Visual neuroscience research in China

YAO HaiShan†, LU HaiDong†* & WANG Wei†*

Institute of Neuroscience, State Key Laboratory of Neuroscience, Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences, Shanghai 200031, China

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Historically, vision research in China was one of a few distinct research programs within the Chinese Academy of Sciences (CAS). With improved funding opportunities and research environment in neuroscience, vision research at several research institutes within the academy has made significant progress not only in the quantity of publications, but also in the quality of the work. Based on our own expertise, this review is mainly focused on the findings that have advanced the understanding of visual processing in the central visual pathway, visual perceptual learning, visual development and eye diseases.

visual cortices, contextual modulation, feedback, feature binding, motion processing, perceptual learning, functional brain imaging, eye movement, visual development and senescence

The abiding challenge in neuroscience is to provide a description that links behavior and perception to brain mechanisms. The function and structure of the mammalian visual system serve as a model for this line of research. In the past decade, findings from a variety of research areas, including machine vision, visual psychophysics, visual neurophysiology, developmental neurobiology, brain imaging, and combined electrophysiological and psychophysical studies of behaving primates, are beginning to establish a causal link between neural activity and visual perception. Various Chinese research institutions have made progress in recent years. In particular, the active vision research groups within the Chinese Academy of Sciences (CAS) focus on some key issues such as: neural mechanisms of the contextual effect, the origin of orientation selectivity in Area 17, the rule of feedback projections in the visual cortices, motion processing in the mammalian extrastriate cortex, perceptual learning, visual development and senescence.

1 Recent progress

1.1 The neural mechanism of the contextual effect

Visual stimuli have a complex spatiotemporal context [1,2] and the perception of local visual features (e.g. size, edge, motion) are influenced by their context. For neurons in the early visual pathway, regions beyond the classical receptive field (CRF), although ineffective alone in driving responses, suppress or facilitate the response to stimuli presented in the CRF [1,3]. Termed as the “non-classical” receptive field (nCRF) or extra-receptive field (ERF), these surrounding regions can convey the context where the stimulus is presented, and play important roles in the processing of contextual information [4]. Researchers in China in the past decade have extensively investigated the interaction between CRF and nCRF for cortical and sub-cortical neurons, the perceptual relevance of the nCRF modulation, the morphological basis of nCRF modulation, and cortical organi-
zation with respect to the nCRF summation property [5–13]. These studies have greatly contributed to our understanding of the role of nCRF in processing contextual information.

Many studies suggested that nCRF may be involved in figure-ground segmentation and perceptual pop-out [14–16]. To examine the neural mechanism of such perceptual phenomenon, Li and colleagues [9] in the Shanghai Institutes for Biological Sciences of CAS asked whether V1 neurons in alert monkey are sensitive to the relative spatial phase (RSP) between the gratings in the CRF and the nCRF. They found that V1 cells exhibited RSP tuning, in which response amplitude to the out-of-phase gratings was much higher than that to the in-phase gratings, suggesting that V1 cells are capable of detecting the center-surround discontinuity. The RSP sensitivity was maximal when the phase difference was generated at or near the CRF/nCRF boundary, and the effect was reduced by inserting a gap between the displaced gratings. Li's laboratory [10] showed that the sensitivity to the center-surround discontinuity was cue-invariant. A single V1 neuron was able to signal the CRF/nCRF discontinuity defined by multiple visual features, including luminance, contrast, color, orientation, spatial frequency, and velocity. The degree of discontinuity sensitivity was strongly dependent on the strength of nCRF suppression. These results suggest that CRF/nCRF interaction may contribute to cue-invariant object perception [17].

Psychophysical experiments showed that motion context also influences the perceived speed of motion [18,19]. To examine the role of nCRF in this psychological phenomenon, Li and colleagues [6] measured the speed tuning of neurons in Area 18 by displaying a moving stimulus in the region surrounding the CRF. They found that the speed tuning of the neuron depended on the contrast of speed between the stimuli in the CRF and the nCRF. The peak of the speed tuning curve shifted to a higher (lower) value when the speed of the surround stimulus was lower (higher) than the optimal speed presented at the CRF. The repulsive shift in peak speed was observed when the surround grating moved at the optimal speed but in opposite directions, indicating that such effect can not be accounted for by temporal frequency interaction. Such interaction between CRF and nCRF may underlie the contextual effect of speed perception.

By independently varying the stimulus orientation in CRF and nCRF, it was found that stimulation of nCRF affects the orientation selectivity [5,13,20–22]. As with many other tuning properties in the visual cortex, V1 orientation tuning exhibits complex temporal dynamics [23]. Li and colleagues [23] measured the spiking responses to a random sequence of oriented gratings at multiple stimulus sizes, and used the reverse correlation method to analyze the dynamics of orientation tuning [8]. They found that stimulation of the nCRF sharpened the orientation tuning, consistent with the previous finding that nCRF stimulation increases the selectivity of V1 neurons [24]. The nCRF stimulation increased the magnitude of the shift in the preferred orientation and the bandwidth over time, suggesting that nCRF stimulation may increase the computational power of the visual cortex. This study also provides useful information concerning the possible neuronal circuitry underlying tuning dynamics.

Cortical cells with similar CRF properties, such as orientation selectivity and ocular dominance, are clustered into columns [25]. Yao and Li [7] measured the neuronal responses to circular grating stimuli of various sizes to test the influence of the nCRF stimulation on the CRF response, and mapped the distribution of neurons with different nCRF properties. Consistent with previous studies, they found two types of neurons with respect to the spatial summation property of nCRF. The majority of cells exhibited inhibitory nCRF, which showed a decreased response to a stimulus larger than the CRF. The minority of cells showed facilitatory nCRF, in which a stimulus larger than the size of the CRF increased the response. Neurons with inhibitory or facilitatory nCRF were clustered together, and the clusters were randomly distributed within the cortex in a manner neither columnar nor laminar. Both the inhibitory and the facilitatory clusters were roughly isotropic in shape, and similar in size. Given that these clusters were randomly embedded in all cortical layers, it may ensure that contextual analysis takes place within all parts of the visual field in the early visual pathway. Such clustered organization with respect to the nCRF property may also help to minimize the length of axons required for long-range integration, and allow an efficient processing of global visual information. This work was published in Neuron [7], which was the first Neuron publication from China.

Previous studies showed that the size of the CRF and the spatial extent of nCRF depended on stimulus contrast [26,27]. By accurately measuring the size of CRF using an occlusion test, Song and Li [11] found that the CRF size of V1 neurons was constant, independent of stimulus contrast, while the spatial summation property of nCRF is either contrast dependent (CD) or contrast independent (CID). For CD neurons, the suppressive effect of nCRF was stronger at a high stimulus contrast and weaker or even turned to facilitatory at a low contrast. Conversely, CID neurons showed similar facilitatory or suppressive summation at low and high contrast. Song and Li labeled the neurons with biocytin, and found that CD and CID neurons were respectively pyramidal and non-pyramidal cells. The CID neurons with inhibitory spatial summation were smooth-dendrite interneurons, and those with facilitatory spatial summation were spiny stellate neurons. The distinctions between cell types provided implications on the circuitry basis underlying the summation property of nCRF: the pyramidal neurons may form long-range horizontal connections, which play important role in the dynamics of spatial summation properties, whereas the interneurons may be critically involved in the summation of neurons whose nCRF properties
depend on the local connectivity.

For subcortical neurons, Shou’s group in Fudan University in Shanghai reported that drifting gratings of lower spatial frequency over a large area beyond the CRF could evoke significant responses from retinal ganglion cells in cats. These large surround fields alone may determine the orientation bias of the cells, because a quarter of the cells did not exhibit an orientation bias for a stimulus presented in the CRF [13]. The CRF preferred higher spatial frequencies at a particular orientation, and the surround field preferred lower spatial frequencies at a different orientation, which may contribute to texture segmentation. The large surround area beyond the CRF of LGN neurons also showed similar responses to drifting gratings of lower spatial frequency at a preferred orientation. These responses depended on and increased with the size of stimulus outside the CRF, which showed spatial summation property [12]. Thus, the nCRF of retinal ganglion cells and LGN cells also play important roles in the processing of contextual information.

Contextual effects in vision are ubiquitous and reveal fundamental principles of visual information processing. Because the effect involves a large-scale integration over multiple image regions, it was believed that the representation of contextual effects takes place in higher visual cortical areas and the small receptive field size of neurons in early visual cortical areas puts a constraint on this kind of integration. However, this view has been challenged. In a series of studies, Fang and colleagues [28] at Peking University used functional magnetic resonance imaging (fMRI) to investigate contextual effects in the human early visual cortex. In the first study, perceived size was found to modulate the distribution of V1 activity, closely matching psychophysical perception. In the second study [29], it was found that grouping line segments into a shape resulting in a reduction of V1 activity, relative to the ungrouped condition. In the third study [30], border ownership was found to be represented as early as in V2. Overall, these results demonstrate that contexts significantly modulated neural activities in early visual areas and suggested the crucial role of early visual areas in the context representations. Fang and colleagues also found that the modulations were largely dependent on attention and indicated that feedbacks from higher cortical areas might be critical for the context representations.

1.2 Origin of the orientation selectivity of Area 17

Following systematic studies of the subcortical origins of orientation and the direction selectivity of neurons in the primary visual cortex in cats [31–33], Shou’s laboratory was the first in China to set up in vivo optical imaging based on intrinsic signals in 1998. Combining optical imaging and retrograde tracing, Shou and colleagues found that relay cells that projected to a single orientation column in V1 representing the horizontal meridian were clustered in the LGN, some of which were aligned on a line parallel to a horizontal meridian of the visual field projection, providing anatomical evidence for Hubel and Wiesel’s model of simple cell receptive fields [34]. Using optical imaging alone with in vivo application of AMPA, NMDA and GABA receptor antagonists, Shou’s group [35] demonstrated on a large scale of primary visual cortex that glutamate-mediated excitatory input, rather than the GABAergic inhibition, was essential for the orientation selectivity of cortical neurons.

1.3 The rule of feedback projections in the visual cortices

Throughout different hierarchies of visual areas, both feed-forward and feedback connections play important but different roles in generating visual signal abstractions [36]. However, the precise functions of the feedforward, feedback, and lateral connections remain to be elucidated. In a series of studies on the functions of feedback projections from higher-order cortical areas to lower ones, Shou and colleagues [37] have found that cortical area 21a in the cat (corresponding to V4 in the monkey) exhibited a neuronal “oblique effect” that was much stronger than that in area 17. The feedback from area 21a improved the spatial frequency tuning of neurons in areas 17 and 18 [38] and enhanced the neuronal oblique effect in area 17 [39,40]. The feedback from area PMLS in the cat (corresponding to V5 or MT in the monkey) sent positive input to Area 17 and improved the direction selectivity but not the orientation selectivity in area 17 [41]. These findings support the idea that higher-order cortical areas within the hierarchical visual streams (either M or P pathway that responsible for form or motion processing respectively) may exclusively modulate the response property of the cells in the lower-order areas.

1.4 Visual feature binding

The organization of the visual system can be described as a stepwise processing of the retinal input through a hierarchy of areas that build increasingly complex abstractions of the visual world. At higher levels these areas in turn are broadly described as two streams, the ventral stream (also known as the “what pathway”) concerned with form processing and the dorsal stream (the “where pathway”) that processes the information of motion and spatial location [42–44]. The connections and functional interactions between these streams are particularly interesting for their abundant lateral or intermediate level interaction. However, the functional consequences of the interactions between these two streams are not clear.

Using fMRI at the Institute of Biophysics of CAS in Beijing, Chen and his colleagues [45] have examined whether form perception plays a role in the human visual perception of apparent motion (AM), created by sequential
presentation of a pair of adjacent motionless images. Like real motion, short-range AM as well as other illusory motion is processed in the dorsal stream particularly within the MT area, with little contribution from the form pathway [46–49]. Long-range AM with a plastic shape change, however, is more naturally associated with form-level processing [50] and was hypothesized to actually associate with global form perception [50–52]. Chen and colleagues [45] found that, in contrast with short-range AM, long-range AM (with larger separation of the two images) caused significant activation of the anterior temporal lobe in the ventral ‘what’ pathway. The degree of activation was directly proportional to the geometric differences between the pair of images, with highest activation when the topological property of the image was changed. Their result clearly indicated that long-range AM was associated with form perception, which strongly supports the notion that cross stream interaction is crucial in the visual feature bindings in the perception of long-range AM. The result also suggests that the abundant connections between the dorsal and ventral streams may allow the visual system to dynamically adapt to the changes of natural environment. Their results are consistent with the view that the topological property of the visual image is the first to be perceived as primary elements in form perception [53,54]. The ‘holistic’ view of this topological perception is drastically different from the traditional ‘bottom-up’ view based on the binding of local features of the visual image into a more global perception [54].

1.5 Motion processing in the cat extrastriate cortex

Visual motion perception is one of the most prominent functions performed by the mammalian cerebral cortex. In cats, the LS (lateral suprasylvian) area is an essential area involved in motion analysis. It is often considered to be functionally analogous, even homologous, to the middle temporal area (MT) of primates [55,56]. Neurons in this area have large RF, and are selective to the direction of motion. Diao and Li’s laboratory of the Institute of Biophysics of CAS investigated different aspects of this motion area, including its contribution to pattern motion detection, to optical flow sensitivity and its motion adaption.

Moving images are commonly considered to be processed in two stages. The first-stage neurons are sensitive to the motion of one-dimensional oriented components, and their outputs are combined at the second stage to perceive the global motion of the entire pattern. Alternatively, the pattern motion may be signaled by monitoring a distinctive feature of the image, such as a line-end or a corner. Li, Diao and their colleagues [57] examined the direction tuning in the posteromedial lateral suprasylvian (PMLS) area of cats using ‘random-line’ patterns, which consisted of identical thin line segments moving perpendicularly or obliquely to their common orientation. When the component lines were much shorter than the size of the RF, the majority of cells were selective in the direction of the pattern motion while a small subset of cells was sensitive in the direction of the component motion. By contrast, the response profiles of most cells became more component-motion-selective with the increase of the line length of the oriented elements. These findings imply that the two-stage theory might be insufficient in describing visual motion analysis. At relatively low levels of the visual system, non-orientation-based processing may coexist with orientation-sensitive processing. These 2 processes dynamically compete. Depending upon the strength of the orientation elements in the stimulus, one process rises as another falls, so that under some circumstances it becomes possible to signal the actual direction of pattern motion.

The processing of optic flow information has been extensively investigated in the medial superior temporal area (MST) of the macaque. It is unclear whether or not the functionally analogous area in the cat—the postero medial area and the posterolateral area in the lateral suprasylvian cortex (respectively PMLS and PLLS)–have comparable functions in analyzing the optic flow information. Li, Diao and their colleagues [58] examined the responses to optic flow patterns in PMLS and PLLS, using stimuli of random dots (including expansion and contraction, clockwise and counter-clockwise rotation, and translation) and moving bar. About 90% of the neurons were found to be excited by the optic flow stimuli and most of them were responsive to different flow patterns. Only 20%–25% of the cells were specific to specific optic flow modes, while their direction preference was fairly modest in general. The optic-flow-selective cells in PMLS and PLLS showed stronger direction-selectivity to both the flow field and the moving bar than those of nonselective cells. However, their optic flow response properties were not well correlated with the direction preference to moving bars. In accordance with previous findings, PMLS was analogous to the middle temporal area of the macaque in many respects. As for the PLLS cells, they were sensitive to fewer types of flow stimuli, but responded better and more selectively to radial motion. These findings suggest that these two lateral suprasylvian areas are unlikely specialized for the analysis or discrimination of different flow patterns, rather playing an intermediate relay role in optic flow processing.

Diao and colleagues [59] further examined the responses of neurons in the dorsal lateral suprasylvian (DLS) cortex to large field optic flow stimuli containing translation and spiral motion in different directions. They found that most cells were responsive to both kinds of movement with fairly good direction selectivity. Generally, the responses were better to spiral motion than to translation, and better to radiation than to rotation. The direction tuning for spiral motion was broader than that for planar motion. The dot size in the stimulus patterns had no definitive influence on the responses and direction preference. These results suggest that DLS might be substantially involved in the detection and
analysis of complex optic flow information, and to some extent, in favor of the radiation component in the stimulus.

It is also unclear how motion adaptation influences the motion processing in these extrastriate cortical areas. Diao and colleagues [60] investigated the changes in neuronal responses during and after adaptation to prolonged optic flow stimulation in the PMLS of cats. In comparison with translation stimuli, the complex optic flow patterns (radiation and rotation) produced more pronounced adaptation and after-effects by inducing a larger response reduction, and sharply altered the direction selectivity of many neurons as well. Generally, the adaptation effects were direction-specific for radiation/rotation, but independent of the direction of the test stimulus for translation. These results suggest that PMLS may play an important role in the perception of motion after-effects to complex optic flow fields, while the adaptation to simple translation might be generated at a relatively earlier level of the visual system.

1.6 Visual perceptual learning

Visual perceptual learning suggests that the visual brain is highly plastic and modifiable. However, little is known about how stimulus temporal factors affect perceptual learning. Yu’s laboratory (of Beijing Normal University) [61] demonstrated the essential role of stimulus temporal patterning by showing that “unlearnable” contrast and motion direction discrimination (resulting from random interleave of stimuli or “roving”) was readily learned when stimuli were practiced in a fixed temporal pattern. This temporal patterning did not facilitate learning by reducing stimulus uncertainty. Learning enabled by temporal patterning could later generalize to randomly presented stimuli.

In a follow-up study, Yu’s laboratory further found that stimulus rhythm was necessary for temporal patterning to take effect during practice. Learning consolidation was subject to roving disruption up to 4 h after each practice session [62]. After completion of temporal patterned learning, performance was undisturbed by extended roving training. They also found that roving was ineffective if each stimulus had a distinct identity. These results suggested that for multi-stimulus learning to occur, the brain may need to conceptually “tag” each stimulus, in order to switch attention to the appropriate perceptual template. Stimulus temporal patterning assists in tagging stimuli and switching attention through its rhythmic stimulus sequence.

Perceptual learning of many visual tasks is found to be specific to retinal location, in which learning transfers little to an untrained retinal location. In most perceptual learning models, this location specificity is interpreted as a pointer to a retinotopic early visual cortical locus of learning. Yu and colleagues [63] developed a novel double-training paradigm that employed conventional feature training (e.g., contrast) at one location, and additional training with an irrelevant feature/task (e.g., orientation) at a second location, either simultaneously or at a different time. This additional location training enabled a complete transfer of feature learning (e.g., contrast) to the second location. This finding challenges location specificity and its inferred cortical retinotopy as central concepts of many perceptual learning models, and suggests perceptual learning involves non-retinotopic, higher brain areas that enable location transfer.

The conventional point of view of visual cortical processing emphasizes a hierarchical order of the processing streams: information about simple stimulus components such as line segments is first extracted in the early visual cortex, while more complex stimulus features are subsequently processed in higher-order visual areas. In the primary visual cortex (V1), response properties of neurons have long been thought to be rather stereotyped or hard-wired. By establishing direct links between neuronal responses in V1 and the behavioral responses of monkeys performing visual discrimination and detection tasks, Li (of Beijing Normal University) and colleagues [64] have recently challenged the standard model of feedforward visual processing, and their study has revealed that the analysis of the visual image depends on countercurrent streams of processing. They found that V1 neurons changed their functional properties according to the task being performed. Repeated performing of the same perceptual task, steered the repetitive invoking of top-down influences specific to the task, and further potentiated the adaptive changes in V1 useful for solving the perceptual task. Their observations suggested that learning dependent changes occurred in the primary visual cortex under task-specific top-down control. These findings indicated that the primary visual cortex acts as an adaptive processor, running and refining different processing “programs” appropriate for different perceptual tasks. This reflected a general processing mechanism in the sensory cortex.

1.7 Aged-related degeneration in the visual cortex and neuronal mechanisms of anisotropic amblyopia

Human visual function declines with age. Much of the decline cannot be accounted for by optical factors alone and most likely reflect an aged-related degeneration in visual cortical areas. Through international collaborations, Zhou and his colleagues at the University of Science and Technology of China (USTC) have carried out extracellular single unit studies on the RF properties of V1, V2 and MT cells in young and old animals, including monkeys, cats and rats. Their results have shown significant age-related degradation of neural function in cortical areas, which may underlie the declines in visual function that accompany normal aging [65–68]. Zhou and colleagues also found that V2 cells in older animals exhibited decreased orientation and direction selectivity, increased visually driven and spontaneous activities and decreased signal to noise ratio [66]. In addition, they found that contrast sensitivity was affected by
aging more severely in MT cells than in V1 cells [69]. Their findings represent a useful first step towards understanding the mechanisms underlying age-related reduction in visual perceptual abilities.

Amblyopia is a developmental visual disorder characterized by reduced vision in the absence of any detectable structural or pathological abnormalities, and this reduced vision does not improve with refractive correction. Although amblyopia has been identified as a cortical impairment resulted from abnormal visual experience in early life, its neural basis remains unclear [70–72]. In clinical practice, patients older than eight years are left untreated [73]. However, recent studies on perceptual learning suggest that the adult visual system retains a large degree of plasticity [74,75], and perceptual learning might be a potential treatment for adult amblyopia. Through the collaboration with Dr. Lu’s group in USC, Zhou’s group at USTC have investigated amblyopia. Their work has primarily concerned the identification of the mechanisms of amblyopia, exploring the neural plasticity of the amblyopic visual system and attempting to find possible therapy for adult amblyopes.

The value of perceptual learning as a potential therapy for amblyopia has been evaluated since the pioneering work of Campbell and colleagues [76]. Zhou and colleagues [77] trained adult and teenager amblyopic subjects in a simple visual detection task and evaluated the effects of perceptual learning on visual acuity and CSF. Their results showed that retention of the training effects was excellent with the practice of sine-wave grating detection near the cut-off frequency, indicating that significant performance improvements were due to training rather than re-testing. Perceptual learning in the amblyopic eyes that generalize to a wide range of untrained stimuli and task conditions would provide a basis for effective training regimen. To evaluate and compare the generalization of perceptual learning in amblyopic and normal vision, Zhou and colleagues [78] estimated the bandwidth of perceptual learning in both normal and amblyopic subjects. They found that the estimated bandwidth of perceptual learning was much broader than the bandwidth of their spatial frequency channels and was consistent with previous reports [79]. These results implied that the impact of perceptual learning generalizes across spatial frequency channels in amblyopic eyes.

Zhou’s laboratory [80] have measured CSFs in treated amblyopes using more carefully controlled standard psychophysical procedures with sine-wave grating stimuli. In contrast with other studies [81–83], they found that contrast sensitivity was significantly higher in the previously fellow eye (pFE) than in the previously amblyopic eye (pAE), and the difference depended on spatial frequency. Their results indicated that treated amblyopes remained deficient in spatial vision [80]. Qiu et al. [84] conducted a study primarily concerned with local motion processing in amblyopia. They found that the apparent local motion deficits in anisometropic amblyopia could be largely accounted for by deficits in moving grating detection. Complementing an earlier study on strabismic amblyopia [85], these results suggest that local motion-sensitive mechanisms are largely intact in anisometric amblyopia; the apparent local motion deficits in anisometric amblyopia are also modeled with deficits in contrast sensitivity functions.

1.8 Ophthalmic glaucoma related vision research

Shou and his colleagues [86] used electrophysiological and optical imaging methods to study cortical functional changes during brief elevation of intraocular pressure (IOP), which was similar to the condition of the acute angle-closure glaucoma. It was found that all the cortical neurons in Area 17 of cats decreased their responses to grating stimuli during the elevation of IOP. However, the simple cells of the visual cortex were more sensitive than complex cells to IOP elevation. Cortical cells that preferred higher spatial frequencies lost orientation columns more than those preferring lower ones in the IOP elevated cats [87]. They demonstrated that the cortical functional decline induced by elevation of IOP was caused by the retinal ischemia, as the effect in the visual cortex was reversed by increasing the blood pressure of the animal [86,87]. The cortical events induced by brief elevation of IOP are readily explained because the previous findings in the same group have shown that X (β- or small) type retinal ganglion cells and relay cells in the lateral geniculate nucleus were more sensitive than their accompanier Y (α- or large) cells to the acute elevation of IOP in cats [88–91]. The opposite was observed in chronic glaucomatous cats, in which the large cells in the retina decreased in cell density, shrunk in dendritic structure and declined in visual response more significantly than the small cells did [92–94], suggesting that there may be different mechanisms underlying acute and chronic glaucoma.

1.9 Visual processing in non-mammals

Wang’s group (Institute of Biophysics, CAS, Beijing) uses pigeons as an animal model and studies important questions that are common to the visual system of both mammals and non-mammals (e.g. how orientation selectivity is raised).

In daily life, humans and other foveate animals frequently move their eyes to rapidly search for or smoothly track a target of interest, or make optokinetic and vestibulo-ocular reflexes. In homing pigeons, Wang’s group found two types of eye movement signals: rapid eye movement (saccade) signals originating from the brainstem raphe complex, and slow eye movement from two optokinetic nuclei including the nucleus of the basal optic root in the accessory optic system and the pretectal nucleus lentiformis mesencephali. They found that the traditionally named fast-phase of the optokinetic nystagmus was actually a saccade with a shorter duration. Before the onset of a saccade,
raphe neurons sent signals to oculomotor neurons to make a saccade, and they also sent efference copies of the motor signals or corollary discharges to telencephalic nuclei and visual thalamus. As a result, the blurred retinal images caused by saccades were suppressed by corollary signals and thus a clear and stable visual world was maintained [95,96].

In their study in pigeons, Wang’s group [97] found that tectal neurons computed the time-to-collision of an approaching target, whereas thalamic neurons computed the distance-to-collision of an approaching surface [97]. Pretectal cells encoded all three physical parameters of visual motion (i.e. direction, speed, and acceleration). In a broad range of speeds, the firing rates of these neurons depended on the changes of speeds over time (acceleration) but not on speed per se. In addition, they responded equally to real and illusory contours. Some of them produced inhibitory (or excitatory) after-responses to the cessation of prolonged motion in the preferred (or null) directions. Because their excitatory and inhibitory RFs possessed opposite directionalities, after-responses in one direction created illusory motion in the opposite direction [98].

Wang’s group [99] found that the nucleus isthmi in vertebrates is a visual center, and they have identified the synaptic nature, transmitters and receptors in the tecto-isthmic system. The magnocellular and parvocellular divisions of the avian nucleus isthmi are separate. They modulate the excitatory and inhibitory RFs of tectal neurons, revealing a dual modulation. All of the visual neurons in a tectal column were found to converge onto an isthmic cell and their excitatory RFs formed the elongated excitatory RF of an isthmic neuron, suggesting the most possible neuronal mechanisms underlying an elongated RF and orientation selectivity.

In the visual system of both mammal and non-mammal vertebrates, visual information is transmitted and processed from the retina to the telencephalon. In ground-feeding birds such as pigeons, however, the brain also sends messages back to the retina via a centrifugal pathway that originates from the isthmo-optic nucleus. Wang’s group [100] found that tectal axons contact isthmo-optic neurons in a one-to-one fashion mediated by glutamate (AMPA receptors) and nitric oxide. Electrical synapses and field effects are critical for synchronizing neuronal activities within the nucleus. Together with the facts that the isthmo-optic nucleus receives input mainly from the dorsal retina via tectum and projects directly to the ventral retina, topographic modulation of tectal activity by isthmo-optic neurons implies that this structure may be involved in switching visual attention to a predator when it appears in the sky.

1.10 Vision research groups in the Institute of Neuroscience in Shanghai

In the past ten years, China has experienced substantial improvement in the research environment of neuroscience, largely due to increased funding. As a result, there has been a significant increase in the number of talented neuroscientists who have received extensive training abroad and have returned to China, as well as an increased number of new research institutions, such as the Institute of Neuroscience (ION) in Shanghai. Several vision research groups were established in ION during the last few years, including Dr. Yao’s group, Dr. Wang’s group, Dr. Lu’s group, and Dr. Zhang’s group.

Yao’s laboratory uses multi-electrode array and in vivo patch recording to study how the early visual system processes information in complex visual scenes (in particular, natural scenes) and how the visual circuits adapt to different patterns of visual stimulation. Yao and colleagues [101] have examined the functional role of LGN spatiotemporal frequency tuning in the processing of natural scenes. They found that LGN neurons exhibit inseparable spatiotemporal frequency tuning in a manner consistent with the feature of optimal filters that maximize information transmission of natural scenes. They also analyzed the spatiotemporal power spectrum of natural scenes and found that some frequencies exhibit larger variation in power across different scenes. The preferred frequency of ensemble LGN neurons matches the range of frequencies in which the natural power spectrum varies most. Comparison of neural discrimination for natural stimuli and for artificial stimuli with similar mean power spectra but different variation structure showed that the match between LGN tuning and natural spectra variation enhances neural discrimination for natural stimuli. Their results indicated that, in addition to removing redundancy, the spatiotemporal frequency characteristics of LGN neurons facilitate neural discrimination of natural stimuli.

Wang’s laboratory focuses on the neural circuitry and functional organization of feedback in form and motion perception, which are two main functions of the visual system. They investigate the function and integration of different neuronal populations within the loop among LGN, layer 4, and layer 6 in the cat primary visual cortex [102,103] and within the complicated integrated circuits among LGN, primary visual cortex, MT, and V4 in primates [104]. Wang’s laboratory consider these issues: (i) The functional role of extrastriate visual cortices such as V4 in illusory and kinetic contour perception; (ii) the functional role of higher order visual area MT in direction of motion perception (iii) whether or not V1 cells response to visual features with awareness; (iv) the function of layer 6 feedback cells in the primary visual cortex. Dr. Wang’s laboratory, mainly funded by the Chinese Academy of Sciences, brings together a range of multi-disciplinary techniques, including visual stimulation, in vivo optical imaging [105], in vivo simultaneous recording of different cortical brain areas and layers using extracellular multi-electrode recording arrays and multi-iontophoretic drug application [102]. Anesthetized and awake animal preparations are currently performed in...
Wang’s Laboratory.
Lu’s laboratory uses multiple approaches (awake monkey optical imaging, single-unit recording and psychophysics) to study the representations of visual features in the primates' visual cortex, and how such representation is modulated by top-down control (e.g. attention). With the intrinsic optical imaging technique, sub-millimeter functional structures in the monkey visual cortex are visualized in vivo. Such cortical “maps” (e.g. ocular dominance map, orientation map, retinotopic map and color map) are used for evaluating the activity levels of visual response (bottom-up driven) or for measuring the modulation from cognitive tasks (top-down driven). Such maps are also used as a guidance for further electrophysiology recording. Lu’s laboratory is one of the few research groups in the world using such techniques on awake behaving monkeys.

Zhang’s laboratory study the neural basis of cognitive function, focusing on the role of the posterior parietal cortex (PPC) in visual attention, the intention of motor plans, working memory, and decision making. The research interests of Zhang’s laboratory are: (i) the relationship between eye position signals in the somatosensory cortex and gain field signals in PPC; (ii) the neural mechanisms underlying the phenomenon that working memory causes inaccurate saccadic eye movements; (iii) the role of the excitatory and inhibitory inputs in cognitive modulation in PPC neurons. The behaving primates are their primary research subjects.

2 Perspectives and concluding remarks

The progress and efforts made by these visual neuroscience laboratories in CAS has advanced the understanding of the functional logic of the myriad interactions in the visual system, and provided additional information for better models of visual processing at the systems level. Detailed understanding of the central visual mechanism may also give insight into the neuronal mechanisms underlying visual disability. Both retinal lesion and changes in the central visual circuitry cause visual disability, and age-related macular disease has become a major problem in human society with increasing longevity. Basic research on visual neuroscience is critical for understanding the mechanisms of visual disability, and may help to develop new ways of medical treatments for the restoration of normal visual function.

The studies reviewed above were mainly conducted in China and have been published in peer-reviewed international neuroscience journals. Like basic research in other fields of neuroscience, rigorous vision research in China will inevitably result in increased international recognition. In particular, younger visual neuroscientists from abroad, who were originally trained in the CAS institutes, are beginning to return to China and set up their own research laboratories, primarily in Beijing and Shanghai. The combination of Chinese scientists trained in China with those returning from abroad has created a large workforce with expertise in a variety of disciplines, which will further strengthen visual neuroscience research by targeting fundamental questions on the mysteries of the brain. Findings with major impact on the field of vision research may occur in the coming decades.

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Laboratory Introduction

Yao’s laboratory studies how the early visual system processes information in complex visual scenes, and how the visual circuits adapt to different patterns of visual stimulation. The lab uses in vivo whole-cell patch recordings or multi-electrode recordings to examine visual responses at the synaptic, cellular, and circuitry level. The research projects include: (i) Neural representation of motion-in-depth signals and the interaction between motion and depth signals in the early visual cortex; (ii) cellular and circuitry mechanisms of cortical modification induced by visual stimulation of natural scenes; (iii) stimulus selectivity and experience-dependent plasticity of cortical connectivity.

Lu’s laboratory studies the structure and the function of the primate visual cortex. With multiple approaches (“optical imaging”, “single-unit recording”, “animal behavior” “histology” and “psychophysics”), the lab focuses on two questions: First, how different visual features (e.g. shape, color, motion, depth etc.) are represented in the early visual cortices (V1, V2, V4). Second, how such visual representations are modulated by animal behavior (e.g. attention). These studies facilitate improved understanding of human perception of the external world.

Wang’s laboratory explores the details of the neural interactions between the higher and lower visual areas, especially the functional role of top down and feedback from the high stages of hierarchical visual cortices for visual form and motion processing. Their intermediate experimental goals are to reveal the neural circuitry and functional organization of visual illusion and second order motion processing across different neuronal populations within the complicated integrated circuits among LGN, primary and extrastrate visual cortices including MT and V4 in primates, through in vivo custom built Intrinsic Optical Imaging and simultaneously multielectrode array recordings. Both anesthetized and awake animal preparations are carried out in Wang’s laboratory.