human populations with a characteristic distribution (slightly earlier in males) of ages of onset. Given that the predisposition (which presumably is genetic) is associated with a procreative disadvantage why do such illnesses persist? Here it is suggested that these conditions are a manifestation of genetic diversity in the evolution of the specifically human characteristic of language, an innovation that has occurred by a process of progressive hemispheric specialization – the establishment of dominance for some critical component of language in one or the other hemisphere. Individuals who develop schizophrenic symptoms show lesser anatomical and functional asymmetries than the population as a whole; such symptoms may reflect 'dominance failure' for language.

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IN THE COURSE of a lifetime, approximately 1% of the population will suffer from a 'schizophrenic' illness. These individuals may experience hallucinations (most characteristically voices that provide a running commentary on the individual's actions) or develop delusions (that thoughts are inserted or removed from their head, or that their thoughts and actions are 'controlled' by an outside force). In addition, the ability of sufferers of schizophrenia to express or even experience emotion can be severely blunted, and they may become withdrawn and socially isolated. Such symptoms tend to persist and recur, are associated with an increased (at least 20-fold) risk of suicide, substantial loss of employment capacity and disruption to social and family relationships. What causes such destructive psychological change?

From the World Health Organization Ten Country study of incidence, Jablensky *et al.*[1] concluded: '…schizophrenic illnesses are ubiquitous, appear with similar incidence in different cultures and have clinical features that are more remarkable by their similarity across cultures than by their difference.'

Such constancy suggests that the disorder is independent of the environment. Indeed the search for common environmental precipitants (birth injury, viruses and social stressors) has yielded little hard evidence that they are relevant to the core process[2]. By contrast, a genetic factor gains credence from studies demonstrating increasing risk for psychosis with genetic proximity to an affected individual[3] and a concordance rate of approximately 48% in monozygotic (MZ) twins versus 17% in dizygotic (DZ) pairs[4]. Although less than 100% MZ concordance suggests that factors other than genetic are relevant, careful lifetime histories of discordant MZ pairs have failed to reveal consistent environmental differences between ill and well twins[5]. If the only contribution to aetiology is genetic, discordance in MZ twins requires explanation. One possibility is that random factors, such as those invoked in some theories of neural development[6], play a role.

Two demographic features of the disease process provide clues to the nature of the genetic contribution. Onsets occur from late adolescence through middle adult life, an epoch coinciding with the reproductive phase. In view of the documented decrease in fecundity associated with the disease[7] the question arises[8,9], how can these genes survive in the face of a biological disadvantage? Genes for thalassaemia and sickle cell anaemia persist in spite of associated disadvantages but only in populations in which they provide protection against malaria. Genes predisposing to schizophrenia survive in all populations without a balancing advantage being apparent. The second puzzle is a sex difference in age of onset, with males presenting a mean two to three years earlier than females. This suggests that pathogenesis is determined by some normal anatomical or physiological difference between the sexes. Here I advance a hypothesis to explain the persistence of these genes in the light of the morphological changes in the brain, what is known about the neuropsychological profile in schizophrenia, and the recent evolution of modern *Homo sapiens*.

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