**INTRODUCTION**

Good morning everyone and thank you all for being here today,

I would like to express my sincere thanks to the professors Sophie Schwartz, Michael Schredl and Yves Rossetti for accepting to be members of my PhD jury. I also want to thank my thesis advisor Perrine Ruby, without whom none of the work I will present today would have been possible.

The general outline of my presentation is shown here. First I will introduce dreaming and some of the main issues related to its scientific study. In the second and most substantial part of my talk, I will detail several studies that we have conducted in the aim of understanding the mechanism of dream recall. In the third section, I will describe a study which aimed at characterizing the relationship between waking-life and dream content and in the fourth section, I will briefly describe an open-source software that I co-developed dedicated to the visualization and analysis of sleep data.

I am going to talk about for the next 45 minutes is dreaming, and even if dreaming is something that probably everyone in this room has already experienced, there are still many things we don’t know about its nature or its mechanisms. For example, even today there are still no consensual definition of dreaming. In its simplest form, one can say that dreaming is a mental experience which occurs during sleep. And upon awakening, this mental experience can be either recalled or forgotten depending whether the dream content is successfully encoded into memory or not. And if the dream is recalled, then it can be reported using for example words or pictures. There is a potential loss of information between each of these steps, for instance, we often have the impression that we only recall a fragment of our dream, and it is even more frustrating when we try to describe it to others. This loss of information is due in part to forgetting, reconstruction, sometimes censorship and description difficulties.

Then goes the question of when does dreaming occur during sleep. Again this is not a simple question, and before answering that one I would like first to introduce some basic notions of sleep and the methods to study it. Sleep is not a passive and homogenous state but rather an evolving process during which the brain pass through several distinct states, or sleep stages. The gold standard for the identification of sleep stages is polysomnography, which consists of simultaneously recording brain activity (EEG or electroencephalography), eye movements (EOG or electrooculography) and muscle activity (EMG or electromyography). Using those information the identification of sleep stages is then performed visually by inspecting consecutive segments of polysomnographic recordings. The five sleep stages are Wakefulness, N1 sleep, N2 sleep, N3 sleep and REM sleep. They all have distinctive electrophysiological properties. For instance, resting wakefulness is characterized by a predominance of the alpha rhythm and a high muscular activity, whereas N3 sleep, sometimes called deep sleep is characterized by large amplitude slow waves. A normal night of sleep, in humans at least, consists of a repetition of four or five ninety minutes long cycle in which sleep stages follow each other in a specific order.

Back to our question of when does dreaming occur during sleep. We know today that contrarily to what was believed for several decades, dreaming can occur during any sleep stages. That said, there is a higher rate of dream recall after awakening from REM sleep than NREM sleep (about 80% of recall versus twenty to fifty percent), and we currently don’t know whether it means that people dream more in REM sleep or that people recall better from REM sleep. Because dreaming can occur in each and every sleep stages, there is no electrophysiological signature of dreaming that would allow sleep researchers to be 100% sure that a person is currently dreaming, and this represents a big issue to the study of the cerebral correlates of dreaming because the only way to know whether someone is dreaming or not is to awaken him or her.

Does dreaming have a functional effect? This question has fascinated mankind since the dawn of time. In ancient Egypt and Greece, dreams were believed to have a religious or mystical signification. Then, the father of psychoanalysis, Sigmund Freud, proposed in the beginning of the twentieth century that each dream is a wish fulfillment during which unconscious desires come to awareness, but in a distorted form to avoid sleep disturbances, and that thus they were the “guardians of sleep”. More recently, and in a more psycho-cognitive view, dreams have been proposed to play a role in psychological individualism, emotional regulation, memory consolidation, threat or social simulation. However, there are still few evidences either supporting or refuting these hypotheses, and I will detail later in my presentation a study that we did with Perrine in which we decided to find some evidence by looking closely at the relationship between

Finally, the last question of my introduction, which will take up a great deal of our attention, and which was already asked by Aristotle more than two thousand years ago, relates to why is there a large variability in dream recall, both among one person over successive mornings, but also, between people. In other words, why do we remember or forget our dreams? This question was the central focus of my thesis, and one of the method to explore it is to compare the personality traits and brain functioning of people who recall their dreams every day and people who almost never recall a dream.

And doing so, dozens of studies have shown that high recallers and low recallers differ on many aspects. In their personality, high recallers tend to have specific personality traits, such as higher openness to experience and anxiety, they tend to have higher creative-thinking abilities, and they generally also report an overall higher interest in their dreams.

They also differ in the way they sleep. And this was demonstrated by a previous study conducted in the lab by Perrine and Jean-Baptiste Eichenlaub who was a PhD student some years ago. They recorded the sleep, using polysomnography, of 18 high recallers and 18 low recallers, and while they found that high recallers had in average longer awakening during sleep, namely 2 minutes in average versus 1 minute for low-recallers. This finding is consistent with the arousal-retrieval model proposed by Koulack and Goodenough in the seventies which postulate that a period of wakefulness must occur immediately after dreaming in order to successfully encode dream content into long term memory and therefore remember it on the following morning.

In this very same study, they also looked at the differences in the brain between high and low dream recallers, for that they asked participants to wear earplugs while being awake and while sleeping. In the earplugs was played an oddball novelty paradigm in which first names are randomly and rarely played among pure tones which are more frequent. And they measured the brain responses to these first names during wakefulness but also sleep. Remarkably they found that high recallers have a higher brain reactivity to first names, and more broadly speaking, to auditory stimuli, during both sleep and wakefulness, as you can see in yellow on this figure.

Furthermore, Jean Baptiste and Perrine also conducted another study in which they compared the spontaneous regional cerebral blood flow of 20 high recallers and 20 low recallers using PET scan. They found that high recallers had a higher activity in two specific brain regions, the medial prefrontal cortex, and temporo parietal junction, which have been previously described as critical for dream recall. Indeed, lesions within one or both of these regions induce a global cessation of dream recall. The important message here is that in addition with having some differences in their personality, high and low dream recallers have also differences in the functioning of their brains.

Now that I have talked a bit of what we know about dreaming, I want to state the unresolved issues that we addressed during the years of my thesis.

First, I said earlier that awakening are critical for dream recall, and yet, we still do not know precisely what happens in the brain after the first minutes after awakening. So we designed an EEG-fMRI study to explore that and at the same time test whether the post-awakening brain state could explain why do we sometimes recall our dreams or not. For that we compared the brain activity of high and low dream recallers in the minutes following awakening.

Next, I said before that high dream recallers have a higher brain reactivity to auditory stimuli as well as an increased proportion of wakefulness during sleep. This suggests that there might be a causal link between these two factors, for instance a greater reactivity to sound during sleep could induce more and longer awakenings, which would in turn give more opportunities to encode dream content into memory. We tested that hypothesis by re-analyzing the polysomnographic data of Perrine and Jean-Baptiste, and at the same time we took the opportunity to measure a whole bunch of parameters of the sleep microstructure to see if we could find any differences between high and low dream recallers.

I also did during my thesis a behavioral study on dream content. In that study, we asked participants to record their dreams for a week and to write down every elements of their dreams that they felt was related to their waking-lives. And this allowed us to quantify and qualify the characteristics of the memory sources of dreams and in turn it gave us insights about the possible function of dreaming.

Finally, I worked a lot on sleep data during my thesis, and I was a bit surprised by the fact that there were very few free and open source softwares that allowed me to do all the analyses I wanted. During the last year of my PhD I started to work on a personal project, which thanks to my fellow PhD student Etienne Combrisson, who I guess is here today, quickly turned into a bigger and comprehensive software, that I will be very happy to present you briefly in the last part of this presentation.

**RESULTS: INERTIA**

I am now going to move to the result, and I will start by detailing the EEG-fMRI study. This study was the central work of my thesis and it took us more than one year to acquire the data for the 55 participants.

Immediately upon awakening, the brain is in a transient state between sleep and wakefulness that is called sleep inertia. Sleep inertia is characterized by impaired cognitive and physical performances, reduced vigilance, a strong desire to return to sleep, and a rapid vanishing of dream content. Surprisingly, while sleep inertia is a phenomenon that we all experience at different level each morning, still very little is known about the brain alterations during this period.

For this study, we recruited a total of 55 participants, among which 28 were high dream recallers, meaning that they usually recalled more than 6 dream per weeks. 27 were low dream recallers, recalling about one dream per month. The two groups were paired in age, gender, education level and habitual sleep duration.

The major points of the protocol are the followings. Participants were asked to sleep for about 45 minutes inside an MRI scanner. We monitored the sleep stages online and awakened them if possible in N3 sleep. Our protocol was designed to maximize sleep inertia, for that participants were partially sleep deprived on the night before, and they took a nap during the circadian low of early afternoon. We also measured the cognitive impairments during sleep inertia using a validated task, namely the descending subtraction task in which subjects were asked to subtract backwards 9 then 8 then 7 and so on to a three digits number for two minutes.

The full protocol of the study is shown here. Subjects arrived at the sleep unit of Alain Nicolas in the Vinatier Hospital at 8 pm. During two hours, I stayed with them and made them perform several behavioral and cognitive tasks to assess for example creativity, arithmetic and memory abilities. They stayed from about 11pm to 5 am under the supervision of night nurses and were asked to go to sleep at 5 am in the morning until 8 am, meaning that they slept a total of 3 hours in the night. After lunch at noon, subjects were led to the CERMEP neuroimaging center and they were set up with EEG electrodes in order to monitor online the sleep stages. They then performed the behavioral arithmetic task, DST, and their brain was scanned for 6 minutes during which they were just told to stay awake and focus on a fixation cross. We then switch off the light and told them that they could sleep if they wanted to. About 45 minutes later, we awakened them, if possible in N3 or deep sleep, and we immediately scanned their brain and performed again a behavioral task. And we did the same thing again about 25 minutes after awakening. So for both the cognitive performances and the brain functioning, we had three measurements points, before sleep, 5 min post-awakening and 25 min post-awakening. Our general hypothesis is that we should observe a reduction of arithmetic performances and brain alterations specifically at 5 minutes post-awakening compared to pre-nap and 25 minutes post awakening, because it corresponds to the moment where sleep inertia is at its maximum.

[ RESULTS ]

**AROUSAL**

We now arrive to the second study we did to better understand the mechanisms of dream recall. This study was in fact the work my Master 2 that I did in the lab and it was published in early 2017 in the journal frontiers in human neuroscience.

If you remember the beginning of my presentation, I said that one of the issue we wanted to test was whether there is a causal link between the increased brain reactivity in HR to first names, and the increased proportion of wakefulness during sleep in these same participants. And a secondary goal that we also test was whether we could see any differences between high and low dream recallers in more subtle sleep parameters, and namely parameters of the sleep microstructure. To test these two hypothesis, what I did during my master 2 was to re-analyze the EEG data of the previous EEG study of Jean-Baptiste and Perrine.

The analysis that we did, and that took quite a lot of time was to visually score arousals, which are short awakenings occurring several times per hours of sleep. We did this time-consuming visual scoring of arousals in order to be able to perform reliable auditory evoked potentials analyses to the first names that induced or not either a full awakening or a short arousal reaction. And while this type of analysis had already been done by the team of Helene Bastuji with painful stimuli, it had never been done with auditory stimuli. At the same time, and because we were re-analyzing all these data, we decided to push it further and analyze several features of the sleep microstructure in order to compare them between HR and LR, and again, this had never been done before. For this, we used either automatic or visual scoring, and on this example you can see an algorithm for the automatic detection of rapid eye movements during REM sleep.

**WLE**

I will now move to the third part of my talk in which I will present a behavioral study that we conducted to specifically look at the relationship between waking-life and dream content.

This study was recently published in the journal Plos One.

To put this study in context, we know both by subjective experience and scientific study that dream content is somehow related to the waking-life of the dreamer. However, the characteristics of the waking life experiences incorporated into dreams are still poorly known, and we don’t know precisely the filters that dreaming applies to waking-life. Yet, a better understanding of that filter could be of crucial importance to improve our knowledge of the possible function of dreaming.

The classic paradigm that is used to investigate the relationship between dreaming and waking life is the content matching paradigm, in which people are asked to write down everything they did during the day on a day diary, and everything they dreamed of during the night on a dream diary, and typically they do that for about fifteen days. After that period of time, either the participant or an external person will rate the level of matching between the days and dream diaries. Yet, one of the obvious problem with this method is that it is unlikely that the participants will be able to write down every single actions or thoughts he or she had during the day, and therefore there might be a bias towards highly emotional waking-life experiences and fewer mundane events. In addition, one of the inherent limitation of this paradigm is that it limits the span of the matching between waking life and dream content to the fifteen days or so of the experiment. And I think we have all already re-experienced in our dreams some situations that dated from several months or several years ago.

Therefore, we decided to do a new version of this paradigm that would overcome these limitations. We asked 40 participants to record their dreams immediately upon awakening during 7 consecutive days, and to subsequently report any connections they could make between their waking-lives and their dreams. After recording their dreams with a Dictaphone, participants had to fill in the first questionnaire, displayed on the left side, to quantify and qualify some general aspects of the dream, including the number of characters, emotional intensity and so on. And the last question of that questionnaire related to whether some elements of their dream made them think about an experience that they had during their waking-lives. And if they could see one or more, they had to fill in another form for each incorporated waking life elements. In this form they had to describe the element as it was originally experienced in waking life, as it was experienced within the dream, and for both they had to quantify some aspects of it on a scale of 1 to 10.

For example, I will show you the dream report and associated waking life elements of one subject of the study. His dream report was as follows: “in my dream, I saw my ex-girlfriend and her new partner. Suddenly, I felt really angry and started to push them down the stairs. They fell down and I shouted at them”. For him it was clear that this part of the dream was related to one situation that he experienced three years ago, during which he bumped into his ex-girlfriend and her new partner, and he was particularly rude and unkind to them.” And for him this waking life experience was mostly negative, it was also very rare because it only happened one time, it was something very personal, very important, and that he considered as personal concern, and even three years after his encounter with his ex-girlfriend.

If we now look at all the participants, we obtained a total of 247 dreams, or around 6 dreams per participants during the 7 days of the experiment, a figure which is high but was expected given that one of the inclusion criteria for this study was being a high dream recallers. About 80% of the dream reports were related to one or more waking life experiences and we obtained nearly 500 waking life experiences incorporated into dreams.

In agreement with our hypothesis, we found that the majority of the incorporated WLE were either from the day before or from the distant past, and it seems therefore that dreams incorporate in an almost equal proportion events from the day before or from several years ago. Another key result of this study is that dreaming attenuate the intensity of waking emotional memories. If we go back to the example I showed you before, if you remember the participants rated the emotional intensity of its original encounter with his ex-girlfriend as something very negative (2 out of ten). But, interestingly, if we looked at how he rated the emotional intensity of the encounter within the dream, you can see that it is slightly higher, meaning that he perceived as less emotionally negative within the dream than within waking-life. And if we look at all the participants, we have the same pattern, negative waking life experiences tend to be perceived as a bit less negative within the dream, and positive waking life experiences tend to be perceived as a bit less positive, while neutral experiences stay at the same level. This is one of the first experimental evidence supporting the emotional regulation theory of dreaming, which postulates that dreaming is involved, or at least reflects, emotional regulation processes.

These results led us to propose that dreaming can be best understood as an open window on several cognitive processes taking place at the same time during sleep. These processes involve emotional regulation, memory consolidation of relevant experiences, or forgetting of insignificant experiences. And notably the emotional intensity of an experience could be the tag to decide whether this specific waking memories should be consolidated or forgotten. In turn, this reorganization of the global memory schema could explain the creative insights and problem solving frequently observed in dreams.

One of the limitation of this study is that it only includes morning dream reports, and we know that there is a time of the night effect on the relationship between dreaming and waking-life, with for instance more references to the day before on the first part of the night. So it would be interesting to evaluate this time of the night effect using our protocol. Secondly, while our study provide a strong argument for the emotional regulation role of dreaming, there is currently very few evidence that dreaming is associated with memory consolidation processes. During my PhD I helped in a study designed by Jane Plailly and Perrine, which aimed at assessing whether recalling a dream related to a recent learning experiences could help memory consolidation, however we did not find a significant effect and therefore future research are needed.

**SOFTWARE**

We now arrive to the fourth section, in which I am going to present you a software that I developed during the last year of my PhD, and I want to emphasize that it was not intended originally in my PhD and it started more as a personal project. The motivation for this software came when I started working with sleep data and realized that there were few free and open source solutions that were dedicated to sleep research. So in early 2017 I started to work on a simple Matlab prototype that was intended for my personal use and which allowed me to visualize and score the sleep stages. And one day I showed this software to my friend and fellow PhD student Etienne Combrisson and we decided to rewrite it in Python and implement it into his excellent package Visbrain. We worked together for several months and quite quickly we obtained a full interface with many features. In September of this year, we released a stable version of this software, called SLEEP, and at the same time we published it into a peer reviewed journal, frontiers in Neuroinformatics.

Here you can see the main interface of the software. It is comprised of several different modules. On the top center are the polysomnographic signals in which it is possible to navigate, they are displayed by default by epochs of 30 seconds but you can adjust that windows on the bottom of the software. One of the important specifications of this software was that it should be able to read natively several commercial and public file formats. In its current version, the software is capable of handling all the main international file formats, including for example Brainvision, European data format, Micromed, and so on. Below the polysomnographic signals is the spectrogram, which is the time frequency representation of the full recording, and which is useful to see at a glance variation in spectral properties of the signal. Below that is the hypnogram that you can of course edit from an existing one or create from scratch and then save in several possible file formats again. On the left side of the software is the setting panel which allows the user to perform several actions, such as changing the visibility and amplitude of the channels, running a bunch of signal processing tools, computing sleep statistics, and one particular aspect I want to emphasize, running automatic detection of phasic events, such as spindles, K-complexes, rapid eye movements and so on. And I think that one of the strength of this software is that these detections are directly embedded within the interface, both on the signals but also on the hypnogram.

To finish, I would like to mention that the development of this software is still ongoing and we are currently implementing a function to automatically identify and score the sleep stages. I am happy to say that we obtain so far very good performances, with a percentage of agreement between our algorithm and a human visual scoring of about 80%. This is a nice result given that it took less than 5 seconds to our software to compute this hypnogram, while for an expert human it would take at least 2 to 3 hours!

**CONCLUSION**

We now arrive to the end of this presentation in which I showed you four studies that we conducted to explore dreaming. I would like to put back the quote by Aristotle that I showed you in the introduction, and ask, what did we learn of the mechanisms of dream recall? All our results combined led us to propose an integrative model of dream recall, which combines the strengths and insights of previous existing theories and experimental data.

The main assumption of this model is that the recall of dream is function of the successful memory encoding of dream content into long-term memory. And there are many factors that can promote or prevent this encoding. For instance, we know that age, gender, personality, interest in dreams and some cognitive abilities, notably creativity can drastically influence the process of dream recall. For instance, individuals with higher creativity can have more salient dreams, meaning that they are more bizarre or highly emotional, and we know the salience of dream can dramatically influence dream recall and that’s why we typically recall more often dreams with bizarre elements or high emotional content. Moreover, people who are highly interest in their dreams will voluntarily focus on their dream content upon awakening and therefore reduce the interference within the encoding process. In contrast, if right upon awakening you think of something else, like what you are going to eat for breakfast, then there is a good chance that the dream content will quickly vanish.

In addition with these psycho-cognitive factors, we propose that the baseline brain functioning is also a predictor of dream recall, and notably the activity within the default mode network. One of our prediction is that a fast re-establishment of this default mode network activity in the first minutes following awakening from sleep is essential for a successful dream recall. And consistent with this we have found in the EEG-FMRI study that upon awakening from N3 sleep the functional connectivity within the brain is highly disrupted, and less disrupted upon awakening from N2 sleep, and based on some of the neuroimaging studies that looked at what happens in the brain during REM sleep, we have reason to think that the default mode connectivity is way less altered following awakening from this sleep. And while this remains to be tested, it could provide a good explanation for why people generally recall their dreams better upon awakening from REM sleep than non-REM sleep. Another consequence of the high activity in the default mode, and notably in the temporo-parietal junction, a region which is known to be involved in attention orienting mechanisms, could be an increase of wakefulness during sleep, with the idea that long nocturnal awakenings could allow the encoding of dream content into memory. And for that our results led us to propose that there might be a threshold duration of 2 minutes for a successful reactivation of the encoding ability of the hippocampus.

Finally, one aspect that need to be further explored but that is promising is that maybe this specific brain functioning is directly linked to the psycho-cognitive parameters. And we have many evidence to believe it should be like that. For instance, women, who typically recall their dreams better than men, also have a higher average functional connectivity in the DMN as well as a tendency for higher creativity and more awakenings during sleep. We know also that DMN connectivity tends to decrease with age, as do dream recall frequency and also the propensity to have episodes of day-dreaming and mind-wandering during the day.

To sum up, during this presentation we have explored this fascinating phenomenon that is dreaming through several studies and methodologies. Our experimental data have brought new knowledge regarding the mechanism of dream recall, as well as on the relationship between dream content and waking-life. These data have resulted in several theoretical advances, notably an integrative model of dream recall, as well as one of the very first and few evidence in favor of a role of dreaming in emotion regulation. And, last but not least, we have also contributed to the development of a more open and comprehensive sleep science, through the development of a software which will hopefully be useful for students and sleep researchers around the world.

I would like to finish by saying that given the time I chose to only present you four of the main studies of my PhD, but I was a part of several other works, including for example a survey of the sleep and dream habits of students of Lyon University, which is currently under review at Journal of Sleep research, as well as many others studies which aimed to improve our knowledge of dreaming and dream recall. And of course I will be happy to talk a bit more about these studies if the jury members have some questions about them.

Last but not least, I would like to thank again everyone for being here, and especially Perrine Ruby which has made all of this possible, the whole DYCOG team for this unforgettable four years that I lived in this lab, the participants of our studies of course for lending us their brains and dreams, and I want also to express my thanks to my family and friends who have always been there for me.