The functional roles of feedback projections in the visual system

Tian-De SHOU

Vision Research Laboratory, Center for Brain Science Research and School of Life Sciences, Fudan University, Shanghai 200433, China

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Abstract: Neurons in the nervous system make connections with ascending feedforward projections and descending feedback projections, as well as projections from neural structures at the identical hierarchical level. These neurons form extremely complicated neural networks and pathways. Compared with the role of the feedforward projection, much less is known concerning the functional roles of the feedback projection. Visual cortex is a good model for studying functional roles of cortical feedback projections which involve many high functions, such as attention, searching and cognition. The present review mainly focused on the functional roles of feedback projections in the visual system.

Keywords: feedback projection; feedforward projection; visual system; visual attention; oblique effect

1 Parallel and hierarchical visual pathways in the brain

Visual information from the outside world is first processed in the retina and then transferred to the dorsal lateral geniculate nucleus (LGN) in the thalamus of monkeys and cats. The LGN neurons are organized into different layers, each of which receives input only from one of the 2 eyes. In the monkey, there are 6 layers of neurons in the LGN: layers 1 and 2, which are called magno-cellular layers composed of large cells, and layers 3-6 which are called parvo-cellular layers composed of small cells. Functionally, parvo-cells are more sensitive to fine gratings of high contrast and color, while magno-cells are more sensitive to motion (velocity and direction) and rough gratings of low contrast, but not to color^[1-4]. Furthermore, in monkeys, there exist a small amount of cells called kino-cells in regions between the LGN layers.

These kino-cells are related to color vision, and they project to blobs in layers 2 and 3 of V1^[5,6].

One of the most important progresses in cerebral cortex study in the last century is the discovery of 2 parallel pathways of visual information processing, i.e., the dorsal magno-stream and the ventral parvo-stream in the monkey's visual cortex. These pathways involve more than 30 cortical areas and process visual information of motion/position and shape/color, respectively^[3,7-10]. Along each hierarchical stream, the sizes of receptive fields of cortical neurons gradually increase^[1-4,8,10]. Importantly, neurons in a given visual cortex receive not only feedforward input from the LGN and lower cortical area projections, but also feedback input from higher areas of visual cortex, as well as horizontal input from neurons of the local circuitry. Over the past half-century, much has been known about the roles of feedforward projection and local circuitry in the visual cortex. However, the feedback projections, which may be associated with many important functions such as attention, target search and other higher functions of the brain, are poorly understood and still need more investigations.

Corresponding author: Tian-De SHOU

Tel: +86-21-65642355

E-mail: tdshou@fudan.edu.cn

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In the visual system of monkeys, there are 3 (parvo-, magno- and kino-) pathways in parallel from the retina to the primary visual cortex V1 via the LGN, and then to other extrastriate cortices. In later stages, two streams of visual information processing pathway become significant due to the 2 gates that they respectively pass: area V4 and area MT (V5). Area V4 serves to be a gate of the ventral form/color stream, and area MT is the gate of the dorsal motion stream. Similarly, in the cat visual cortex, form and motion informations are processed by 2 streams gated by areas 21a and PMLS/PLLS, which are to a certain extent, equivalent to V4 and MT in the monkey, respectively^[11]. In both species, almost all areas of the visual cortex have reciprocal connections, with few exceptions in the cat^[12], and both the feedforward and the feedback projections between cortical areas are mostly sent by pyramidal cells via glutamatergic excitatory synapses to the target cells^[13,14]. However, the monosynaptic inhibitory synaptic potential between cortical areas of the same or the opposite hemisphere has not been reported^[15]. Like the cortico-cortical connections, cortico-geniculate connections are predominantly excitatory^[16,17]. Hierarchically, the “retina-LGN-V1-higher cortical areas” feedforward pathway provides the main driving force for the response properties of neurons^[3,15,18-22]. Generally, the feedback projections from higher-level areas exert modulatory effects on the lower areas^[22-24].

2 The roles of cortico-thalamic feedback projection

Layer 6 in the visual cortex is the location where cortical neurons send the corticofugal signals to the dorsal LGN of the thalamus. With synaptic distribution area and retinotopic regions much larger than those of retinal projection to the LGN, the feedback projections from cortical neurons are able to dynamically modulate the response patterns and spatio-temporal properties of the LGN neurons^[25].

The spiking trains of LGN neurons during period of visual stimulation are divided into 2 periods: burst and tonic modes. The burst firing in the LGN cells improves stimulus detectability and is thought to provide a high-security signal to focus the circuitry on the new feature, and to drive attention in the cortical activities. The tonic firing of cells in the

LGN has better linearity for accurately relaying information to visual cortex^[26]. In the experiments of simultaneous dual recording from a LGN neuron and a cortical neuron, while feedback from layer 6 neurons of the primary visual cortex could be activated by local application of GABAb receptor antagonist CGP55845, Sillito and his colleagues found that the enhancement of feedback signals would lead to a significant shift in the burst/tonic ratio for 68% of LGN cells studied (43% showed a shift from tonic to burst and 25% from burst to tonic) (Fig. 1)^[25,27]. These findings indicate that changes of the responses of layer 6 cortical cells can clearly switch the firing mode of LGN cells. Thus, the role of cortico-thalamic feedback is that it may contribute to selective attention via its influence on geniculate firing mode. With the complex input from the natural visual world, selective adjustment of the transfer property of the LGN provides a means of alerting the visual system to salient change, and simultaneously optimizes its capacity to relay accurate information about what the system has worked.

Sillito's group have shown that the corticofugal projection from layer 6 of area V1 to the LGN enhances inhibitory mechanisms underlying length tuning, and is highly responsible for the length tuning of LGN cells. This suggests that the inhibitory effects derived from the corticofugal feedback exhibit characteristics of the response properties of orientation-tuned layer 6 cells^[28]. Furthermore, they observed that the enhancement of the inhibitory surround leads to an increased sensitivity to orientation, direction, and temporal contrast, when 2 independent grating stimuli covered the center and surround regions of the receptive fields of LGN neurons, respectively. The sensitivity to difference in orientation of the LGN neurons is greatly reduced in the absence of feedback input^[29-31]. Many experiments have demonstrated that the orientation-sensitive corticofugal feedback influences not only the center-surround interactions, but also the spatial frequency tuning of neurons in the LGN of cats^[29,32]. Thus, the cortico-thalamic feedback enhances response precision in the visual system^[33].

Cortico-thalamus feedback also contributes to synchronization of geniculate neurons' activity. No synchronized response is found when 2 separate and neighboring recep-

Fig. 1 Changes in the visual response mode of LGN neurons induced by local application of GABA receptor antagonist CGP55845 into layer 6 of cortical area 17 (adopted from Sillito and Jones, 2004)^[25]. **A:** An experimental diagram showing multimicropipette at layer 6 of the cortex for drug injection and single unit recording of visual response, and single pipettes at LGN for recording. **B:** Visual response amplitude of cortical layer 6 before, during and after excitation by CGP55845 application. **C:** Two LGN neurons shifting in visual response mode induced by the enhancement of feedback signal from layer 6 of area 17. Upper panel: the neuron response shifted from the burst mode to tonic mode. Lower panel: another neuron shifted from the tonic mode to burst mode.

tive fields of neurons in cat LGN are stimulated with a pair of flashing spots. However, as soon as a light bar simultaneously drifts across the 2 receptive fields, the 2 neurons respond in synchronization strongly. The synchronized responses would cease soon after ablation of the visual cortex^[34]. This suggests that geniculate synchronization is generated via cortico-thalamic feedback mechanism, which may be involved in visual attention.

3 Retinotopic relationship of feedback projections of the visual cortex

Compared with the convergent feedforward projections, the feedback projections from high level cortical areas are distributed more diffused in the low level areas^[21,35-37]. However, early studies have shown that the retinotopic relationship is better in the feedforward than in the feedback projecting areas, although the good retinotopic expression declines gradually with hierarchical feedforward pathways in visual cortex^[21,38-40]. Therefore, feedback projections can

be used to mix information from distant regions of the visual field. Stimulating areas 18 and 19 initiate responses of neurons in layers 2 and 3 of area 17 in a precise retinotopic way^[41,56]. The most significant feedback effect can be found when the receptive fields of 2 neurons located at a higher area and a lower area, respectively, are overlapped in the visual field^[42,43]. In the cat, the functional morphological distribution of the cortico-geniculate synaptic buttons exhibits a strong tendency that cortical cells in the contralateral eye dominant column mostly project to layer A of the LGN that solely receives the inputs from the contralateral eye, while cells in the ipsicontralateral eye dominant column mostly project to layer A1 that receives only input from the ipsilateral eye^[44,57].

4 Excitatory influence of feedback projections in the visual cortex

To study the roles of cortical feedback projections, the functional changes of neurons in the lower cortical areas are

revealed by electrical or optical imaging techniques, when the higher cortical areas are affected by electrical stimulating, physical cooling, chemical activating or even lesioning. Stimulating the areas 18 and 19 of cat can induce the response increase of cortical neurons in layers 2 and 3 of area 17^[45]. In rat, depolarization of neurons in area 17 can also be observed when the higher area is stimulated electrically^[20]. Inactivation of area pLS can decrease visual responses of neurons in area 18 significantly^[46]. Moreover, visual responses of neurons in areas 17 and 18 are declined by inactivation of area 21a^[42,47]. In monkey, inactivation of area MT causes significant decreases in responses of neurons at areas V1, V2 and V3^[48,49]. These reports support the general view that cortical feedback projections exert an excitatory effect on neurons in the lower cortical areas. However, at the single cell level, inactivation of a cat's area 18 neuron causes not only response reduction, but sometimes also increase of those area 17 neurons, depending upon their receptive field locations, within the center or surround the receptive field of the given area 18 neuron^[50]. Thus, either increase or decrease in responses of layers 2 and 3 in area 17 was recorded when layers 2 and 3 in area 18 were locally inactivated^[43]. Alonso *et al.* have found that 40% of the neurons in layer 5 of area 17 show increased responses to stimuli of low velocity when the corresponding region in layer 5 of area 18 is inactivated, suggesting that the preference to low velocities of neurons in layer 5 of area 17 is partially due to an inhibitory effect of area 18 that responds to high velocities^[51,52]. The effects are strong and can often be observed when the inactivated area 18 neurons have overlapped receptive fields and the same response properties as those of recorded neurons in area 17. These are understandable because within a cortical area, both the pyramidal cells and the GABAergic inhibitory interneurons interact with each other at local circuits^[53].

5 Feedback projections modulate tuning properties of neurons in the visual cortex

The feedback input from higher levels of visual cortex finely modulates receptive field properties of neurons, in addition to facilitating responsiveness. Inactivation of layer 5 neurons in area 18 can cause significant alteration of half-

widths of the orientation tuning curves in approximately 46% of the cells in layer 5 of area 17 in cats^[52]. In contrast, the half-widths of layer 2 and 3 neurons in area 17 are not affected by inactivation of layers 2 and 3 neurons in area 18^[42,43]. These facts imply that feedback projections even from the same area may have different effects on the lower areas.

In the form information processing pathway, Wang *et al.* find that the shapes of orientation tuning curves of approximately half of the neurons in area 17 are sharply changed by inactivation of area 21a, although the neurons' preferred orientation is not changed. Interestingly, little change is found in their direction selective and length selective curves in their single unit recording study^[42]. On the other hand, Shou's group find that the feedback from area 21a significantly facilitates and improves neuronal activities of areas 17 and 18 in a spatial frequency-dependent manner^[47]. In the motion information processing pathway, an optical imaging study has shown that inactivation of layer 5 in cat's area pLS influences direction selectivity of area 18 neurons and their direction map pattern, but not orientation pattern^[46]. By using the same technique, Shou and his colleagues find that besides increasing the responsiveness of neurons in area 17, the feedback input from area PMLS can also modulate direction maps, but not orientation maps of neurons in area 17 of cats^[54]. The question that whether the feedback signals from higher levels in the form or the motion information pathway solely modulate the corresponding properties of neurons in the lower levels still needs further investigation.

6 Visual attention and feedback projections

Attention to a visual stimulus increases the gain of neuron responses in most visual cortical areas^[55,56]. Interestingly, these effects are strongest for low contrast stimuli and weak for high contrast stimuli^[56,59]. Similarly, the feedback connections from MT to areas V1, V2 and V3 potentiate the strength of the inhibitory effect of the receptive field surround on the response elicited by stimulating the receptive field center. This effect is found to be specific to stimuli of low salience, such as a low contrast moving bar on a noisy background, but not to the stimuli of high salience^[49,57]. This suggests a possibility that the mechanisms revealed by inactivating feed-

back projections may be involved in an attention-directed modulation effect on the sensitivity of lower level areas. The first direct evidence supporting this idea is from Myiashita and his colleagues. Using a slit brain preparation, they distinguished activation by feedback projections of the frontal cortex, which transfers information about categorization signals of visual images, from that by feedforward projections in area IT neurons in monkey^[58].

The front eye field (FEF) in the frontal cortex is the primary cortical area that generates saccades and for controlling gaze shift through direct and indirect pathways to the superior colliculus, which plays a crucial role in the control of eye gaze shift^[59,60]. Electrical stimulation of the FEF causes saccades to a particular position in the contralateral visual field. Damage of the FEF is usually temporary, but combined with the damage to the superior colliculus, it will produce a permanent deficit in generating voluntary gaze shift^[61]. On the other hand, the lateral intraparietal area (LIP) of the parietal cortex plays a major role in the process of visual selection of gaze shift. Inactivation of neurons in area LIP dramatically reduces the frequency of movement towards the affected portions of the visual field, although it does not cause large deficits in the timing and accuracy of gaze shift, suggesting a visual neglect of stimuli in the affected region^[62]. Clinically, damage of the parietal cortex in human also produces a neglect syndrome with similar deficits in attention.

7 Visual psychology and feedback projections

The oblique effect is a well-known psychological and behavioral phenomenon in humans and mammals that have a better visual ability in perceiving and discriminating horizontal and vertical contours than in oblique ones in the visual field^[63-68]. This effect has been usually referred to as an event generated in the primary visual cortex, since more neurons there preferentially respond to the horizontal and vertical meridians than to the oblique ones^[63-65,69-71]. Many similar reports have revealed less than 7% overexpression of cardinal contours than oblique contours in area 17 of ferrets, cats and humans^[72-77]. However, the weak neuronal oblique effect seen in area 17 alone may not be sufficient to cause the psychological and behavioral effects. Recently, by using

optical imaging, Shou and his colleagues have revealed that area 21a of the cat, which corresponds to V4 or V3v in the monkey, exhibits a much stronger oblique effect $[(24.0 \pm 3.9)\%$ overrepresentation of horizontal and vertical preference] than the primary visual cortex does $[(5.2 \pm 0.72)\%$ overrepresentation]^[78], which can help explain the psychological or behavioral consequences. The fact that cat's area 21a exhibits a much stronger oblique effect can be reasonable for explaining the psychological or behavioral consequences. Area 21a in the cat receives inputs mainly from area 17 and to a less extent from areas 18 and 19 separately^[40,79]. Why and how the neurons in area 21a generate such a strong oblique effect remain to be elucidated.

Furthermore, Shou's group find that injection of glutamate or GABA into area 21a in cats significantly influences the visual response amplitude of neurons in area 17. Reversal activation of area 21a by glutamate significantly facilitates responses of neurons in area 17, while inactivation by GABA produces the opposite effect. Strikingly, the neuronal oblique effect in area 17 is largely enhanced by activation of neurons in area 21a, but decreased by inactivation of area 21a via shifting the preferred orientation of some neurons in area 17 (Fig. 2)^[80,81]. These findings support that the co-activation of areas 21a and 17 may greatly strengthen the neuronal basis of the psychological or behavioral oblique effect, indicating that feedback projection from higher level of cortical areas influence neurons' activities in the lower level that are even related to neuronal basis of psychological or behavioral phenomena.

Feedback signals either from magno-pathway or from parvo-pathway may re-enter the lower areas and co-activate the neurons there, even initiating synchronizing discharges of neurons in many cortical areas. The primary visual cortex has the finest retinotopic representation of the visual field and receives a large number of projections from higher areas, where the motion and form/color signals are separately processed in the visual system. Thus, it is possible to provide a platform for spatio-temporal integration of visual information in the primary visual cortex via neuronal co-activation or synchronization that is presumably necessary for perceiving an object, although this hypothesis needs further studies.

Fig. 2 Enhancement of neural oblique effect in visual cortical area 17 induced by feedback of cortical area 21a in the cat (adopted from Liang *et al.*, 2007^[80]). **A-D**: Functional orientation columns of area 17 revealed by optical imaging of intrinsic signals before (**A**), during glutamate (**B**) and GABA (**C**) application, and in recovery (**D**), respectively. Scale bar=1 mm. **E-H**: Preferred orientation distribution histograms of all pixels in **A-D**, respectively. Note that more pixels in area 17 preferred to horizontal and vertical orientations (0°, 180° and 90°) than the oblique (45° and 135°) in control (**E**) and recovery (**H**), showing the oblique effect, which was significantly enhanced by glutamate excitation (**F**) and declined by GABA inhibition (**G**) in area 17. **I** and **J**: Net change in preferred orientation distribution histograms caused by application of glutamate (**I**) and GABA (**J**) in area 21a. Some pixels that preferred to the oblique were shifted to the horizontal and vertical by glutamate application (**I**), and some pixels that preferred to horizontal and vertical were shifted to the oblique by GABA application (**J**). Positive number denotes newly increased pixels, and negative number is for pixels that disappear. **K**: Surface vessel map of the visual cortex. White dot line denotes the border between areas 17 and 18, and black line indicates the region of interest in the study. A, anterior; L, lateral. Scale bar=1 mm.

More interestingly, multisensory convergence of inputs from auditory and polysensory cortices and multimodal integration have been found in the primary visual cortex^[82,83]. These findings may be related to the recent psychophysical report of sound-induced illusory flash effect, in which a human subject perceives a single flash as two when the single flash is accompanied by 2 auditory beeps^[84]. A similar visual illusion can also be produced by touch stimuli^[85].

Singer points out that neuronal combination related to

the synchronized discharges of neurons in the brain conforms to the Gestalt criteria^[86]. According to the principles of Gestalt psychology, pattern features of an object tend to be organized together to form a subjective perception that human perceives by using those features of neighboring, similarity, continuation, and common fate^[87]. Engel and his colleagues provide evidence supporting that the interaction between neurons at different levels of cortical areas meets Gestalt criteria of continuity and common fate^[88]. In their

experiments, two cortical cells were simultaneously recorded respectively from areas PMLS and 17 whose receptive fields were spatially separated and aligned, with an identical preferred orientation. When a long moving bar was drifting in the preferred direction across the 2 receptive fields, strong synchronized responses were elicited. Two short bars moving simultaneously in the preferred direction evoked relatively weak, but significant synchronized responses. Interestingly, the synchronized response disappeared completely when the bars were moving in opposite directions.

8 Conclusion

Recent research on the functional roles of feedback projections has been developed rapidly in the visual system. More than 30 reciprocally connected cortical areas in the visual system provide an ideal model for elucidating the important roles of feedback projections, especially when much has been known about the roles of feedforward projections in the visual pathway after 3 decades of research. Feedback signals from multiple cortical areas interact with feedforward signals and horizontal projections in a local circuitry, and precisely shape response properties of neurons in a given cortical area along the hierarchical visual pathway. The relative contribution of these signals remains unclear at the synaptic level. In addition, the roles of feedback signals in modulating gain control of neurons in the visual system need to be investigated in detail.

On the other hand, whether the feedback signals from margo- and parvo-pathways have different preferences and how they interact with each other to modulate the lower cortical areas remain still elusive. Furthermore, whether the functions of feedback signals directly from distal areas differ from that from near areas in information processing needs to be further determined.

Feedback projections play very important roles in descending signals that are related to higher-order processing functions, such as visual attention, searching and controlling gaze. Elucidating these aspects is a difficult and long-lasting task, due to the complexity of anatomy and function of the brain. Certainly, novel research tools, especially noninvasive techniques with high resolution need to be

developed for *in vivo* psychological and behavioral studies in human and monkey. New imaging techniques, such as functional MRI, optical imaging and two-photo confocal imaging, combined with largely developed substances for labeling neurons or axons, have been showing great power in the studies.

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视觉系统中反馈投射的功能作用

寿天德

复旦大学脑科学研究中心, 生命科学学院, 视觉研究实验室, 上海 200433

摘要: 在神经系统中, 神经元既接受下级结构神经元的投射输入, 又接受上级和同级神经结构神经元的输入, 形成了极其复杂的神经网络和通路。目前, 对于神经系统向前的投射通路的功能作用已有相当深入的了解, 但对脑内反馈的投射通路的功能知之甚少。视觉皮层是研究反馈投射通路的较好模型, 其下行反馈的投射涉及注意、搜索和认知等高级功能。本文主要对有关视觉系统中反馈投射的功能作用做一综述。

关键词: 反馈投射; 前馈投射; 视觉系统; 视觉注意; 倾斜效应