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

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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 interactifs commentés et accompagnés de figures animées.

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# 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. Then, 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 information 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 psychophysics experiment with simple artificial stimuli such as straight bars or gratings.

But this kind of stimuli are intrinsically limited in their relevance to study the rich dynamic involved in the vision of natural (Yoshida & Okhi, 2020). 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. While it is possible to probe the primary visual cortex with natural images, natural images are complex and sometimes difficult to control, but the use of natural stimulation avoids unnatural bias that can come from artificial stimulation (Olshausen & Field, 2005). On the other hand, 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 “natural-like” stimuli in order to separate the different theories of representation of orientation in V1. This approach offers a compromise between the need for naturalistic stimuli to study ecological brain mechanisms and the desire to keep a fine control over the experiments. 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 psychophysics experiment.

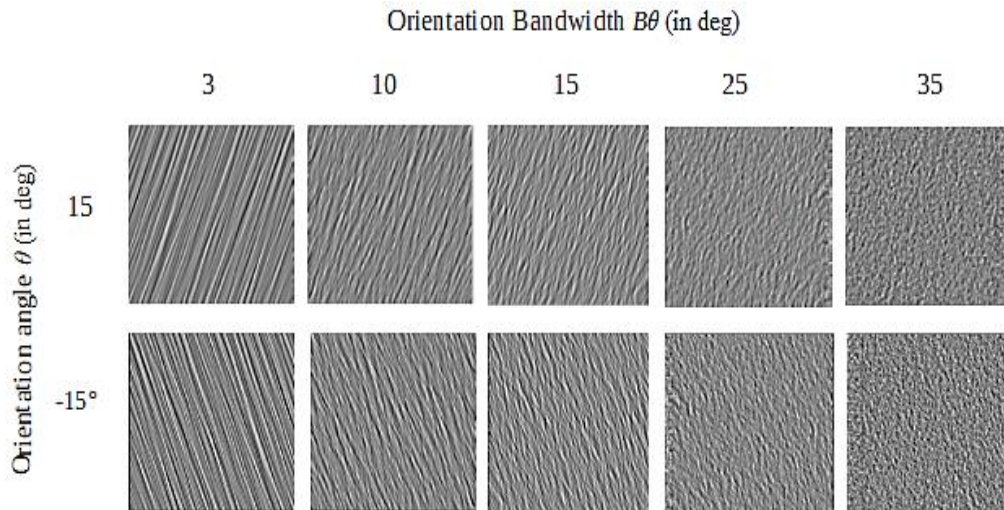
# Methods

## a. Participants

Five healthy volunteers (1 author and 4 participants naive as to the purpose of the experiment, age  $23.2 \pm 0.25$ ) 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 band-pass filtered white noise textures called Motion Clouds that provide parametric control over the content of the stimuli while retaining the statistics of natural images (Leon et al., 2012). Motion Clouds are synthetic oriented textures who model the distribution of orientation in natural visual scene. They can be easily controlled by playing with different parameters and we decided to focus on 4 different parameters: the orientation angle  $\theta$ , the orientation bandwidth  $B_\theta$ , the bandwidth spatial frequency  $B_{sf}$  and the spatial frequency  $sf$ .  $\theta$  is drawn from a uniform distribution ranging between  $\pi/8$  and  $\pi/8$  with respect to vertical,  $B_\theta$  drawn from a uniform distribution ranging between 0 and  $\pi/3$ , the spatial frequency bandwidth  $B_{sf}$  also draw from a uniform distribution ranging between 0.06 and 1 c/deg and  $sf$  ranging between 0.01 and 0.125 c/deg (fig.1). The visual stimuli were generated using PsychoPy (Pierce, 2007) and displayed in 100% contrast. A new stimulus was generated for each presentation.



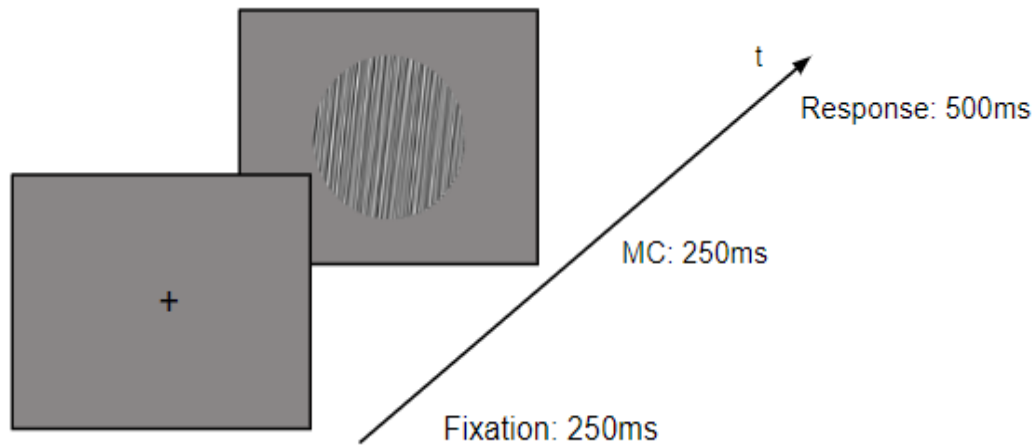
**Figure 1.** Representation of the visual stimuli: Motion clouds are random textures imitating natural pattern. Here, we illustrate the effect of increasing the orientation bandwidth  $B_\theta$

### 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 Motion Cloud ( $20^\circ$  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 measured at various combinations of angle orientation, spatial frequency, spatial frequency bandwidth and orientation bandwidth of the oriented stimuli.

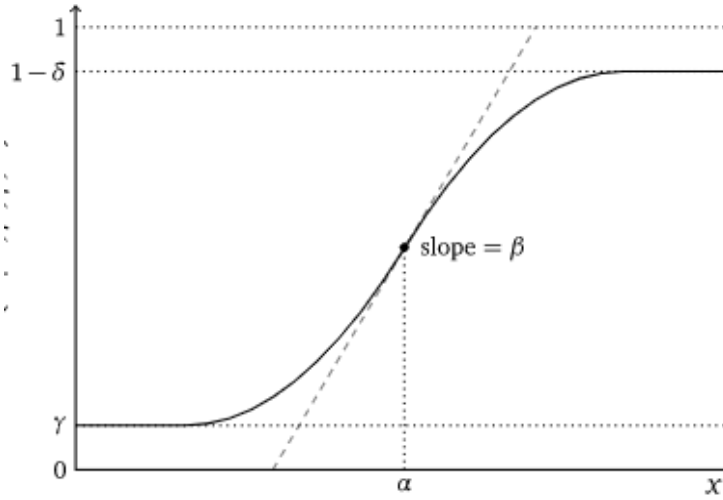
Each participant had to perform 3 sessions of 750 trials:

- first session: for each trial,  $B_\theta$  was randomly chosen out of 5 possibilities and  $\theta$  out of 30 possibilities.  $B_{sf}$  (0.5 c/deg) and  $sf$  (0.125 c/deg) were fixed.
- second session: for each trial,  $B_\theta$  and  $B_{sf}$  were randomly chosen out of 5 possibilities and  $\theta$  out of 30 possibilities.  $Sf$  (0.125 c/deg) was fixed.
- third session: for each trial,  $B_\theta$  and  $sf$  were randomly chosen out of 5 possibilities and  $\theta$  out of 30 possibilities.  $B_{sf}$  (0.1 c/deg) was fixed.

### e. Fitting

In psychophysics, subject responses to a 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.

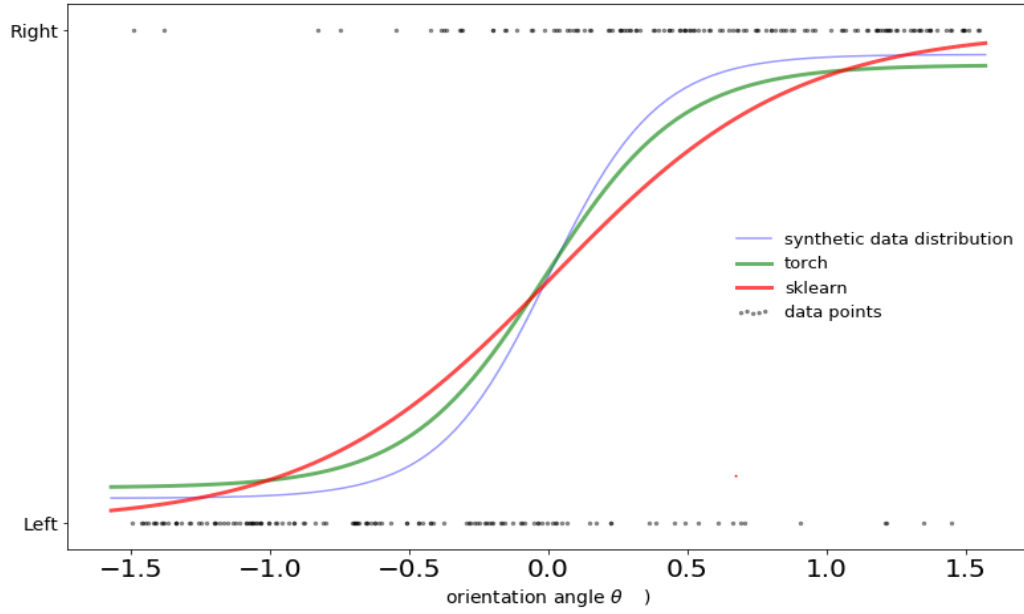




**Figure 3.** Diagram of the psychometric function with the intensity of a stimulus  $x$ , the base rate of the performance in the absence of signal  $\gamma$ , threshold  $\alpha$ , slope  $\beta$  and the lapse rate  $\delta$ .

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).

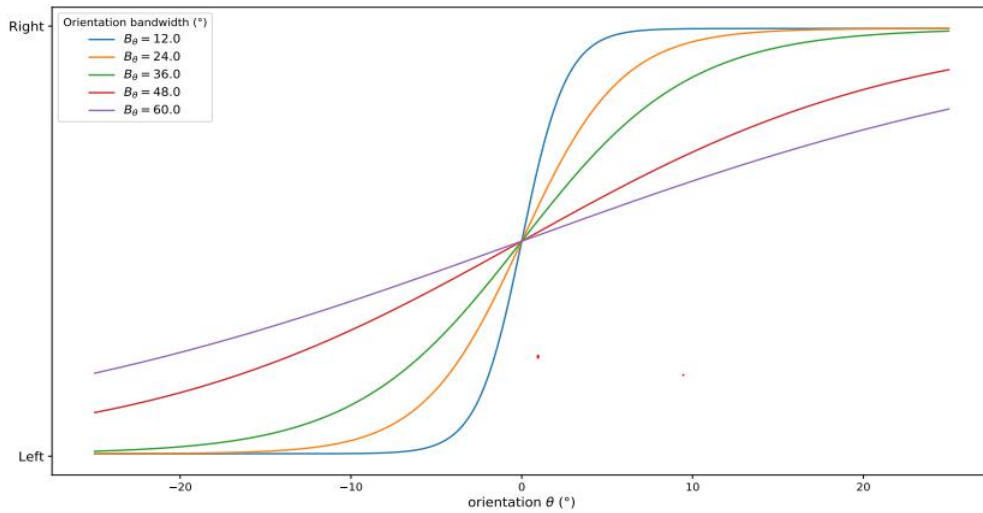
In order to limit this type of bias, we have performed a preliminary theoretical analysis. We first generated synthetic data corresponding to participants binary responses to a two alternative forced choice task and added a lapse rate ( $\delta = 0.1$ ). Then we defined a fitting method using Pytorch (<https://pytorch.org/>) and we included in the model a metric corresponding to the lapse rate. We also defined another fitting method using Scikit-learn (<https://scikit-learn.org>) not-including the lapse rate than 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 Scikit-learn 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.

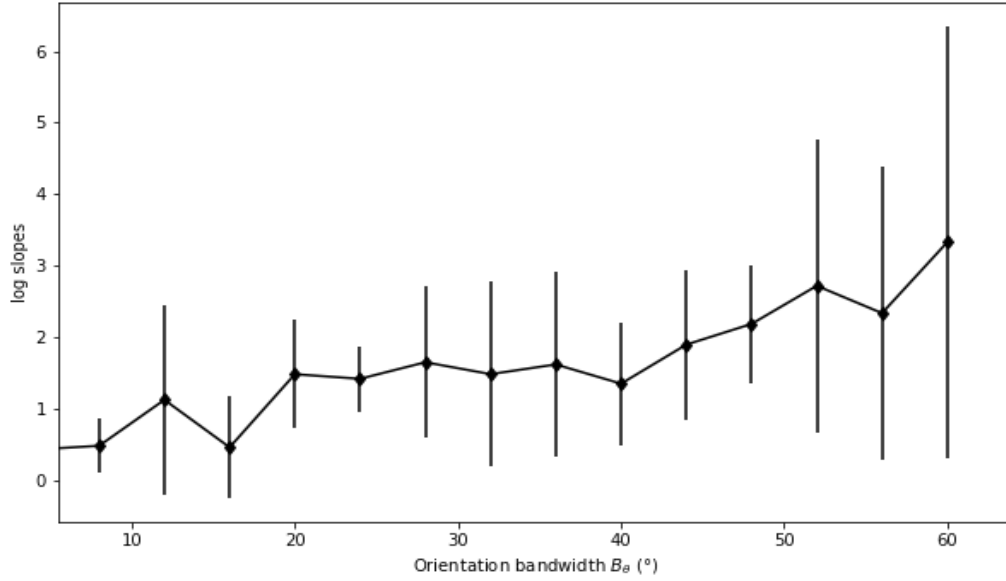
## Results

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’, and fig.5). Overall, the percentage of correct responses from participants is  $80.5\% \pm 6.2$  (mean  $\pm 1$  SE) for the first session,  $74.1\% \pm 5.4$  for the second session and  $71.5\% \pm 5.2$  for the third session.



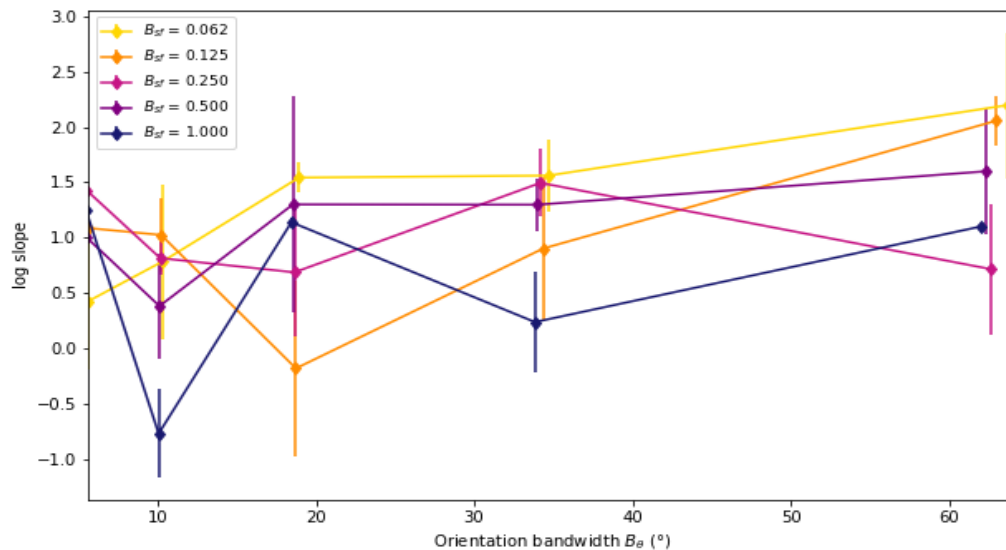
**Figure 5.** Psychometrics curves of the participant JF as a function of the orientation bandwidth  $B_\theta$  (between  $\sim 6^\circ$  and  $\sim 60^\circ$ ). Curves were fitted based on 750 stimulus-response pairs. Only 5 curves were represented here for the sake of representation.

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 a significant discrimination error. If we analyse the results of the first session where only the orientation angle and the orientation bandwidth of the visual stimulus varied, we notice a positive correlation between the slope and the orientation bandwidth. Moreover, the variability between the participants seems to increase gradually with the highest values obtained for a  $B_\theta$  greater than  $50^\circ$ .



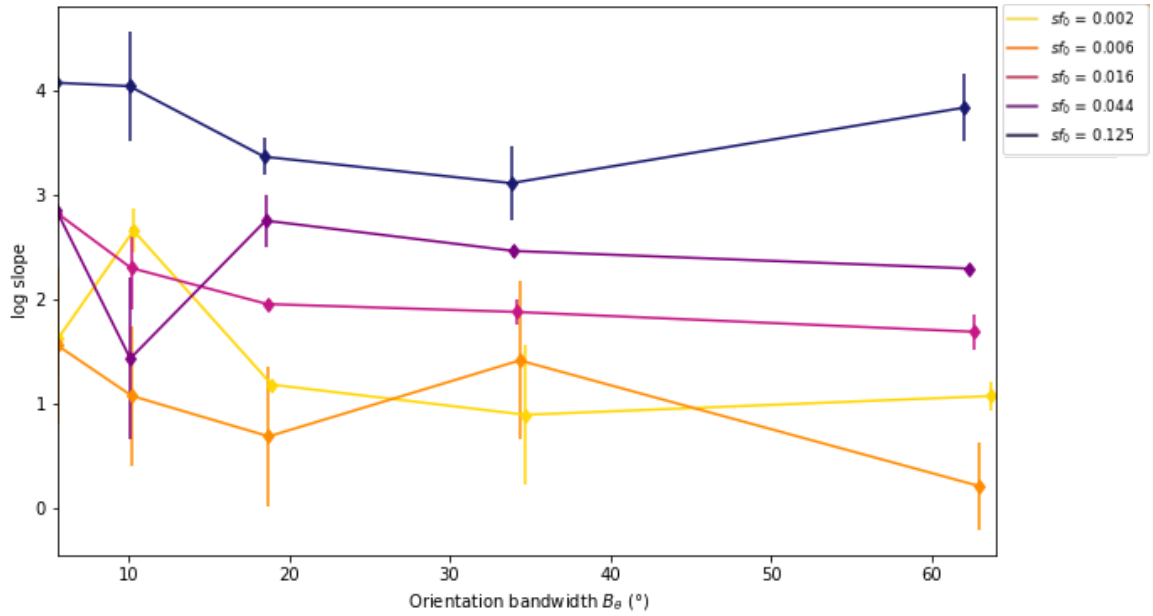
**Figure 6.** Mean log slope of all the participant psychometrics curves obtained during the first session. Error bar represents  $\pm 1$  SE.

In the second session, we changed the orientation bandwidth, the orientation angle and the spatial frequency bandwidth. We observe a similar behaviour: the error rate does seem to increase with the bandwidth. But the slope even tends to decrease for a  $10^\circ$   $B_\theta$  for the highest  $B_{sf}$ . Despite the mixed results, it seems that the spatial-frequency bandwidth of the visual stimuli used in the experiment discrimination did not impact the performance of our participants (fig. 7).



**Figure 7.** Mean log slope of all the participants psychometric curves for the second session as a function of the orientation bandwidth (between  $10$  and  $60^\circ$ ) and the spatial frequency bandwidth (between  $0.062$ - $1$  cpd). Error bar represents  $\pm 1$  SE.

Concerning the last session data, we notice that the orientation bandwidth does impact on the performances. For  $B_\theta$  below  $20^\circ$ , the log slope is negatively correlated with the orientation bandwidth for almost all the spatial frequencies beside  $0.002$  c/deg. It also seems that the spatial frequency affects the ability to discriminate orientation. Indeed if we pass the mixed results obtained for narrower  $B_\theta$  (below  $20^\circ$ ), we see that the slope gradually increases with the spatial frequency (fig.8).



**Figure 8.** Mean log slope of the all the psychometrics curves generated with the results of the third session as a function of the orientation bandwidth  $B_\theta$  and the spatial frequency (between  $0.002$  to  $0.125$  c/deg) . Error bar represents  $\pm 1$  SE.

## 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 orientation bandwidth does not directly impact the performances but does increase the participants responses variability. This observation has already been reported in various publications ( Heeley et al., 1997; Heeley & Timmey, 1988). 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 and thirist session data sets suggest that no effect of the spatial frequency bandwidth on the acuity to discriminate orientation but a significant impact of spatial frequency. In several psychophysical studies, the threshold were measured for discriminating the orientation of sinusoidal gratings of varying spatial frequency and found to decrease monotonically with increasing spatial frequency (D.C.Burr & S.A Wijesundra, 1991). Results from single unit physiology studies also provide similar conclusion. T.Pasternak and L.J.Leinen (1986) recorded single unit activity of v1 neurons in adults cat and measured the orientation selectivity to moving sinusoidal gratings. They showed that cat visual acuity was the best for low spatial frequencies and observed a slight loss of visual acuity for higher frequencies. Further studies by Allison, Melzer, Ding, Bonds & Casagrande (2000) and Devalois, Cottaris, Mahon Elfat & Wilson (2000) on macaque monkeys cortex also support this conclusion.

This original psychophysics study thanks to the use of Motion Clouds allowed us to know more about the influence of the different spatial parameters of a 2D grating on our capacity to discriminate its orientation. But this study was done online with a limited numbers of participants and one disadvantage of online data collection is the experimenter's lack of control over the setting in which participants provide their responses. This is important to consider in cases like us where lighting or capability of computing equipment could affect the experimental outcomes. 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 fMRI. 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. A possible extension of this study could be to propose a modelling approach with the aim of explaining to results obtained in our discrimination tasks. Another possible extension could 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 participants to the exact same discrimination task. The goal could be to build a new neural network based on learning architecture close to that of the human visual cortex with a discrimination acuity similar to ours.

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