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The Role of Cortical Feedback Circuitry on Functional Maps of V2 in Primates: Effects on Orientation Tuning and Direction Selectivity

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1. Introduction

Extensive work in anatomy, neurophysiology and brain imaging has approached the challenge of understanding visual processing in human and non-human primate brains. This approach has been very successful in generating a roadmap of the primate brain: identifying a large number of different cortical areas associated with different functions and cognitive skills. Recent developments in multi-unit recordings combined with inactivation paradigms have provided powerful methods for the study of cortical circuits and novel insights into cortical dynamics.

In monkeys, visual cortical information has been considered to be the result of ascending projections and local processing through a series of hierarchical cortical visual areas [1]. At each station, horizontal connections reinforce the interplay between groups of neurons with similar properties [2]. Both feed-forward and intrinsic circuits contribute to the extraction of complex attributes of the visual scene at each successive processing stage. The feed-forward connections are excitatory and make non-specific synaptic contacts with different compartments of post-synaptic cells [3]. These connections are visuotopically organized, converging in clusters, and they are paramount for the receptive field properties of post-synaptic neurons [4,5]. Indirect feed-forward projections to area MT (via V2 and V3) contribute to the response to fast moving stimuli and for binocular disparity tuning [6,7]. The role of caudally directed (feedback) projections is less clear. The exuberance of the feedback connections between different cortical areas, the speed of electric signal propagation along these connections, and

the latency of visual response all suggest that feedback connections could affect the functional performance of neurons beyond a “modulatory” role [8-11]. Some studies have demonstrated the influence of feedback circuits on the receptive field properties of target neurons [8,12-14,17], whereas others have not found any influence [18,19].

In primates, the second visual area (V2) is the largest extrastriate area. The visuotopic organization of V2 in *Cebus apella* was described using extracellular recordings. V2 area is located in the opercular region of the occipital pole. V2 forms a continuous belt of variable width around the primary visual area (V1) except at the most anterior portion of the calcarine sulcus. It contains a complete visuotopic representation of the contralateral visual hemifield [20]. V1 and V2 are part of both dorsal and ventral pathways of visual information processing.

The prestriate visual area MT is an area of the dorsal stream of visual information processing. It is strongly involved in motion and depth perception and it contains an abundance of motion-coding cells. The medial temporal area is a small area that exists in the temporal lobe of all primates, including human [21]. In *Cebus*, MT is an oval area located mainly in the posterior bank of the superior temporal sulcus (STS). MT contains a continuous representation of the coarse and contralateral segment binocular visual field. As in V1 and V2, the superior field is located ventrally and the lower field is located dorsally. the representation of the fovea is located at the lateral posterior bank of the superior temporal sulcus while the periphery is located medially. The average area of MT is 70 mm² [22].

The prestriate visual area V4 is an area of the ventral stream of visual information processing. It is strongly involved in shape and color perception and it contains an abundance of color-coding cells [23,24]. It is defined as a strip of cortex from 10 to 12 mm in width anterior to V3 that extends dorsally from the anterior margin of the lunate sulcus. V4 contains a topographically organized representation central of 35° 40° of the visual field. The representation of the central portion of the visual field is greatly expanded compared to the periphery. The receptive field size increases with increasing eccentricity, while the cortical magnification factor decreases [25,26].

The pulvinar nucleus is a diencephalic structure located in the posterior region of the thalamus whose evolutionary development occurred in parallel with the expansion and differentiation of the temporo-parieto-occipital cortex. Its involvement with visual function has been demonstrated by the presence of a retinotopic organization, and by its connections with the different cortical visual areas.

It has been suggested that some receptive field properties of cortical neurons, such as orientation selectivity and direction selectivity, may be attributed to the inhibitory influence of intrinsic circuits on incoming information [30,31]. The inactivation of intrinsic inhibitory processes impairs both orientation and direction selectivity [32,33]. In primary (V1) and secondary (V2) visual areas of monkeys and cats, the orientation and direction selectivity depend on the inhibitory influence of basket cells projecting to orientation- and direction-selective functional modules [30,31,34-36]. However, evidence indicates that excitatory intrinsic inputs also contribute to V1 orientation selectivity and direction selectivity [30,36]. We have investigated whether feedback projections from area MT, V4 or pulvinar directly interfere with the orientation and direction selectivity of V2 neurons. We studied the receptive

field properties of V2 neurons before and after the inactivation of a large topographically corresponding portion of area MT, V4 or pulvinar in the capuchin monkey (*Cebus apella*). Several aspects of the visual system of this New World monkey, including photoreceptor distribution [37], ganglion cell topography [38], thalamic organization [39-41], morphology and physiology of the M and P ganglion cells [42-44], intrinsic circuitry of V1 [45-47] and the topographical characteristics of areas V1, V2, MT, and V4 [20,22,26,48,49] have been studied for almost two decades, making this monkey a suitable experimental model.

In this chapter we will describe the role of feedback circuits to V2 from two cortical visual areas and one subcortical nucleus and compare these inactivation results with the direct inactivation of V2. We will also address the cortical dynamics using an illusory motion paradigm.

We have also investigated feedback influence on early visual cortices related to perception of illusory motion stimulus. Mapping of cortical visual areas suggests that cortical feedback from higher visual areas induces a selective increase of activity in the early visual stage along the cortical representation of illusory stimuli [27-29].

2. Inactivation paradigm

The stimulus consisted of a thin white bar (18 x 0.5 degrees) that appeared in four random orientations (0°, 45°, 90°, or 135°), crossed the screen in a direction perpendicular to its orientation at a velocity of 10 degrees/sec, and passed through the receptive fields of all the recorded neurons. We continuously tested the direction of motion selectivity before and after GABA injection. We did not segregate orientation selectivity from axis-of-movement selectivity.

To locate the topographically corresponding portions of areas MT, V4, pulvinar and V2, we penetrated the cortex with 1M Ω -impedance tungsten microelectrodes, using stereotaxic coordinates and sulcal landmarks [20,22,26,39,50].

Areas MT, V4 and the pulvinar were individually inactivated by pressure injections of GABA 0.25 M until virtually all recorded activity at the injection site in these areas were silenced. Data collection resumed immediately before and after the injection, and several blocks of recording protocols were acquired until recovery of MT, V4 and pulvinar cellular activity. The recording sessions typically continued for 24–30 h.

After the corresponding topographical site was localized in area V2, a single microelectrode was replaced by a two-electrode recording system, with the electrodes placed 800 μ m apart, to record V2 neuron activity. Single-unit activity from area V2 was recorded using tungsten microelectrodes. The activity was amplified and filtered, and single spikes were sampled by a waveform discriminator system (SPS-8701, Signal Processing System, Malvern, VIC, AU). Extracellular single-unit spike events were stored using the CORTEX software (Laboratory of Neuropsychology, NIMH/NIH, Bethesda, MD, USA) for offline analysis (MATLAB toolbox, Mathworks Inc., Natick, USA). The receptive fields were initially localized and mapped using a hand-plot mapping procedure. To determine the statistical significance of the effects on V2

neuron direction selectivity before and after GABA injection into area MT, V4 or pulvinar, the cell activity under each condition was analyzed using a two-way ANOVA. We also performed a statistical evaluation of the recovery after GABA injection by evaluating the cell activity in the control condition, before GABA injection and after the GABA-induced effects had vanished, using a two-way ANOVA. Selectivity of the neurons was examined with a standard test of circular tuning in order to determine the magnitude of the GABA-induced changes in both direction and orientation selectivity across the population.

The receptive field automatic mapping procedure was based on computing the latency-corrected neuronal activity in response to elongated bars moving in one of eight directions of motion. Initially, Peristimulus Time Histograms (PSTHs) were computed based on 10 stimulus presentations, using a bin width of 10 ms. Single-trial spike trains used to produce the PSTHs were aligned to stimulus onset. The PSTHs were then smoothed, using a normal convolution filter of 200 ms time-window, resulting in the Time Spike Density Function (TSDF). The TSDF characterizes the dynamics of neuronal firing pattern well, as it is a continuous and derivable function [51].

3. Evaluation of the early and late effects of GABA inactivation

GABA inactivation of area MT produced an early and short (10-30 min) decrease in both spontaneous activity and responsiveness followed by a transitory change in the V2 neuronal direction selectivity. The difference in the time course of these effects resulted in an intermediate improvement (20-40 min) of the signal-to-noise ratio of the stimulus driven activity. After a variable time period, this improvement disappeared. GABA inactivation in area MT produced either an inhibitory effect, a significant change of direction tuning or a complete loss of directional selectivity in most (72%) of the V2 neurons. During the 15 min following GABA inactivation, a clear inhibitory trend in the response pattern was observed. Additionally, 56% of the V2 neurons exhibited a significant change in directional selectivity. For 6% of the V2 neurons, a general suppression of activity was observed after GABA injection into area MT - even though no change in direction selectivity was observed. In 3 cells, GABA inactivation had no discernable effect on the direction or orientation selectivity.

GABA inactivation of V4 induced a statistically significant effect in the majority (72%) of V2 neurons studied. Statistical analysis of the first five minutes of the response of the V2 neurons after GABA inactivation of V4 showed a change in direction selectivity in 46% of these neurons; of these, 23% showed a change from pandirectionality to directional selectivity. The remaining 23% showed a change from directional selectivity to pandirectionality. In seven neurons, there was no change of direction selectivity, although there was a statistically significant effect on the strength of the response. There was no significant effect in the remaining three cells.

In the pulvinar nucleus, GABA injections resulted in a significant decrease of cellular activity, and 5 minutes after the injection the activity was, in average, 40% that of the initial level. We studied 33 cells in V2 before and after GABA injections in the pulvinar. All cells had their receptive fields within 10 degrees of the representation of the central visual field. Most cells

studied in V2 (67%) during pulvinar inactivation showed changes in the response to visual stimuli and/or in the spontaneous activity. We observed a change in the direction and/or orientation selectivity in 91% of the cells during pulvinar inactivation. Most of these cells (55%) showed changes in both directional index (DI) and orientation index (OI), while 15% showed changes only in DI and 21% only in OI.

Figure 1 shows an example of a V2 cell after inactivation of visual area V4. The cell was pan-directional with good response to virtually all directions. One minute after inactivation the spontaneous activity and the driven activity were drastically reduced.

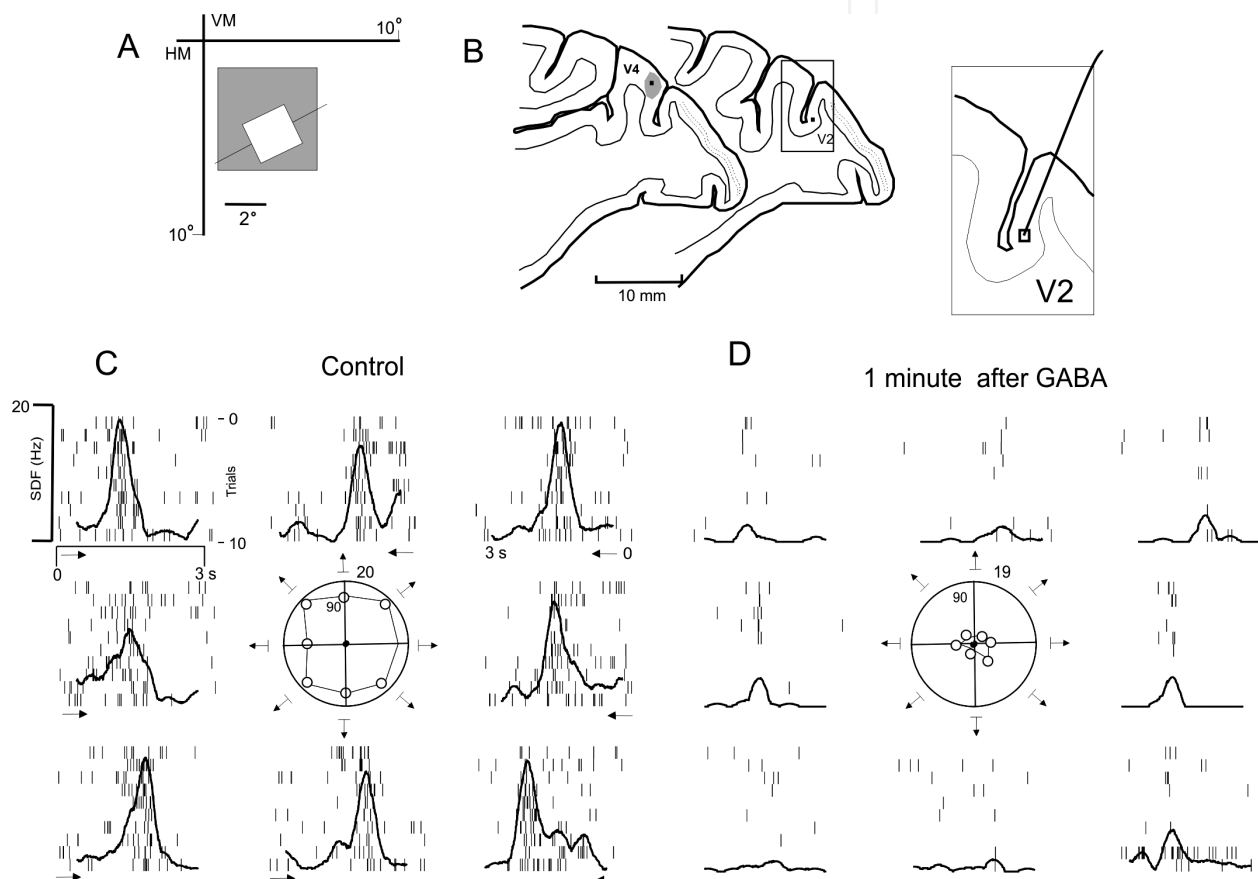


Figure 1. The effect of GABA inactivation of a portion of V4 in the visual response of a V2 neuron. A: The visual field location of the receptive fields of the neurons of V4 and V2 that were studied in this experiment. The large and small rectangles correspond to the V4 and V2 receptive fields, respectively. The approximate positions of the recordings sites are indicated by small rectangles; B: Parasagittal sections of the Cebus brain, showing the locations of V4 and V2. The approximate positions of the recordings sites are indicated by small rectangles; C: A pandirectional selective V2 neuron ($p < 0.05$) recorded at the V2 site. The polargrams depicted at left illustrate the V2 neuron mean firing rate elicited by bars moving in eight directions orthogonal to its preferred orientation before (control condition, polargram at the top) and one minute after GABA (D) ($p < 0.05$). The polargrams represent the response magnitude relative to each direction of motion. These SDFs represent the cellular activity in the space domain. The vertical ticks represent spikes, and each line of spikes corresponds to the total span of visual stimulation during each trial.

GABA inactivation of area MT, V4 and pulvinar produced early (up to 20 min) and late (from 20 to 160 min after GABA injection) effects on V2 neurons. These effects consisted of an early

general decrease in neuronal excitability, which corresponded to a depression in the spontaneous and driven activities, and late effects, which generally reflected changes in the orientation and/or direction selectivity of the V2 neurons. In general, a loss of direction or orientation selectivity was observed during the 25 min after GABA inactivation. As an intermediate effect, an improvement in the amount of driven activity inside the classical receptive field relative to that outside the classical receptive field was observed 15 to 25 min after GABA inactivation. This effect was transient and was followed by a longer-lasting decrease in neuronal excitability.

The greater the amount of GABA injected the longer the inactivation duration period and the time needed for the neurons to recover [52]. This last result is in agreement with our observations for MT, V4 and pulvinar. Neurons required 40 min to recover to baseline after a 0.9- μ L injection of GABA 0.1M [19]. This recovery period coincided with the time required by V2 neurons to regain baseline activity after a 0.8-1.0 μ L GABA (0.25 mol/L) injection into area MT and V4. Considering the extent of area MT and V4 [22,26], we extended preceding predictions [52] regarding the relationship of the injected volume and occupied extracellular volume. We predicted that injection volumes between 0.8 and 10 μ L would inactivate between 2.3 and 33.3% of area MT and 0.7–3.22% of area V4.

4. Population circular tuning when areas MT, V4, pulvinar or intrinsic V2 were inactivated

When area MT was inactivated, both increase (62%) and decrease (38%) of direction circular tuning was observed in the V2 neurons. In addition, some cells significantly changed their orientation selectivity. However, a significant change in the mean orientation circular tuning of the V2 neurons was not observed after GABA inactivation in area MT. When a change greater than 0.2 was used as criterion, only 38% of the neurons altered their direction or orientation circular tuning.

When area V4 was inactivated both increase (72.2%) and decrease (27.7%) of direction circular tuning were observed in the V2 neurons. In addition, we found that 72.2% of these cells decreased while 27.7% increased their orientation selectivity, thus presenting an opposite effect for direction and orientation circular tuning. When changes greater than 0.2 were used as criterion, only 25% of the neurons changed their direction or orientation circular tuning. There was no statistical segregation of GABA effect for directional or orientation index in this sample (χ^2 test $p=0.1$). Although the number of cells that increased OI is similar to the number that decreased DI, there was no bias toward increase or decrease in the sample (χ^2 test $p=0.1$).

GABA and lidocaine-induced inactivation of the area V2 changed direction and orientation tuning in 37.4% of V2 cells. When changes greater than 0.2 were used as criterion, 29.2% of the neurons changed their direction or orientation circular tuning. There was no trend in the sample of cells toward increase or decrease in selectivity. Sixteen percent of V2 neurons increased while 20.8% decreased their direction selectivity after injections of GABA or lidocaine. In addition, some cells decreased (2/24) while others increased (3/24) their orientation selectivity. The effect of intrinsic inactivation of V2, unlike the effect produced by

inactivation of MT and V4 areas, decreased the indices of orientation or direction circular tuning.

GABA inactivation of the pulvinar induced both excitatory and inhibitory change in the V2 neuronal activity and produced a decrease in orientation selectivity. The effects of inactivation of the visual area MT are quantitatively different from those of inactivation of area V4. While inactivation of MT, on average, decreases DI, the inactivation of V4 increases DI [51,53]. In addition, inactivation of MT, on average, increases OI, while inactivation of V4 or the pulvinar decreases OI [51,53,54]. Thus, the feedback connections of MT are different from those of V4, but both promote inhibitory modulations in V2, while the projection of pulvinar produces both excitatory and inhibitory modulations on the target cells in V2.

4.1. V2 neurons that became selective with GABA

There have been some neurons that became direction and orientation selective with GABA injection in areas MT, V4 or pulvinar. There was a pan-directional V2 neuron that had high spontaneous activity before GABA injection in MT. It became directionally selective 1 min after a 10- μ L injection of 0.25 M GABA into area MT. Under GABA-induced inactivation, the unit acquired a bi-directional response pattern ($p < 0.01$), and an inhibitory flank could be observed when a bar moving at 180° was presented.

4.2. V2 neurons that lost direction or orientation selectivity with GABA

The loss of selectivity was the most frequently detected receptive field alteration in the V2 neurons after GABA inactivation in areas MT, V4 or pulvinar. Two V2 neurons lost their direction selectivity after GABA-induced inactivation in area MT ($p < 0.01$). These cells exhibited directional selectivity during the control condition and became pan-directional 1 min after GABA injection ($p = 0.9$ and $p = 0.7$ respectively). After 14-15 min, the cells recovered their directional selectivity ($p < 0.01$).

4.3. Hypothetical circuit

We propose the following hypothetical model to explain our observations (Figure 2). If the feed-forward projections of the cortical areas are considered to be excitatory [55], the feedback circuits would probably modify the properties of the receptive field through the excitatory and inhibitory neurons present in the intrinsic circuits. The most common effect observed during the 10 min after GABA injection into area MT, V4 or pulvinar was a decrease in the spontaneous and the driven activity in the V2 neurons. We propose that pyramidal neurons within direction selective modules in area MT, V4 and pulvinar containing GABA_A receptors [30] are inhibited by the GABA injection. A decrease in neurotransmitter release to the superficial and deep layers of area MT, V4 and pulvinar would then ensue. As a result, the excitatory caudally directed synapses become inhibited, causing a decrease in the spontaneous and driven activity of the V2 neurons. The injections affect each direction-selective column, resulting in a decrease in the spontaneous and driven activity of the neurons for all directions.

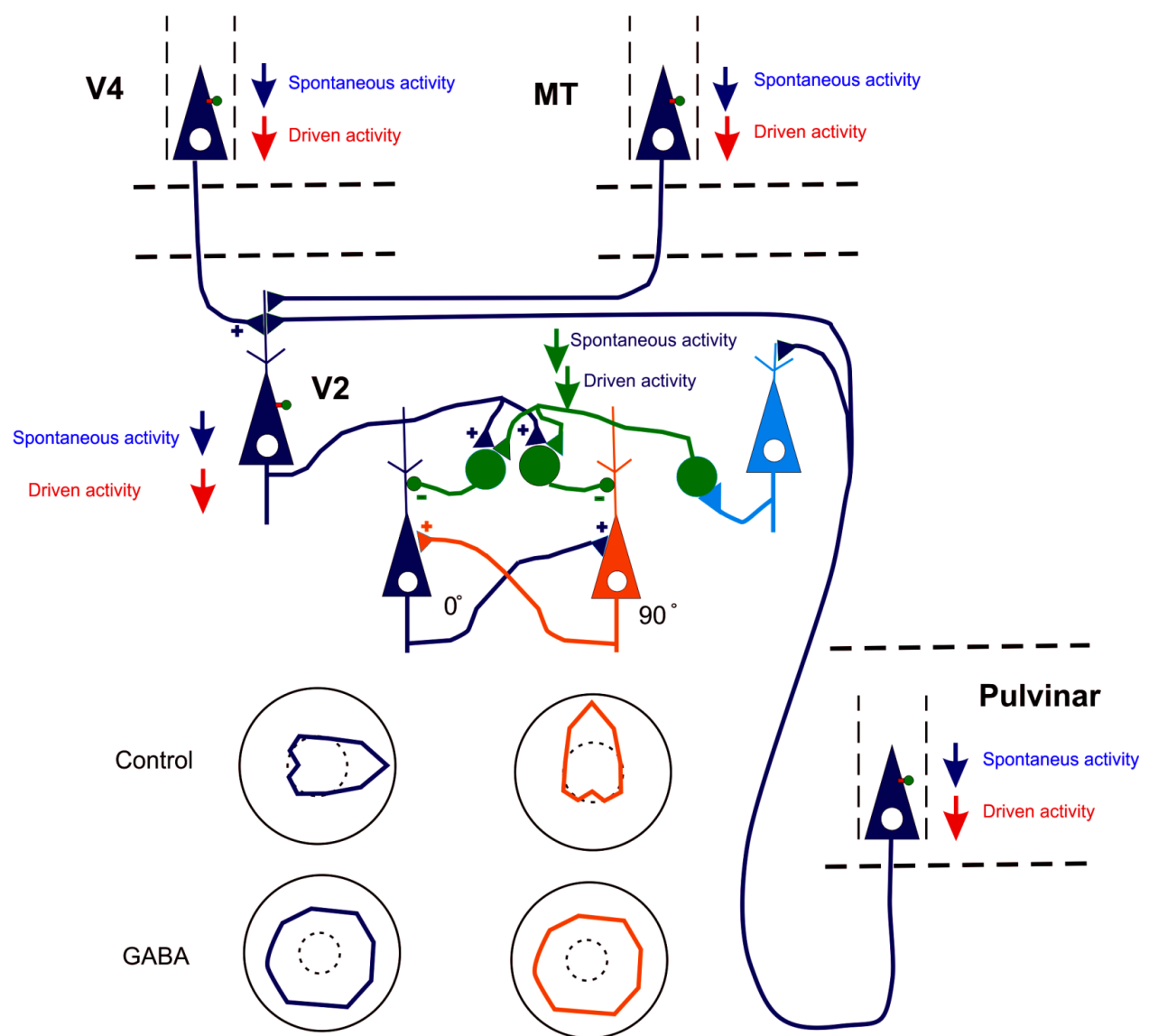


Figure 2. Hypothetical circuit of the GABA effect. Schematic diagram of cortical cells (blue triangles) and the pulvinar showing a circuit that generates loss of direction selectivity in V2 neurons after injection into MT, V4 or pulvinar. In these circuit direction selective pyramidal neurons in target areas, containing GABA_A receptors capture the GABA injected, resulting in decrease of the firing rate activity of these neurons. The arborization neurons project back to the superficial and deep layers of V2. Neurons in MT, V4 or pulvinar decreased neurotransmitter release, and the frequency of firing rate in excitatory synapses result in a decrease of the spontaneous activity of neurons in V2.

A loss of selectivity was the most frequent receptive field alteration in the V2 neurons after GABA inactivation of the topographically corresponding portions of area MT, V4 or pulvinar. We hypothesize the existence of a circuit involving projections from deep and superficial layers of area MT (probably pyramidal neurons) containing GABA_A receptors. The excitability of these neurons would decrease after the activation of GABA receptors. This decrease in excitability would influence the pyramidal neurons in V2 that receive these projections and would also influence intrinsic inhibitory neurons. Intrinsic inhibitory interneurons decrease the influence of neuronal afferents to neighboring columns and cause a loss of direction

selectivity for the majority of neurons. The directionality of the remaining 10% of the neurons in our population became selective after the GABA injection. Therefore, we propose that the inactivation of area MT, V4 or pulvinar have partial and asymmetrical effects, causing some direction columns to remain active whereas others are suppressed. This asymmetrical inhibition would generate direction selectivity in neurons that were pan-directional before the injection.

4.4. Other interpretations

These results of GABA inactivation challenge the notion that serial hierarchical processing and lateral projections are the only responsible for the construction of receptive-field properties in early cortical visual areas. We propose that larger recurrent networks may also contribute to the construction of response properties of single cells and those properties are established after several cycles of feed-forward and feedback information.

The paradigm used in this study does not allow the distinction between an intrinsic change in direction/orientation selectivity and a change in the shape of the receptive fields or their surround. For instance, if GABA or lidocaine caused the RFs to become smaller, this would presumably show up as a decrease in responsiveness. Likewise if they became asymmetrical, this would be evident as a change in orientation selectivity. A superficial analysis of changes in receptive field structure of V2 neurons with GABA injections in MT did not revealed however any systematic effect. Future experiments with a selected sample of cells are necessary to further exam the spatial structure of the intersection maps before and after GABA or lidocaine inactivation.

5. Contribution of feedback projections to illusory motion processing in V2

Neurons in the secondary visual cortex (V2) are capable of responding to illusory contours [56]. A classic illusion to which V2 neurons are responsive is the Kanizsa triangle. In this visual phenomenon we can see an illusory well defined triangle, apparently having higher luminance than the background. Single neurons in V2 respond to the illusory contour of the Kanizsa triangle in a similar manner as to the presentation of a real triangle.

Visual illusions have been defined as misperceptions of the real world. This interpretation is a contradiction to the traditional feed-forward concept of visual information processing, inasmuch as the visual signal is not physically presented. Therefore, how do V2 neurons respond to something that does not exist? How does a non stimulated area of the retina generate action potentials in cortical neurons? To answer these questions we need to look into high hierarchical areas in the brain. As we go from early to advanced stages of the visual processing, the size and the structure of the visual receptive fields go from small and simple [1,48] to large and complex [22,26]. Based on these data, one should think that early visual areas have limited capacity for complex visual phenomena processing, unless they receive

visual clues from visual higher-order brain areas, where neurons could integrate information from the global visual scene and send it back to neurons to the early visual stages.

A paradigm to test the functional influence of feedback projections to V2 neurons is to induce visual motion processing in a large area, with apparent motion (AM) stimuli. V2 has motion detector neurons, which are tuned to the direction of the movement. This means that the displacement of a stimulus in a preferred direction increases the firing rate of the neuron, while displacement in the opposite direction (null direction) decreases the firing rate. Visual motion processing implicates that neurons must integrate information from a defined area of the visual field, covering the distance of the motion trace. Neurons with large receptive fields, as those in higher visual areas, could integrate the information about large spatial locations in space, while neurons in the early stages would be spatially restricted due to their small receptive field sizes. The spatial distance of the motion trace can be manipulated in a monitor display by using the paradigm of apparent motion illusion. This illusion was formally described by Wertheimer in 1912 [57] and a classic representation is two static stimuli presented transiently and alternately at two different locations in the visual field. The brain interprets the two static stimuli as a single moving stimulus. The use of the apparent motion paradigm allows controlling spatial and temporal variables of the motion information. By keeping constant the temporal interval, different spatial intervals can be used to determine the exact range of the spatial integration carried out by neurons with small receptive fields. If the maximal spatial range is much greater than the receptive field size of these neurons, one could suggest that information from higher visual areas with large receptive fields is being added to the neuronal computation performed by the lower visual area neurons. The maximal spatial range can be determined by increasing the separation of the stimuli until suppression of the directional neuronal response. In this case, neurons could not discriminate the direction of the illusory motion, inasmuch as the static stimuli far from the receptive field could not be 'seen', or information sent by higher visual areas would not be enough to produce a response.

It is not yet understood how feedback signals influence the spatial integration of visual signals by V2 neurons. In regard to apparent motion processing, strong evidences show that the visual middle temporal area (MT) of nonhuman primate is a critical area for the perception of apparent motion [58], inasmuch as its specialized motion detector neurons and the large receptive fields can cover a large area of the visual field. Also in humans, activation of an area analogous to area MT in primates, the human complex hMT/V5, is directly associated with the AM perception [59].

We indirectly investigated the feedback contribution in V2 neuronal response by using an apparent motion paradigm. We delineated an experiment where short and long-range apparent motion stimuli were generated to adequately stimulate both V2 and MT, although only V2 activity was recorded. We determined the spacing (ΔS) for consecutive (directional) visual stimuli and we looked for the responses to the stimuli that fell in the center of the receptive field. A methodology for precisely mapping the receptive fields was required so that the spatial distribution of the stimuli could be correctly arranged when the illusion of apparent motion was induced at the cellular level. Extracellular multi-unit recordings were made in the secondary visual cortex of an anesthetized and paralyzed adult *Cebus* monkey (*Cebus apella*)

and single-units were studied by comparing the neural activity response to AM conditions versus a smooth motion condition. The neuronal activity acquired was classified as to belong to individual neurons by 'spike sorting' software. The apparent motion condition was generated by a white bar presented at 30 Hz with different spatial intervals (gaps) producing apparent speeds from 15°/s to 135°/s. The smooth motion condition was given by the same stimulus presented in a 60 Hz refresh rate monitor and moving at 15°/s. To infer that neurons were detecting motion, the neuronal response was quantified by calculating a directional selectivity index which takes into account responses for the best and null directions of the stimulus. The presence of direction selective neurons would suggest that V2 is able to process AM in that particular space and time intervals. However, we found directional V2 single-units that stopped to discriminate directions of motion with stimuli spatially separated that exceeded the receptive field size of the neuron, suggesting that these neurons would not process long-range apparent motion. Figure 3 shows a single-unit example of such a neuron.

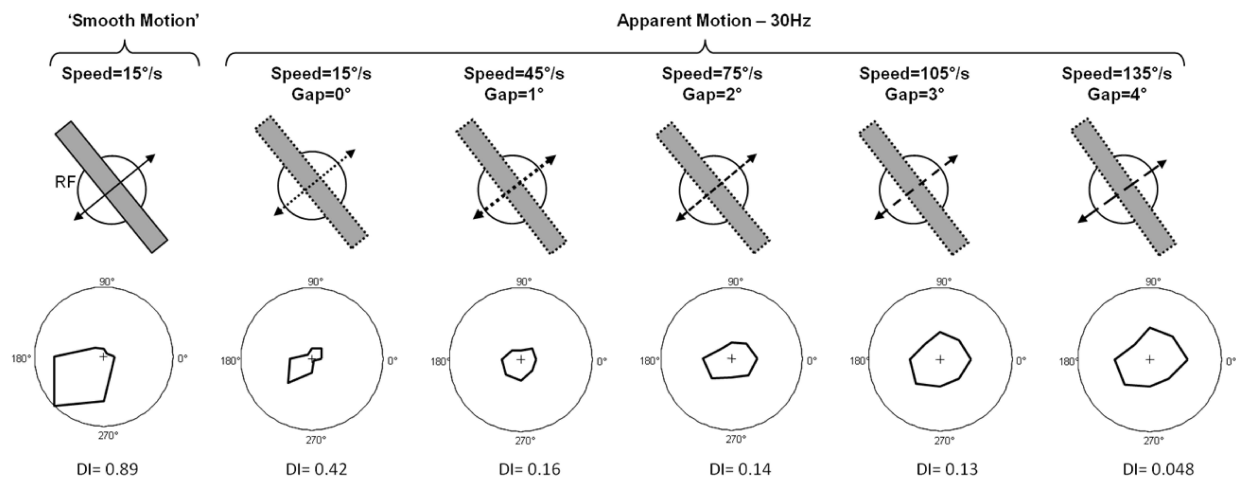


Figure 3. Representation of single-unit responses of a V2 neuron to a smooth motion stimuli and to apparent motion stimuli. Directional selective responses are represented by polargrams and quantified in directional indexes (DI) values. Each condition (column) generates a directional response when the stimulus crossed the center of the receptive field (RF). The same bar stimulus (in gray) was presented in smooth motion (bar in continuous line) and in 30 Hz apparent motion (dotted line). Apparent speeds were produced by increasing the distance (gap in degrees). Increasing the distance of the flashed bars increased the speed of apparent motion. The directional response was extracted by the bar in smooth motion (left column). In this particular example, it is possible to see by polargram and by the directional index (DI=0.89) that the neuron is unidirectional (from 45° to 215°). However, when the bar was presented in apparent motion condition the directional response (DI=0.42) was maintained just at the first condition (no gap between the bars). By increasing the distance between the bars the neuron loses its directional selectivity.

To study the range of spatial integration in V2, and to indirectly illustrate the role of feedback or intrinsic circuitry in apparent motion processing in V2, new experiments will be needed to analyze directional response to apparent motion of different spatial and time intervals. The exact functional role of feedback contribution to V2 neuronal response to illusory motion remains a topic of current research.

6. Conclusion

The inactivation of feedback connections from MT or V4 to area V2 produces a general decrease in the excitability of the V2 neurons, which included an increase in spontaneous activity, a decrease of the stimulus-activity, and sometimes changes in directional selectivity. These changes in selectivity were toward an increase in directional selectivity and a decrease in orientation selectivity. The effects of inactivation of the cortical visual area V4 are different from those of inactivation of visual area MT or from the inactivation of subcortical nuclei, such as the pulvinar. Inactivation of the feedback connections of V4 and MT promote inhibitory modulations in V2, while inhibition of the pulvinar produces both excitatory and inhibitory modulations on the target cells in V2. GABA inactivation of areas MT and V4 produced an early and short decrease in both spontaneous activity and responsiveness, followed by a transitory increase of spontaneous activity and change in V2 neuronal direction and orientation selectivity. GABA inactivation of the pulvinar induces both excitatory and inhibitory changes in V2 neuronal activity and produces a decrease in orientation selectivity. The effects of inactivation of the visual area MT are quantitatively different from those of inactivation of area V4. While inactivation of MT, on average, decreases DI, the inactivation of V4 increases DI [51,53]. In addition, inactivation of MT, on average, increases OI, while inactivation of V4 or pulvinar decreases OI [51,54].

We also attempted to study the role of feedback from higher visual areas to V2 by designing a study in which spatial integration was accessed by using an apparent motion paradigm. Preliminary results suggest a minor contribution of the feedback projections to the apparent motion processing in V2.

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