GRATING STIMULI DO BIAS OUR CONCEPTS ON CORTICAL GAMMA SYNCHRONIZATION: A STUDY IN CAPUCHIN MONKEY V1

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Trabalho apresentado ao programa de pós-graduação em neurociências da Universidade Federal do Rio Grande Do Norte como requisito parcial para a obtenção do Grau de Mestre

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ABSTRACT

Cortical gamma oscillations (30 - 90 Hz) have been implicated in various cognitive processes, such as perceptual binding and attention. So far, most evidence in support of this hypothesis is based on studies that used artificial and simplified stimuli, such as moving gratings and bars. Recently, experimental work using natural images led to conflicting conclusions. In a paradigm that required human subjects to maintain fixation, electrocorticogram signals (ECoG) showed gamma for grating stimuli but not for static images or pink noise (Hermes et al., 2015). On the contrary, analysis of ECoG in the early visual cortex of macaque monkeys revealed strong gamma components for free viewing of natural scenes (Brunet et al., 2015). Here, we aim to clarify these discrepancies using a paradigm that allowed direct comparisons between fixation vs. free viewing conditions, for both simplified stimuli (moving and static gratings) and natural scenes (static and moving images). Recordings of spiking activity and local field potentials (LFPs) were obtained from the central and the peripheral representations of V1. Our results show that in capuchins (N= 3 monkeys), as previously described in macaques and humans, gamma is characteristically strong when stimulus parameters, such as size, orientation, and speed are set at to optimal values. Comparisons between fixation vs. free viewing conditions and gratings vs. natural stimuli revealed that gamma is always high for optimal grating stimuli, regardless of viewing condition (N= 93 recording sites, 2 monkeys). However, gamma is surprisingly absent during free viewing of natural images and movies. Similar negative findings were also obtained when the monkeys were exposed to real-world scenes, such as objects and other animals in the laboratory. The present results suggest that strong, narrow-band, gamma responses in V1 are primarily associated with the selective activation of cell populations sharing similar response properties. Therefore, gamma may be seen as a resonance phenomenon of the underlying cortical connectivity. Overall, our results belittle the importance of gamma as a critical cortical mechanism for vision.

KEYWORDS: gamma, synchronization, V1, visual perception, capuchin monkey.
Resumo

As oscilações corticais gama (30 - 90 Hz) têm sido implicadas em processos cognitivos como a ligação perceptual e a atenção. Até agora, a maioria das evidências que servem de suporte para esta hipótese é baseada em estudos a partir do uso de estímulos simples e artificiais, como grades e barras luminosas. Recentemente, no entanto, estudos experimentais utilizando imagens naturais levaram a conclusões conflitantes. Em um paradigma em humanos que requeria fixação mantida, sinais eletrocorticográficos (ECoG) mostraram gama para grades, mas não para imagens estáticas ou ruído rosa (Hermes et al., 2015). Contrariamente, a análise dos sinais ECoG no córtex visual de macacos-reso revelou fortes componentes gama para a livre observação de cenas naturais (Brunet et al., 2015). Neste estudo, temos por objetivo esclarecer essas discrepâncias utilizando-se de um paradigma que permitiu comparações diretas entre uma condição de fixação vs. uma condição de observação livre, tanto para estímulos simplificados (grades móveis e estáticas) quanto para cenas naturais (imagens estáticas e em movimento). Registros de potenciais de ação e de potenciais de campo locais (LFPs) foram obtidos para a representação central e periférica de V1. Nossos resultados demonstram que em macacos-capuchinhos (N = 3), como descrito anteriormente para macacos-reso e humanos, a gama é caracteristicamente forte, sempre que os parâmetros do estímulo, como tamanho, orientação e velocidade, são definidos para a ativação ótima das células. Comparações entre condições de fixação e de livre observação e grades vs. estímulos naturais revelaram que a gama é sempre forte para grades de orientação ótima, independentemente da condição de visualização (N = 93 sitios de registro, 2 macacos). No entanto, a gama está surpreendentemente ausente durante a livre visualização de imagens e filmes naturais. Achados negativos semelhantes também foram obtidos quando os macacos foram expostos a cenas do mundo real, como objetos e outros animais no laboratório. Os presentes resultados sugerem que, no córtex visual primário, a atividade gama é principalmente associada à ativação seletiva de populações neuronais que compartilham propriedades de resposta similares. Portanto, a gama pode ser vista como um fenômeno de ressonância da conectividade cortical subjacente. Em geral, nossos resultados minimizam a importância da gama como um mecanismo cortical chave para a visão.

Palavras-chave: gama, sincronização, V1, percepção visual, macaco-prego.
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The major problems in the world are the result of the difference between how nature works and the way people think.

Gregory Bateson
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1. INTRODUCTION

1.1. Neuronal representations

A remarkable aspect of the visual system is its ability to handle vast amounts of information from a continuous stream of images. In real life, because of eye movements, retinal sampling of the world is at best sparse and fragmentary. These highly variable and incomplete inputs are in sharp contrast to our conscious experience, which is continuous and unified. Thus, the visual system does not passively record a series of 2D images but rather actively integrates the raw sensory inputs into coherent and stable percepts. Our understanding of the nature of these integrative processes represents one of the most significant challenges in contemporary neuroscience.

It is known that the visual system can analyze complex natural scenes fast and efficiently. It takes just 120 to 130 ms for humans to recognize an object and to shift the eyes towards it (Kirchner and Thorpe, 2006). The time constraints imposed by eye movements are considerable. In natural viewing conditions, fixations have relatively short duration, ranging from 150 to 350 ms in monkeys (Berger et al., 2012; König and Buffalo, 2016; Maldonado et al., 2008) and from 290 to 340 ms in humans (Henderson, 2003; Smith and Mital, 2013). These brief epochs of relative gaze stability are interrupted continuously by saccadic movement of the eyes that shift the center of the gaze to a new location. Saccades are genuinely ballistic movements since there is no time for course corrections by sensory feedback mechanisms (Kandel et al., 2000). One can readily appreciate how fast, and efficient the visual system is considering that, in a recognition task, a saccade towards a target face is done in less than 110 ms (Crouzet et al., 2010).

Since Adrian (1926, 1928), it became widespread the notion that sensory stimuli are primarily encoded by the average responses of the cells. Later, a seminal series of experiments carried out in the
primary visual cortex of cats and monkeys gave the concept of neuronal representation a significant leap forward (Hubel and Wiesel, 1959, 1962, 1968). A paradigmatic discovery was that cortical neurons are highly selective to specific properties of a stimulus, such as such as orientation and direction of movement. This selection mechanism would be key for building a neuronal representation. According to experiments of Hubel and Wiesel (1962), the receptive fields of cells in the visual cortex are not equal to those found in the retina and lateral geniculate nucleus (LGN). Based on their RF properties, the cells in the primary visual cortex can be divided into two major functional categories: simple and complex cells. At first glance, simple cells may be thought to have RFs with similar properties as the LGN neurons (or the retinal ganglion cells), since they respond to light discs an show clear excitatory (ON) and inhibitory (OFF) subregions. Unlike the LGN, however, RFs of simple cells do not have a concentric organization, but instead, they are formed by the apposition of slab-shaped subregions. More importantly, as Hubel and Wiesel have shown in their seminal studies, cortical neurons show selective responses to oriented bars. Later, complex cortical cells were classified by Gilbert (1977) into two categories: standard complex cells, which showed summation, and special complex cells, those that did not.

According to the model proposed by Hubel & Wiesel, abstract representations emerge from the integration of elementary features elicited by neurons (Hubel and Wiesel, 1968). Thus, as one moves further downstream across hierarchical levels, the response of single cells become progressively more specific related to more complex features of a scene (Barlow, 1972). In accord with this view, different aspects of an image are analyzed by different modules or areas across hierarchical levels in the visual system.

Several studies served to establish orientation preference of V1 neurons (Hubel; Wiesel, 1959, 1962, 1974; De Valois; Yund; Hepler, 1982). It has been detected through the strength of the
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obtained evoked responses, although there are V1 neurons that respond for all oriented bars crossing their receptive field (non-oriented cells) (Campbell et al., 1968).

In this respect, neuronal responses at higher levels will acquire more and more sparseness, since a cell will only fire for a particular constellation of features, such as a grandmother’s face. The idea of a sparse coding in natural vision became attractive as it would allow for maximization information transfer with a minimal redundancy and metabolic cost (Vinje and Gallant, 2000).

It became challenging to conciliate this firing rate-based visual processing with the evidence that recognition of an object is indeed swift. There is no doubt about the fact that action potentials are a fundamental mechanism for information transmission in the brain. Nevertheless, a consensus on how spike trains encode information is still missing (Guyonneau et al., 2004).

1.2. BINDING BY SYNCHRONIZATION

An alternative concept postulates that the fine temporal patterning of the responses is a crucial mechanism for building
neuronal representations. This mechanism is thought to operate at two levels: (1) encoding of stimulus properties, (2) feature binding.

In accord to the temporal code model, the timing of spikes or patterns of spikes across population carries feature stimulus information. Among concepts that use temporal coding we have: the timing of the first spike after the stimulus onset, sparse coding, and neural oscillations.

An oscillation can be defined as a repetitive variation in time of some measure. For neuronal proposes, an oscillation is a burst of action potentials that occur at regular intervals. Through history, the spectral bands received a Greek letter, and, although these frequency bands are object of discussion, they are usually taken as delta, 0.5 - 4 Hz; theta, 4 - 8 Hz; alpha, 8 - 12 Hz; beta, 12 - 30 Hz; gamma, above 30 hertz (Buzsáki, 2006). Gamma band oscillation can be considered as concentrated in a center frequency between 30 and 90 Hz (Bosman; Lansink; Pennartz, 2014; Fries, 2015). Although, the hypothesis that that oscillation within and between groups of neurons may convey information has been applied to the different frequency-band, it is the gamma-band that received the most attention, as it has been extensively discussed in the last 30 years.

The first studies showing that gamma oscillations depend on stimulus properties were those of Gray and collaborators (1987), followed by Eckhorn et al. (1988). In these studies in the anesthetized cat, gratings stimuli were capable of inducing strong, coherent responses within a cortical column, between columns and even between different visual areas (areas 17 and 18). Other experiments using light bars led to similar results. Gray and collaborators (1989) using arrays of electrodes with well-defined distances between them, could demonstrate that gamma synchronization appears in responses of cells with similar orientation preferences, but not for cells with different preferred features characteristics. Notably, synchronization was stronger for one single bar across the receptive fields of two recording sites, suggesting that
not only the stimulus is significant, but also its global properties, including continuity, orientation and common direction of movement.

Later on, in a series of seminal studies, Gray and collaborators realized that gamma synchronization might be necessary for visual processing, in particular for figure-ground segregation. Simultaneous recordings of the local field potential (LFP) and the spiking activity in area 17 of anesthetized cats in response to light bars suggested that gamma synchronization contributes to an intra-cortical mechanism involving cells in the same column sharing the same orientation preferences. Specifically, cells synchronized their spikes at the same phase, corresponding to the negative oscillation phase of the LFP (Gray e Singer, 1989). This synchrony could also be verified in spatially separate regions of visual cortex (Eckhorn et al., 1988). The LFP is the electric field that reflects transmembrane currents flowing about the neuronal population around the electrode and is an indicator of average population activity (Salinas and Sejnowski, 2001).

Gray and Singer (1989) have also shown that neurons presented with an optimal stimulus probably fire at a frequency near 40Hz (42±7Hz), but this peak showed considerable variability and was never the same on different trials. They also analyzed the type of cells and found that especially the cells with complex receptive fields were entrained into gamma rhythms (Gray et al., 1989, 1990).

Overall, these findings led to the notion that gamma-band oscillations were responsible for the perceptual binding (Eckhorn et al., 1988; Gray et al., 1989; Singer, 1999). Although much has been learned about how the cell responses analyze particular aspects or features of the image, it is still unclear how the visual system brings together these bits of information into a coherent representation of the perceived object. This has been called the binding problem. Gamma-band synchronization has been pointed out as a mechanism that could in principle solve the binding problem. Rhythmic synchronization in the gamma-frequency band may provide the spatial
As mentioned before, gamma synchronization in neuronal responses is stronger for neurons sharing similar orientation preferences. For stimuli with an angle > 30 degrees larger than the preferred orientation, oscillatory modulation amplitude decreases sharply (Gray et al., 1990). Accordingly, early studies showed that in the cortex responses to stimulus orthogonal to the optimal are weak (Campbell et al., 1968; Hubel; Wiesel, 1979). Moreover, experiments using oriented light bars (Gray et al., 1990) or plaid stimuli (Lima et al., 2010) showed that gamma is strongly reduced or abolished when an optimal stimulus is presented superimposed with a non-optimal stimulus. Gamma also depends on several visual stimuli parameters, for example, stimulus orientation and velocity. Dynamic stimulus, such as moving bars and gratings are more effective in inducing cell activation than static stimuli (Hubel; Wiesel, 1959, 1962), and causes

**Figure 2. Pro and contra evidence for BBS.** Left, evidence of synchronization of spiking responses in area MT of an awake monkey (from Kreiter & Singer, 1996). Synchronization is strong for a single bar crossing the RFs, but weak for two conflicting bars. Observe that the correlograms show weak signs of gamma oscillations. Right, a similar experiment made by Palanca et al. (2006) led to diverging conclusions.
stronger gamma oscillations (Gray et al., 1990; Tovee; Rolls, 1992).

In V1 of monkeys and cats, it has been found that neurons fire more for gratings at a specific orientation than to bars and that they are more tuned (Albrecht; De Valois; Thorell, 1980). One possible explanation for that is the fact that the bars have a broad spatial frequency, which does not happen with the gratings. Gratings and plaids are excellent stimuli because they are periodic and allows a continuous stimulation of the cells.

Gray et al. (1990) showed that gamma oscillation frequency is strongly dependent on the speed of the stimulus. In their experiments, they found that the preferred average velocity that showed gamma oscillation was 1.3 to 2.7 degrees per second, and none oscillation was observed when the speed exceeded 13°/s. Eckhorn et al. (1988) found that the binocular stimulation provoked more gamma than monocular, likewise Gray et al. (1990), who demonstrated greater gamma oscillation amplitude with binocular stimulation.

An important question is whether the oscillation is induced by the visual stimuli or phase-locked with the stimulus onset. Overall, most of the experiments in the anesthetized cat have shown that gamma oscillations are not phase-locked with the stimulus, but stimulus-induced (Eckhorn et al., 1988; Gray et al., 1990).

Since then, gamma synchronization has been systematically studied over the years and verified through a variety of species, as cats (Engel et al., 1991), monkeys (Eckhorn et al., 1993; Livingstone, 1996), mice (Saleem et al., 2013); pigeons (Neuenschwander and Varela, 1993), and humans (Hadjipapas et al., 2007; Hall et al., 2005; Hoogenboom et al., 2006; Muthukumaraswamy et al., 2010). Furthermore, different cortical areas such as V1 (Lima et al., 2010; Womelsdorf et al., 2012), V4 (Brunet et al., 2014; Vinck et al., 2013), and MT (Kreiter and Singer, 1992), motor cortex (Donoghue et al., 1998) and auditory cortex (Brosch et al., 2002) have shown oscillations at the gamma frequency-band. Several studies have also
demonstrated gamma synchronization between cortical areas (Bosman et al., 2012; Engel; König; Singer, 1991; Jia; Xing; Kohn, 2013) and also in non-cortical structures, as the retina (Neuenschwander et al., 1999), optic tectum (Neuenschwander and Varela, 1993) and hippocampus (Montgomery and Buzsáki, 2007). Also at different cognitive states, as anesthetized (Castelo-Branco; Neuenschwander; Singer, 1998) and awake state (Brunet et al., 2014; Neuenschwander et al., 1993), is possible to detect gamma.

Cortical gamma processes have been implicated in various cognitive processes, such as attention (Fries, 2001; Gregoriou et al., 2015), memory (Montgomery and Buzsáki, 2007; Pesaran et al., 2002), perception (Melloni et al., 2007), temporal expectation (Lima et al., 2012) and binding of different features of a stimulus (Singer, 1999; Uhlhaas et al., 2009). In this study, we will focus on the correlation of gamma-band frequency oscillation and two cognitive processes: stimulus encoding and attention.

1.3. Gamma coherence and attention

Attention can be seen as a collection of processes involved in pointing out which information is relevant for a specific behavior (Buschman; Kastner, 2015), and which is not (Desimone; Duncan, 1995). In other words, attention can be understood from a dual perspective: it increases saliency but also filters out irrelevant information. From a computational point of view, attention is required given the vast amounts of information available from a visual scene. The brain, as any computational system, has a limited capacity. Attention provides a mechanism for reducing drastically the information to be processed downstream in the system. It is likely that these selection or gating mechanisms operate at early levels in the cortex. The nature of these mechanisms has been the subject of a heated debate.

Recently, it has been proposed that, besides a role in visual integration, gamma synchronization may have also a role in attention.
Experimental evidence has been provided by a series of experiments in humans and monkeys. Using EEG techniques, Gruber and colleagues described an increase in gamma-band (35 - 51 Hz) amplitude when subjects were cued to attend a visual stimulus. Later, evidence has been also found for the somatosensory cortex in monkeys (Steinmetz et al., 2000). In this study the monkeys had to shift their attention between two sensory modalities, either by visually discriminating a oriented bar or tactically, the letters of the alphabet. Results revealed that pairs of neurons in the somatosensory cortex oscillate synchronously, and the degree of this synchrony increased at about 80% when the monkey attended specifically the tactile stimuli. Interestingly, synchrony was found to be dependent on task difficulty, when the attentional demand was at its most.

A link between gamma synchronization and visual attention was first established by Fries et al. (2001) in area V4 (Figure 3). In this study, two monkeys were trained to attend to a behaviorally relevant visual stimulus in detection task. The monkeys were required
to hold their gaze onto a fixation point and, after a variable time, two grating stimuli appeared simultaneously at the upper and lower quadrants of the visual field. Attention to one of the quadrants was cued by the color of the fixation point: if red, the monkey had to pay attention to the upper quadrant; if green, to the lower quadrant. The monkeys had then to signalize by a lever release a subtle change in the cued stimulus. Responses associated with attention directed to the stimulus covering the RF were marked by a heightened amplitude of gamma, as characterized by spike triggered averaging of the LFP. Notably, attentional effects were not seen during spontaneous activity, suggesting that gamma modulation related to attention is dependent on cell activation. The functional implication of gamma rhythms into attentional selection mechanisms has been posteriorly reinforced by a series of experimental and theoretical studies (Fries, 2015).

The aforementioned body of work led to the proposal of a new conceptual framework about the role played by gamma oscillations in the cortex, known as the communication-through-coherence (CTC) hypothesis (Fries, 2005, Figure 4). According to this hypothesis, the precise phase relationship between local spikes

**Figure 4. The CTC hypothesis.** According to this hypothesis, the precise phase relationship between local spikes and oscillatory population signals controls information flow among distributed neuronal networks.
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and oscillatory population signals controls information flow among distributed neuronal networks (Vinck and Bosman, 2016; Nikolic et al., 2013; Womelsdorf et al., 2012; Fries et al., 2007). More specifically, action potentials emitted by cell populations in phase with the gamma cycle are more effective to generate post-synaptic spikes as compared to non-coherent schemes of pre-synaptic activation (Fries, 2005). In principle, this mechanism could explain how the brain select channels of information, as required by attentional mechanisms (Fries, 2015).

1.4. IS GAMMA REQUIRED FOR NATURAL VISION?

So far, most of the experimental evidence in support of gamma synchronization has been derived from responses to simplified, artificial stimuli, such as gratings and bars. Although such class of stimuli are very effective in triggering strong and sustained gamma responses, it does so only when stimulus parameters, such as...
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size, orientation, spatial frequency, speed, and contrast are set at optimal values (Gieselmann et al., 2008; Lima et al., 2010; Ray and Maunsell, 2010). These conditions, however, are in sharp contrast to what happens in a real-world, natural environment. First, natural scenes contain complex spatiotemporal patterns, very different from gratings stimuli, which are characterized by single spatial and temporal frequencies. Second, in real-life, eye movements and blinks make the sampling of the image discontinuous and sparse. Thus, under natural conditions, the visual input is mainly distinguished by its transient, non-stationary components. This mode of operation represents a challenge for coding strategies that assume continuous and steady-state processes, as it is the case for any mechanisms based on oscillations.

To address this problem, Kayser et al. (2003) carried out an elegant experiment in the behaving cat. Using a small head-mounted

Figure 6. Gamma oscillations in ECoG signals of V1 of a macaque monkey during free viewing of natural scenes. Mass activity signals in the visual cortex show strong gamma for static natural scenes (modified from Brunet et al., 2013).
camera, they were able to acquire real scenes from the perspective of a cat's eye. Comparisons were made for responses to natural scenes, gratings and various noise stimuli derived from the movies. All stimuli were presented on a computer screen, and the cats were set to look at it passively (ideally not moving the eyes, although eye movements were not controlled). Analysis of LFP responses revealed high-amplitude, narrow-band gamma (40–80 Hz) for the gratings. Surprisingly, narrow-band gamma was absent for natural movies. For this condition, the spectral profiles were broad and included high-frequency components (100 - 200 Hz). Similar profiles were also found for non-structured images. This latter finding was paradoxical, as one would have expected marked response differences for images with and without contours. Overall, these results belittle the notion that gamma is relevant for contour integration.

Using similar approaches, recent experiments in monkeys and human subjects led to diverging conclusions. Ito et al. (2011) described strong beta components (20 Hz) in V1 responses of capuchin monkeys freely viewing images, such as pictures of birds, leaves, and faces. Notably, in this first study gamma was not found in the spiking responses of V1. Later, in a following-up study (Ito et al., 2013), the authors reported that gamma components in the LFP are locked specifically to the saccade onsets (and not the fixation onset). So, it is possible that gamma also contributes to active oculomotor parsing of the visual scene.

Brunet et al. (2013), using a free-viewing task similar to Maldonado et al. (2008), reached very different conclusions. In an electrocorticographic (ECoG) study in macaque monkeys, mass activity was recorded from 252 subdural electrodes covering a vast area of the early visual cortex (V1 and V4). The monkeys were free to inspect a series of color or gray pictures during a few seconds. Spectral analysis of ECoG signals showed strong narrow-band gamma components (50 to 80 Hz) for each of the images tested, suggesting that gamma is an integral part of the cortical dynamics
The above results, however, were challenged by Hermes et al. (2014), who used similar recording techniques in humans. During a fixation task, responses to static images (objects, houses, and faces) or pink noise revealed broad spectral components. These findings were in sharp contrast to the narrow-band gamma described by Brunet et al. (2013) in the monkey. Interestingly, in humans, high gamma was found only for grating stimuli, resembling the results of Kayser et al. (2003) in the cat. Overall, these experimental controversies further galvanized debates around the relevance of gamma in natural vision (Brunet et al., 2014; Hermes et al., 2015).

In the present study, we aim to solve this puzzle using a paradigm that allows direct comparisons between fixation vs. free viewing conditions, for both simplified stimuli (moving and static gratings) and natural scenes (static and moving images). Our analysis focuses on characterizing gamma oscillations in spiking responses.
2. Goals

The primary goal of this study is to evaluate gamma responses in capuchin V1 to gratings stimuli (static and moving) as compared to natural scenes (images and movies) in two different viewing conditions: maintained fixation and free-viewing. With this paradigm we hope to be able to disentangle stimulus from viewing condition effects, given that eye saccades impose discontinuities in the visual input, which potentially may interfere with ongoing gamma activity.

2.1. Specific goals

- To record, for the first time, V1 responses in capuchin monkeys performing a 2000 to 4000 ms fixation task.
- To quantify, for the first time, gamma responses in V1 with respect to basic properties of the stimulus, such as size, speed and orientation.
- To compare gamma responses to gratings with those to natural scenes movies during maintained fixation.
- To assess whether gamma activity is present during free viewing of grating stimuli and natural scenes (both images and movies).
- To assess, for the first time, whether gamma responses is present during free viewing of real-world scenes, as featured by familiar objects, monkeys and humans.
3. METHODS

All procedures and methods in this study were previously approved by the Ethics Committee of our University (Protocol number 053/2012, CEUA-UFRN).

3.1. MONKEYS

Three capuchin monkeys (*Sapajus sp.*) of both sex participated in this study. The monkeys were initially obtained from the Brazilian Institute for the Environment and Renewable Resources (IBAMA - Natal, SISBIO authorization number: 35425-4, 2013 - 2017), and housed at the monkey facility of the Institute (BISIC, Instituto do Cérebro - UFRN).

Currently, our monkey facility houses seven capuchin monkeys. The facility comprises two interconnected enclosures (total of 7.5 m², 2.65 m high) built in stainless-steel (304 steel, 4 mm rods, 150 x 40 mm spacing). The two areas are separated by a gate that can be closed for cleaning and maintenance purposes when the monkeys are moved into one of the two areas. An opening in the ceiling allows proper ventilation and direct sun light. Wooden shelves mounted horizontally provide resting platforms and, alongside with wing ropes and nets (PlayTeam, Hasselbach, Germany), environmental enrichment. A large primate-cage (0.75 x 0.85 x 1.18 m) affixed to the enclosure serves as an anti-chamber for taking the monkeys into the lab.

The monkey facility is located next to our laboratory, where the recordings were taken place. Consequently, the monkeys got quickly familiarized with procedures and experimental apparatuses. Differently from macaque monkeys, capuchins can learn all these steps without being deprived of water. Thus, only positive reinforcement was necessary. According to our experience, three reinforcement items were very efficient: dry spaghetti, condensed milk, and sunflower seeds. For the training and recording sessions, we used liquid refreshment as a reward. Noteworthy, Gatorade® (especially orange, tangerine and passion-fruits flavor) was found to be incredibly useful. Upon returning
to the animal facility, the monkeys were fed *ad libitum* with vegetables and fruits (watermelons), and occasionally with chicken and eggs.

**Figure 7. Habituation to the laboratory.** Capuchin (Monkey 3) awaiting the start of a training session in the laboratory (Vislab, Brain Institute - UFRN, May 2017). Observe details of the monkey-chair (designed by Sergio Neuenschwander, Heitor de Oliveira and J-B de Saint Aubert).

### 3.2. Habituation

Before starting the training sessions *per se*, the monkeys went through a series of steps for getting acquainted with the laboratory and training procedures. First, they learned to respond to verbal commands and enter into the monkey-chair. Then, they learned to put their heads out of the chair, a step that usually took 2 to 3 months. After being at ease with these routines, they were brought to the recording setup box on a daily basis. During all procedures, the monkeys received abundant rewards (condensed milk, pieces of fruits).

After completion of this initial habituation program, the monkeys underwent surgery for implantation of a head fixation prosthesis. We allowed 2 - 3 months for full recovery from the surgery. Then we began to train the monkeys to have their heads fixed, initially for a brief period, and later for longer times (up to 2 hours). It was only when the monkeys felt truly safe and comfortable with all procedures
that the training in a visual task began.

Our monkey-chair was designed by Sergio Neuenschwander, Heitor de Oliveira, and Jean-Baptiste de St. Aubert, based on an original model made for the Rhesus in Würzburg, Germany. The chair has two lateral acrylic plates (45 X 26 mm) mounted on a frame welded to a steel base (34 X 26 cm), which gives excellent stability and durability. The access door (28 X 27 cm) is at the back of the chair. On top, an oval opening allows the passage of the head. A guillotine plate restrains the monkey in place. We used good M6 stainless-steel screws (DIN 464-M6-25NI, Elesa+Ganter, Germany) for fixating all moveable parts of the chair.

A stainless-steel table (36 X 40 X 72 cm) fitted with rollers (75 mm of diameter) was used to carry the monkey-chair. The base of the chair was fixed to the table by two M6 screws.

3.3. IMPLANTS

Before starting with the training sessions, the animals were submitted to a surgical procedure for implanting a head fixation prosthesis and a recording chamber, which gave access to the cortex.

The head fixation prosthesis was designed in our laboratory by
Sergio Neuenschwander and Heitor Oliveira, following a model put forward by Nikos Logothetis at the Max-Planck Institute for Biological Cybernetics, Tübingen, Germany. Our version consisted of two parts, a base and a rod (12 mm of diameter), fixed together with an M4 steel screw. The base had an X-form, with a series of holes for placement of the bone screws. The base was relatively thin (2 mm) so that one could easily bend it to fit onto the curvature of the skull.

The recording chamber had a diameter of 9 or 14 mm. To close the chamber, we used a cover made of PEEK, a biocompatible polymer that has been widely used as a substitute of the titanium alloys (Sagomonyants et al., 2008). Silicone paste was applied to the lid for sealing the chamber.

Both the head fixation prosthesis and the recording chamber were made of a titanium alloy (Titanium grade II), a light material that has excellent corrosion resistance and strength (Niinomi, 1998).

During the recording sessions, the chambers were opened under sterile conditions. We used a customized tool to hold the lid when removing it from the cylinder (developed by Manuel Messias in our...
workshop). The lids (with sealing applied to it) and their respective holding-tools were sterilized together, so that, later, one could safely recap the chamber. The chambers were cleaned at least once per week by saline irrigation and aspiration using a Pasteur pipette. If necessary, iodine solution or antibiotic were applied directly into the chamber (Iodopovidona, Povidine Antisséptico Tópico, Ultrafarma).

In our experiments, the dura mater always remained intact.

3.4. Surgery

All surgical procedures were conducted under general inhalation anesthesia and near-aseptic conditions.

During the preparatory phase, the monkeys received Meloxicam (Maxicam®, Ourofino, 0.2 mg/Kg, i.m.), a non-steroidal anti-inflammatory and potent analgesic, combined to atropine (Atrofarma®, Farmace, 0.05 mg/Kg i.m.) used for controlling salivation and respiratory tract secretion. To induce anesthesia, we employed xylazine (Xilazin®, Syntec, 0.25 mg/Kg i.m.), which is an analgesic, sedative and muscle relaxant, in combination with ketamine (Cetamin®, Syntec, 10 mg/Kg, i.m.).

Surgical anesthesia was maintained using 1.0 - 1.2% halothane (Tanohalo®, Cristália) administrated in a mixture of oxygen (30%) and nitrous oxide (70%). Infections were prevented with the administration of a large-spectrum antibiotic (ceftriaxone, Ceftriaxona Sódica, Eurofarma, 100 mg/Kg, i.m.).

The monkeys were submitted to skin asepsis with hair removal, washing, and rinsing. Hydrogen peroxide was administrated for antisepsis. An endotracheal tube with cuff (B. Braun, Germany, 3.5 to 4.0 mm) was placed into the trachea with the aid of gel lidocaine 2% (Xylestesin, Cristália, Brazil). After that, the animals were placed into a customized (David-Kopf compatible) stereotaxic-apparatus. The head was fixed into the stereotaxic-apparatus using two bars placed bilaterally at the external acoustic meatus, and two placed at the infraorbital margin. Another bar, crossing the mouth behind the canines,
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held the maxillary bone.

During the surgical procedures, the monkeys were artificially ventilated (Dual Phase Control Respirator, Harvard Apparatus, USA) with a fixed volume set at 40 to 50 ml. The ventilatory pressure was kept approximately constant between 7 to 10 mBar. Fluid losses were compensated with continuous intravenous infusion of saline delivered by an infusion pump (Perfusor VI, B. Braun, Germany). Body temperature was kept at 37°C with the help of a hot water heating pad (T/Pump, Gaymar, Germany). Vital signs were continuously monitored by a medical life monitoring system (Dash 3000, GE Healthcare, USA) fitted with a gas analyzer module (SMART, GE Healthcare, USA). The system provided information about the electrocardiogram (ECG), expiratory CO2 (2.6 to 3.5%) and SPO2 curves, respiratory rate (14 to 20 strokes/min) and temperature, as well as the inhalation and expiration partial pressure values of O2 and halothane.

Before the implantation surgery, all surgical instruments were cleaned, dried and sterilized in an autoclave (Sercon, model AHMC 12L, Germany).

For the implantation surgery, a median sagittal incision was made in the scalp. The layers of skin and muscle were shifted laterally,
and the skull exposed. Then, the head fixation prosthesis was placed over the bregma, with an angle of approximately 75°. The recording chamber was positioned over the occipital pole, in the opercular region, corresponding to the central representation of V1 (1 to 3 degrees; Gattass et al., 1987). Approximately 13 orthopedic screws (Synthes cortical screws, Germany; 2mm) were used to fixate the implants onto the skull. The screws were distributed laterally in the exposed bone area, in the frontal, parietal and occipital regions of each side. Bone cement (Palacos® MV+G, Medium Viscosity, Heraeus Medical, Germany) was spread in successive layers to cover the skull, anchoring in place the implants and fixation screws. Palacos® has an excellent bone compatibility and contains antibiotic (Gentamicin). After applying the cement, the prosthesis as a whole was covered with a layer of dental acrylic (Paladur®, Heraeus Kulzer, Germany), which gave extra stability and protection to it.

Approximately 60 days after surgery, the cicatrization was complete, and the animals were fully recovered. The implants did not represent a significant inconvenience to the monkeys, who accepted them as if they were parts of their own body.

3.5. Training sessions

Initially, the monkeys were required to make a simple fixation task, which consisted of maintaining the gaze at a point centered on a computer screen (fixation point, FP). As the training progressed, we systematically increased the duration of the time required to complete the task, from 200 to 3000 ms. The fixation point was set to be large (6 to 10 pixels) at the beginning of the training. Later on, depending on the performance of the monkey, we progressively make it smaller, to a minimum of 2 pixels. The fixation point could be red or white.

For each trial, the monkeys had to bring the gaze to the fixation point and hold it for at least 200 ms within a 1° window. If they inadvertently moved the eyes from the center, the trial would not start, and the point will appear again a few seconds later. In this case, the
monkeys got no warning sound (and obviously no reward). Upon trial start, the monkeys had to maintain fixation without blinking until the end of the trial (maximum of 4000 ms). If successfully doing so, the monkeys received a liquid reward (typically 1 to 5 ml). A sound feedback indicated whether the trial was successful or not. Repeated fixation breaks were punished next trial, by a longer inter-trial interval. Overall, our capuchins typically did 700 to 1000 correct trials in a single training session, which could last for 3 to 4 hours (the best performance was 2600 correct trials in a single experimental session).

After the monkeys were able to fixate reliably, we introduced distractor stimuli of increasing saliency (static and moving stimuli of variable contrasts and colors). In general, the distractors appeared at 500 ms after trial onset. We used various stimuli, such as patches of static or moving gratings and images.

Typically the monkeys needed 20 to 30 days to fully accomplish the fixation task. As a reward, we always used Gatorade®.

All stimuli were presented on a computer screen (Monitor CRT CM803ET, HITACHI, USA, refresh rate 100 Hz, spatial resolution 1024 X 768 pixels) placed about 60 cm from the eye. In these conditions, 1° of visual angle corresponded approximately to 26 pixels, so the total display area was of about 40° X 30°.

The behavioral tasks were controlled by a set of customized LabVIEW programs developed by Sergio Neuenschwander at the Max-Planck Institute for Brain Research. Essentially, the software consists of 4 components: (1) the Monkey Experiment Control (MEC), a master program that sets the timing of the task and reward; (2) the StimPlayer, a program that handles the commands for stimulus display; (3) ActiveStim, a stand-alone visual presentation software (developed by Danko Nikolic at the Max-Planck Institute for Brain Research); and (4) Look!, a program for monitoring eye movements. The MEC and Look! programs run on one Windows PC and the StimPlayer and ActiveStim in another (DELL computers fitted with National Instruments multi-function acquisition boards). The two computers are set to communicate through
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Figure 11. FIX-FREE visual paradigm. During the fixation epoch, the monkeys were required to maintain their gaze at fixation point (red point). During the free-viewing epoch the fixation point was hidden. At least four different conditions were presented: gratings drifting (1) at optimal and (2) non-optimal direction, and natural scenes drifting (3) at optimal and (4) non-optimal direction. Note the difference in size and position of stimulus for each epoch.

a fast ethernet port. The MEC controls the StimPlayer program (IP communication), which in turn sends control commands to ActiveStim (Windows Active-X communication protocol). A user interface (MEC) allows for setting timing values and decisions about the stimulus, and also the definition of a fixation window (Look!). The ActiveStim program has a high timing accuracy (stimulus onset jitter below 1 ms). It allows the display of multiple simultaneous objects (BMP images, and movies made of image sequences), which can be controlled by a series of functions, such as show, hide, move, set color, at a precise point in time (temporal resolution, 10 ms). The stimuli were generated by another program (StimPaint) and stored on disk as .bmp files that were later loaded into RAM.

For eye gaze tracking, we employed the system developed by Keiji Matsuda and colleagues at the Japan Science and Technology Corporation (Tsukuba, Japan, https://staff.aist.go.jp/k.matsuda/
iRecHS2). This system is based on an HD infrared camera (Grasshopper3 GS3-U3-41C6NIR-C, Point Grey, USA). The program computes the parameters of an ellipse fitted to the pupil in combination with the location of the Purkinje image center to estimate the visual axis. Measurements can be obtained with a sampling rate of up to 250 Hz and a spatial resolution of 0.2°, thus providing good estimates of the time course of the saccades.

Eye tracking calibration was carried out with a 5-point square grid centered on the monitor (horizontal distance between the points, 4°). For the calibration, the fixation point was presented randomly at one of the five preset positions (50 trial repetitions).

3.6. Stimuli and visual paradigms

The electrophysiological recording sessions were initiated as soon as the monkeys achieved good performance in the fixation task. Typically, the recording sessions took place 1 - 3 times a week and had a duration of 5 hours.

At the beginning of each experiment, we employed the method proposed by Fiorani et al. (2014) to estimate the position and size of the RFs. This method consists of obtaining a response matrix to a single large moving bar (1000 x 5 pixels), presented systematically at 16 directions (22.5° intervals). In our experiments, the bar was set to cover about 40 degrees of visual angle in 2000 ms (speed of 20°/s). Each condition was repeated five times (total of 80 trials). The RF maps were computed with a resolution of 0.2° of visual angle (corresponding to 10 ms).

After knowing the position of the receptive fields, we applied a stimulus protocol to quantify the orientation preferences of the cells. Square gratings were displayed through a circular aperture mask (diameter of 100 to 300 pixels) centered on the RFs. In case the RFs were non-overlapping and distant, we repeated the protocol multiple times, targeting each RF (or group of RFs) at a time. As before, the stimulus was shown systematically at 16 directions with angular
intervals of 22.5°. In general, the parameters of the gratings were set to elicit vigorous responses in V1 (high contrast, spatial frequency of 2 cycles/degree, speed of 1 to 2 degrees/ s, duty cycle of 0.3). For every recording site, we compiled the condition of maximal gamma response (optimal condition) and the condition of minimal gamma response (non-optimal condition).

Occasionally, we have also obtained tuning responses for other parameters of the gratings such as size, velocity, and spatial frequency (see Results).

Two behavioral paradigms were used in this study: (1) maintained fixation only and (2) maintained fixation followed by free-viewing.

In the first paradigm, the monkeys were required to maintain fixation continuously for an extended period (2000 to 3000 ms). Besides applying it for RF mapping and tuning curves as described above, this paradigm was used to compare the neuronal responses to gratings with those to natural scenes. As in the case of gratings, natural scene movies (see example in Fig. 18) were presented within a circular aperture mask and centered over the RFs. The scenes consisted of desaturated video clips of a football game originally shot in Super 8 film (black & white Kodak Tri-X). Five different clips were used. All of them showed a fine grained texture associated with high contrast objects in the scenes.

The second paradigm was designed specifically to compare within the same trial the two viewing conditions: (1) maintained fixation (FIX epoch) and (2) free-viewing (FREE epoch). The FIX epoch had a duration of 1500 ms and started after a blank of 500 ms. The FREE epoch followed the FIX epoch, after another blank of 500 ms. The fixation point appeared at trial onset until the end of the FIX epoch. During the whole period (total of 2000 ms) the monkeys were required to maintain fixation. If the eyes deviated from the FP, the trial was immediately aborted. During the FREE epoch, the monkeys were allowed to freely move their eyes and blink. Thus, if the FIX epoch was
completed, the monkeys always received a reward at the end of the trial.

The stimuli displayed during the FIX and FREE epochs were identical, although presented through different aperture masks (different sizes and positions). For the FIX epoch, the stimuli were 200 to 300 pixels wide and centered at one of the RFs (or group of RFs), while for the FREE epoch the stimuli were 600 pixels wide and centered at the whole screen. Ideally, we should have the same size and spatial relationships between the stimulus and RFs in the two viewing conditions, so that comparisons could be made for perfectly matching stimuli. Of course, this was not possible in our paradigm, since during the FREE epoch we couldn’t control the actual position of the RFs in relation to the stimulus. To minimize this problem, we also used an aperture mask (although larger) for the FREE epoch, thus making a compromise between the size of the stimulus in the two viewing conditions.

In this second paradigm, we always presented gratings along with natural scenes stimuli as different, randomly interleaved trials. The
gratings, as the natural scenes, were generated as large pictures (much larger than the screen size) of 2000 X 2000 pixels in size. During the presentation, we used the function *MoveObject* of ActiveStim to make the stimuli drift on the screen under an aperture mask. Besides moving the picture, this function also set its orientation (or direction of movement). Typically, a full protocol consisted of (1) a static gratings at optimal orientation, (2) a static gratings at non-optimal orientation, (3) a static image, (4) a drifting gratings at optimal orientation, (5) a drifting gratings at non-optimal orientation, (6) a drifting image at optimal orientation, (7) a drifting image at non-optimal orientation. Every condition was shown with 20 receptions (a total of 140 trials).

The natural scenes stimuli were derived from a variety of pictures collected on the internet, with a broad range of motifs, from human faces to objects and fruits. The images were presented in color or gray levels (see examples in Fig. 12). For the presentation, the original pictures were resampled, cropped and exported as 8-bit .bmp files in Adobe Photoshop. The image color space was downscaled to 100 values. The images were selected avoiding large homogenous surfaces, thereby maximizing the chance to evoke robust responses to contours present within the RFs.

It is important to emphasize that the primary goal of this study was to draw comparisons between gamma responses to gratings and natural scenes. It was not our intention to evaluate the responses to any particular aspect of the images.

### 3.7. Recordings

Recordings of neuronal responses were made using quartz-insulated electrodes (Thomas Recording, Germany). Quartz electrodes allow extracellular recordings of spiking and LFP signals with an excellent signal-to-noise ratio (Reitboeck, 1983). They have a relatively small diameter (80 µm) and small tip angle, resulting in little damage to the neural tissue. The electrodes we used were manufactured in our laboratory from raw fiber material (quartz fiber with a 25 µm metal core
made of 95 % platinum and 5% tungsten). For this, we employed a special grinding machine, which allows accurate control of the metal core exposed (DIECKL-ST, Thomas Recording, Germany). The tips of the electrodes were carefully inspected after every insertion into the brain. Electrodes with blunt tips were discarded. Since we couldn't measure the impedance of the electrodes, a mere visual inspection was the only option we had to evaluate whether or not an electrode should be used. Despite this, most of the time, we got beautiful spikes during the recordings.

In chronic experiments as ours, the dura at the recording chamber usually becomes thicker with time, making difficult to cross it without breaking the electrodes. To overcome this problem, we used a fine hypodermic needle inserted into a guide tube, a method originally proposed by Bruss Lima (Max-Planck Institute for Brain Research). Two needles (0.3 x 23 mm; Ehrhardt Supra Einmal-Kanülen, Germany) were mounted back-to-back within a third long one (0.6 x 80 mm; Sterican, Braun, Germany) that served as a guide tube. The back-to-back configuration allowed us to fit the electrodes in both directions (bottom-up and top-down), making exchanges very easy. The needles were glued with an instant adhesive (Super Bonder, Loctite, Brasil) applied with the help of a capillary tube.

The placement of the electrodes in the cortex was made with the help of a customized recording device developed by Sergio Neuenschwander (Max-Planck Institute for Brain Research). This device consists of 2 to 5 hydraulic manipulators (MO-95, Narishige, Japan) mounted on a movable platform. It allows a fine vertical positioning of each electrode individually (via the microdriver units, 10 µm resolution), but also a coarse control of all electrodes together (via a single vertical screw, 0.10 mm resolution). The guide tubes (0.6 mm needles) are fixed in a central grid at the device base. All parts of the recording device were made in PEEK.

The recording device has a simple mechanism for moving the electrodes. A glass tube (3 X 30 mm) mounted into each one of the
guide tubes works as a piston, sliding up and down. The glass tube, in turn, is linked to the axis of the micromanipulator with an L-shape metal bridge (made by bending a 0.3 needle). A drop of solder fixes the electrode and a thin wire (1.0 mm) to the inner wall of the piston, also providing electrical connection to the electrodes (the distal end of the electrode is made bare by breaking the quartz insulation with a pair of tweezers). The soldering of the electrode is made by applying hot air to the surface of the glass tube (soldering hot air blower). All these procedures are carried out under a stereo microscope.

The guide tubes and electrodes (descended maximally) were sterilized by immersion in an aqueous solution of alcohol (70%) for at least 1 hour before the recordings.

The recording device was mounted into a customized table based on a Narishige X-Y positioning apparatus (part of the Narishige MO-95 recording system). Thus, before the placement of the electrodes, it was possible to target a desired point in the dura by adjusting the X-Y table. The distance of the base to the chamber was adjusted by sliding the recording device into the two guiding rods that X-Y table has.

The recording device provided two scales for depth readings of the base and the coarse movement of the electrodes, respectively. From these readings we could estimate two important parameters: (1) the distance of the guide tubes to the dura (dura 0-point); and (2) the point at which the electrode tips left the guide tubes (electrode 0-point). We kept a record of these values in our experiment notebook.

The procedures during the recordings were as follows. First, the recording chamber was opened and cleaned. A piece of surgical drape (having a central hole) was placed around the recording chamber. Then the X-Y table adapter was screwed into the chamber, and the X-Y table was fixed to the adapter. After this, the recording device was carefully fitted to the guiding rods of X-Y table. Both the recording device table and all electrodes were then lowered taking into account the 0-point values. The grounding and reference cables were connected, and the whole device was wrapped with a shielding
aluminum folium. At that time, each electrode could be moved into the cortex with the help of their respective remote control units (full rotation of the unit knob, 500 µm; minimum graduation, 2 µm; maximal displacement in the brain, 10,000 µm).

Noteworthy to mention that the monkeys were completely unaware of the placement of the electrodes in the brain and that all procedures above were painless.

Two neuronal signals were obtained: spiking activity (MUA) and local field potentials (LFP). The MUA consists of action potentials of a small group of neurons located around the electrodes. The LFP expresses mass action potentials from synaptic and membrane potential oscillations. The acquisition of MUA and LFP was made with a sampling frequency of 32 kS/s and 1 kS/s, respectively. The signals were conditioned and amplified by a Plexon amplifier with gain of 1000x (PBX2/ 32 sp-G1000-700 Hz-6 kHz / 32fp-G100, headset HST/ 16o25-18P-GR; Plexon Inc., USA). The bandwidth of the MUA signal was set between 0.7 and 6 KHz, while the LFP signal was set from 0.7 to 170 Hz.

Data was acquired by SPASS, a non-commercial system developed by S. Neuenschwander at the Max Planck Institute for Brain Research. The SPASS system is written in LabVIEW (National Instruments, USA) and it is based on two multi-function E-series NI acquisition boards. Spikes were detected after a simple amplitude threshold algorithm, typically set to twice the noise level. The SPASS software provides modules for on-line visualization of neuronal response, LFP oscillation, spike waveform, auto and cross-correlation.

3.8. DATA ANALYSIS

For the spectral characterization of oscillatory signals (MUA and LFP), methods provided by the Chronux group (Chronux, Partha Mitra, Cold Spring Harbor, http://www.chronux.org) were used, incorporated into the NEUROSYNC system (developed by Sergio Neuenschwander in LabVIEW). Estimates were compiled for (1)
orientation selectivity index, (2) oscillation strength at the gamma band, (3) oscillation frequency.

A spike sorting classifier based on principal component analysis (SpikeOne, developed by Sergio Neuenschwander) was used to define unit cells for different register channels. In the program, classification is performed by an automatic definition of 12 groups (clusters), which can be merged or deleted after the observation of autocorrelation graphs, orientation selectivity curves, histogram of intervals. The program allows also evaluation the stability of the responses.

To evaluate the oscillatory synchronization of unit and multi-unit responses, autocorrelation and cross-correlation were computed for each trial (with time resolution of 1ms and time lags of ± 80ms) and averaged for the same conditions (presented with 10 to 20 repetitions). A shift predictors were also computed to characterize the phase-locking with stimulus onset. A gabor function were be adjusted to the correlogram (König, 1994) to describe the strength of the oscillation (MA, modulation amplitude) and its frequency.

The special components of the responses, both for spiking activity (MUA and SUA) and for the LFP, were evaluated using the multitaper method (Thomson, 1982) proposed by Partha Mitra (see review in Mitra and Bokil, 2009). This method is implemented as a collection of MATLAB (Mathworks Inc., Natick, USA) routines in the Chronux 2.0 package, an open source software available at http://chronux.org. The great advantage of the multitapering techniques is that they reduce the variance of spectral estimates by multiplying the given data to multiple orthogonal tapers, known as slepian functions. Frequency decomposition of multiple data segments results in a set of independent spectral estimates that, after averaging, becomes more reliable against data noise.
4. RESULTS

Spiking and LFP data was collected from V1 of 3 monkeys (Monkey 1, bit; Monkey 2, ded; Monkey 3, juj).

All three monkeys participated in a maintained fixation task (FIX paradigm, N= 3 monkeys). Only monkeys 2 and 3 participated in the maintained fixation followed by a free viewing task (FIX-FREE paradigm, N= 2). Additional data was collected for free viewing of real objects and scenes for all monkeys (REAL paradigm, N= 3).

We obtained a total of 163 recording sites (Monkey 1, N = 53; Monkey 2, N = 36; Monkey 3, N = 74). During the recordings we searched for robust oscillatory responses to grating stimuli independent of layer position in the cortex. The median eccentricity of RF for the central representation of the visual field was of 2.1°, range of 0.7° to 4.4° (73 recording sites, RS); for the para-central representation was of 8.8, range of 5.1° - 9.9° (39 RS) and for the peripheral representation was of 16.1°, range of 10.2° - 23.1° (112 RS).

In the present study our analysis is primarily focussed on evaluating the gamma oscillations in spiking responses.

4.1. Gamma responses to grating stimuli during maintained fixation

Initially, we set out to assess the multiunit responses in V1 of the capuchin monkey to gratings stimuli. The monkeys were required to fixate for 2000 ms, while high contrast square granting stimuli were displayed and centered above the RFs. In this study, we obtained tuning curves for MUA and gamma (in LFP and spiking signals) as a function of stimulus direction of movement (16 conditions), size (9), speed (11) and spatial frequency (7). For the tuning curves computed for the direction of movement, speed, and spatial frequency, we used relatively large gratings (200 to 300 pixels, about 5 times the size of the RFs), known to elicit robust gamma responses. Tables 1-3 show the number of recording sites and stimulus parameter ranges for all recordings.
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Similar to the primary visual cortex of the macaque, MUA responses in V1 of the capuchin typically exhibit a robust tuning for stimulus orientation. Figure 13 shows multiple tuning curves compiled for the direction of movement of drifting gratings for the three monkeys. Observe that the gamma ratio of the LFP tended to follow the tuning properties of the spiking responses strictly. The gamma ratio metric was obtained after dividing the area corresponding to the gamma band (30
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Figure 14. Gamma depends on the size of a grating stimulus. Observe that an increase in stimulus size induces a marked suppression of the MUA responses and a concomitant positive gain in gamma power. Oscillation frequency decreases from 58 to 48 Hz. Stimulus size ranges from about 1° to 20°. RF eccentricity, 25°. Data obtained for Monkey 3.

to 90 Hz) by the total of the power spectrum. Interestingly, orientation selectivity was explicitly found for the gamma band and not for alpha or beta. This indicates that gamma strength is significantly more dependent on the orientation of the stimulus than the other oscillatory bands. Notably, the selectivity in the cell responses tends to follow the selectivity for gamma of the LFP. For this reason, in general, we could identify the same preferred condition from the two metrics.

Gamma oscillatory strength and gamma oscillation frequency
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were strongly dependent on stimulus size (Fig. 14). Typically, if a small patch of gratings, about the size of the RFs, was used to activate the neurons, gamma was absent from the LFP and spiking activity, although the responses were vigorous. If the stimulus, however, covered an area of about twice the size of the RFs (~4° at an eccentricity of 20°) gamma appeared, becoming progressively stronger as a function of the stimulus size. Notice that the firing rates showed an inverse trend. For large stimuli the responses were sparse, and the gamma had high-amplitude. In the example indicated in Figure 14 gamma amplitude reaches a plateau at 400 pixels (about eight times the size of the RFs). Interestingly, gamma oscillation frequency was strongly dependent on stimulus size. In Fig. 14 the peak frequency in the power spectra of the LFP (at the gamma band) decreased by 20% (from 58 to 48 Hz). Similar

Figure 15. Gamma frequency depends on the speed of the stimulus. Notice that an increase in stimulus speed leads to faster oscillations. Data obtained for recordings corresponding to the central and peripheral representation of the visual field (1° and 17°, respectively). For the central representation oscillation frequency increases steeply from 65 to 90 Hz (~40%), while for the peripheral representation it increases moderately from 45 to 55 Hz (~20%).
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Figure 16. Gamma is absent for natural movies. Gratings drifting at the optimal direction induced strong gamma synchronization (oscillation frequency about 53 Hz). When a natural scenes movie was presented over

Figure 17. Gamma power of the LFP is high for gratings and absent for natural movies. Notice that the high and narrow gamma peak at 52 Hz is present only for the gratings stimuli (colored trace). Remarkably, beta is present for both stimulus conditions (peak at 21 Hz). For these recordings the monkeys were required to hold fixation for 2500 ms. Thus beta activity may be present independently of saccadic eye movements. Stimuli were presented over the RFs. Same recording sites as in Figure 16.
results were found for recordings corresponding to the central representation (data not shown).

Besides being affected by the size of the stimulus, oscillation frequency was also strongly dependent on the speed of the gratings. Figure 15 shows data obtained from recordings corresponding to two different points in the visual map (1° and 17°, corresponding to the central and peripheral representation of the visual field, respectively). Notice that increasing stimulus speed led to faster oscillations. These effects were more pronounced for the center as compared to the periphery. For the recordings from the operculum (center), gamma frequency increased steeply from 65 to 90 Hz (~40 %), while for the calcarine (periphery) it increased moderately from 45 to 55 Hz (~20%).

4.2 NO GAMMA IN RESPONSES TO NATURAL SCENES DURING MAINTAINED FIXATION

We initially trained one monkey (Monkey 1) in a simple fixation task to evaluate the oscillatory behavior of the responses to gratings as compared to natural scenes. All stimuli were dynamic (drifting gratings and movies) and were presented during a fixation period of at least 2000 ms.

After mapping of the RFs, we used drifting grating stimuli presented over the RFs to estimate the tuning characteristics of the cells to the direction of movement (16 conditions, steps of 22.5°). Comparisons were made with natural scene movies, which consisted of clips of high contrast black & white film. The clips were obtained from a Super 8 shooting, and consisted of highly grained images of a football game (see Figure 16). Correlation analysis of the responses revealed robust gamma for the gratings that matched the preferences of the recorded neurons (Figure 16, green dots in the tuning curves insets). Notably, gamma oscillation frequency invariably decreased over time, reaching a plateau about 400 ms after stimulus onset. Similar trends could be observed for the individual channels and also for the cross-correlogram (in this case, RFs were partially overlapping, at about 10°
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of eccentricity). Oscillation frequency mean was around 53 Hz (55.4 Hz for channel 1 and 52.1 Hz for channel 2). In sharp contrast to gratings, the natural scenes movies elicited no gamma responses, as the individual autocorrelations (computed for each channel) and the cross-correlograms were flat (Figure 16, lower panels). The shift predictor controls computed for all conditions were also flat (not shown in the figure), indicating that the strong gamma responses induced by the gratings arouse from neural coordination and could not be explained as mere entrainment of the responses to the computer screen (refresh rate of the screen, 100 Hz).

Analysis of the LFP signals yielded similar results. As shown in Figure 17, the power spectrum of LFP responses recorded from the same electrodes exhibits a high amplitude, narrow-band peak at 52 Hz only for the gratings stimuli (presented at the optimal direction). For the responses to natural scenes movies, the spectral components at the gamma-band were absent. These dramatic differences in the LFP reflected the results obtained for the spiking responses. Interestingly, a robust peak at 21 Hz (beta band) was observed invariably for both stimulus conditions, observing that in the present task the monkeys were required to maintain fixation over several hundred milliseconds. Thus, contrary to the conclusions of Ito et al. (2011), robust beta activity in capuchin V1 may arise even in the absence of saccadic eye movements, during a passive task.

4.3. Does the viewing condition make a difference?

A primary goal in this study was to compare gamma responses for gratings and natural scenes stimuli during two distinct viewing conditions: (1) prolonged fixation and (2) free-viewing. We used a paradigm that the required the monkeys to first hold the eyes for a few seconds and than, after a brief blank period, let them freely scan the images or movies. So, we could make comparisons within the same trial for the two viewing conditions.
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Figure 18 presents raw LFP data (single sweeps) showing the dramatic effects of gratings stimuli on the oscillatory dynamics of the responses. After stimulus onset, the LFP begin to exhibit regular, high amplitude fluctuations, at the gamma-band (around 50 Hz in this case). Observe how oscillation frequency slowly changes over time. Gamma frequency is higher at the beginning of the response, becoming gradually slower towards the end of the trial (asymptote is reached.

Figure 18. Comparisons of raw LFP traces obtained during maintained fixation (from 500 to 200 ms) and free-viewing (2500 to 4500 ms) conditions for gratings (upper trace) and natural scenes (lower trace). Notice the strong, high-amplitude fluctuations of the LFP in responses to gratings during the prolonged fixation. For the natural scenes, although the stimulus was as the gratings at an optimal direction, gamma oscillations were comparatively weaker or absent.
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Figure 19. Gamma responses to a gratings at optimal direction during FIX and FREE epochs. Left panel, average sliding window analysis. Upper right panels, average autocorrelation function computed within a fixed 500 ms window (vertical lines in the sliding-window plot). Bottom panels, multitaper spectral analysis. Notice the strong and persistent gamma oscillation during the FIX epoch. Strong gamma is also evident for the FREE epoch.

Figure 20. Gamma responses to static vs moving gratings, FIX-FREE paradigm. Upper panels, static gratings. Lower panels, drifting gratings. Notice that gamma is invariably stronger for a moving gratings. Both stimuli were shown at the preferred orientation of the cells. Oscillation frequency was slightly higher for the dynamical stimulus. Analysis was made after detection of the fixation periods (in collaboration with Adrien Brilhault) and does not include the saccades.
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around 200 ms after). Gamma is strongly dependent on the presence of the stimulus. Upon the first saccade, when the stimulus and fixation point disappeared on the screen, the ongoing gamma of the LFP ceases abruptly.

Correlation and spectral analysis of spiking responses (Figures 19 to 22) confirm what we observed in the LFP. Independent of the viewing condition, gratings stimuli are capable of generating a reliable and robust gamma oscillation, whenever the orientation of the gratings match the properties of the cells. Natural scenes, in general, did not evoke any gamma oscillatory responses. It is important to stress that the differences in gamma for the two stimulus conditions were dramatic, even though the firing rates did not differ so much.

These effects were observed for a fixed window analysis (Figures 19 and 22), but taking into account only the fixation periods (after analysis of the eye movement data, Figures 20 and 21). In the latter case, the correlograms tended to assume a triangular shape, since the mean fixation period (around 150 ms) had a value near the time lag used to compute the correlograms (-80 to 80 ms). Despite

Figure 21. Gamma responses to gratings vs natural scenes, FIX-FREE paradigm. Gamma, which appear very robust to gratins, is completely absent from the responses to natural scenes. The differences are dramatic. Analysis was made after detection of the fixation periods and does not include the saccades.
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these methodological limitations, a clear modulation was seen in the correlograms for the grating stimuli, even in the free-viewing condition.

Figure 22. Gamma responses to gratings vs natural scenes, FIX-FREE paradigm, comparisons across monkeys. Notice that the strong gamma responses for the gratings during the Fix epoch. In contrast gamma is absent for the responses to natural scenes, both during the FIX and FREE epochs. Data obtained for two monkeys (recordings were made in V1 at the central representation in Monkey 3, and at the peripheral representation in Monkey 2). Analysis was made for fixed 500 ms windows as indicated in the sliding-window plots.
Figure 23. Gamma modulation to gratings vs natural scenes, FIX-FREE paradigm, population data. Gamma modulation amplitude obtained for all recording sites (N = 51 recording sites, 2 monkeys) during presentation of gratings and natural scenes both for during maintained fixation and free-viewing conditions. Only 3 recording sites showed gamma oscillation for natural scenes stimuli, all during the maintained fixation epoch.

Figure 24. Gamma in response to textures stimuli. Texture stimuli were made by the superposition of gabor patches at different orientations (jitter in orientation increases from 10° to 90°). Notice that gamma decreases with the increase of complexity of the stimulus (from A to D).
Population results are presented in Figure 23.

To show how sensitive gamma is to the orientation of the gratings we created texture stimuli made of the superposition of Gabor patch elements. By introducing a jitter in the orientation of each element, we could build stimulus patterns of varying complexity (from pure gratings to multiple orientation components textures, Figure 24). Correlation analysis shows that introducing a jitter in the orientation had an enormous impact on gamma, both in the FIX and FREE viewing conditions. These results reinforce the notion that gamma is a special-class dynamics which emerges from the massive activation of cells in V1 sharing the same tuning properties.

4.4. FREE-VIEWING OF REAL-WORLD SCENES

In a series of experiments, we allowed the monkeys to inspect freely real-world scenes (for example, a monkey sitting in a monkey-chair and eating dry spaghetti) while recording the neuronal responses in V1. This approach, albeit less controlled, provided us with valuable data for the naturalistic condition since it allows for high attentional

Figure 25. Eye movement data obtained during free viewing of real-world scenes. In this case the monkey was freely observing another monkey (in this case a monkey in a monkey chair, eating spaghetti). Left plot, eye movements showing periods of fixation (ordering numbers) and saccades (10 seconds recording). Right plot, distribution of fixation durations.
load, contextualized stimuli, bridging multiple dimensions in perception (visual-auditory integration, active vision). Moreover, real-world objects carry important visual features that can be only inferred from images displayed on computer screens, such as texture, shading, and 3D. As documented by the eye movement data shown in Figure 25, the monkeys actively explored the real-world scenes.

The results we obtained in this overtly naturalistic condition were surprisingly negative. Cross-correlation analysis of spiking responses yielded flat correlograms, indicating that gamma activity was largely absent in V1 during free-viewing of real-world objects and scenes. In the example shown in Figure 26, the correlations were computed after parsing of the eye movement data (saccadic and eye blinking events were excluded from the analysis), encompassing only the fixation periods.

Overall, these negative findings confirmed our previous results, showing dramatic differences in gamma for the gratings stimuli as compared to any other stimulus (textures, images, natural scenes movies, real-world scenes).
Figure 26. No gamma for responses to real-world scenes. Autocorrelation and cross-correlation analysis. Gamma is completely absent in the spiking responses. Recording sites at the peripheral representation in V1, overlapping RFs. Analysis was made after detection of the fixation periods (in collaboration with Adrien Brilhault) and does not include the saccades.
5. DISCUSSION

5.1. CAPUCHIN V1 DOES SHOW GAMMA RESPONSES

Recent studies of temporal coding in the primary visual cortex of capuchin monkeys using a free-viewing paradigm led to some unexpected results. Analysis of spiking responses using unitary event analysis (Grün et al., 2010) showed neuronal synchronization related to the saccades, without signs of gamma activity (Maldonado et al., 2008). Moreover, a more recent analysis of the same data set (Ito et al., 2011), showed modulations in the LFP modulations concentrated in the beta-(centered at 13-16 Hz), but not in the gamma-band. These results are in contradiction with the results of Brunet et al., (2013). Using a free-viewing paradigm similar to Maldonado et al., 2008, the authors show in ECoG signals robust gamma responses to natural scenes. This paradox is difficult to conciliate with the fact that gamma oscillations have been found across many species (see Introduction), including an another new-world-monkeys species, the squirrel monkey (Livingstone, 1996).

Our present results clarify some of these apparent discrepancies. First, gamma oscillations are robust mostly for responses to grating stimuli (or bars). Different from the study of Livingstone (1996) in the squirrel monkey, or several other studies in the macaque, Ito et al. (2011) have never employed gratings in their studies in capuchin V1. As pointed out before, simplified stimuli such as light bars, dots, and gratings are known to evoke strong responses in the gamma-band in monkeys and cats (Eckhorn et al., 1988; Feng et al., 2010; Gieselmann; Thiele, 2008; Gray et al., 1989), but also in humans (Self et al., 2016, Figure 27). Thus, the absence of gamma oscillation in the absence of grating stimuli should not be a surprise. In our study, for the majority of recording sites (23 out of 51 recording sites), gamma oscillations were particularly high and sustained for responses to gratings presented at the optimal direction, both during the fixation and free-viewing epochs. Even when gratings were presented at the
orthogonal direction, some recording sites showed gamma responses (20 out of 71 recording sites), although with lower modulation amplitude and power, in accord with previous studies in the cat (Gray et al., 1990).

It is also important to emphasize that in the Maldonado’s experiments the monkeys were not required to maintain fixation for a long period. For decades, the study of vision has been driven by a paradigm that employs a fixation point to control for the eye movements and stabilization of the image in the retina. Although it may seem unnatural to maintain the eyes fixed for several seconds, this viewing condition proved to be the best choice to ramp up cortical gamma. Experiments using a more naturalistic approach, on the other hand, are not completely established yet, and findings are still inconclusive. Another problem is the fact that none of the studies of Maldonado employed receptive mapping techniques. Thus, in their study, the precise position of the RFs was largely unknown. Finally, another potential problem was the use chronically implanted electrodes, which probably led them to record the activity from infra-granular layers. It
was demonstrated by a previous study (Buffalo et al., 2011) that synchronization at gamma-band frequency varies with layers from visual cortical areas (V1, V2, and V4). Gamma frequency was predominant in superficial layers, whereas infra-granular layers showed synchronization at the alpha and beta (6-16 Hz) frequency ranges.

Our results conclusively show that the neuronal dynamics of V1 responses in the capuchin monkey are very similar to those found in the macaque. There is a dramatic increase in gamma modulation with increasing stimulus size. As stimulus size increased, also did increase the strength of the inhibitory surround, which caused a reduction in firing rates. These results are in line with earlier reports in macaque monkeys (Gieselmann; Thiele, 2008; Ray; Maunsell, 2011). Furthermore, our data also showed a decrease in oscillation frequency, an effect also observed in the macaque by Gieselmann and Thiele (2008). Neuronal responses in capuchin V1 depend on stimulus speed, showing an increase in oscillation frequency with the increase of velocity. Similar results for speed selectivity were reported in macaque monkeys (Eckhorn et al., 1993; Lima et al., 2010) and cats (Gray et al., 1990). Finally, as in other studies that analyzed interactions between gamma frequency and orientation selectivity in the macaque (Frien et al., 2000; Womelsdorf et al., 2012), our results show a strong dependency between modulation amplitude of gamma frequency and orientation selectivity.

Overall, our findings point to the notion that gamma depends not only on the properties of the stimulus but also on the visual map. Accordingly, capuchin monkeys share with macaques a similar topographic organization of the primary visual cortex (Gattass et al., 1987). Our study is the first to demonstrate that the visual cortex dynamics is also very similar across the two species. These new findings in a new-world monkey reinforce the notion that the functional architecture of the visual cortex may constrain the neuronal dynamics more than expected before.
5.2. Artifactual Dynamics from Artificial Stimuli?

Our data emphasize the concept that synchronization at gamma-band frequency induced by gratings, especially for optimal orientation, is a special-class cortical dynamics. In real-world conditions, as for stimuli such as natural scenes, movies of natural scenes and textures, gamma synchronization was weak or absent.

These results make us ask why visual cortical gamma is so special? The bulk of experiments that link gamma to cognitive processes, such as perceptual binding and attention, is based on paradigms that used artificial, simplified stimuli, such as moving bars, dots and gratings (Eckhorn et al., 1988; Feng et al., 2010; Gray et al., 1989, 1990; Gray; Singer, 1989; Woelbern et al., 2002; Womelsdorf et al., 2006). Gratings are a unique class of stimulus because they have a fixed spatial frequency, contrast, and orientation. In the past, Campbell and Robson (1968) argued that the visual system could analyze an image using a Fourier-based process. Gratings stimuli selectively activate large populations sharing the same properties within columns in the visual cortex, which are preferentially connected (Schmidt et al., 1997).

Studies using more complex stimuli led to divergent conclusions. Experiments with a superimposed bar-stimulus approach have been used to test the scene segmentation (Engel; König; Singer, 1991; Gray et al., 1989; Kreiter; Singer, 1996). Recordings were obtained for groups of neurons with overlapping receptive fields but differing in their selectivity for the direction of movement of the stimulus. Responses from a single-bar stimulus in an intermediate orientation between the two receptive fields were used as a control, known to evoke gamma response. Indeed, when presenting a single-bar stimulus, cross-correlation showed oscillation in the gamma range. However, gamma synchronization was absent when two separate bars with optimal movement direction for each group of neurons were presented. Kreiter and Singer (1996) analyzed the neuronal dynamics of the middle temporal area (MT) from two alert macaque monkey,
whereas Engel et al. (1991) recorded from Area 17 of eight anesthetized cat visual cortex. It has been suggested that these findings were due to active neuronal processes and not in response to feature characteristics of the stimuli, in support to the binding by synchrony (BBS) hypothesis.

Also, paradigms with plaids were used in an attempt to test the BBS hypothesis. Plaids are stimuli formed by superimposed gratings in different orientation or direction of motion and are ideal for the sustained activation of neurons and luminance manipulation, which can lead to the creation of two segmented surfaces crossing upon each other in a non-coherent manner, or a single pattern. Castelo-Branco et al. (2000) analyzed visual responses in anesthetized cats in response to pattern coherent and non-coherent plaids, and reported synchronization for coherent plaids (pattern motion of the plaids), but not for non-coherent plaids (component motion of the plaids). Nevertheless, using similar stimuli, other studies have come to contrary results (Lima et al., 2010; Palanca; DeAngelis, 2005; Thiele; Stoner, 2003). Lima et al. (2010) studied V1 of four awake monkeys using plaids, and an innovation of their work was a delayed superposition of the second grating in the formation of plaids. Evidence of synchronization at gamma-band frequency was found when the first component of the plaids appeared, as it occurs to optimal moving gratings. With the presentation of the second plaid component, oscillation was interrupted, without a drop in the firing rates. Even with gradual appearance of the second component, a strong attenuation of oscillation power and a shift in oscillation frequency was observed, demonstrating that the remaining oscillation could not be attributed as a sustained response for the first component.

Furthermore, textures were presented to V1 of alert monkeys, and synchronous response for nearby and distant recording sites showed similar results, even though the responses signalized an object or the background (Lamme and Spekreijse, 1998).

In a more naturalistic paradigm using faces as stimuli, Tovee
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and Rolls (1992) have not found any oscillatory pattern in the responses, in disagreement with the BBS hypothesis. Finally, a now-classic study in the awake cat compared the gamma dynamics for several stimuli, including gratings, pink noise and a natural scenes movie made while a camera was placed on the top of the cat's head (Kayser et al., 2003). Results showed a broad-band LFP power increases between 100 and 200 Hz for movies and pink noise. On the contrary, the responses for grating showed a narrow-band gamma frequency (40-80 Hz). Our data in the capuchin monkey fully confirm these observations in the cat. Altogether, these results weak the notion that gamma is necessary for perceptual binding.

5.3. DOES GAMMA PLAY A ROLE IN VISION?

Our paradigm could disentangle two confounding factors: (1) the stimulus per se (gratings or natural scenes) and (2) the viewing condition (fixation or free-viewing).

A novel contribution in our study is the use of gratings in a free-viewing condition. Our correlation analysis demonstrates a pronounced gamma modulation amplitude after stimulus onset for optimal moving gratings (23 of 51 recording sites). On the contrary, natural images did not induce such a strong oscillatory synchronization pattern. We have seen signs of gamma for natural scenes rather exceptionally, in a few recording sites (4 of 51 recording sites). In all these cases gamma appeared during the fixation epoch and for images moving at the optimal direction. In none of these cases we have seen gamma in the free viewing epoch.

Previous work of Gallant et al. (1998) used a similar paradigm consisting of gratings displayed during a fixation period, and natural images in both viewing conditions. In this study, however, the authors only analyzed modulation in firing rate associated with eye movements. Moreover, gratings stimuli were used just as a control condition during the fixation periods, and not during free viewing. Another study in V1 of macaque under free viewing conditions used a light bar embedded
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within a natural scene or a uniform gray background. The authors report that responses “tended to be higher with a uniform rather than natural background” (MacEvoy, Hanks e Paradiso, 2008). This latter work did not follow oscillatory patterns either.

The use of a passive fixation task in visual paradigms has been criticized by not providing attentional engagement to the stimulus. In our work, the prolonged fixation epoch was important as a control condition for gratings but essential to test whether this type of stimulus-induced gamma oscillations and thus encoded information, as the CTC hypothesis predicts.

In our experiments, the absence of gamma for natural images is in accord with the study of Ito et al. (2011). In this study, the LFP responses to static natural scenes were largely dominated by the beta-band (around 20 Hz) and not the gamma band. These results differ from those of Brunet and colleagues (Brunet et al., 2015). In their work, in particular, images of oranges and bananas were capable of inducing surprisingly high gamma-band oscillations. The authors argue that “the particularly strong gamma-band activity might be due to the familiarity and the appetitive character of these stimuli.” We find this interpretation insufficient, since the monkeys in laboratory receive their fruits in pieces or slices, and not the whole fruit as used for stimulus presentation. It is unclear whether the monkeys recognized or not the

Figure 28. ECoG responses to gratings and different types of noise in humans. The gamma oscillations can be conspicuous and robust, but because they are absent for many stimuli, which observers can see and recognize. We can conclude that gamma is not necessary for vision. Modified from Hermes et al., 2014.
oranges and bananas when present on a screen monitor. Even though, in our study, images of watermelon and orange slices were presented, and despite a large number of times they were shown, gamma oscillation pattern was not induced during the free-viewing epoch.

Furthermore, another significant difference between our studies from Brunet et al. (2015) is the nature of the recorded signals. In our study, we recorded spiking activity, while Brunet et al. obtained population ECoG signals.

Finally, our results are corroborated by a previous study in the human visual cortex (V1/V2/V3) using ECoG arrays (Hermes et al., 2015; Figure 28). This study shows a strong narrow-band gamma oscillation for gratings stimuli and a broad-band non-oscillatory pattern (80–200 Hz) for textures, natural images, and noise. As discussed by Hermes et al. (2015b), the few cases we could observe gamma responses for natural scenes are more likely to be related to the spatial structure of the images. Overall, these studies do not support the current notion that gamma oscillations are necessary for vision.
6. CONCLUSION

In this study, we show for the first time that gamma in V1 of capuchin monkeys share the same general properties as those found in macaques and humans. Gamma depends on stimulus size, orientation, and speed. Size and speed also impact on gamma frequency: bigger the stimulus, slower the oscillation; faster the stimulus, faster the oscillation. These similarities reinforce the notion that capuchins, macaques, and humans share a profound kinship in their functional organization of the visual system, despite the fact that Platyrrhines split from Catarrhines at around 35 MYA. Moreover, we show that grating stimuli presented at optimal conditions are exceptional in inducing long-lived, high-amplitude gamma responses. Complex stimuli, which likely activate large populations with different response preferences, such as images, movies or textures, elicit weak or no gamma. These results could be verified in both maintained fixation and free-viewing conditions. Notably, when the monkeys were exposed to real-world scenes, a condition that unequivocally requires a high attentional drive, gamma was absent from the spiking responses. Overall, these results weaken the notion that gamma is necessary for natural vision.
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8. TABLES

<table>
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<th>Monkey</th>
<th>Tuning protocol</th>
<th>N of recording sites (RS)</th>
<th>Range studied</th>
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<td>Real task</td>
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