Université Paul Sabatier TOULOUSE III

M2 NEUROSCIENCES, COMPORTEMENT, COGNITION

Sélectivité à l'orientation des neurones
du cortex visuel primaire :
une étude psychophysique

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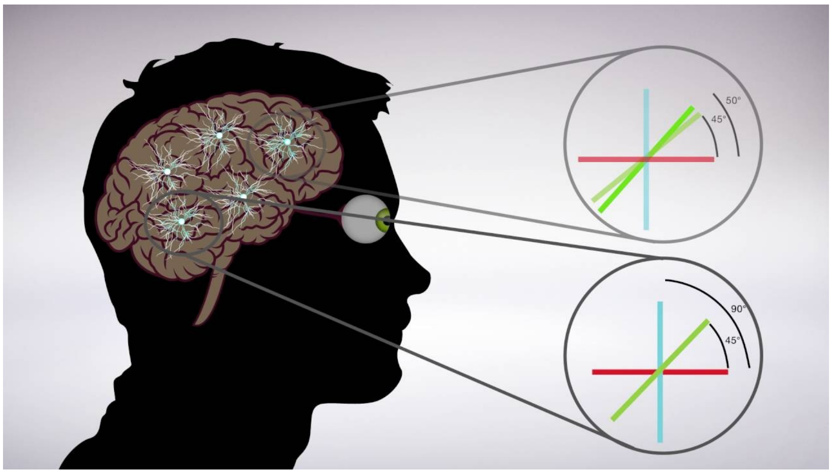

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Avant propos

Ce rapport comporte 14 pages dont 9 figures. Les codes informatiques utilisés pour réaliser l'expérience de psychophysique ainsi que l'analyse des données sont en accès libre sur https://github.com/jennafradin/MSc-Internship sous la forme de notebook commentés, accompagnés de figures.

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Résume

L’aire visuelle primaire (V1) est l’une des régions les plus caractérisées du cortex de part son implication centrale dans le traitement de l’information visuelle. Les neurones de V1 sont sélectifs pour de nombreux attributs dont l’orientation, la direction du mouvement ou la fréquence spatiale et temporelle. Cette sélectivité à l’orientation des neurones du cortex visuel primaire est l’une des propriétés les plus étudiées mais les mécanismes qui sous tendent cette sélectivité restent encore incomplètement compris.

Dans le but d’en savoir plus sur ces mécanismes, nous avons mené une expérience de psychophysique sous la forme d’une tâche de discrimination. Des textures orientées pseudo-aléatoires appelées Motion Clouds (MC) étaient présentées aux participants et ils devaient deviner l’orientation de ces patterns. Nous nous sommes focalisés sur 4 paramètres impliqués dans la génération des MC à savoir l’angle d’orientation, la fréquence spatiale, la largeur de bande (orientation bandwidth) et la largeur de bande de la fréquence spatiale (spatial-frequency bandwidth). A chaque session et pour chaque essai, nous avons fait varier ces 4 paramètres. Chaque participant a réalisé 3 sessions de 750 essais. Nous avons recueilli les données et généré les courbes psychophysiques associées.

Nous observons que la largeur de bande influence l’acuité à discriminer l’orientation. En effet, plus celle-ci est importante plus la précision de l’orientation diminue et il devient donc difficile de deviner l’orientation des pattern. Ce seuil de discrimination en fonction du bruit ne semble varier de façon linéaire avec la largeur de la bande. La fréquence spatiale a tendance a diminué également le seuil de discrimination. Aussi, la largeur de bande de la fréquence spatiale lorsqu’elle est augmentée diminue les performances des participants à la tâche de discrimination pour des petites largeurs de bande. Ce comportement est la signature d’un mécanisme neural potentiellement nouveau dans V1.

Nous avons mis en évidence ici le rôle de différents paramètres d’une image orientée sur la capacité à discriminer son orientation.

Introduction

One of the main objectives of Neurosciences is to understand how the sensory inputs we receive are integrated with our expectations about the world around us to generate behavior. As visual sensory information travels through our nervous system, it undergoes transformation in its representation. First, the visual sensory information reaches the photo-receptors, which are neurons specialized on the reception and conduction of visual stimuli found in the retina. Than, this information is converted into an electrical stimulus that travels to other retinal layers through neurotransmitters. From photo receptors, this impulse is transmitted to the bipolar cells and then reaches the retinal ganglion cells. The retinal ganglion cells relay the electrical message to the lateral geniculate nucleus (LGN). Each layer of the LGN receives informations from the retinal hemi-field of one eye.(De Moraes, 2013). The LGN, which in primates receives the majority of the output of the retina, relays this visual information to the first neocortical visual area, the primary visual cortex. V1 is the site where the neural representation of the visual world undergoes drastic transformations and this profound changes along the visual pathway has positioned V1 as a system model for studying the circuitry that underlies neural computations across the neocortex. V1 neurons are sensitive to multiple visual stimulus attributes including contrast, temporal frequency or orientation and this selectivity is in many cases exquisitely sensitive (Priebe, 2016).

Orientation selectivity was first described by D. Hubel and T. Wiesel by recording electrical activity of neurons in the cat visual cortex. They demonstrated that neurons in adult visual cortex of cats respond with the highest firing rates to preferred oriented stimuli. They also showed that preferred orientations of neurons are organized in a specific pattern, where cells with similar selectivity are clustered in iso-orientation domains also known as orientation columns (Hubel & Wiesel, 1962). In mammals, this orientation columns are arranged smoothly, with the preferred orientations shifting in a graded manner. Neurons with close orientation selectivity are located next to each other (Zhang et al., 2018).

Being simple and tractable, the orientation selectivity is one of the most investigated sensory feature in the mammalian brain. However, its underlying neural mechanisms are still not completely understood. Many competing theory have been proposed for which no consensus has been reached. These theories are often based on recordings or psychophysic experiment with simple artificial stimuli such as straight bars or gratings.

But the classical toolbox of standard stimuli is largely outdated and insufficient to understand how the primate brain achieves an efficient visual processing in a short time.

The choice of the type of stimuli (artificial or natural) to be used for the study of the primary visual system continues to be debated today. Natural images are complex, with many parameters that are difficult to control, but the use of natural stimulation avoids unnatural bias that can come from artificial stimulation (Olshausen & Field, 2005). Artificial stimuli are easily controllable and allow to test particular characteristics present in natural images such as oriented edges, spatial frequencies, but they sometimes remain too simplistic. The aim is to increase the complexity of artificial stimulation yet keeping a reasonable numbers of parameters.

Here, we will propose to generate optimized synthetic textures in order to separate the different theories of representation of orientation in V1. The objective is to study in more detail the influence of different parameters such as bandwidth or spatial frequency on this selectivity by carrying out a psychophysic experiment.

Methods

a. Participants

Five healthy volunteers (1 author and 4 participants naive as to the purpose of the experiment, age 23.2 ± 0.25, 3 female) with normal or corrected-to-normal vision took part of the experiment. The experiment was carried out according to the ethical standards specified in the Declaration of Helsinki.

b. Stimuli

Visual stimuli had to be less complex and more controllable than natural images but effective enough to elicit a sufficient response. We chose to work with natural-like random textures called Motion Clouds (Leon et al., 2012). Motion Clouds (MC) are synthetic oriented textures who model the distribution of orientation in natural visual scene. MC can be easily controlled by playing with different parameters and we decided to focus on 4 different parameters: the orientation angle θ**,** the orientation bandwidth B_{θ}**,** the bandwidth spatial frequency B_{sf} and the spatial frequency *sf.* θ is drawn from a uniform distribution ranging between π/8 and π/8 with respect to vertical, B_{θ} drawn from a uniform distribution ranging between 0 and π/3, the spatial frequency bandwidth Bs_f also draw from a uniform distribution ranging between 0.06 and 1 cpd and *sf* ranging between 0.01 and 0.125 cpd fig.1). The Stimuli were generated online and a new stimulus was generated for each presentation.

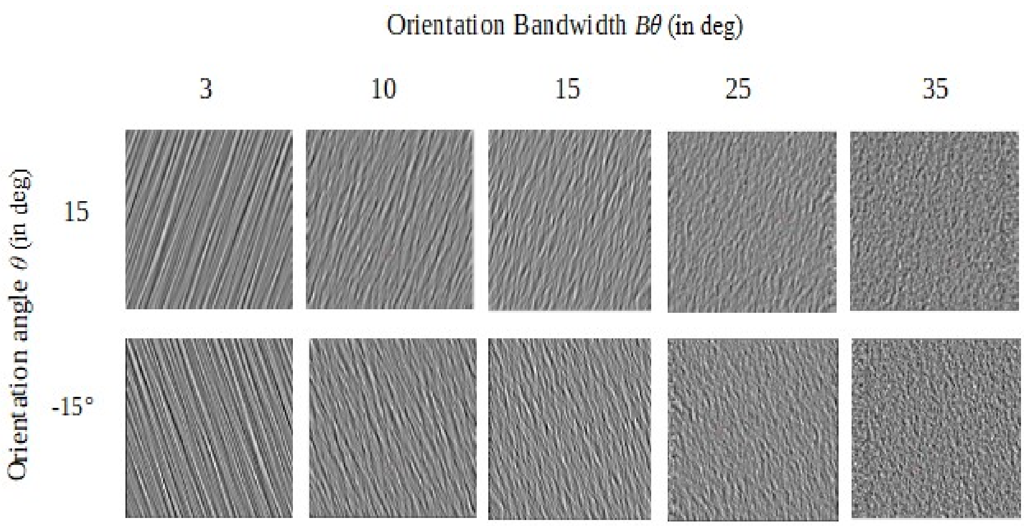


Figure 1. Representation of the visual stimuli: Motion clouds are random textures imitating natural pattern. Here, we illustrate the effect of increasing the orientation bandwidth B_{θ}.

c. Apparatus

Psychophysical protocol was controlled using PsychoPy 3.2.4 (Peirce, 2007). Participants had to do the experiment with their own computer.

d. Procedure

The target used in the experiment was a static MotionCloud (20° diameter) that was presented at the centre of the screen, on a grey background. Each trial started with a central fixation cross displayed for 250 ms. Then the target was presented in the centre of the screen for 250 ms. After that, the participant had 500ms to report the pattern's orientation they perceived using the mouse. If the orientation was clockwise of the vertical, they had to move the mouse to the right; otherwise they had to move it to the left (fig.2).

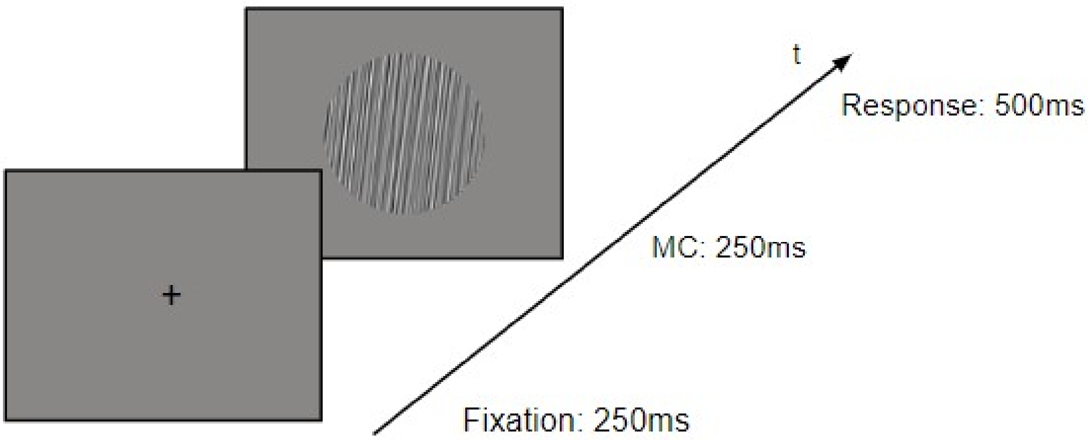


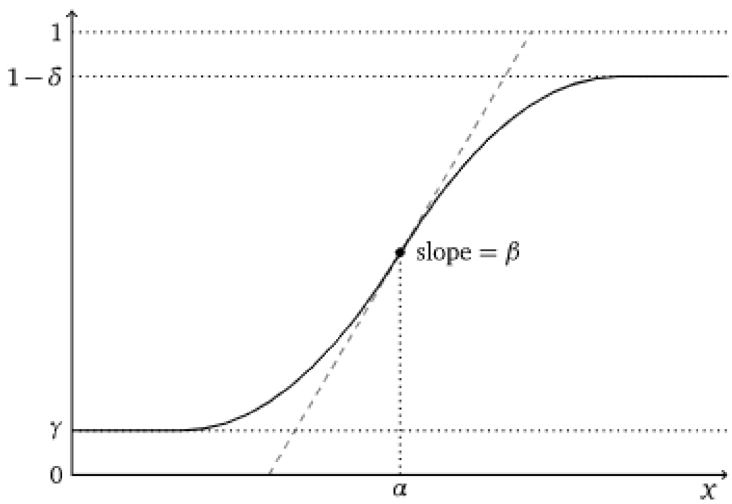
Figure 2. Two-alternative forced choice task design. Orientation acuity (discrimination threshold) was measure at various combinations of angle orientation, spatial frequency, spatial frequency bandwidth and orientation bandwidth of the oriented stimuli.

Each participant had to perform 3 sessions of 750 trials:

- first session: for each trial, B_θ was randomly chosen out of 5 possibilities and θ out of 30 possibilities. B_{sf} (0.5 cpd) and sf (0.125 cpd) were fixed
- second session: for each trial, B_θ and B_{sf} were randomly chosen out of 5 possibilities and θ out of 30 possibilities. Sf (0.125 cpd) was fixed.
- third session: for each trial, B_θ and sf were randomly chosen out of 5 possibilities and θ out of 30 possibilities. B_{sf} (0.1 cpd) was fixed.

e. Fitting

In psychophysics, subject responses in the psychophysical task constitute binary data: correct/incorrect or yes/no. The function relating the behaviour on a given psychophysical task to some quantitative characteristics of the stimulus (length, luminance or spatial frequency) is called the psychometric function. The shape of this curve is determined by the slope and the threshold (fig.3). The goal is to find the distribution that fits the best to our sample data.



However, fitting the psychometric curve can be a difficult task and if it is not well done it can lead to serious bias. Participant can make incorrect responses which are independent of stimulus intensity. The probability of this carelessness errors is called the lapse rate. The lapse rate is always low (in the order of 5% to 10%) but it has been shown that the threshold and slope estimate of a psychometric function may be severely biased when it considers equals zero but lapse does in fact occur (Wichman & Hill, 2001).

In order to limit this type of bias, we have performed a preliminary theoretical analysis. We first generated synthetic data corresponding to participants binary responses to a two alternative forced choice task, we added a lapse rate ($\delta = 0.1$). Than we defined a fitting method using Pytorch (https://pytorch.org/) and we included in the model a metric corresponding to the lapse rate. We also defined an other fitting method using Sklearn (https://scikit-learn.org) not-including the lapse rate than we draw the dataset and plot the psychometric curves obtained by the two different method (fig.4). It shows the importance of including the lapse rate in the model to increase the goodness of fit. We kept the Pytorch model to fit the future psychometric curves to our actual experimental data.

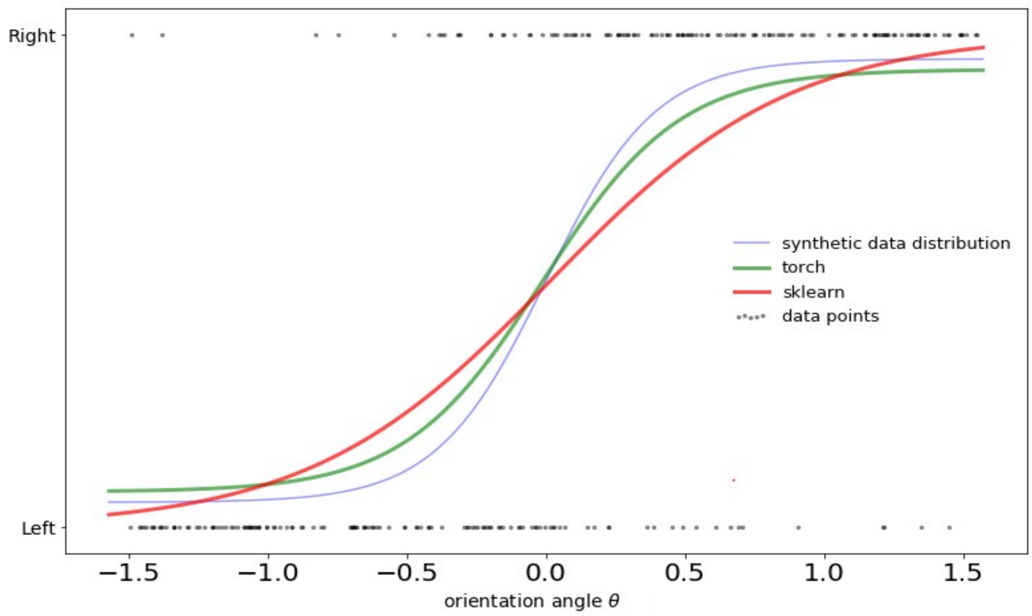


Figure 4. Qualitative comparison of the two methods. In blue: distribution of our synthetic data, in green: the psychometric curve obtained with the Pytorch model including the lapse rate, in red: the psychometric curve obtained with the Sklearn model non-including the lapse rate, in black: data points. The goal is to find the curve that fits the best with the synthetic data distribution that is normally unknown. The torch model seems to find the best.

Results

The analysis of the data obtained from the psychophysics experiment is based on the study of the slope of the psychometric curve obtained with our model (see'Methods- Fitting').

Overall, the percentage of correct responses from participants is 80.5% ± 6.2 (mean ± standard deviation) for the first session, 74.1% ± 5.4 for the second session and 71.5 % ± 5,2 for the third session.

Concerning the results of the first session where we only modified the orientation angle and the orientation bandwidth of the MC, we noticed the accuracy was the best for B_θ lower than 36° and it undergoes a collapse for B_θ greater than 36°. So if we increased the orientation bandwidth, we lowered the slope, in other words the lower the precision of the orientation, the higher the error (fig.5). The discrimination threshold as a function of the precision did vary smoothly as would be expected .

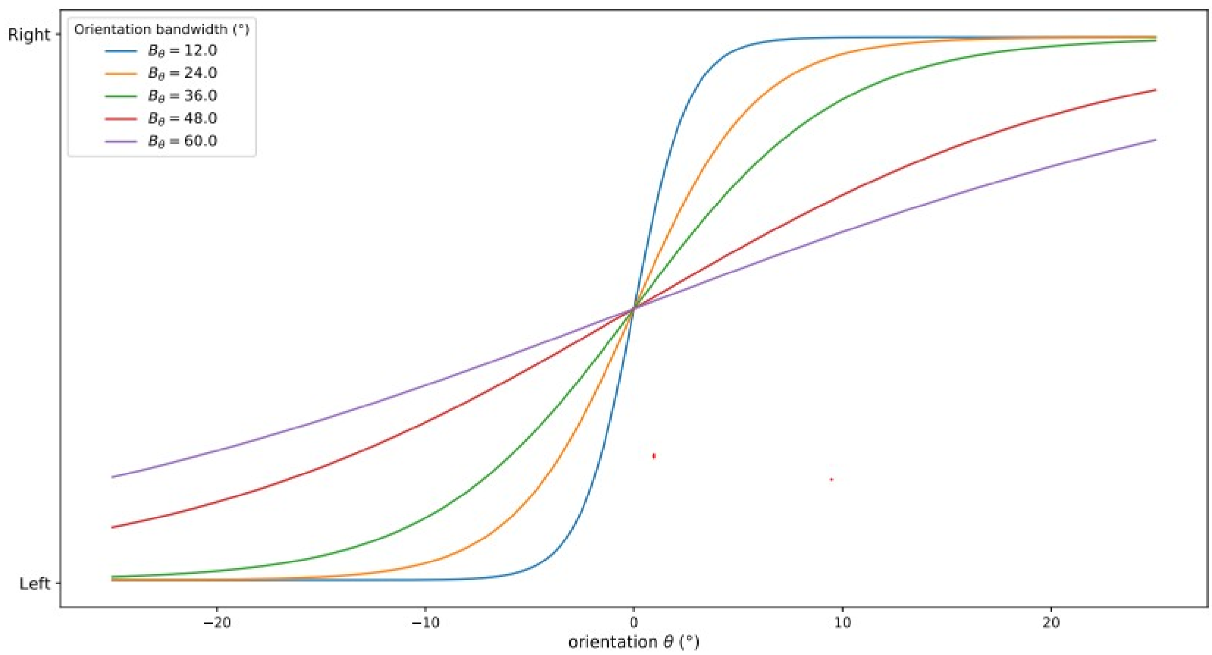


Figure 5. Psychometrics curves of the participant JF as a function of the orientation bandwidth B_θ (12-60°). Curves were fitted based on 750 stimulus-response pairs. The more vertical the curve, the better the results. Here the slope of the curves increases with the orientation bandwidth.

Another way to represent the data is to show the evolution of the log of the curve as a function of the orientation bandwidth (fig.6). A high log slope means discrimination error is significant. The results are quite similar, the slope increases with the orientation bandwidth. from a log 0.5 to log 1.3 for a bandwidth between 4 and 40° than for a bandwidth greater than 40°, we observed a sharp augmentation from log 1.5 to log 3.2.

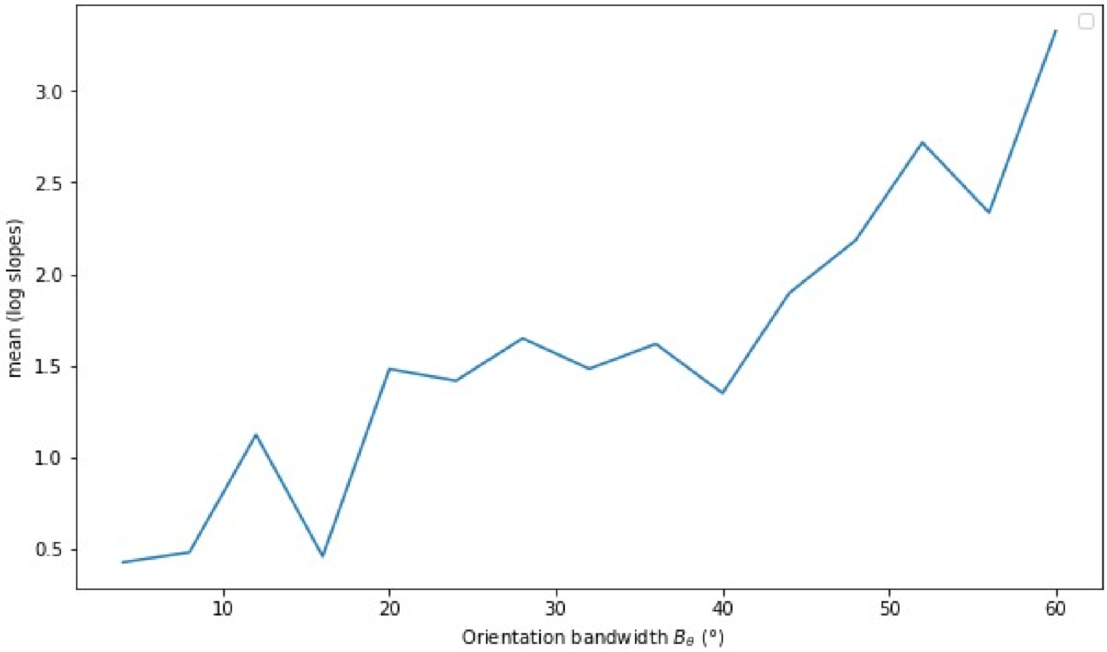


Figure 6. Mean log slope of all the participant (N=5) as a function of the orientation bandwidth (in deg).

In the second session we changed the orientation bandwidth, the orientation angle and the spatial frequency bandwidth. We observed the same behavior: the error rate increase with the bandwdith. Despite noisy results, it seems that the more the spatial frequency bandwidth increases, the more orientation discrimination errors participants make. (fig.7).

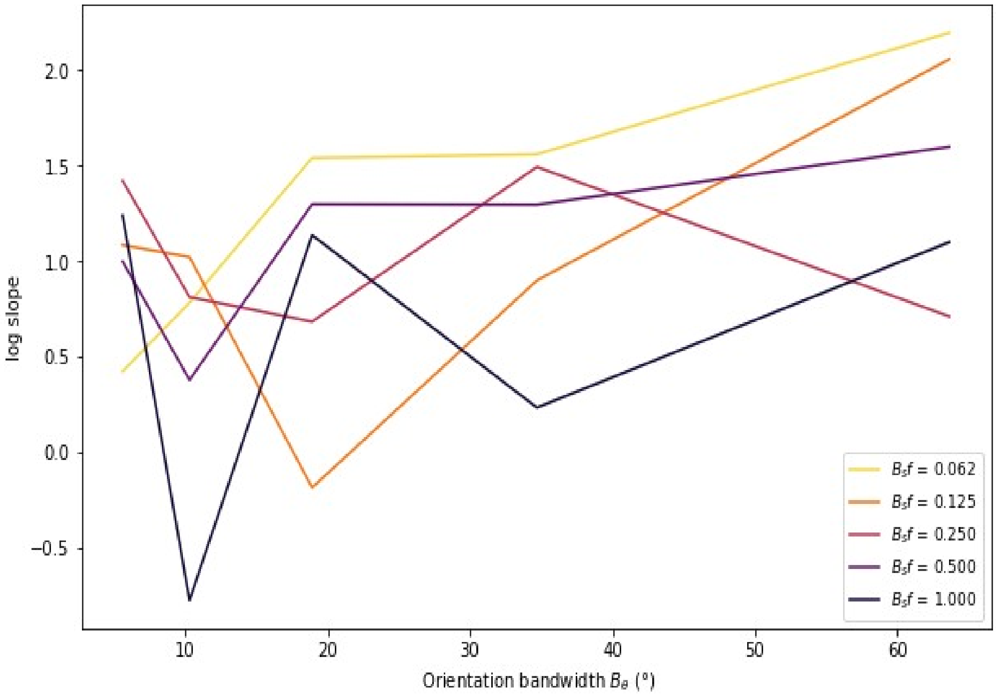


Figure 7. Mean log slope of all the participant as a function of the orientation bandwidth (3-60°) and the spatial frequency bandwidth (0.062-1 cpd).

For the third session results, we observed a similar profile which is that the error rate increased with the orientation bandwidth. Concerning the spatial frequency of the MC, the accuracy seems is the best for smaller spatial frequency (Sf > 0.016 cpd). (fig.8).

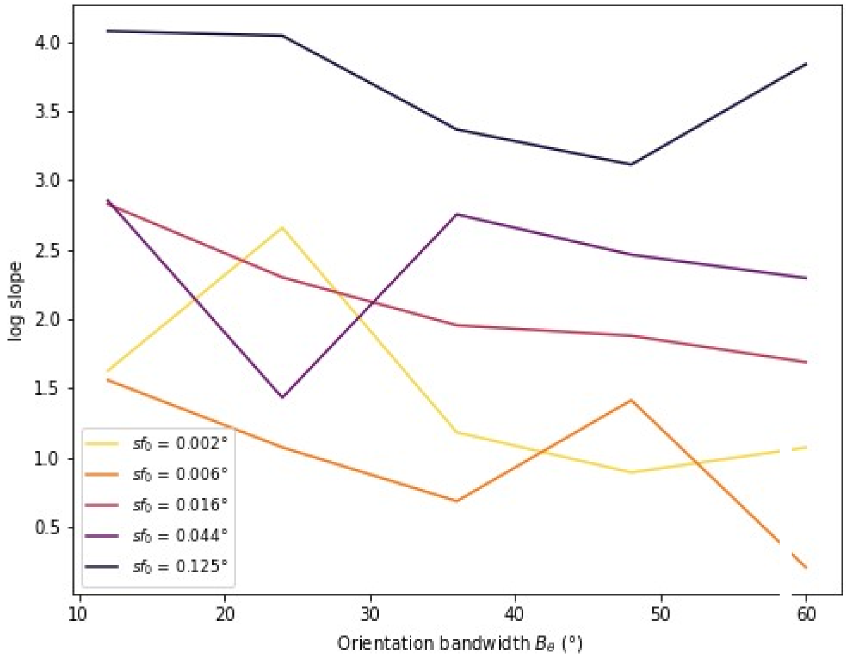


Figure 8. Orientation discrimination error rate of the all the participant as a function of the orientation bandwidth B_θ (12-60°) according to the spatial frequency (0.002 – 0.125 cpd) of the MC presented.

Discussion

In this work, we have highlighted the role of different parameters (orientation angle, orientation bandwidth, spatial frequency and bandwidth spatial frequency) on the ability to discriminate orientation. We have shown that the acuity decreases as the orientation bandwidth of the stimulus is increased. This observation has already been reported in various publications (Heeley et al., 1997; Heeley & Timmey, 1988) and therefore validates our observation. It suggest the stimulus orientation bandwidth act as a source of external noise. The manner in which acuity declines is suggestive of a relatively straightforward statistical summation of the different noise processes. The psychophysical threshold could be the result of combining several sources of uncertainty, which for the sake of simplicity can be referred to generically as “noise”.

The second session data sets suggest that by reducing the spatial frequency bandwidth, we increase the precision. Other publications suggest the same hypothesis: by increasing the spatial-frequency bandwidth of the gratings, they decrease the precision with which the human visual system is capable of discriminating between gratings which differ in their spatial frequency (Greenlee, 1992; Howard 1987). Viewed in the spatial-frequency domain, the effect of decreasing the spatial frequency bandwidth constant of the Gaussian envelope is equivalent to adding higher and lower spectral components to the frequency spectrum of the grating.

We also observed that the accuracy seems to get lower with the spatial frequency. However, several psychophysical masking and adaptation studies suggest the opposite: they indicate that bandwidth decreases with spatial frequency (Phillips & Wilson, 1984; Holopigian, 1985). Which means that if we increases the spatial frequency, we reduced the noise, thus improve the acuity. Results from single unit physiology also provide results that are similar. In the monkey striate cortex, Devalois et al (1982) obtained data that suggest the same relationship between the orientation bandwidth and spatial frequency. Differences in the stimuli used in these studies (2D simple gratings) and the stimuli that we used (Motion Clouds) could be responsible for these differences.

This original psychophysics work thanks to the use of Motion Clouds allowed us to know more about the influence of the different spatial parameters of a grating oriented on our capacity to discriminate its orientation. The limit of this work is the study of a small number of parameters of an “image”, we could also have been interested in luminance or contrast. We used static gratings, the utilisation of moving gratings could also be interesting. The small numbers of participants and the fact that they had to run the experiment themselves could lead to certain biases in the results.

However, this preliminary work could serve as a basis for a larger study on orientation discrimination. It would be interesting to find out more about the behavior of primary visual cortex neurons when performing an orientation discrimination task by measuring their activity during this task using electrophysiological tools or even two-photon imaging. The psychophysics task could be carried out by an animal possessing a primary visual cortex with an organization similar to that of human, namely a nonhuman-primate or a cat (fig.9).

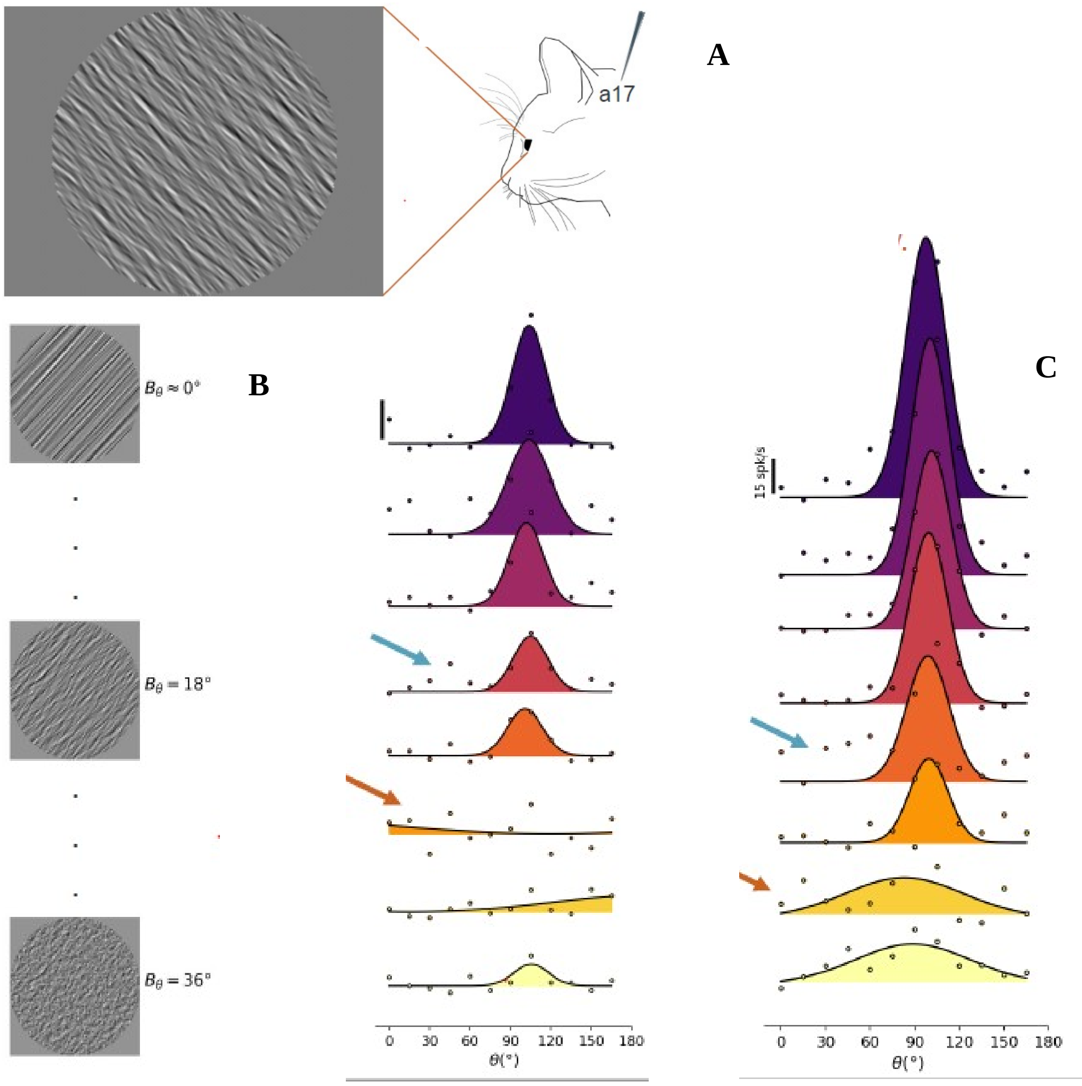


Figure 9. A: Experimental setup. A cat implanted at v1 level could be placed in front of a screen where MC would be displayed. B: Stimulus. We could also play with the orientation angle and orientation bandwidth. C. Theoretical results for 2 neurons. The activity of V1 neurons as a function of the orientation bandwidth and angle could be measured and presented as tuning curve. The goal will be to find the preferred θ et Bθ of V1 neurons (H.Ladret).

Another possibility would be to propose a new model of orientation selectivity that will based on deep-learning which performance will be evaluated with the same orientation discrimination task proposed before. The performance of the neural network will be compared with the performance of human to the exact same discrimination task. The goal could be to build a neural network based on biological learning architecture, sort of bio-mimetic.

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