

# BEHAVIORAL AND NEURAL PROPERTIES OF CONSCIOUS AND UNCONSCIOUS EXPECTANCY EFFECTS



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**PICNIC Lab (Physiological Investigation of Clinically Normal and Impaired Cognition)**

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A Doctoral Thesis in Cognitive Neuroscience

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## A K N O W L E D G M E N T S

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## A B S T R A C T

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While psychologists have long debated whether it is consciousness or unconsciousness that has a stronger hold on human behavior, a more fruitful endeavor is to explore how they work together. Recent research has shown that the links between conscious and unconscious processing are so extensive that it is almost impossible to get a complete picture of mental life without understanding their interactions. In this work, our main goal was to understand to which extent unconscious processing influences conscious representations, and impacts behavior. Furthermore, consciousness appears to be required for a representation to be actively maintained, and flexibly accessed, to most cognitive processes including strategic control and episodic memory. In several experiments, unconscious representations observed both with behavioral and functional brain-imaging tools are typically very short lived. However, we hypothesized that such vanishing unconscious representations may still elicit long-lasting processes. Indeed, recent research has shown that attention and motor preparation can be manipulated unconsciously. This led us to explore whether expectancy of an upcoming visual stimulus, which engages both attentional and motor processes, can be triggered by unconscious processes. To this aim, we designed a series of masked cueing experiments in which we explored the possibility of initiating unconsciously a sustained expectancy effect. Through four complementary experiments using behavioral measures, high-density EEG and intra-cranial recordings, we demonstrate that an unconsciously perceived visual cue can modulate a long-lasting (>1 second) event related potential (ERP) component (the contingent negative variation, CNV) and that this neurophysiological expectancy effect has a behavioral counterpart. These results underline the importance of distinguishing a fast decaying unconscious representation, from its possible long-lasting influences on cognitive processes. The iEEG results also revealed a dissociation between conscious and unconscious effects. We report early effects in temporal regions similar for conscious and unconscious cues, followed by late and sustained frontal effects for the conscious effects only. Taken together, these results converge towards a two-stage model of the underlying mechanisms of expectancy.

## R E S U M E

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Tandis que les psychologues débattent depuis longtemps la question du conscient et de l'inconscient pour savoir lequel a le plus d'influence sur le comportement humain, une approche plus fructueuse serait d'explorer comment ces deux aspects fonctionnent ensemble. En effet, les recherches récentes montrent que les liens entre les processus conscients et inconscients sont si étroits qu'il serait quasi-impossible d'avoir une compréhension générale de l'appareil psychique humain sans comprendre leurs interactions. De plus, la conscience semble être nécessaire pour qu'une représentation mentale puisse être maintenue et accessible à divers processus cognitifs tels que le contrôle stratégique ou la mémoire épisodique. Plusieurs expériences comportementales et d'imagerie fonctionnelle montrent que les représentations inconscientes sont typiquement de très courte durée. Toutefois, nous avons émis l'hypothèse que ces représentations inconscientes éphémères pourraient également provoquer des processus de plus longue durée, comme le suggère l'observation récente de préparations motrices et attentionnelles pouvant être manipulées inconsciemment. Ceci nous a poussé à explorer si l'attente d'un stimulus visuel imminent – qui sollicite des processus moteurs et attentionnels – est modulée par des processus inconscients. Ainsi, nous avons développé une série d'expériences d'amorçage masqué pour explorer la possibilité d'initier inconsciemment un effet d'attente soutenue. A travers quatre expériences complémentaires qui utilisent des mesures comportementales, de l'EEG à haute densité ou des enregistrements intra-crâniens, nous démontrons qu'un signal perçu inconsciemment peut moduler un composant ERP (la variation contingente négative, CNV) de longue durée (>1 seconde) et que cet effet d'attente neurophysiologique va de pair avec une facilitation comportementale. Ces résultats soulignent l'importance de distinguer les représentations inconscientes éphémères de la possibilité d'une influence de plus longue durée sur les processus cognitifs. Les résultats iEEG ont mis en lumière une dissociation entre les effets conscients et inconscients. Nous trouvons des effets précoces comparables dans les régions temporales pour les signaux conscients et inconscients, suivis par des effets frontaux de longue durée uniquement pour les effets conscients. Ces résultats convergent vers un modèle en deux étapes des mécanismes sous-jacents de l'attente.

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## FOREWORD

Over the past three years, I have traveled about 1740 times between my apartment and the lab. This trip has six stops on the subway line N°1 of Paris. As a result, I have been exposed 10440 times to the following situation: While I am in the train, I hear a recorded voice indicating the name of the next station, shortly after, the train begins to slow down which forces me to hold onto something or balance myself one way or another. Six seconds later, the voice repeats the name of the station and the subway fully stops. Finally, one second later, the doors open, people get in and out. Approximately 13 seconds later, an audible signal rings for two seconds, indicating that the doors are about to close. Five seconds later, the train restarts for a new cycle. This repetitive exposure during my daily commutes over the past three years led me to overlearn the contingencies and timings of the metro line N°1. These subway trips often happen in the morning when I am not entirely awake, or in the evening while I engage in a conversation with some labmates. Nevertheless, I am still able to balance myself when needed or to prepare to get out at the right time. I feel that I can now travel between my home and the lab in a very automatic way. My brain seems to process the contingencies and temporally attend each stimulus automatically. This is anecdotal, of course, but may it suggest that consciousness is not required for me to form expectancies and adjust accordingly as I navigate through this urban environment.





**CHAPTER 1**  
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**INTRODUCTION**

*In this chapter we will review the extents of the cognitive processes that can occur in the absence of consciousness but also the limits of unconscious processing, we will also address a specific cognitive process that is the ability that our brain has to expect upcoming events, that allows for attention orientation and preparation. Finally, we will present the scientific question of this thesis.*



## 1 Unconscious processing

Navigating the world requires us to integrate rich amounts of information and to perform infinitely complex actions. Yet, in our daily lives, we have the subjective impression of performing all these actions with a relative simplicity and we are not overwhelmed by the quantity of information that reaches us. The reason for this is that we seem to be aware of only a limited amount of these complex cognitive processes that are required for us to navigate through our day-to-day life. Our brain identifies patterns, uses heuristics, makes predictions and applies rules of which we are mostly unaware. They allow us to orient ourselves in the world with an apparent ease. It is precisely the extent of this unconscious mental life that we will review in the following part.

### ● 1.1 Definition and experimental paradigms

#### 1.1.1 Definition

In order to study the scope of our unconscious cognition, it is necessary for us to define what differentiates an unconscious process from a conscious one. The most common and intuitive definition of conscious processing is that a conscious process provides the person with a subjective experience. We, therefore, consider an unconscious process as any representation in the brain that is not accompanied by a subjective experience. To assess this experience the most straightforward way is to ask for a subjective report; if a person is not able to report their experience (provided that this person can articulate a response) we consider that they are unconscious of that representation.

#### 1.1.2 Dissociation between conscious experience and cognitive processes in patients

With this definition in mind, researchers have explored the extent to which information can be processed in the brain without reaching awareness. The first observations of information processing in the absence of awareness came from early studies on brain-lesioned patients. Some patients, suffering from cortical blindness, had lost all conscious visual experience in part of their visual field;

when visual stimuli were presented in their blind visual field they were unable to detect them and had no conscious experience of them but yet were able to direct their eyes towards the luminous dot they were not perceiving consciously (Pöppel et al., 1973). This was the first evidence of a dissociation between conscious experience and cognitive abilities. Patients were unable to report seeing the stimuli presented in their blind visual field. Yet, they were able to perform better than chance when simply asked to make a saccade towards these stimuli. Further studies on so-called blindsight patients showed that these unconscious cognitive abilities were not only limited to perceptual and motor processes. Patients' attention could be manipulated by stimuli in their blind visual field (Kentridge et al., 1999) and these patients were, in fact, able to categorize more complex images, like emotional faces (de Gelder et al., 1999), revealing the possibility to process emotion unconsciously.

In a similar way, patients suffering from prosopagnosia, are unable to recognize familiar faces. They do not have conscious access to the identity of the face, but yet an image of a familiar face can trigger a measurable emotional bodily response (Bauer, 1984); illustrating here again how an unconscious representation can induce an emotional response.

Witnessing these dissociations between conscious experience and cognitive processing, led scientists to investigate the following question: to what extent of abstraction can information be processed unconsciously?

These observations of cognitive processing in the absence of awareness were only the first of many to come. With the use of experimental paradigms hereafter described, scientists were able to explore in healthy subjects the richness and diversity of content that can be processed unconsciously.

### 1.1.3 Studying unconscious cognition in healthy participants

The study of unconscious processing was mainly made possible by the development of a set of experimental paradigms in which healthy subjects are presented information that they cannot consciously perceive. With the use of these techniques, researchers were able to study the range of cognitive tasks our brains are able to perform on unconscious stimuli, as well as the differences in brain activations elicited by conscious versus unconscious representations.



Because unconscious processing was mainly explored in the visual dimension, we will present only the main paradigms in the visual domain.

One of the challenges of “unconsciousness research” is to be able to present an information without it being consciously perceived, the most intuitive solution to bypass conscious perception of information is to present that information at a very low detection threshold. This method is called near-threshold visual presentation. It consists in varying the contrast, intensity or duration at which a stimulus is presented and estimating the detection threshold under which it is impossible to discriminate it. Stimuli are then presented just above that threshold. Depending on fluctuations in attention, some of them will be consciously perceived while others will remain unconscious; hence allowing for the comparison of the processing of identical visual stimuli either consciously or unconsciously perceived.

Another efficient way to deliver visual information, without it accessing awareness, is to add conflicting information. This classical technique is called temporal masking (Breitmeyer et al., 1984). A stimulus presented even for a few milliseconds may be visible, but if immediately after this stimulus, another stimulus (called a mask) is presented, this mask will provide additional visual information interfering with the processing of the initial stimulus preventing it from being consciously perceived. A commonly used one is the metacontrast mask (Werner, 1935). It consists in reducing the visibility of a stimulus by presenting it immediately before a non-overlapping mask stimulus that fits the contours of the first stimulus. Another common mask is one that consists of various shapes adding noise at the location where the stimulus was presented.

The conflicting information can also be presented at the same time, in the case of spatial masking. The crowding paradigm consists in presenting a visual stimulus in the peripheral vision accompanied by other visual stimuli surrounding it, the presence of these other stimuli, and the eccentricity of the stimuli, will render the conscious perception of the masked stimuli impossible.

Apart from acting on the physical properties of the stimulus, another way of altering the awareness of visually presented information, is to act on the way the visual information is delivered to the eyes. Thus a famous masking technique consists in presenting different visual information to each eye. Using this paradigm called dichoptic presentation, one eye receives a stimulus and the other eye

another stimulus, because of binocular rivalry, the subject's conscious experience will alternate between these two images (Blake and Logothetis, 2002). Continuous flash suppression (CFS) (Tsuchiya and Koch, 2005) is a very similar method to mask visual information. Using dichoptic presentation, the masked image is presented in one eye and the other eye is continuously flashed with noisy images (Mondrian patterns), this way the masked image can remain outside of awareness and this suppression can last a few seconds. Measuring the time it takes for an image to break the suppression and to reach awareness is a way to evaluate the salience of the image.

Finally, one last way to modulate the awareness of visual information is to manipulate the attention of the subject. Experimenters do so by using the attentional blink (AB) paradigm: images are displayed in a rapid serial visual presentation (RSVP), when the subject is instructed to respond to a target that appears in this RSVP, his attention will be drawn to that first target, and if quickly after (200ms), another target follows, the subject will fail to report that second target (Raymond et al., 1992).

Using these techniques, scientists were able to present visual information to healthy subjects without them consciously perceiving them. Similarly to what was observed in blindsight patients, subjects' behavior was impacted by the unconscious information. These various experimental techniques have allowed the exploration and the uncovering of a wide range of cognitive processes that can occur unconsciously.

## ● 1.2 Diversity of unconscious content

### 1.2.1 Unconscious semantic priming

Several scientists have attempted to explore the limits of unconscious cognition. Semantic representations have been considered the ultimate form of abstraction; such a representation requires the brain to integrate the visual information, to identify the word form and to access its semantic content. This explains why many of the early visual priming experiments tested the possible influences of a masked word on the behavior.

In the early 1970's, scientists noticed that a word was recognized faster when it was preceded by a word of the same semantical category (Meyer and Schvaneveldt, 1971) this phenomenon is known as priming, and occurs not only for semantic but also for perceptual stimuli. Later, scientists by presenting masked words as primes have studied the influences of masked words on the priming effect in what is called a masked priming experiment. Early studies have shown that masked words could indeed activate abstract semantic representations. In a classic experiment (Marcel, 1983), masked words were followed by a color patch that the subjects had to discriminate. These words would facilitate the response to a target color presented right after. Despite some methodological flaws in Marcel's initial design, these early works triggered an interest for the field of unconscious semantic processing. Greenwald investigated unconscious semantic access with a more rigorous methodology (Greenwald et al., 1996). In order to assess the visibility of the masked cue, Greenwald and colleagues designed an additional task that subjects performed at the end of the experiment. In this task, subjects had to categorize the masked stimulus in the form of a forced choice task. The results were then analyzed according to the signal detection theory target, detection and false alarms were reported in order to calculate the d-prime ( $d'$ ) criterion, which reflects the signal to noise ratio. A null d-prime criterion indicates a null detection. Ensuring, in this way, that the subjects were not aware of the primes, Greenwald confirmed the existence of masked semantic priming. Interestingly these results also showed a limit to this priming: for a stimulus onset asynchrony (SOA) separating cue and target longer than 100ms, this priming effect disappeared. The discrimination task used in this experiment to assess the visibility of the cues has become a classic way to ensure that masked information is indeed not consciously perceived.

Later Naccache & Dehaene showed that masked information could reach levels of processing including numerical quantity. In their experiment, masked "Arabic" notations of numbers or "verbal" notations of numbers primed numerical quantities and facilitated the response to target numbers (Dehaene et al., 1998). They also showed that the masked information was processed as far as to prime the motor response given to the target. Further studies ensured that the unconscious information would undergo real semantic processing and was not only the object of a direct stimulus-response type of process and replicated these semantic priming results (Koechlin et al., 1999; Lionel Naccache and Dehaene, 2001).

All these studies demonstrate that masked primes facilitate responses for short prime target SOA's (Stimulus Onset Asynchrony), which suggests the activation of automatic semantic processes but also points out a first limit to unconscious processes: their influence on behavior seems to be very short term (of only a few milliseconds).

Using fMRI (functional Magnetic Resonance Imagery) and EEG (Electroencephalography) to observe the activations elicited by masked words scientists further characterized unconscious semantic processes showing that activations of the visual word form area (vwfa) could be recorded intracerebrally as early as 150ms (Dehaene et al., 2001) after the presentation of a masked word. Furthermore masked emotional words were capable of activating the amygdala (Naccache et al., 2005a).

### 1.2.2 Unconscious motor preparation

The early studies of blindsight patients that we previously mentioned shed light on the possibility of a direct unconscious perceptuo-motor link. Patients were able to execute saccades (Pöppel et al., 1973) or hand movements (Weiskrantz et al., 1974) in the direction of visual stimuli they could not consciously perceive, being the first evidence in favor of a motor response activated by unconscious information.

This hypothesis of an unconscious motor influence was later confirmed in experiments with healthy subjects; Neumann and Klotz (1994) showed that masked symbolic cues could prime a motor response to a target by lowering reaction time and increasing accuracy. This motor priming effect was also reported when the primes carried semantic information. So far this only proved that motor actions could be influenced by subliminal information but did not provide evidence for an unconscious motor preparation. The evidence for that was provided by Dehaene et al. (1998) and Leuthold and Kopp (1998) who showed that the processing of unconscious stimuli reached motor areas involved in programming and executing motor commands. In experiments where masked cues were presented to subjects, they were able to measure an early-lateralized readiness potential (LRP) 200-400ms after cue onset triggered by masked primes. fMRI results localized the precise occurrence of this effect in the motor cortex (Dehaene et al. 1998).

Recently, an fMRI study even reported that unconsciously triggered motor-related brain activity could occur despite the absence of a target stimulus, when no movement is executed. Subjects presented an activity in the medial premotor area reflecting an unconsciously triggered motor preparation (D'Ostilio and Garraux, 2012a).

After reviewing evidence that unconscious information can trigger motor preparation, the next question is whether this unconscious information can reach higher cognitive functions that are modulating the motor commands. We will now review the extent to which unconscious information can influence executive functions.

### 1.2.3 Unconscious influences on executive functions

Executive functions such as error detection, conflict resolution, response inhibition, and task switching seem to be complex cognitive processes that might require consciousness. Indeed these functions are associated with activations in the prefrontal cortex, which is believed to be part of a network for conscious processing (Dehaene et al., 2003). But the latest research shows that unconscious information can go as far as to influence these high order cognitive processes.

The inhibition of an automatic behavior requires strong cognitive control and relies on activity of the prefrontal cortex. Negative compatibility effect (NCE) is a first evidence of a form of unconscious inhibition. When a masked arrow primes the response to a target, with a short SOA, it facilitates the response to this target but in the case of longer SOA 100-200ms as compared to 0-60ms the prime has the inverse effect, due to an automatic inhibition effect that suppresses the primed motor response (Eimer and Schlaghecken, 1998; Klapp and Haas, 2005; Schlaghecken and Eimer, 2004) The NCE seems to be a rather automatic form of inhibition that is mediated by activity in the caudate and thalamus (Aron et al., 2003) as well as the supplementary motor areas (SMA) (Sumner et al., 2007).

Recent studies tested the possibility of triggering a more « voluntary » form of inhibition with masked cues. Using a Go/NoGo task they tested the possibility of inhibiting an already planned response. The mask Nogo signals triggered an inhibition effect which was correlated with the fronto-central N2 ERP in EEG (van

Gaal et al., 2008) and activations in the pre-SMA and inferior frontal cortices (van Gaal et al., 2010).

The influences of unconscious information on executive functions is not limited to inhibitory processes. Other executive functions, such as error monitoring or task switching can be subject to unconscious influences. For example when subjects were asked to perform different tasks on target words, either phonological or semantic depending on the instructions they were presented with, if an earlier masked cue primed them for another task (incongruent condition) they could observe slower RT as well as activations for the irrelevantly cued task, activity in the dorso-lateral Pre-Frontal Cortex (dlPFC) is associated with this priming effect (Lau and Passingham, 2007a). These findings later replicated (Reuss et al., 2011; Zhou and Davis, 2012) indicate that subject can prepare for the execution of a task in the absence of consciousness.

We have just reviewed how two important executive functions can be affected unconsciously, subliminal stimuli can extend their influences to other executive functions. Scientists have shown that in case of unconscious conflict or incongruency subjects show higher activity in the Anterior Cingulate Cortex (ACC) a region known to participate in the conflict detection and resolution (D'Ostilio and Garraux, 2012b; Ursu et al., 2009). Similarly in case of an unperceived error, scientists have noted an error-related negativity (ERN) that originates in the ACC showing a possibility of processing of errors outside of awareness (Dhar et al., 2011; Hester et al., 2005; Klein et al., 2007; Nieuwenhuis et al., 2001; O'Connell et al., 2007). There also seems to be a possibility of subliminal influences on decision-making and goal pursuit (Custers and Aarts, 2010; Pessiglione et al., 2008)

The motivational system participates in executive functions by attributing value to objects in order to optimize decisions. Interestingly, scientists were able to modify motivational states with subliminal rewards. Participants when presented with high subliminal rewards made increased physical effort, and showed improved performances on cognitive tasks and stronger Blood-Level-Oxygen-Level Dependent (BOLD) activations in the basal forebrain (Aarts et al., 2008a; Capa et al., 2011a; Custers and Aarts, 2005, 2010; Pessiglione et al., 2007).

### 1.2.4 Unconscious allocation and manipulation of attention

Attention is the process by which our brain selects information based either on saliency or relevance; this selection then allows the brain to distribute its limited processing resources optimally. We can distinguish two types of attention: endogenous attention, which qualifies a top-down process of voluntarily orienting our attention according to our intentions; for example when a Ph.D. student tries to focus on writing her introduction. But if this student were to be suddenly interrupted by a loud noise in the lab, her attention would be exogenously grasped even though she intended to stay focused on her introduction, this type of attention constitutes a bottom-up process irrelevant of intentions that is called exogenous attention.

Attention was historically defined as being tightly associated with consciousness as we are most of the time conscious of what we attend and we attend to what we are conscious. However, a long body of research has shown that there is a double dissociation between attention and consciousness. Attention can occur in the absence of consciousness and consciousness in the absence of attention, proving that those are two distinct processes (Koch and Tsuchiya, 2007).

#### **Attention amplifies unconscious processing**

Scientists have observed that the processing of unconscious information was influenced by attention. When attention is carried towards an unconscious stimulus it facilitates the processing of this stimulus, in the case of masked priming when attention is oriented towards the masked prime, unconscious priming effects are enhanced. Unconscious priming effects are affected by temporal attention (Naccache et al., 2002) by spatial attention (Lachter et al., 2004; Marzouki et al., 2007) and stimulus set (Kunde et al., 2003).

#### **Unconscious stimuli can manipulate attention**

We will review in the following part the extent to which attention can be manipulated in the absence of awareness.

When a blindsight patient was presented with visual cues in his blind visual field priming for the spatial location of the target, he was faster and more accurate

in responding to the latter. These findings suggest the possibility for unconscious information to direct attention to specific locations (Kentridge et al., 1999).

Similarly in healthy subjects, when presented with targets either to the left or to the right of a fixation point, they were quicker to respond when an imperceptible cue had been flashed to the same location shortly before (McCormick, 1997) supporting the hypothesis that attention can be captured even in the absence of awareness. These results of an orientation of spatial attention by unconscious information were replicated using various different paradigms. With a CFS display, Hsieh (2011) were able to mask pop out displays (one singleton among distractors) and showed that subjects were more accurate when performing a task at the location of the singleton.

Attention can also be manipulated by stimuli requiring a higher level of integration like threatening (Lin et al., 2009), emotional (Brooks et al., 2012; Vuilleumier and Schwartz, 2001), erotic (Jiang et al., 2006), or socially relevant stimuli (Sato et al., 2007)

All these results indicate the possibility of a bottom-up orientation of attention by subliminal stimuli but they give us no clue as to whether endogenous attentional top-down processes can occur in the absence of awareness.

Subjects presenting biased attention towards masked threatening stimuli had a higher occurrence of a polymorphism in the promoter of a serotonin transporter gene, one possible consequence of this polymorphism is an altered amygdala-anterior cingulate attention network (Hariri and Holmes, 2006; Pezawas et al., 2005) This suggests that the amygdala-anterior cingulate attention network plays a role in orienting spatial attention in response to threat and that perhaps these attentional effects are in fact modulated by subliminal stimuli in a top-down way (Carlson et al., 2012)

Several scientists suggested that unconscious orientation of endogenous attention may be specific to conscious processing. McCormick (1997) showed that learning to attend left when cued on right seemed possible consciously but not with masked cues. When cues are presented unconsciously, subjects seemed unable to avoid the exogenous attentional orienting of the cue and couldn't exert an endogenous orienting at the opposite direction. Recently Palmer and Mattler



(2013) used centrally presented masked cues to assess the possibility of orienting endogenous attention without the exogenous attention orienting bias caused by the presentation of the cues laterally. They were able to show a modulation of shifts in endogenous attention by masked cues, suggesting possible unconscious influences on endogenous attention orienting.

### ● 1.3 Unconsciously elicited brain activity

Defining what differentiates conscious from unconscious brain activity appears crucial in understanding the brain mechanisms allowing the emergence of consciousness.

As we previously evoked, unconscious information can elicit activity in many cortical areas. From early sensory cortices to associative areas, motor cortices and even frontal regions. There doesn't seem to be any region that escapes influences from unconscious information.

However, scientists by comparing brain activity elicited by the same physical stimulus either perceived consciously or unconsciously were able to tell some differences between conscious and unconscious processing in the brain. Unconscious processing seems to elicit more localized activity and these activities do not seem to be sustained in time. Moreover, the frontoparietal network seems to be preferentially activated when an information is processed consciously. Scientists have observed two stages in the processing of conscious information, a first stage that is mainly an occipitotemporal activation and that seems to depend on the intensity of the stimulus, this phase seems common in conscious and unconscious processing. The second phase, however, is similar to an all or none type of process, with sustained and more widespread activities particularly involving the frontoparietal network. This led scientists to postulate the importance of the fronto-cingulo-parietal network in consciousness. The global neuronal workspace (GNW) model is a model of conscious access in which information is processed unconsciously at a local scale; if the information is salient enough and is attended it reaches this global network which allows the information to be broadcasted to wider regions and for its representation to be sustained in time (Baars, 2005; Dehaene and Naccache, 2001). Another theory of consciousness states that for information to gain conscious access it has to be the object of a recurrent processing between higher order regions providing feedback to lower regions. Un-

conscious processing is considered in this theory to only withstand feedforward types of processing (Lamme, 2006).

The unconscious information does not seem limited by the type of brain regions it can influence but rather by the type of activations it can elicit. They seem to undergo only localized and evanescent processings.

#### ● 1.4 Summary

- Unconscious representations by definition do not produce reportable subjective experiences.
- Various brain lesions can lead to dissociations between cognitive processing and conscious content.
- Masking visual information allows the presentation of information without it being consciously experienced or reported.
- Unconsciously presented information can undergo complex abstract processing like semantic processing.
- Unconscious information can affect motor preparation by eliciting a RP.
- Subliminal information can influence executive functions such as inhibition and motivation in particular by modifying the activity in the ACC and SMA.
- Spatial attention can be affected and reoriented by unconscious information.
- Unconscious information can affect activity in most of cortical areas.





## 2 Limits to unconscious processing

There seems to be no apparent limit regarding the extent to which unconscious information can be processed, it can undergo various types of processing ranging from visual sensory processing to semantics, it can trigger motor preparation and even influence motivation. This wide range of unconscious processing raises the question of what are the limits to processing information in the absence of awareness, and thus, what is the role of consciousness in cognition.

### ● 2.1 Durability of unconscious processing

#### 2.1.1 Vanishing unconscious representations

The first limit that we previously evoked is the question of the longevity of subliminal representations. Unconscious representations seem to have fleeting behavioral and neural effects.

#### 2.1.2 Decay of behavioral influences with time

In the classical experiment by Sperling (1960), they illustrate the evanescence of unconscious information in an elegant way. Subjects presented with a grid of letters that was flashed briefly were able to report only 5 letters of the whole grid. But if immediately after the grid, they were informed, by a cue, of which row they had to recall, they were able to report all of the rows, showing that they, in fact, have access to that information. Interestingly, the longer the delay between the grid and the post-cue, the less they were able to recall the letters. The fact that they can potentially recall all the letters shows that the unconscious information is available and can be accessed, but only a limited amount of this information gains consciousness. The decrease in performance with time shows that subjects can access that unconscious information only for a short amount of time; this temporarily available information is called iconic visual memory. Results of replicating a fast decay of iconic visual memory were also provided by Lu et al. (2005). Access to consciousness appears to be necessary for an information to access working memory, to be stored more lastingly and for its influences to last over time.

Gentilucci, using the Muller-Lyer illusion, provided another illustration of fast-decaying unconscious representations. In the Muller-Lyer illusion subjects consciously perceive segments to be longer or shorter than they really are. However, when asked to execute a movement towards the segments, the subjects execute the movement according to the real physical dimension of the segments and not according to the perceived dimension (Gentilucci et al., 1996). This indicates that the visuomotor pathway uses an exact representation of the segments that do not reach consciousness, whereas the conscious representation that the subject reports is provided by the ventral pathway and is affected by the illusion. Interestingly, they noticed that when the movement was delayed to 5 seconds after the visual presentation of the segments, the subjects would now execute the movement to the perceived dimension of the segment, relying solely on their conscious experience, illustrating here again, how unconscious representation vanish with time.

A wide range of other experiments exposed the ephemeral nature of unconscious representations. Scientists, with the use of masked priming studies, varied the duration between masked primes and targets to explore the duration of influences masked cues could have on behavior. Early masked priming studies revealed that subliminal priming effects disappeared for SOAs longer than 100ms (Greenwald et al., 1996). Using a repetition priming paradigm Ferrand et al. (1996) showed that masked primes facilitated the response to the following target for SOA's of 150ms, however that repetition facilitation effect disappeared for SOA's of 500ms. Similarly, in a masked speech priming experiment, Dupoux et al. (2008) showed that masked primes could affect behavior past 100ms, however that effect seemed to decrease with SOA length and disappeared for SOA's longer than 600ms. As described by these masked priming experiments subliminal influences on behavior seem limited to a couple hundred of milliseconds.

#### *2.1.2.1 Decay of elicited neuronal activity with time*

This apparent limit in the behavioral influences of subliminal stimuli can be in part explained by the fact that subliminal stimuli seem to elicit brain activity that vanishes with time. Indeed many studies report a decay of brain activity with time and seem to agree on the fact that the activation of a population of neurons coding for a representation decays and vanishes after a couple of milliseconds, unless that representation gains awareness. Scientists have used various tech-

niques to distinguish the temporal dynamics of conscious and unconscious processing, they seem to concur on a similar early processing for consciously and unconsciously perceived stimuli up to 270ms, followed by an amplification of information only in the case of conscious processing (King et al., 2014; Salti et al., 2015; Schurger et al., 2015).

This view is also supported by results of intracranial recordings in monkeys, when the monkeys were presented with unmasked faces they recorded neurons in the face-selective area were firing up to 350ms after presentation; but in the case of masked faces these neurons fired only very briefly (20-30ms) (Rolls, 1999; Rolls and Tovee, 1994).

The short-lived nature of unconscious representations can be explained by the current theories of consciousness. According to the GNW theory of consciousness, if a representation is not salient enough and/or is unattended, it won't reach consciousness and thus will not access the global network required for it to be amplified, maintained as an active representation and memorized (Dehaene and Changeux, 2011; Dehaene and Naccache, 2001). Similarly, the Recurrence Theory, predicts that an invisible stimulus will only undergo a feedforward response across the brain, and won't be followed by recurrent processing, thereby, the activity it elicits will decay (Lamme and Roelfsema, 2000).

Several scientists have reported unconsciously elicited activations lasting longer than 500ms. For example, reporting a modulation of the activity in the amygdala following the presentation of masked emotional words up to 800ms after presentation (Naccache et al., 2005b). Some even claimed to have observed unconscious modulations of the P3 component occurring more than 500ms after the presentation of the masked stimulus (Bernat et al., 2001; Silverstein et al., 2015; van Gaal et al., 2011).

However, only a minority of studies were able to report unconsciously elicited neuronal activity lasting over 500ms and considering the amount of evidence pointing towards the vanishing nature of unconscious neuronal processing, scientists tend to agree on the fact that unconscious representations are not sustained in time.

### 2.1.3 Long lasting effects of subliminal stimuli

Some have postulated that despite the fact that unconscious representations seem to vanish quickly, they might be able to exert lasting influences by modifying the synaptic weights of local neuronal networks.

#### *2.1.3.1 Facilitation effect upon repetition of subliminal information*

Watanabe et al. tested this hypothesis, they repeatedly presented subliminal stimuli of directed motion and observed that this repetitive exposure affected the performance on a motion detection task (Watanabe et al., 2001). Furthermore, Gaillard et al. showed that unconscious information had long-term effects on neuronal activity: when an unconscious information was repeated several seconds to minutes later, it elicited a repetition effect measured in SEEG (Gaillard et al., 2007). Later, Reber et al. (2012) found that repeatedly presented masked word-pairs could influence decision-making one minute later and that this influence was reflected by changes in hippocampal BOLD signal. These studies demonstrate that masked repeated stimuli can exert long-lasting influences on behavior and neuronal activity, although incapable of eliciting durably maintained representations.

#### *2.1.3.2 Unconscious working memory: a possible explanation of these long-lasting influences*

Most of the theories of working memory postulate that the information has to be conscious in order to be maintained (Baars and Franklin, 2003; Squire and Dede, 2015). However, lately, the link between information maintenance and conscious access has been challenged by scientists who have reported late behavioral and neuronal influences of masked stimuli.

Several studies have explored the maintenance of unconscious information across time and have started to mention the possibility of an unconscious form of working memory (Bergström and Eriksson, 2014, 2015; Dutta et al., 2014) in particular Soto et al. (2011) showed that subjects could recall the orientation of a Gabor above chance after a 5 second delay, suggesting the possibility of unconscious working memory. However, the results were barely above chance and subjects could have miscategorized seen trials as unseen. Subjects could also have made an early guess and maintained that guess consciously until asked to give their re-

sponse (conscious maintenance hypothesis). In a recent study, Trübutschek et al. (2017) tested this possibility of working memory in the absence of consciousness by replicating Soto et al (2011) using magnetoencephalography (MEG) recording. They found similar long-lasting (<4s) behavioral blindsight effects. And moreover using MEG, they were able to show that the brain response and the working memory processes at play are different for seen trials and unseen trials. The proposed explanation for an unconscious working memory without sustained activity is that it would rely on changes in synaptic weights that upon reactivation facilitate the response towards the previously exposed stimulus. Their hypothesis is that posterior sensory regions encode conscious and unconscious information with slowly decaying neuronal activity, which later becomes periodically reactivated in the case where this information was to reach consciousness. In the case of repeated exposure, the repeated unconscious activations could durably modify the synaptic weights of the neuronal sensory network facilitating future processings.

### *2.1.3.3 Long-term effects on motivation and cognitive control*

Other studies showed long-lasting effects of masked stimuli on cognitive processes, especially on motivation and cognitive control. Aarts et al. (2008b, 2008a) and Custers and Aarts (2007) showed that subjects exerted more physical effort in a strength task three seconds after being exposed to a mask cue that had been associated to positive visible words, similarly Pessiglione (2007) found that masked monetary cues presented at the beginning of each trial seem to be affecting motivation and efforts subjects were making within that trial. All these results support that unconscious cues could initiate a long-lasting modulation of motivation. Capa et al. (2011b) similarly showed that subliminal cues associated to visible words related to studying had an influence on the cardiovascular reactivity of subjects during a learning task following the priming, reflecting enhanced goal-directed resource mobilization. In another study they used monetary cues to influence motivation prior to each block of task switching, and showed that subliminal reward stimuli had an effect lasting over several seconds (mean time of run 1/4 40.74 sec) on switch cost performances and on the contingent negative variation ERPs reflecting motivation within trials (Capa et al., 2013). In a switch task experiment, masked cues presented 2 to 3 seconds before the target announced switch trials. The predictive masked cues improved performances as reflected by a reduction in switch cost, these results can be interpreted as a long-lasting effect of masked cues on cognitive control (Farooqui and Manly, 2015).



According to the current theories of consciousness, unconscious information can not be maintained as a sustained process, in trying to explain these long-term effects, it is important to ensure that these processes are fully unconscious, one possible hypothesis could be that despite the fact that the cues remain unseen, they might nonetheless induce a conscious modification of the motivational or expecting state of the subjects allowing long-term effects of the masked cues (conscious maintenance theory).

#### *2.1.3.4 Long-lasting unconscious associative learning*

Pessiglione et al. (2008) demonstrated the possibility of unconscious instrumental learning, by showing that subliminal cues biased subjects in their decision, they were able to show that subjects had learned the association between the masked cues and the associated monetary reward presented seconds later. This ability of subjects to learn the association between the masked cues and their corresponding monetary reward, implies that subliminal information can be the object of delayed associative learning. Other scientists presented subliminal combinations of masked faces of persons and written words indicating the occupation of that person. They observed in a 30-40min delayed decision-making task, that these masked associations had influenced participants decisions at a task in which they had to guess the income of the person judging from their face, showing that long-term memories encoded unconsciously can bias delayed decisions (Ruch et al., 2017). Other scientists have observed this long-term associative learning Duss et al., (2011) and have even linked this unconscious relational encoding to hippocampal activity (Duss et al., 2014).

For a long time, hippocampal episodic memory was associated to conscious memory (Moscovitch, 2008; Squire and Zola, 1996; Tulving, 2002) whereas procedural memory was thought to be a more unconscious form of memory. However many new results point towards the involvement of the hippocampus in unconscious memory, they found the hippocampus to have a role in the implicit learning of relations between visible stimuli (Chun and Phelps, 1999; Greene et al., 2006; Negash et al., 2015) and more crucially they found an involvement of the hippocampus in the associative learning of subliminal stimuli (Duss et al., 2014; Henke et al., 2003; Züst et al., 2015).

These new results suggest that unconscious memory could occur via the hippocampal memory network, which could explain a more sustained form of unconscious learning.

## ● 2.2 Complexity of unconscious processing

Complex cognitive operations like integrating and combining information, as well as adopting a novel strategy, have traditionally been considered as the type of operations requiring conscious access (Dehaene and Naccache, 2001).

In the following part, we will review the contribution of consciousness to these cognitive processes.

### 2.2.1 Complex integration of unconscious information

If high-level representational stages such as semantics can be activated unconsciously (Naccache et al., 2005b; L. Naccache and Dehaene, 2001) the question of whether multiple unconscious information can be bound together is still debated.

#### *2.2.1.1 Integration of information in the absence of awareness*

Van Gaal et al. (2014) tested the effect of two successively presented masked cues (good/bad) (not/very) on the evaluation of the emotional valence of a target word, they did not notice any behavioral effects, yet, the N400 revealed a semantic violation, reflecting an integration of both cue and target word. Indeed, the negative cue adjective seemed to have inverted the valence of the word. These results illustrate the unconscious application of a grammar rule. It seems possible for unconscious stimuli to be integrated according to a rule of logic at a semantic level.

However, these unconscious integrations could be limited to combinations of usual information and unusual information integration might require consciousness. Indeed it was found that when an incongruency was present in unconscious information that needed integration, in a CFS paradigm these stimuli broke suppression and accessed consciousness more quickly, this was shown for visual scenes (e.g. basketball player with a watermelon, Mudrik et al., (2011)) and simple sentences (e.g. 'I ironed coffee', Sklar et al., (2012)). These findings suggest

that it might be impossible to integrate incongruent unconscious information and that this information might trigger a premature access to consciousness.

### *2.2.1.2 Unconscious inferences and reasoning*

Scientists have wondered whether this unconscious integration of information could lead to the combination of complex cognitive operations in the absence of awareness; which would suggest the existence of a form of unconscious reasoning.

Recent studies have shown that apparent complex integration of information in the absence of awareness seems possible in certain situations. For example, subjects were able to draw simple inferences from subliminal picture sequences and word pairs (Kawakami and Yoshida, 2015; Reber and Henke, 2012). In the latter, word pairs such as 'winter-red' and 'red-computer' were presented subliminally, a test 1min later revealed an association between 'winter' and 'computer' proving that a transitive link had been between the two pairs of subliminal words.

Complex stimuli requiring high-level integration such as chessboards were shown to be integrated at a strategical level, facilitating responses to tasks requiring to determine whether the king is in check. However, this facilitation was only present in expert chess players suggesting that this level of integration can only occur on information for which subjects are highly trained (Kiesel et al., 2009).

Other complex forms of integration can occur unconsciously, some arithmetic problems can be solved even when presented subliminally (García-Orza et al., 2009; Karpinski et al., 2016; Sklar et al., 2012; Van Opstal et al., 2011), indeed, the approximate average of four masked numbers can be extracted non-consciously (Van Opstal et al., 2011), and some evidence suggests that multi-step operations may be mediated non-consciously (Sklar et al., 2012). Others argue that consciousness seems required for the association of multiple operations (Sackur and Dehaene, 2009).

The integration of several cognitive operations might be possible for the case of well-trained operations, but consciousness does seem required for a more elaborate combination of cognitive operations.

### *2.2.1.3 Integration over time without consciousness*

We have previously evoked the possibility of creating associations of masked stimuli across long periods of time, yet, consciousness seems required for complex integration of information. Particularly in the case of integration of multiple stimuli over time, where consciousness seems necessary. Scientists designed a paradigm allowing the presentation of series of repetitive sounds with rules being broken at a short time scale (local deviant), meaning that information needed to be integrated over a short time to allow a detection of the irregularity, or at a longer time scale (global deviant) meaning that to detect the irregularity subjects have to integrate more information across a longer time. The local deviant typically elicits a Mismatch Negativity (MMN) measured in EEG which is associated with the detection of irregularities at a short time-scale and the global deviant elicits a P300 reflecting the processing of irregularities at a larger time scale (Bekinschtein et al., 2009). Patients with disorders of consciousness were exposed to this experimental paradigm and elicited brain activity were recorded using EEG. The patients showed an MMN in response to local deviants, indicating that the processing of irregularities at a short time scale does not depend on the level of consciousness. However global deviants only elicited P300 effects in conscious patients (Bekinschtein et al., 2009; Faugeras et al., 2012) indicating that consciousness seems required to integrate information at a larger timescale.

### 2.2.2 Learning novel strategies

Learning new associations seems possible in the absence of awareness, however learning a new strategy is different, it requires the ability to combine cognitive operations in a novel way, but also to memorize and apply this new combination. The importance of consciousness seems crucial for this process.

Merikle et al. (1995) tested the possibility of unconsciously performing a task in an unusual way by applying a novel strategy and inhibiting a habitual behavior. In a Stroop-like task, subjects had to categorize a target word according to its color (red or green), the targets were preceded by the words « GREEN » or « RED ». As predicted by the classic Stroop effect, subjects were faster when word cues predicted the color of the target. However, in blocks where the cues were 75% incongruent, subjects could establish an inversion strategy preparing for the opposite color and thus become faster for incongruent trials than congruent trials. Crucially this inversion in strategy was adopted only for unmasked cues, when the

cues were not perceived consciously, subjects were unable to adopt this inversion in strategy.

In a similar paradigm El Karoui et al. (2017), found that consciously instructed strategy of Stroop inversion had no behavioral evidence for unmasked trials but they did find a modulation of the P300 component in masked trials due to a transfer of strategy inversion from conscious to unconscious trials.

According to these results, consciousness seems to be required to inhibit the automatic Stroop effect and to inverse the strategy. Applying a strategy unconsciously might be possible only if it has been previously consciously learned and automatized.

### ● 2.3 Generating intentional behaviors unconsciously

The question of whether consciousness is required to generate intentional behaviors has divided philosophers in the debate about the existence of free will. Intuitively, intentional behavior seems inseparable from consciousness. For example, the patients suffering from blindsight, despite being unable to report visual stimuli in their blind visual-field are able to perform tasks on them when told to, yet they seem unable to initiate spontaneous behavior towards them when they aren't told to (Weiskrantz, 1997). This suggests that intentional behaviors might only occur consciously. However, scientists have explored the possibility for intentional behavior to be initiated outside of awareness. In a famous experiment, Libet (1983) measured subjects' RP before initiating a spontaneous hand movement and asked participants to report the exact moment they became conscious of their intention of moving their hands, interestingly they found that subjects elicited RPs 500ms before they reported having made the conscious decision to move their hands. This result suggests that the motor preparation was initiated before the participants were even aware of their intention of moving. However, this striking result received several critics. Firstly, the fact that the task itself was not probing purely intentional behavior since subjects were specifically told to generate the intentional behavior, puts into question the real intentionality of the hand movements. Also the observation of a beginning of RP before conscious intention does not mean that the decision to move has been made, indeed the beginning of the RP might not reflect actual fixed decision to move. This view is supported by the fact that movements can be vetoed after the RP has started (Libet et al., 1983).

According to the accumulator model of spontaneous self-initiated movement, the early RP reflects the pre-decisional processes leading to the initiation or not of a motor command . The first part of the RP might not reflect the intention to move but maybe more the cognitive processing leading to this intention. The conscious intention seems to come after this pre-decisional step. Specifically, this view is supported by the results of Desmurget (2009), in an experiment showing the involvement of the inferior parietal cortex. The authors showed that this conscious intentionality could be dissociated from the execution of the movement itself when stimulating subjects in the inferior parietal cortex.

Overall no evidence demonstrates the possibility of unconscious intentionality but there rather seems to be a prior unconscious process leading to the formation of conscious intentions.

## ● 2.4 Summary

- Unconscious priming effects seem to be limited to a few hundred of milliseconds.
- Unconscious neural representations elicit short-lived activity vanishing after 500ms.
- Facilitation effects upon repetition of subliminal information are observed at a behavioral and neuronal level.
- Unconscious working memory could possibly be induced by changes in synaptic weights.
- Masked stimuli can affect durably motivation and cognitive control.
- Associative learning mediated by the hippocampus seems possible in the absence of awareness.
- Integration of unconscious information might be limited to usual combinations and impossible for novel and unusual combinations.
- Simple combinations of cognitive operations are possible unconsciously.
- Consciousness seems required to combine complex cognitive operations.
- Integration of information over time requires consciousness.
- Applying a strategy unconsciously seems possible only if it has been consciously learned and automatized.
- Consciousness seems necessary to initiate an intentional behavior.





### **3 Sustained temporal attention processes**

As we reviewed, attention is one of the many cognitive processes that can be influenced unconsciously. Most of the studies investigating unconscious influences on attention have done so by studying the influences of subliminal stimuli on the orientation of spatial attention. However, attention can also be oriented in time and some attentional processes can be sustained over time. It is precisely these types of processes that we will review in the following part.

#### **● 3.1 Orienting attention in time**

Attention refers to the processes that allow us to prioritize and optimize how the brain treats information. It can help us prioritize the processing of events according to their spatial occurrence, but also according to their type, or their moment of occurrence. To do so, attentional resources can be allocated to a specific area of space as well as to specific features of the sensory information. Besides, they can also be oriented towards a specific moment in time; it is typically the case when we are expecting the occurrence of an event at a given moment.

Expecting an event implies orienting attention in time, which allows us to prepare for the occurrence of that event. Scientists have shown that when attention is oriented to a specific moment in time subjects exhibit better performances at that specific moment (Miniussi et al., 1999). It seems like a critical ability that facilitates how we apprehend our environment and anticipate the actions we make in response to that environment. We constantly perform these anticipations in our daily lives. For instance, in the case of a race when a referee shouts « ready, set, go! », we are highly aware of the contingency between those words, the « ready, set... » message announces the « go ». The first two words trigger expectancy towards the third, by orienting attention in time and preparing for an action. Similarly, in the subway, when the door signal rings, it alerts us and creates an anticipation of the closing of the doors. These are typical situations in which our attention is oriented toward a specific future moment in time, allowing us to anticipate particular events. Similar types of anticipation are also at play in a variety of situations, ranging from motion perception to music and speech perception as well as situations that require a motor action like in sports, driving, or in the case



of speech production. All these situations require us to allocate our attention to a given moment in time and to build expectations towards the upcoming events.

### ● 3.2 Studying expectancy with the use of the foreperiod paradigm

By recreating situations of expectancy like the ones we described, scientists have studied how the brain processes contingencies in the environment, allocates attentional resources in time and builds expectations in response to these events. To this purpose, a classical paradigm, called the foreperiod paradigm, has been developed. In this paradigm, a warning stimulus (S1) is followed by an imperative stimulus (S2), both separated by a foreperiod of about 1 to 4 seconds. Once the contingency between S1 and S2 is learned after a few trials, the presentation of S1 triggers an expectancy towards S2. The brain response triggered by the warning stimulus S1 can be measured using EEG. S1 elicits a series of ERPs N1, P2, N2, P3 followed by a slow negative potential, called the contingent negative variation (CNV). This slow negative potential gradually increases until the presentation of S2, and terminates by settling back to baseline level shortly after the appearance of S2 (Walter et al., 1964).

The global CNV can be divided into 2 components. The early component, or initial CNV (iCNV), starts 450ms after the appearance of S1, reaches its maximum between 550ms and 750ms, and lasts up to one second after S1. This early component is distributed over frontocentral regions and reflects the orientation of attention; it depends mainly on the properties of S1 (Gómez et al., 2001; Loveless and Sanford, 1974).

This early phase is followed by a late phase or terminal CNV (tCNV), starting around 1s to 1,5s after S1, and lasting until the appearance of S2. This late phase is distributed over centro-parietal regions and is associated with the expectation as well as with the preparation of the motor response to S2 (Brunia and van Boxtel, 2001; Brunia, 2003; Rohrbaugh et al., 1976).

In the example mentioned earlier, we can see how the words « ready, set » can act as S1 and trigger an expectancy towards the word « go » which acts as S2. It is quite obvious through this example that expectancy is a rather complex phenomenon, which reflects processes of stimulus anticipation, temporal estimation, and motor preparation. In the following part, we will try to shed light on the contribution of each of these processes to the CNV.

### ● 3.3 Interpretation of the CNV

#### 3.3.1 The CNV an indicator of expectancy

The CNV occurs when a contingency between two stimuli has been learned. When a stimulus S1 announces a stimulus S2, after being presented with the S1-S2 pair for approximately 30 trials, the stimulus S1 triggers the appearance of a CNV (Walter et al., 1964). After a few trials of the un-paired stimulus (S1 alone), scientists observe a disappearance of the CNV, indicating that the CNV occurs only when there is an expectation towards S2. Moreover, the amplitude of the CNV is correlated with the probability of occurrence of S2 (Walter et al., 1964). These results imply that the CNV depends on the contingency of S1 and S2 and the expectation of the upcoming of S2. In these early studies, authors described the CNV as an « expectancy wave».

Further investigations of the CNV using longer foreperiod paradigms revealed that it was in fact composed of two waves, with two negative peaks (Connor and Lang, 1969). These two components were probably confounded in the paradigm with shorter foreperiod. What they noticed, in particular, is that the late component seemed to vary mainly depending on the motor response required by S2 (Loveless and Sanford, 1974), which led scientist to wonder if this second wave was not composed only of a motor preparation regarding S2.

#### 3.3.2 Temporal orienting and the CNV

When an event is presented at an attended time, attention is oriented towards that specific moment in time, a process known as temporal orienting (TO). This temporal orienting allows the brain to prepare for the processing of an event resulting in a facilitation effect. Temporal orientating of attention is reflected by enhanced early sensory processing with a larger P1 component for stimuli appearing at the attended moment as well as enhanced components such as N2 and P300 reflecting decisional and motor preparation (Correa et al., 2006). This orientation of attention is conferring enhanced cognitive resources at a given time and is accompanied by an improvement in performance at that given time. Scientists observed shorter RT on trials where participants were validly cued towards the moment in time in which the target appeared (Coull et al., 2001; Miniussi et al., 1999; Naccache et al., 2002).

A situation of expectancy typically requires orienting attention in time. In the following section, we will review the contribution of temporal attention to the CNV.

Tecce and Scheff (1969) showed the contribution of attentional processes to the CNV. Using a classical foreperiod paradigm, they presented distracting auditory stimuli and they asked the participants to pay attention to these auditory stimuli in order to perform a task. What they observed is that during the foreperiod, there was a decrease in the amplitude of the CNV for trials with distractors compared to control trials. Hence, Tecce and Scheff were the first to demonstrate that the amplitude of the CNV depends, in part, on attentional processes. Later, many studies confirmed the attentional interpretation of the CNV, in particular studies revealing that a larger negativity was indicative of greater sustained attention. Rebert et al. (1967), and Connor & Lang (1969) showed that a lower intensity of stimulus S2, which required subjects to pay more attention to perceive S2, elicited stronger CNV amplitudes. Furthermore, individuals with impaired attentional abilities, like children with ADHD, usually exhibit a smaller CNV compared to control subjects (Banaschewski et al., 2003; Perchet et al., 2001; van Leeuwen et al., 1998).

### 3.3.3 CNV and time processing

The CNV has also been studied as a marker of time processing. CNVs have been observed in tasks requiring a time interval judgment or production (Kononowicz and van Rijn, 2011; Macar and Vidal, 2003). For example, in a task in which subjects had to tell if an interval was shorter or longer than a previous interval, the CNV triggered by the second interval had similar length than the CNV of the previous interval, suggesting that the CNV might reflect temporal estimation and time perception (Pfeuty et al., 2005; Tarantino et al., 2010).

This implication of the CNV in temporal tasks led scientists to postulate that the CNV is a marker of time processing in the brain (Macar and Vidal, 2009). Because of the morphological similarities of the CNV and the temporal accumulator described in the pacemaker-accumulator model of time perception (Gibbon, 1977; Gibbon et al., 1984; Treisman, 1963), the CNV constituted a good candidate mechanism at the origin of this temporal accumulator (Macar and Vidal, 2004). Some have argued against this interpretation and prefer the interpretation of the CNV as temporal preparation rather than being the source of pure temporal perception (van Rijn et al., 2011). In any case, temporal estimation seems

required for temporal preparation and the CNV probably reflects in part this temporal estimation.

### 3.3.4 CNV and motor preparation

The investigation of the contribution of motor preparation to the CNV is a long-going topic of investigation. When subjects are asked to perform a movement in response to a stimulus, we typically observe a negativity preceding the execution of that voluntary movement, called the readiness potential (RP). The late phase of the CNV has for a long time been assimilated to the RP. The CNV and the RP were both discovered in the same year 1964, both happen in the seconds preceding a button press, and both potentials are distributed over motor regions corresponding to the motor response expected (Brunia and Vingerhoets, 1980); suggesting that both potentials may reflect motor preparation processes. Furthermore, when no motor task is required the late CNV is very attenuated and can even disappear, this led Rohrbaugh, & Gaillard (1983) to interpret the late phase of the CNV as being identical to a RP. This interpretation is corroborated by the fact that this motor preparation seems to have a behavioral counterpart, as the amplitude of the CNV seems to be inversely correlated to the RT (Haagh and Brunia, 1985; Hillyard, 1969; Hillyard and Galambos, 1967).

### 3.3.5 CNV and sensory expectation

In addition to the clear contribution of motor preparation to the late phase of the CNV, several later findings suggest that the late CNV is not only comprised of a RP, but also reflect cognitive expectancy processes. Firstly, the higher amplitude of the tCNV compared to the RP suggested, from the beginning of CNV research, that the CNV might involve more than motor processes (Kornhuber and Deecke, 1965). Moreover, the CNV can be recorded in the absence of motor response (Nakamura et al., 1975; Ruchkin et al., 1986; Weinberg et al., 1974). Finally, various studies showed that in a foreperiod paradigm, when the motor response to S2 is followed by a feedback, a slow negative potential is elicited after the motor response and prior to the feedback. This potential, called the SPN (stimulus preceding negativity), reflects the purely sensory expectation of the upcoming reward stimulus (Damen and Brunia, 1987). This led them to hypothesize that the tCNV is comprised of both a motor preparation negative potential (RP) and a sensory expectation negative potential (SPN) (Brunia and Damen, 1988) towards S2.

### 3.3.6 Conclusion on the interpretation of the CNV

Overall, we saw that the CNV elicited in paradigms with long foreperiods displays two phases. The early phase reflects the processing of S1 and the orientation of attention it induces. It mainly depends on the properties of S1. The second phase reflects both the expectancy of the sensory stimuli S2, similar to a SPN, and the motor preparation to the response given to S2, similar to a RP. The overall CNV reflects temporal orienting of attention and this temporal expectancy allows for sensory and motor preparation.

### ● 3.4 Neural Origins of the CNV

The CNV reflects multiple cognitive processes involving attentional, sensory and motor preparation. Therefore, this potential is likely the result of the integration of dissociable neural processes.

Scientists often consider expectancy as a top-down process exerted on sensory regions, where prior expectations inform sensory regions by modulating early sensory processing. In the following section, we will see how the knowledge about the neural origin of the CNV might inform this model.

#### 3.4.1 Implication of frontal regions

Measured in EEG, the CNV is located preferentially around the vertex with a rather frontocentral early phase and a more centroparietal terminal phase. It is preferentially measured over left frontal, parietal (Macar and Vidal, 2003), or premotor (Praagstra et al., 2006) electrodes.

Source reconstructions from MEG studies have localized the source of the CNV in frontal regions (Ioannides et al., 1994; Liu et al., 1996) with primary motor, ACC and SMA as the best candidates for the CNV generators. Intracranial recordings also recorded the CNV in central regions like premotor areas, SMA, post central and cingulate areas (Lamarche et al., 1995). Furthermore, Nagai et al. (2004) indexed trial-by-trial CNV fluctuation to active brain areas measured in

fMRI and found enhanced activity in the ACC, SMA, and insula during the CNV task. Moreover, a Positron Emission Topography (PET) study also showed implication of the ACC in sustained attentional processes (Pardo et al., 1991).

These reports are consistent with the implication of these different frontal areas in high-level cognitive processes like motor preparation, attentional orienting and arousal.

The ACC and the SMA are known to be implicated in motor preparation (Ioannides et al., 1994; Lee et al., 1999; Liu et al., 1996) and could contribute to the response anticipation and motor preparation aspects of the CNV.

The ACC and the insula are known for their role in autonomic arousal and their integration of cognitive processes (Critchley et al., 2000, 2001, 2003). The ACC is also implicated in higher cognitive processes such as conflict monitoring, selective attention, and working memory (Barch et al., 2001; Braver et al., 2001; Luks et al., 2002).

The SMA seems to exhibit a phasic increase in activity at the time when the target is expected, which suggests it might be implicated in memorizing fixed time intervals (Pfeuty et al., 2003). It also has been investigated as a potential neural substrate of the temporal accumulator (Casini and Vidal, 2011; Coull, 2009; Macar et al., 1999). The SMA is also involved in the control of voluntary movements, indeed stimulating this region provokes a feeling of urge to move. It has been proposed that the SMA is involved in the triggering of voluntary movement (Ball et al., 1999).

Among frontal regions, the dIPFC is known to participate in the genesis and maintenance of alerting. Using repetitive Transcranial Magnetic Stimulation (rTMS) to inhibit activity in the dIPFC, Mannarelli et al. (2015) induced a decrease in the amplitude of CNV. Moreover, Zappoli et al. (2000, 2002) showed that lesions centered on the dIPFC led to the absence or the reduction of the CNV. In these two studies, the lesions were rather extensive. Finer investigations revealed that patients with focal lesions in the prefrontal cortex had a normal CNV early phase, but a specific reduction in the late phase of their CNV (Rosahl and Knight, 1995). These reports suggest the implication of the prefrontal cortex in the generation of the late phase of the CNV. Funderud et al. (2013) found similar results suggesting that the dIPFC might be implicated in the late preparatory phase of the CNV.

Moreover, these frontal regions seem to be part of a network for temporal attention as revealed by the work of Coull et al. defining a network for temporal orienting of attention, this network involves a fronto-parietal and specifically the left parietal region (Coull and Nobre, 2008, 1998; Coull et al., 2013).

In short, source reconstruction of the CNV with EEG and MEG have localized several potential generators in frontal regions, including pre-motor and cingulate areas, as well as dorsolateral-prefrontal cortex with a causal implication.

### 3.4.2 Implication of subcortical structures

Neurophysiological studies classically report that negative potentials (like the CNV) originate from thalamic afferents depolarizing the dendrites of pyramidal cells, and thus permitting an excitation of extended cortical areas (Birbaumer et al., 1990; Rockstroh, 1989). It is therefore not surprising to find an involvement of the thalamus in the generation of the CNV (Bareš et al., 2000; Nagai et al., 2004; Rektor et al., 2001). Other regions of the basal ganglia have also been implicated in the generation of the CNV. For instance, Bareš (2001) observed a fast phase reversal and strong voltage changes in the basal ganglia indicating that the putamen, pallidum, and caudate nucleus might be candidates for the generator of the CNV. SMA, frontal regions, temporal regions, and basal ganglia insula posterior thalamus all participate in a cortical-subcortical network for anticipation and preparation for stimuli (Bareš et al., 2003).

Dopamine is an important neuromodulator in the basal ganglia, suggesting that CNV may be modulated by the dopaminergic system (Amabile et al., 1986; Kopell et al., 1974; Oishi et al., 1995; Tecce et al., 1975; Tecce, 1991; Tecce and Cole, 1974).

The cerebellum is another structure that could be implicated in expectancy particularly in the learning of temporal contingencies, as revealed by the study of patients with cerebellar atrophy (Trillenberget al., 2004). It also has a contribution to the estimation of durations as shown by its implication in explicit timing tasks (Coull and Nobre, 2008).

### 3.4.3 CNV in temporal and sensory regions

In an EEG study, Gomez et al. (2003) applied source reconstruction to localize the potential regions involved in the generation of the CNV. Apart from the ACC and the SMA, they found an additional involvement of motor and occipital regions particularly in the late phase, they suggested that the ACC and the SMA might initiate the anticipation, followed by the recruitment of motor and perceptual areas required to process the upcoming stimulus.

Lamarche et al. (1995), using an auditory foreperiod paradigm and intracranial recordings of the CNV, also found an involvement of the auditory cortex, in line with the idea that sensory areas prepare for the upcoming of S2.

An alpha-related desynchronization is known to be associated to event anticipation and preparation (Babiloni et al., 1999). It is thus not surprising to observe that the CNV is accompanied by a reduction in alpha power preceding the upcoming of S2 (Bender et al., 2005; Magnani et al., 1998). Recently, Funderud (2012), in a Go/No-go type of foreperiod paradigm showed both an increase in CNV for Go trials, and a power reduction in theta to low gamma bands. Similarly, Rohenkohl et al. (2011) observed an alpha-desynchronization preceding the appearance of the target, suggesting that a reduction in alpha oscillations might be related to temporal expectation.

The CNV is also accompanied by an increase in gamma power (30-100Hz) in frontal regions during anticipation (Fan et al., 2007).

## ● 3.5 CNV and consciousness

### 3.5.1 Habituation and potential link between CNV and consciousness

The CNV is elicited when an attentional process is triggered, and when attention is oriented in time over a couple of seconds. It seems like an active process that depends in part on voluntary top-down control of attention over time. Scientists have long postulated that the CNV might reflect a conscious sustained process.



In early studies on the CNV, scientists observed that the CNV amplitude seems to diminish across blocks revealing a form of habituation. They postulated that the habituation of the CNV reveals that cognitive processes eliciting the CNV are being automatized with time. In other words, the CNV might reflect conscious attentional orienting efforts. Once participants are habituated to the contingency, these preparation processes are automatized and the CNV diminishes (Cooper et al., 1979).

### 3.5.2 CNV a result of both voluntary and automatic temporal orientation

The CNV is thought to reflect a voluntary form of attention coming from an explicit association between S1 and S2. However, more automatic forms of temporal expectation have been recently explored. Thus, the CNV could be modulated more automatically depending on context. This automatic form of temporal orienting is reflected by the sequential effect (SE). This effect is typically displayed in a foreperiod paradigm with variable foreperiod intervals, where the RTs are affected by the length of the foreperiod of the preceding trials. Smaller foreperiods will cause shorter RTs on the following trial (A. Baumeister and E. Joubert, 1969; Drazin, 1961; Los and Heslenfeld, 2005; Steinborn et al., 2008). The CNV is also affected by this sequential effect: shorter preceding foreperiods elicit stronger CNVs in the following trial (Capizzi et al., 2013; Los and Heslenfeld, 2005; Mento, 2013; Trillenberg et al., 2000; Van der Lubbe et al., 2004). Recent studies revealed that the SE is not affected by concurrent working memory tasks, suggesting that it might reflect an automatic modulation of temporal attention. Moreover, SEs are preserved after prefrontal lesions suggesting that this effect involves a different network of temporal attention than the voluntary temporal orienting (TO).

Recent studies manipulated voluntary temporal attention with informative versus non-informative warning cues, while also manipulating automatic temporal attention by the contextual effect of preceding trials with short versus long foreperiods. They showed that automatic and voluntary TO had independent effects that implicated independent networks (Coull et al., 2016; Mento, 2013, 2017).

Similarly, Breska et al. (2014) showed a contextual modulation of the CNV induced by rhythmic presentation of stimuli inducing unintentional modulations of the temporal attention as reflected by the changes in CNV amplitude.

These results support the view that the CNV can be modulated unintentionally by the context, supporting a form of automaticity in the TO reflected by the CNV.

### 3.5.3 Subliminal influences on the CNV

A recent study reported that CNVs elicited consciously could be subject to unconscious modulations by masked reward cues presented before the task (Capa et al., 2013). Participants performed long runs of task switching and were presented at the beginning of each run with masked monetary cues, researchers observed an effect of the monetary cues on performances and on the CNVs initiated during the task. Unconscious monetary cues seemed to induce changes in motivation resulting in modifications of the CNV amplitudes. These results were interpreted as a long-lasting influence of monetary cues on motivation thus resulting in increased CNVs. The CNV is indeed known to be influenced by the level of motivation.

To our knowledge, no study has ever directly tried to probe the initiation of a CNV with subliminal stimuli or directly influence an ongoing CNV with masked cues.

### 3.5.4 CNV and conscious states

The CNV seems to be affected by levels of arousal. Indeed, subjects who had an undisturbed night of sleep show stronger CNVs than participants who were disturbed during their sleep (Yamamoto et al., 1984). These results suggest that arousal might be a key requirement to elicit a CNV.

Hamon and colleagues (1994) tested the possibility of initiating anticipatory attention during sleep. They observed CNVs in awake subjects, and during REM sleep, but noticed that the CNV was absent in deep sleep. Yasuda et al. (2011) also found an absence of CNV in deep sleep and a decrease of CNV amplitude with sleep onset latency. All these evidence points toward the fact that consciousness might be necessary for endogenous anticipatory temporal attention.

The presence of CNV was also probed in patients with disorders of consciousness (DOC). In a study on two comatose patients, Dolce & Sannita (1973) found that after presenting paired auditory stimuli to these patients more than a hundred

times, they were able to observe a negative shift in the EEG between S1 and S2 resembling a CNV. This implies that maybe after long repeated exposure the contingency between S1 and S2 could be learned unconsciously and trigger a CNV-like expectancy process in unconscious patients.

More recently, Faugeras et al. (2012), in a study on the processing of novelties in DOC patients, noted an effect of global novelties only in the group of patients presenting CNVs. This suggests that the CNV might be an indicator of the complexity of information processing, and can serve as an index of consciousness to help in the assessment of DOC patients. However, they also noted the presence of a CNV in several minimally conscious (MCS) and vegetative state (VS) patients (Faugeras et al., 2012). Similarly, Sergent et al. (2017) also observed a CNV in three of four VS patients. Hence, temporal expectancy might also occur in the absence of consciousness.

### ● 3.6 Summary

- Attention can be oriented temporally and improve performance at a given moment in time.
- The CNV is a complex ERP reflecting multiple cognitive processes, but mainly temporal expectancy.
- Motor preparation contributes to the late phase of the CNV as a RP.
- The anticipation of the upcoming stimulus also contributes to the late phase of the CNV similarly as a SPN.
- There is a strong contribution of temporal attention to the CNV.
- The CNV is thought to be implicated in time estimation.
- The CNV main generator is the frontal region, in particular, the premotor areas ACC, SMA and dIPFC.
- The CNV also seems to originate from thalamo-cortical interactions.
- The CNV seems to be accompanied by a reduction in alpha, beta and theta bands reflecting sensory expectation and motor preparation.
- The habituation of the CNV might suggest that the CNV reflects conscious efforts of temporal attention.
- The CNV can be modulated unintentionally in an automatic way.
- The CNV seems to disappear during deep sleep.
- CNVs were observed in DOC patients, suggesting that consciousness is not required.





#### **4 Question of the present thesis**

A clear dissociation between consciousness and cognitive processing can be made since a lot of cognitive processes can occur unconsciously in particular motor preparation, motivation and attention. Several studies have reported long-lasting influences of unconscious information. However, most unconscious information seems to fail in eliciting sustained unconscious representations lasting more than a few hundred of milliseconds.

Knowing that attention and motor preparation can be oriented and initiated unconsciously we wondered if it would be possible to initiate unconsciously a sustained attentional preparatory process. Expectancy processes eliciting CNVs involve attention but also motor preparation, which are known to be manipulable unconsciously. However, expectancy is a sustained attentional state that lasts up to several seconds which is why it is interesting to question the possibility of eliciting such a sustained active process unconsciously. There is contradictory evidence regarding the implication of consciousness for CNV mediated expectancy processes. By revealing the existence of a lasting (> 1 second) and sustained expectancy process triggered by a subliminal cue inaccessible to conscious report, we would extend the field of unconscious cognitive processes.

In the first part, we explored the possibility of probing subliminal temporal attention orientation behaviorally by trying to prime a response to a target with masked warning cues.

In a second part, we investigated whether we could find electrophysiological evidence of unconscious expectancy with the help of EEG and intracranial recordings.

Finally, after demonstrating the existence of such a lasting expectancy process triggered by a non-consciously perceived stimulus, we investigated if this expectancy process could still be consciously introspected. In other terms, we explored the possibility that a complex interplay between unconscious and conscious metacognitive processes could explain this phenomenon.



**CHAPTER 2**

**—**  
**BEHAVIORAL EXPLORATION  
OF CONSCIOUS  
AND UNCONSCIOUS  
EXPECTANCY PROCESSES**



## 1 Introduction

In the classic Posner task (Posner, 1980), cues presented prior to the appearance of the targets can orient attention in space and facilitate the processing of these targets. Similarly, attention can also be oriented in time where cues indicate the time window of appearance of a target. Attentional resources are oriented towards this time window, facilitating the processing of targets appearing at that moment and allowing a faster detection of temporally cued targets (Coull and Nobre, 1998; Doherty et al., 2005; Griffin et al., 2001).

As I have reviewed in the first chapter, various studies that used masked priming paradigms reported that even when cues were not consciously perceived, they were able to facilitate responses to targets. Many different cognitive processes can be primed unconsciously, however, masked priming has only been tested for cues providing information about the nature of the target or its location but never about its temporal occurrence. Whether masked cues can orient attention in time over an extended period (>1sec) is an interesting question knowing that no masked priming effect lasting more than one second has ever been reported.

Unconscious representations are thought to be short-lived. However, it is possible that these evanescent unconscious representations could induce lasting cognitive processes, like for example, expectancy processes requiring sustained orientation of attention. We were motivated by the following question: Can masked cues orient attention temporally and in a lasting manner, towards the moment of occurrence of the target and facilitate the processing of that target by engaging in an expectancy process?

To maximize the effect of the masked cues we decided to test both the effect of time orientation (by contrasting predictive versus non-predictive temporal cues) and also the effect of expectation (by contrasting predictive cues of precise onset of upcoming target versus predictive cues of absence of upcoming target). We used cues providing information about the probability of occurrence of a target in an attempt to manipulate expectancy by creating differences in the amount of preparation and temporal attentional efforts. We used a masked cueing ex-

periment to probe unconscious expectancy behaviorally by presenting two types of cues: 1) a 100% predictive cue of the upcoming of a target appearing after a fixed time-interval; and 2) a cue announcing in most of the trials the absence of a target. This allowed us to measure the behavioral advantage of the 100% predictive cue on the response to the target compared to the mostly unpredictable cue. Crucially, by masking the cues, we tested whether this expectancy effect occurs unconsciously.



## 2 Materials & Methods

All volunteers gave their written informed consent, and experiments were approved by the Ethical Committee (APHP, CPP-IDF VI, Pitié-Salpêtrière Hospital).

### ● 2.1 Participants

Thirty right-handed participants with normal or corrected to normal vision were included. Two participants were excluded because they could perceive the masked cues better than chance level on the discrimination task (75% and 63% correct-response (chance-level = 50%), individual  $d'$ -prime values were 1.37 and 0.67 respectively with t-test p-value against zero  $<10^{-11}$  and  $<10^{-3}$ ). Two other participants were also excluded because they did not take into account the instructions (no significant expectancy effect on unmasked trials). Twenty-six participants were thus included in the statistical analysis (age =  $25.4 \pm 3.81$  ranging from 20 to 35 y.o.; median age = 25; 18 females).

### ● 2.2 Stimuli and procedure

Each trial consisted in the presentation of a fixation cross for 1s followed by the serial alternation of a neutral cue (50 ms), a blank (17 ms) and a mask (33 ms). This sequence alternated for a variable time ranging from 500ms to 1433ms, and was then followed by the presentation of a cue (diamond or square balanced across subjects) that predicted the upcoming presentation of a target within the current trial. These cues could be presented masked or unmasked. Masked cues were presented in the alternation of masks and neutral cues, whereas unmasked



cues were flanked by a 17ms blank allowing a conscious perception (see Figure 2.1).

In an attempt to render the perception of the cues unconscious, we designed masks using a metacontrast masking approach. We tested different modalities of masking on a pilot group of subjects. We chose the most optimal masking by assessing the visibility with a discrimination task and the behavioral influences of the cues with a masked repetition priming task. Interestingly, presenting the masks directly before and after the cues was not effective enough. Indeed, we found that inserting a blank frame between masks and cues allowed better masking, possibly creating similar effects as in the flicker paradigm used to assess change blindness (Rensink et al., 1997). Moreover, we chose to present the cues during a continuous visual sequence in an attempt to mask not only the physical characteristics of the cues but also their temporal occurrences. This also allowed us to limit as much as possible a general expectation generated by the presentation of the masked cues irrespective of their physical characteristics.

One cue predicted the upcoming appearance of a target ('Cue-Tgt'), whereas the other cue predicted the absence of upcoming target within the current trial ('Cue-NoTgt'). Predictability of target presence by the cues was manipulated in order to optimize the efficiency of task instructions on unmasked trials on the one hand, and to increase the number of trials in each condition for masked trials in order to detect a behavioral effect. In the unmasked condition, Cue-Tgt predicted target presentation with 100% certainty, and Cue-NoTgt predicted the absence of a target with 88.46% certainty (184/208 trials). In the masked condition, Cue-Tgt predicted target presentation with 100% certainty, and Cue-NoTgt predicted the absence of a target with 50% certainty.

Cues were then followed by the identical series of neutral cue/blank/mask that initiated a trial, for a fixed interval of 1166 ms. Then either the letter 'W' was presented as a target, or no target was presented, defining thus 6 types of trials (see Figure 2.1). Subjects had to press a response-button with their right index as fast as they could when a target was presented. Stimuli were presented on a DELL P170S 1280x1024 32bits 60Hz using Matlab (The Mathworks, Inc.) psychtoolbox

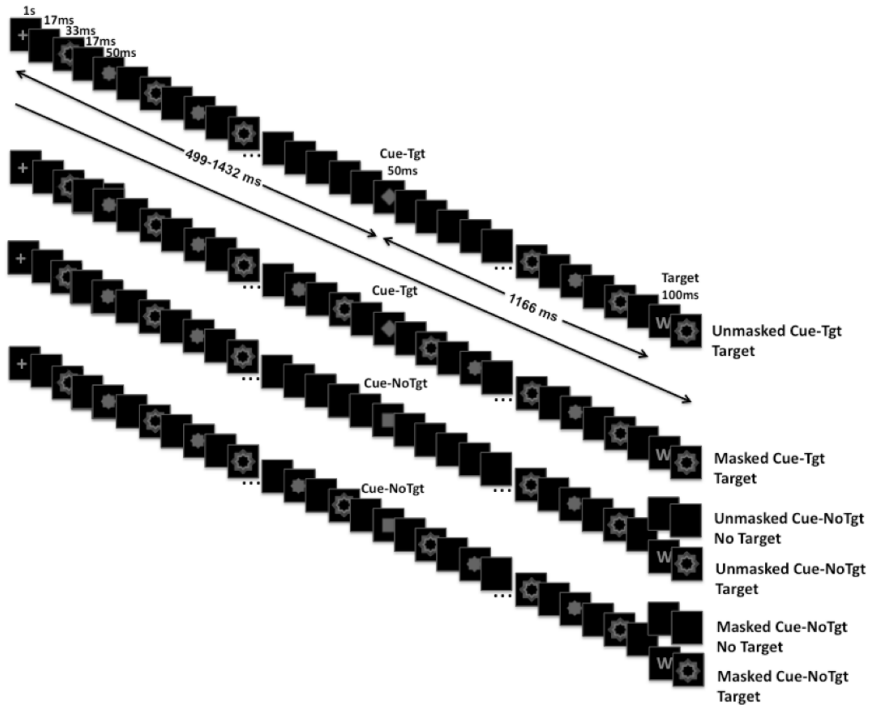


Figure 2.1 Experimental paradigm

Sequences of visual events are shown for the 6 type of trials. Each trial begins with a fixation cross presented 1s followed by the repetition of the following pattern: blank (17ms), mask (33ms), blank (17ms) and neutral cue (50ms), interrupted by the presentation of a Cue-Tgt or Cue-NoTgt followed by a blank or a target (W) according to the 6 possible type of trial.

Subjects underwent a training of 48 trials composed of 100% predictive unmasked cues trials. The main experiment consisted in 8 blocks of 110 trials with the following total number of trials per condition: Unmasked Cue-Tgt target = 208 trials; Unmasked Cue-NoTgt No target = 184 trials; Unmasked Cue-NoTgt Target = 24 trials; Masked Cue-Tgt target = 208 trials; Masked Cue-NoTgt No target = 128 trials; Masked Cue-NoTgt Target = 128 trials). Trials were randomly presented.

In order to assess the visibility of masked cues we gathered subjective and objective measures. A short interview probed subjective report of: “seeing cues within the serial alternation of displays in trials free of visible cues”. Then, partic-

ipants performed a forced-choice prime discrimination task after the main experiment. They were presented with masked cues (50% Cue-Tgt, 50% Cue-NoTgt for a total of 200 trials) presented the same way as in the main experiment, and were forced to categorize the cue using two keyboard response buttons.

### ● 2.3 Instructions

Subjects were instructed to pay attention to the sequence of stimuli appearing on the screen and to press a button as rapidly as they could when the letter 'W' appeared. They were informed that two cues could precede the target: one predicted the upcoming appearance of a target with 100% certainty ('Cue-Tgt') approximately 1 second later, whereas the other cue ('Cue-NoTgt') predicted the absence of upcoming target within the current trial in the vast majority of trials.

### ● 2.4 Data analysis

Analyses were performed on reaction times (RTs) inferior to 1000ms and superior to 100ms. Additionally, RTs exceeding 3 standard deviations of the individual mean were excluded. ANOVAs and Student t-tests were used.



## 3 Results

In this experiment, 30 control subjects participated in a classical temporal expectancy paradigm. A geometrical cue (square or diamond or vice-versa) predicted the presence ('Cue-Tgt') or absence ('Cue-NoTgt') of an upcoming target letter ('W') in the current trial. Cues could be masked or unmasked and were randomized within the same blocks (see Figure 2.1). Subjects were instructed to answer to the target, if it appeared, as fast as possible using a response button with their right index finger. The 'Cue-Tgt' cue was fully predictive of target presentation (100% of trials) both in masked and unmasked conditions, while the 'Cue-NoTgt' cue was 88.5% predictive of the absence of a target in unmasked trials, and non-predictive in masked trials (50% of trials were not followed by a target). This difference was designed on purpose in order to increase the number of trials including a target preceded by a 'Cue-NoTgt' cue in masked trials and

therefore to increase the power to detect a masked cueing effect in RTs.

We analyzed RTs from trials containing a target, with the following ANOVA: Cue-type (2) X Cue-Visibility (2). A major effect of cue-type was found ( $F(1,25)=78.2$ ,  $p<10^{-8}$ ) with faster RTs for 'Cue-Tgt' than for 'Cue-NoTgt' cues (495ms and 578ms respectively, post-hoc  $p$  value  $< 10^{-8}$ ), as well a strong effect of cue visibility ( $F(1,25)=21.5$ ,  $p<10^{-4}$ ) with faster RTs to unmasked cues trials than to masked cues trials (520ms and 554ms respectively, post-hoc  $p$  value  $< 10^{-4}$ ). These two factors interacted ( $F(1,25)=63.0$ ,  $p<10^{-7}$ ; see Figure 2.2) reflecting a stronger expectancy effect for unmasked cues than for masked ones. Crucially, post-hoc tests revealed that both masked and unmasked expectancy effects were significant. Expectancy effect in unmasked cues trials showed an effect size of 163ms ( $p<10^{-8}$ ). Expectancy effect in masked cues trials was much smaller (effect size = 4.4ms) but significant ( $p=0.03$ ).

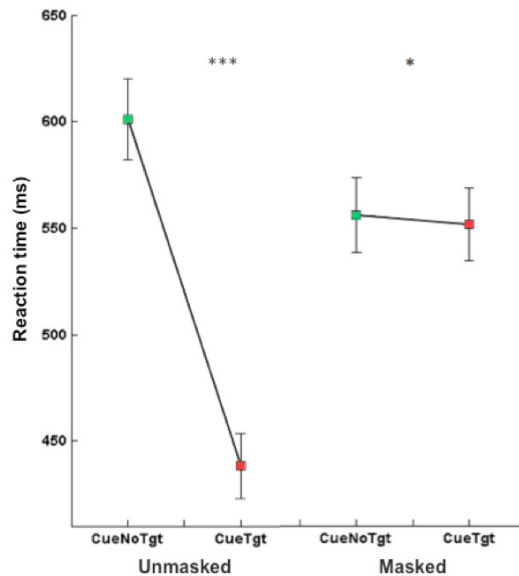


Figure 2.2 Behavioral masked & unmasked expectancy effects

Mean reaction time is shown as a function of masking and of cue type (green and red for Cue-NoTgt and Cue-Tgt respectively). Error bars represent standard error. Subjects presented a strong cueing effect for unmasked cues ( $p<0.001$  \*\*\*) and also displayed a significant but smaller cueing effect for masked cues ( $p<0.05$  \*).

Concerning cue visibility, none of the subjects reported the subjective impression of perceiving predictive cues in the serial alternation of displays of trials free of visible cues. Objective performance confirmed these subjective reports by showing a mean  $d'$  value of  $-0.06$  ( $p=0.1$ ). No correlation was observed between individual  $d'$  values and masked cues trials expectancy effect ( $p=0.17$ ).

This first behavioral experiment showed both a classic expectancy effect for consciously visible cues, as well as a small but significant expectancy effect driven by unconsciously perceived symbolic cues. Crucially, this subliminal expectancy effect spanned in time over more than a second (1166ms), far beyond the usual shorter SOAs previously used to probe masked priming effects (Dehaene et al., 2001; Dupoux et al., 2008; Greenwald et al., 1996).



## 4 Discussion

In this behavioral cueing experiment, we tested the possibility for masked cues to trigger an expectancy effect that would prime behavior. The cues manipulated expectancy and temporal attention by predicting the probability of occurrence of the target. Unmasked cues clearly manipulated expectancy as reflected by a strong conscious cueing effect. More crucially, however, even when the cues were masked, they induced a small 4.5ms cueing effect. This masked cueing effect occurred for an SOA exceeding a second which is, to our knowledge, the first report of such a long unconscious cueing effect.

This masked cueing effect is small but it is assessed on a large group of subjects. Moreover, the visibility of the cues was controlled and did not correlate with the masked cueing effect at the subject level, suggesting that this effect is not driven by a potentially conscious experience of the masked cues.

We chose to present the cues with a variable time interval that separates them from the fixation point in order to avoid the temporal prediction possibility triggered by the fixation point itself. However, this might have impaired the treatment of the masked cues. Indeed, Naccache et al. (2002) showed that when masked cues are not presented at a fixed time in a flow of stimuli, attention can not be

oriented towards the moment of appearance of the cue and this results in poorer processing of the masked cue and reduction of the priming effects. In our paradigm, since masked cues appear at random intervals, it is possible that they are not fully attended and thus their influences are limited.

Another limit to our paradigm comes from the fact that even though we ensured that participants could not discriminate between the two masked cues, the moment of appearance of the cues was slightly perceivable by an irregularity in the continuous visual presentation. This irregularity by itself could have oriented attention temporally irrespectively of the nature of the cue. Moreover, cues that were not predicting a target were still predicting the upcoming end of the trial and could also have oriented attention temporally, limiting our measured effect.

Despite these factors that could limit the measured difference in expectancy, we were still able to measure an influence of masked cues on behavior lasting over a second.

This novel finding puts into question the fleeting nature of unconscious processes and calls an exploration of the temporal dynamics of this process. What is the neural signature of this effect? Our next chapter explores this specific question.





**CHAPTER 3**

**—**

**ELECTROPHYSIOLOGICAL  
EXPLORATION OF CON-  
SCIOUS AND UNCONSCIOUS  
EXPECTANCY PROCESSES:  
EEG STUDY**



## 1 Introduction

In the previous chapter, we observed behavioral effects of unconsciously elicited expectancy on time periods exceeding a second. Here, we explore the neural underpinnings of this unconscious manipulation of expectancy. We were particularly interested in knowing whether we could elicit unconscious modulations of the CNV, an ERP known to reflect sustained expectancy brain process. As reviewed in Chapter 1, Capa et al. (2013) reported influences of masked cues on motivation which led to changes in CNV amplitudes within the following block. However, they did not directly test the possibility for unconscious cues to elicit an expectancy process by affecting the CNV directly.

To investigate possible unconscious modulations of the CNV on a trial-by-trial basis, we used a similar paradigm as the one we previously used to probe unconscious expectancy behaviorally, with the same global structure. Given that our major objective was to maximize the expectancy effect measured electrophysiologically and not necessarily to measure any behavioral effect, we used fully predictive cues (100% correct cues) and compared neural activity elicited by ‘Cue-Tgt’ and ‘Cue-NoTgt’ cues during the 1166ms time-window spanning from cue onset to target onset. We also added a neutral condition corresponding to the absence of any predictive cue, in order to compare RTs and neural activity to a condition without an increased expectancy (see Figure 3.1).

We also modified the task that participants had to perform compared to the behavioral experiment: we used a number comparison task instead of a basic reaction time task. The target was a number between 1 to 9 (but never 5), that subjects had to compare to 5 using two response buttons (smaller/greater than 5). This way subjects had to wait for the upcoming target in order to prepare a specific motor command (right hand or left hand), this allowed us to limit the LRP motor preparation aspect of the CNV.





## 2 Material and methods

### ● 2.1 Participants

Sixteen participants were included (age= 24.2±1.68 ranging from 22 to 27 y.o.; median age 24; 10 females).

### ● 2.2 Stimuli and procedure

Experimental design of stimuli presentation used in this experiment was very similar to the one used in the experiment of chapter two, except that the cues were 100% informative: 'Cue-Tgt' announced systematically a target, and 'Cue-NoTgt' the absence of any target in the current trial. A control condition was added by preceding the target with a neutral cue corresponding to the cue used in every repetitive pattern of the alternating sequence used in all trials (see Figure 3.1).

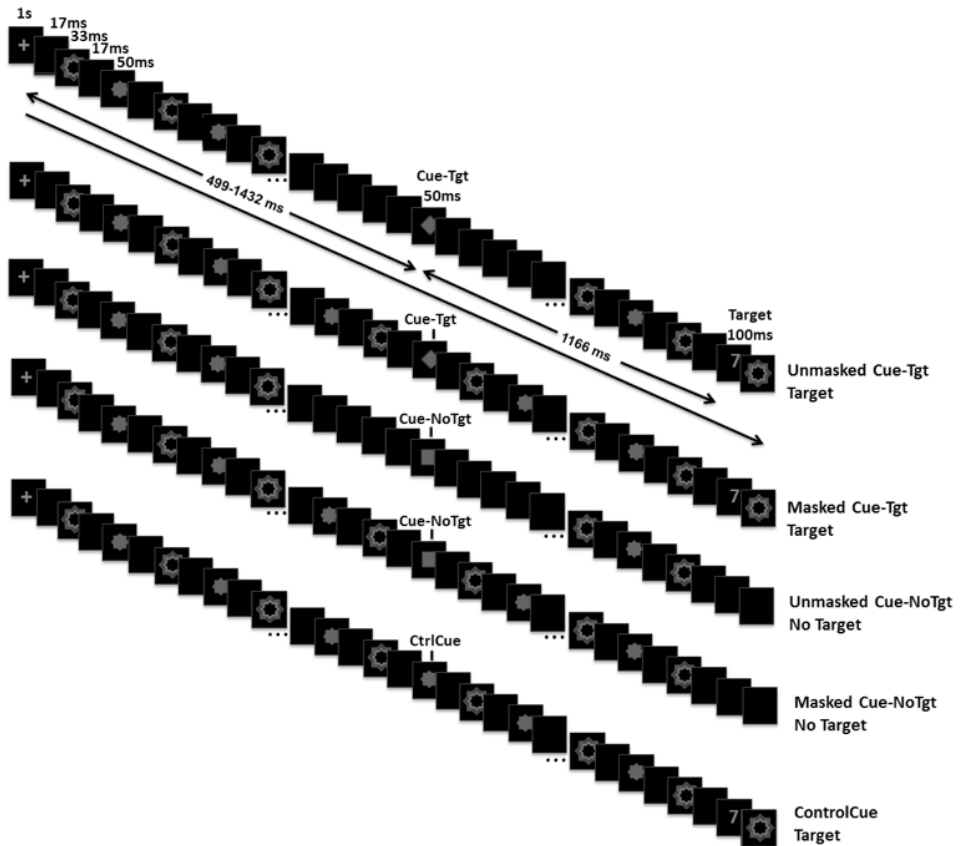


Figure 3.1: Experimental paradigm

*Sequences of visual events are shown for the 5 type of trials. Each trial begins with a fixation cross presented 1s followed by the repetition of the following pattern: blank (17ms), mask (33ms), blank and neutral cue (50ms), interrupted by the presentation of a CueTgt or CueNoTgt followed by a blank or a target (1, 2, 3, 4, 6, 7, 8 or 9) according to the 5 possible type of trial.*

In this experiment the target was a number between 1 and 9, except 5, that the subject had to categorize as larger or smaller than 5. A total number of 550 trials were delivered, corresponding to 110 trials of each of the 5 conditions. Trials were distributed in 10 blocks of 55 trials (11 trials per condition). Trials were randomly presented within each block. A pause was offered after each block.

A training was proposed before the main experiment, and consisted of two blocks of 50 trials with conscious cues, to let the subjects learn consciously the association between each cue and the corresponding target predictability (100%

and 0% respectively).

After the main experiment, we assessed masked cues visibility by collecting subjective reports and by engaging participants in a final forced-choice discrimination task on masked cues trials.

To assess the visibility of the masked cue the participants performed a forced choice prime discrimination task: subjects were presented with masked cues (50% 'Cue-Tgt', 50% 'Cue-NoTgt') presented the same way as in the main part, and at the end of the trial subjects were forced to categorize the cue using two keyboard response buttons.

### ● 2.3 Instructions

Subjects were instructed to respond to a number ranging from 1 to 9, excluding 5, that they had to categorize as being larger than five by pressing the right button, or smaller than five by pressing the left button. Prior to this target categorization, they were presented with a visual sequence and informed that if the visual sequence contained a 'Cue-Tgt' it would be systematically followed by a target approximately one second later, and that if it contained a 'Cue-NoTgt' then no target would follow. Finally they were instructed that in the absence of a visible cue, a target could be presented or not, without specifying any probability.

### **EEG recording and processing**

EEG signal was collected at 250Hz with a 256 electrodes geodesic sensor net (EGI, Oregon, USA) referenced using a common average reference. In order to be sensitive to slow cortical potentials typical of CNV, we deliberately used a 0.1Hz highpass, as well as a 20Hz lowpass filter. We chose the 0.1Hz highpass after trying 0.5Hz and 0.2Hz highpass and observing distortions of the slow potentials (Acunzo 2012). Trials were segmented -200 +1600 ms relative to the appearance of the cue, voltages exceeding 150 $\mu$ V as well as blinks exceeding 100 $\mu$ V and eye movements exceeding 80 $\mu$ V were excluded, electrodes with more than 30% reject rate were excluded, bad electrodes were interpolated trials with more than 10 bad electrodes were excluded, a 200ms baseline correction was applied, all these treatments were applied with EGI waveform tool.

## ● 2.4 Data analysis

### 2.4.1 Behavior

Analyses were performed on reaction times (RTs) inferior to 1500ms and superior to 100ms, and used Student t-tests.

### 2.4.2 ERPs

Regions of interest (ROI's) were adapted from Faugeras et al. (2012) using the EGI (Eugene, Oregon, USA) numbering system, these ROI corresponded to the following groups of contiguous electrodes: Fz centered: 6 7 8 14 15 16 21 22 23; Cz centered: 8 9 45 80 81 90 131 132 186 257; Pz centered: 100 101 110 118 119 126 127 128 129; Oz centered: 137 138 125 149 148 147 101 125 126. For each ROI, voltages were averaged across electrodes and across trials of each condition. Student t-tests were performed and only significant effects lasting over 15 time points (60ms) were kept.



## 3 Results

Mean RTs on correct trials presented a typical numerical distance effect (Dehaene, 1992) (see Figure 3.2): subjects were significantly faster at comparing targets far from 5 (1,2,8 and 9) than targets close to 5 (3,4,6 and 7) ; effect size = 33.3ms, t-test p-value  $p < 10^{-5}$ . Subjects responded very accurately (mean percentage correct = 97.6%  $\pm$  0.5) and showed a typical numerical distance effect on error rates (see Figure 3.2): they were significantly more accurate at comparing targets far from 5 (1,2,8 and 9) than targets close to 5 (3,4,6 and 7); effect size = 3.6%, t-test p-value  $p < 10^{-3}$ . The parallel between RTs and error rates discards a speed-accuracy tradeoff.

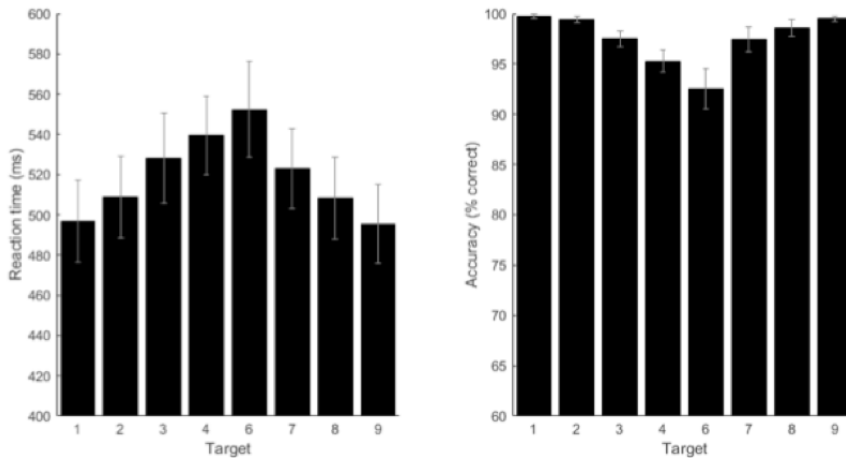


Figure 3.2: Numerical distance effect

*Numerical distance effect is shown on RTs and accuracy. Error bars represent standard error.*

Concerning the effect of the cues, subjects were significantly quicker at responding to targets when they were preceded by an unmasked ‘Cue-Tgt’ compared to when there were no cues (control condition), resulting in a conscious priming effect size of 88.7ms (t-test p-value <10<sup>-6</sup>). A trend to commit more errors for ‘Cue-Tgt’ than for neutral trials in the unmasked condition (effect size=-1.2% p=0.06), may reflect a form of impulsivity triggered by consciously perceived Cue-Tgt signals.

In the masked conditions, a trend was observed in the predicted direction: subjects tended to answer faster to targets preceded by a masked ‘Cue-Tgt’ than to answer cue-free trials (effect size = 5.7ms; unilateral t-test p-value =0.1). Note that given we used 100% correct predictive cues in this experiment in order to maximize ERP effects, behavioral cueing effects are not univocal: they may reflect a specific ‘Cue-Tgt’ effect, or be related to a warning signal irrespective of its symbolic content. No significant masked cueing effect was observed on error rates (p=0.8).

Concerning awareness of masked cues, none of the subjects reported conscious perception of masked cues in the subjective reports collected after the main experiment. Moreover, objective performance confirmed these subjective reports by showing a mean  $d'$  value of 0.02 (t-test against zero p-value=0.8), and

by the absence of significant correlation between individual  $d'$  and behavioral cueing effect (neutral - masked Cue-Tgt;  $r=0.06$  and  $p=0.82$ ). Finally an interpolation analysis revealed a trend for a masked cueing effect for a null  $d'$  (effect size=5.7ms;  $p=0.14$ ) {Greenwald et al., 1996; Naccache and Dehaene, 2001}.

Drawing on these behavioral results, we then moved to the ERP data. Comparisons to baseline activity were used to probe early effects of cues. Moreover, for masked trials only, the cue relevant (Cue-Tgt and Cue-NoTgt) can be contrasted with the neutral cue condition because they all shared the very same temporal structure (see Figure 3.1).

Unmasked cues elicited a series of 3 early successive ERP components on the posterior Oz ROI: a P168, followed by a N280 and a P352 component (all  $p$ -values  $<0.05$  as compared to baseline activity). A late P300 (576ms) response was found over Cz-ROI ( $p$  value =  $10^{-4}$  as compared to baseline activity). The same analyses conducted for masked cues did not reveal consistent effects. However, we could identify an early effect when contrasting relevant cues ('Cue-Tgt' or 'Cue-NoTgt' cues) to control cue trials around 164ms ( $p=0.01$ ).

We then turned to the CNV window. For unmasked trials, we observed a clear CNV, maximal in the midline electrodes, in response to 'Cue-Tgt' cues. The critical statistical contrast between 'Cue-Tgt' and 'Cue-NoTgt' cues trials confirmed the significance of this CNV modulation by cue type (see Figure 3.3). This Cz-Pz midline effect was sustained across the whole temporal window (400-1166ms), with a maximum over the vertex (Cz ROI). Crucially, a less intense but significant CNV effect was also observed for masked cues. This effect was confined to the vertex region (Cz), and reached its peak of significance around 850ms after cue onset. This late and sustained expectation effect elicited by unconsciously perceived masked cues did not correlate with individual  $d'$  values obtained in the cue discrimination task. Importantly, a significant unconscious CNV effect was interpolated for a theoretical null  $d'$  ( $p$ -value=0.015) (see Figure 3.4). Latencies of both masked and unmasked CNVs were very similar (840ms vs 812ms using the  $p=0.05$  threshold, and 632 ms and 632 ms using the 0.1 threshold). In contrast, the masked CNV ceased to be significant around 908ms whereas the unmasked CNV was sustained until target onset (1116ms).

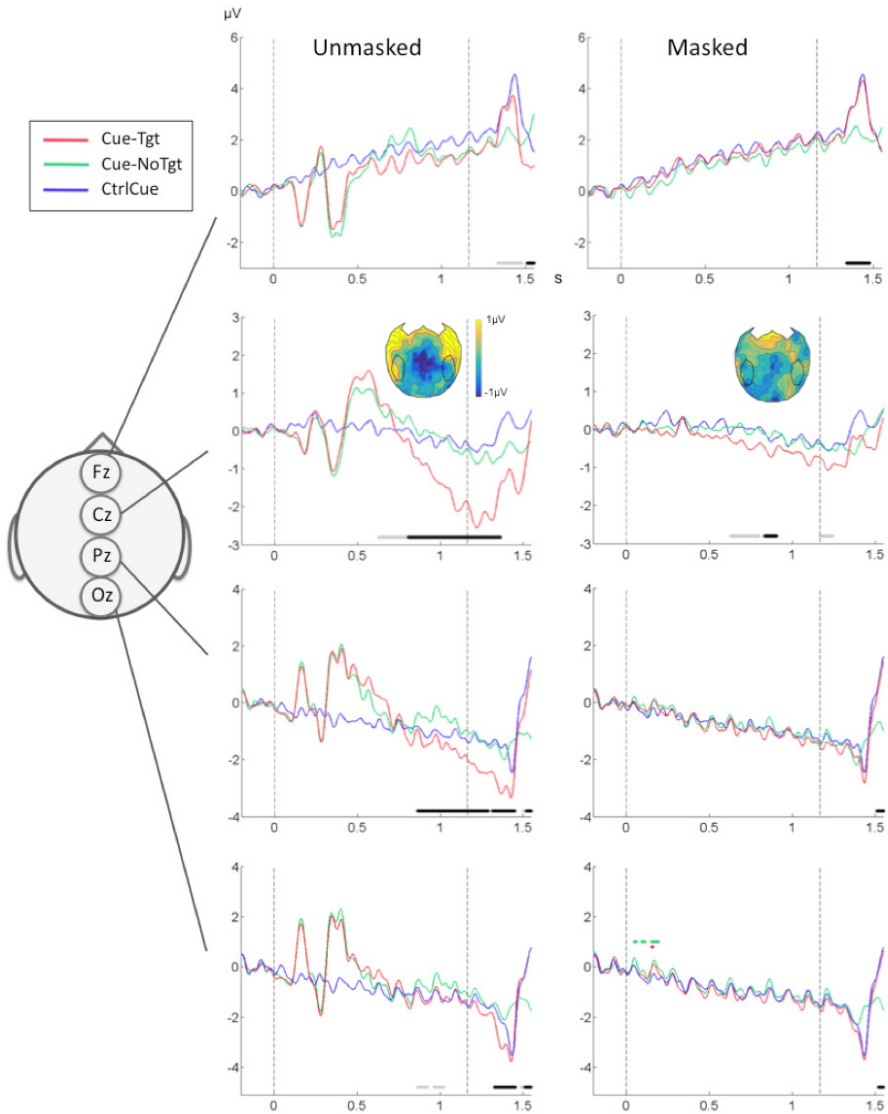


Figure 3.3 : ERPs in the regions of interest

ERP effects are shown for the 4 ROIs (Fz,Cz,Pz,Oz). Averaged ERP waveforms are displayed for Cue-Tgt (red), Cue-NotTgt (green) and CtrlCue (blue) in unmasked and masked conditions. First and second vertical dashed lines indicate the appearance of cue and target respectively. Bold line marks the significance of Cue-Tgt versus Cue-NoTgt conditions (black  $p < 0.05$  grey  $0.05 < p < 0.1$ ), on a minimum of 15 successive samples (60ms)). In the Oz ROI significant early visual effects of the masked cues as compared to the control condition are shown in red for Cue-Tgt and in green for

*Cue-NoTgt. Scalp topographies were computed on the time-window of significance for the Cz ROI prior to target onset, respectively for unmasked (812-1116ms) and masked conditions (840-908ms).*

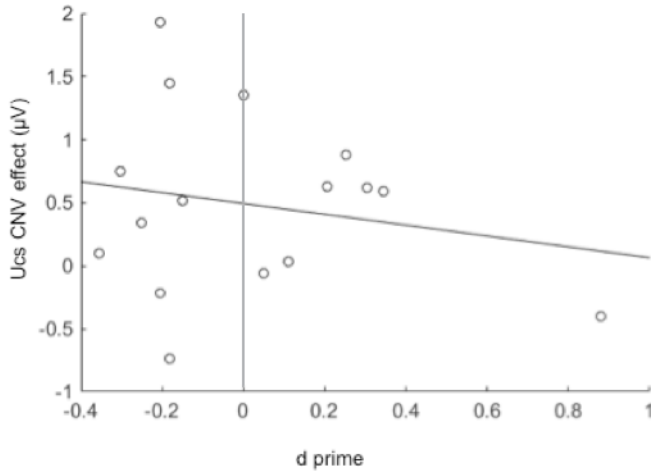


Figure 3.4 : Interpolated d prime

*Linear regression plots showing extrapolated prime-visibility to the point where the discrimination task showed zero sensitivity ( $d'=0$ ) y axis shows subjects differences in mean CNV unconscious effect (masked Cue-Tgt vs masked Cue-NoTgt) during the significant window (632-908ms) and x axis represents the subjects respective d prime.*



## 4 Discussion

In this experiment, we explored the possibility of initiating conscious and unconscious expectancy effects. We found a clear modulation of the CNV induced by conscious cues, with a maximal amplitude in Cz but also extending to Pz: Cue-Tgt strongly increased the CNV amplitude as compared to Cue-NoTgt and control cues. Moreover, this effect increased with time up to the upcoming of the target. Crucially, we also found evidence of a modulation of the CNV by masked cues. This unconscious CNV was more focal, limited to the Cz ROI and lasted up to 900ms.

In addition, we also observed early visual effects of the masked cues in Oz, indicating that the masked cues have been processed in early sensory areas. The



results of the discrimination task, as well as the interpolated CNV effect for a null d prime, suggest that these early effects are fully indeed unconscious.

This more focal scalp topography of masked CNV (confined to Cz region), as compared to a widespread and sustained unmasked CNV, is in line with a large body of literature, and with the global workspace model of conscious access. According to those, the crucial distinction between unconscious and conscious processing is that the former only induces local effects while conscious access is characterized by wide-spread neural effects and recurrent loops (Dehaene et al., 2006, 2001).

In the control condition, the ERP also showed a sustained negativity which could reflect the fact that the fixation cross itself induced expectancy effects towards the occurrence of the end of the trial. Interestingly, the Cue-NoTgt seemed to elicit rather similar CNV effects as the control condition. This suggests that our main effect (Cue-Tgt vs. Cue-NoTgt) may be rather driven by an engagement of attention induced by Cue-Tgt, than by a disengagement induced by Cue-NoTgt.

Capitalizing on these scalp EEG discoveries of masked and unmasked CNV components showing subtle differences in topography and timing, we decided to complement our approach by using intra-cranial recordings that offer a unique combination of space and time resolution.





## CHAPTER 4

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### ELECTROPHYSIOLOGICAL EXPLORATION OF CONSCIOUS AND UNCONSCIOUS EXPECTANCY PROCESSES: iEEG STUDY



## 1 Introduction

Exploring conscious and unconscious manipulation of expectancy, behaviorally and electrophysiologically, led us to conclude that consciousness is not required to manipulate expectancy processes. However, the neural differences between these conscious and unconscious effects are still unclear. In this experiment, we decided to explore expectancy processes using intracranial recordings to better understand the origins of our conscious and unconscious influences on the CNV.

We recruited 14 epileptic patients undergoing a pre-surgical mapping implanted with depth electrodes and engaged them in the same task as the scalp EEG experiment. We performed both single-subject and group analyses of the behavioral data while iEEG analysis was performed at the single-subject level only.



## 2 Material and methods

### ● 2.1 Participants

Fourteen epileptic patients were included (age mean =31.57+-8.41 median=32 yo; 5 males). Neuropsychological assessment revealed normal or mildly impaired general cognitive functioning. These patients suffered from drug-refractory focal epilepsy and were implanted stereotactically with depth electrodes as part of a presurgical evaluation. Implantation sites were selected on purely clinical criteria, with no reference to the present protocol. This experiment was approved by the Ethical Committee of Pitié-Salpêtrière Hospital (Comité Consultatif de Protection des Personnes participant à une Recherche Biomédicale).

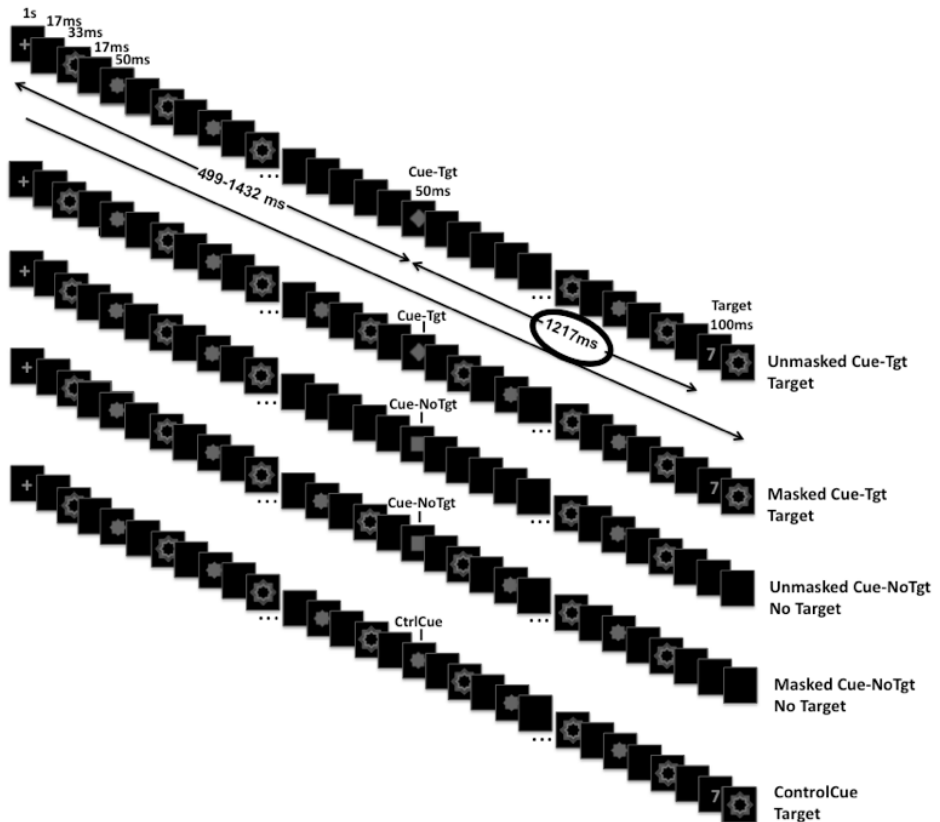


Figure 4.1 : Experimental paradigm

Sequences of visual events are shown for the 5 type of trials. Each trial begins with a fixation cross presented 1s followed by the repetition of the following pattern: blank (17ms), mask (33ms), blank (17ms) and neutral cue (50ms), interrupted by the presentation of a CueTgt or CueNoTgt followed by a blank or a target (1, 2, 3, 4, 6, 7, 8 or 9) according to the 5 possible types of trial.

## ● 2.2 Stimuli and procedure

We used the same stimuli as in Chapter 3 (see Figure 4.1), these stimuli were presented on a Dell precision M4600 32bits with a resolution of 1920x1080 and a refresh rate of 60Hz. The only difference was that ISI was 1217ms. Patients underwent a training block of 50 trials then 6 blocks of 50 trials of the main experiment, followed by a discrimination task of 2 blocks of 50 trials. (3 patients did the main experiment twice). The task and instructions were the same as in the scalp-EEG experiment.

### ● 2.3 iEEG recording and processing

Intracranial data was acquired with an audio–video–EEG monitoring system, 12 patients with Neuralynx and 2 with Micromed with a sampling rate of 4000Hz and 1024Hz respectively and were then resampled to a common sampling rate of 1000Hz. Epochs were extracted (from –200 to 1550 ms relative to the onset of the cue). To avoid artifacts, recording sites exceeding the threshold of  $\pm 300 \mu\text{V}$  in more than 5% of the epochs were excluded. All signals were re-referenced to their nearest neighbor on the same electrode (bipolar montage). From this point on, we will refer to these bipolar montages as “electrodes.” All data were visually inspected to discard any trial with epileptic activity.

To localize all contacts of the intracranial electrodes the following steps were applied (Pérez-García et al., 2015):

1. Patient’s DICOM files were automatically transformed to NIfTI format.
2. Anterior and Posterior Commissures (AC, PC) and an Interhemispheric Point (IH) were interactively localized using Brainvisa’s Anatomist. After that, different brain structures were automatically segmented from the pre-implantation MRI (MRI-pre) using Brainvisa Morphologist Pipeline.
3. The CT and the MRI post-implantation (CT-post, MRI-post) were automatically registered to the MRI-pre using Baladin.
4. The Leksell stereotactic frame was automatically segmented and registered to a predefined model using tools from PyDBS.
5. The electrode contacts were segmented on the CT-post using a watershed transform-based image processing algorithm. After that, the contacts were classified according to different features: size of the artifact, distance to the original trajectory, etc.
6. The automatic electrode localization was manually verified and corrected (if necessary).

## ● 2.4 Data analysis

### 2.4.1 Behavioral

Analyses were performed on reaction times (RTs) inferior to 1500ms and superior to 100ms. ANOVAs and Student t-tests were used.

### 2.4.2 Intracranial

Event-related potentials (ERPs) were obtained by averaging epochs for each condition. Data was filtered similarly to scalp ERPs experiment (Chapter three) with a 0.1Hz high-pass and a 20Hz fourth-order Butterworth low-pass filter in forward and reverse directions in order to avoid phase-shift. A baseline correction was applied by subtracting the mean voltage in the [-200 ms 0 ms] window. To assess the statistical significance of the difference between our conditions of interest, we performed independent sample t-tests and considered effects significant for a minimum of 10 successive samples with a  $p\text{-value} \leq 0.05$ . In order to correct for multiple comparisons, we then performed 1000 permutations and computed sums of t for each cluster satisfying the first-level statistic threshold. Effects were considered significant only if they were observed in less than 10% of surrogate permutations. We reported two levels of significance ( $\alpha < 0.1$  and  $\alpha < 0.05$ ).



## 3 Results

At the group-level, we replicated the classic numerical distance effect: mean RTs on correct trials were shorter for targets far from five (1, 2, 8 and 9) than for targets close to five (3, 4, 6 and 7) (effect size=25.8ms;  $p=0.002$ ). Patients performed the task very accurately with a mean accuracy of 96.7%, and they also displayed a typical numerical distance effect on accuracy rates: they were more accurate at responding to targets far from five than to targets close to five (effect size=2.41%;  $p=0.003$ ).

Regarding the effect of the cues, patients were faster to respond on trials with a 'Cue-Tgt' compared to control cue trials, resulting in a significant con-

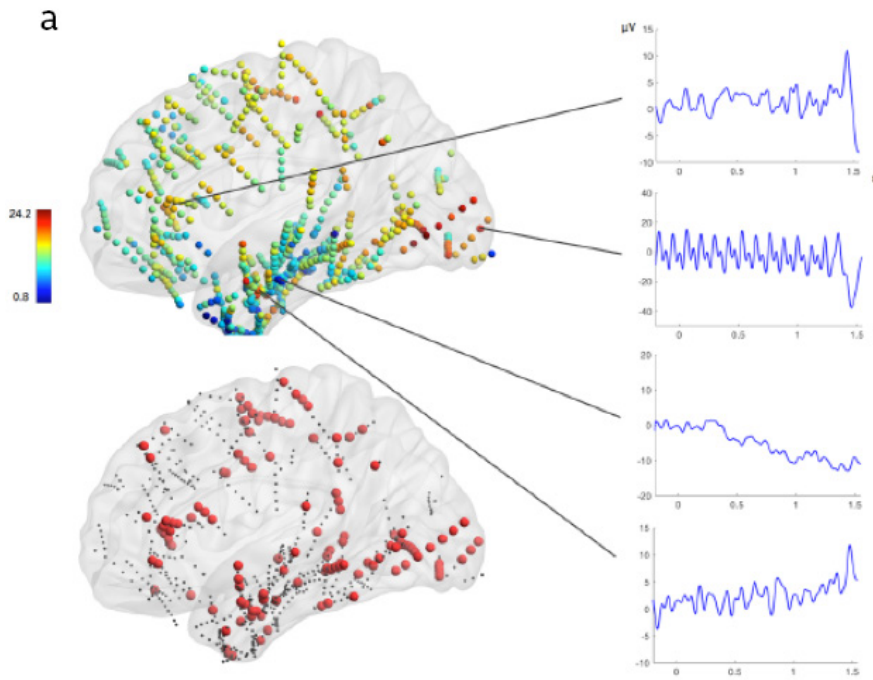
scious priming effect (effect size = 50.3ms;  $p=0.005$ ). There were no such effect for masked 'Cue-Tgt' trials ( $p=0.84$ ). Similarly to the scalp EEG experiment, no significant cueing effect was observed on error rates, neither for unmasked trials nor for masked ones (both  $p$  values  $> 0.25$ ). Concerning masked cue visibility, none of the 14 patients reported conscious experience of masked cues. On the forced-choice discrimination task the mean  $d'$ -prime did not differ from chance-level ( $d'=0.05$ ;  $p=0.44$ ). Individual behavioral data is summarized in Table 1.

We then probed unmasked and masked CNV effects by analyzing iEEG signal recorded from a total of 674 recording sites (mean of 48.2 per patient), with the following lobar distribution: 250 in frontal lobes, 334 in temporal lobes (either internal or external), and 90 in other structures (mostly in occipital and parietal lobes).

Given that masked cues elicited scarce behavioral (see chapter two) and early scalp EEG (see chapter three) effects, we first looked for evidence of masked cue processing within early visual cortex, by comparing ERPs elicited by the relevant 'Cue-NoTgt' or 'Cue-Tgt' trials on the one hand, and by neutral cue trials on the other hand, in an early time-window following cue onset [0-200ms]. We could detect significant masked cue early effects in 10 occipital electrodes (4/19 in one patient; and 6/43 in a second patient) (see Figure 4.4).

Incidentally, visual inspection of occipital sites revealed clear iEEG oscillations at the exact rhythmic frequency (8.55Hz) of our visual paradigm ('cue-blank-mask-blank' repetitive sequence; see Figure 4.1). In order to probe the spatial distribution of sites showing such a visual entrainment, we focused on neutral trials (in which the rhythmic pattern was repeated until target onset without interruption for a masked or unmasked instructed cue) and computed, for each recording site, the mean spectral power centered on this 8.55 frequency (8-9Hz), and normalized this value to the total power within the 1-20Hz frequency band. We then calculated a Z-score for each site, in comparison to the distribution observed in the 673 remaining sites ( $p \leq 0.01$  corrected for multiple comparisons with Bonferroni correction). As expected, this visual entrainment was mostly observed in the occipital cortex (27/62 sites = 43.5% versus 98/612 sites = 16% for all other regions:  $c2$   $p$ -value =  $5.10 \cdot 10^{-5}$ ). Note however that this visual entrainment was also present in the ventral visual pathway, in parietal regions as well as in mesio-frontal structures, including ACC (see Figure 4.2 a). The same analysis conducted on

scalp EEG data yielded very similar patterns of results (see Figure 4.2 b).





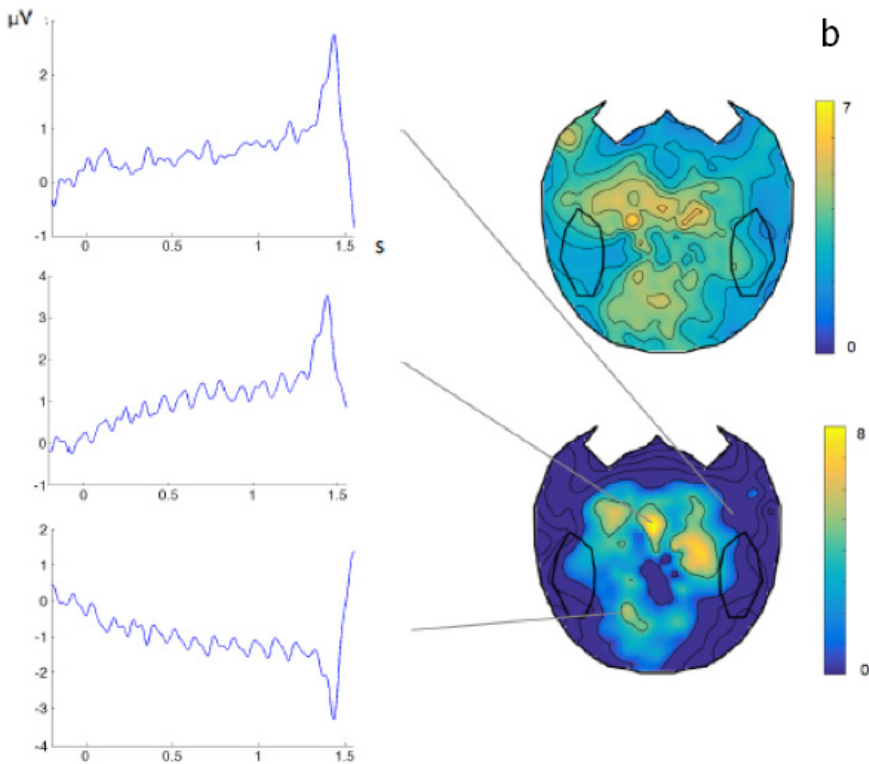


Figure 4.2 Visual entrainment effects

Visual entrainment effects reported for the iEEG (a) the top Figure shows the relative spectral power of all contacts for the 8.55Hz frequency while the bottom topography reports in red the electrodes resisting the Bonferroni correction at  $p \leq 0.01$  on the left, the ERP elicited in the control cue condition are plotted for 4 electrodes as examples of regions visually trained or not. and EEG (b) the top topography shows the relative spectral power for the 8.55Hz frequency while the bottom topography displays the positive Z scores, on the left the ERPs elicited in the control condition are plotted for 3 channels as examples of regions that are visually trained or not.

We then analyzed the cueing effect (Cue-Tgt versus Cue-NoTgt), respectively for the masked and unmasked conditions during the CNV window (see Figure 4.3). In the unmasked condition, a CNV effect was observed both in the frontal lobe (N=30 significant electrodes) mostly in the SMA, the ACC, and the frontal gyrus, and in the temporal cortices (N=7). These effects were sustained over the whole CNV time-window. In comparison, the masked CNV effect was confined to temporal electrodes (N=6 and N=3 for frontal lobe; Exact Fisher test comparing frontal and temporal electrodes in masked and unmasked conditions:  $p=0.009$ ),

and decayed over time.

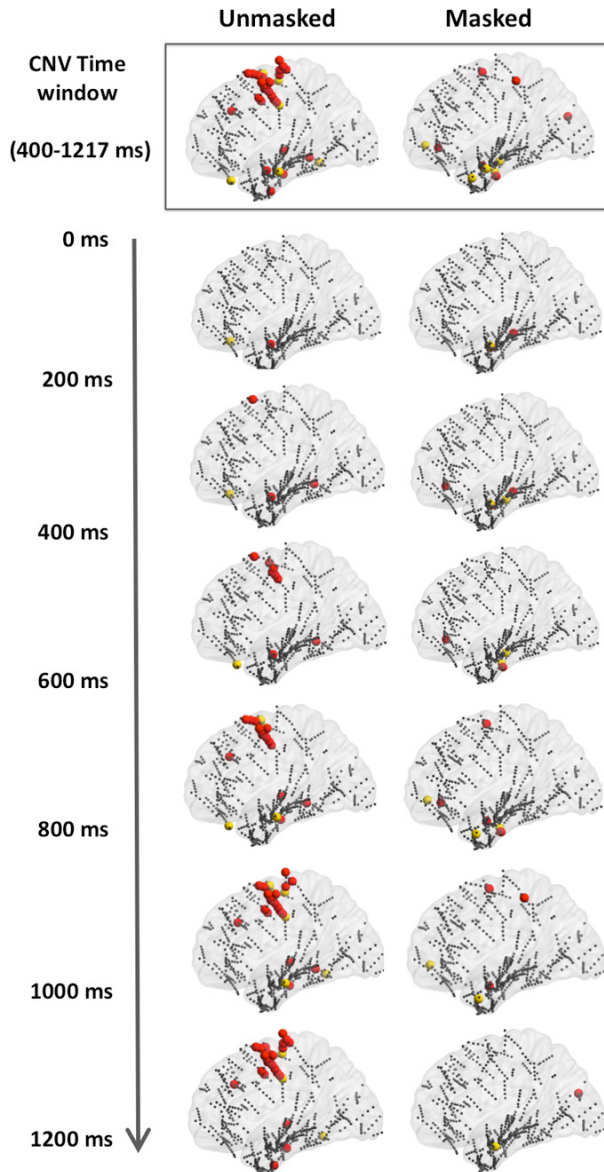


Figure 4.3 Timing of unmasked and masked cueing effects  
 Each black dot represents an electrode. Significant effects (Cue-Tgt vs Cue-NoTgt conditions) are colored in red when  $p_{corr} < 0.05$  and yellow when  $0.05 < p_{corr} < 0.1$ . Left (unmasked) and right (masked) top images summarize significant effects across the CNV time-window (400-1217ms), whereas the six

following rows of images represent the time course of binned (200ms) effects.

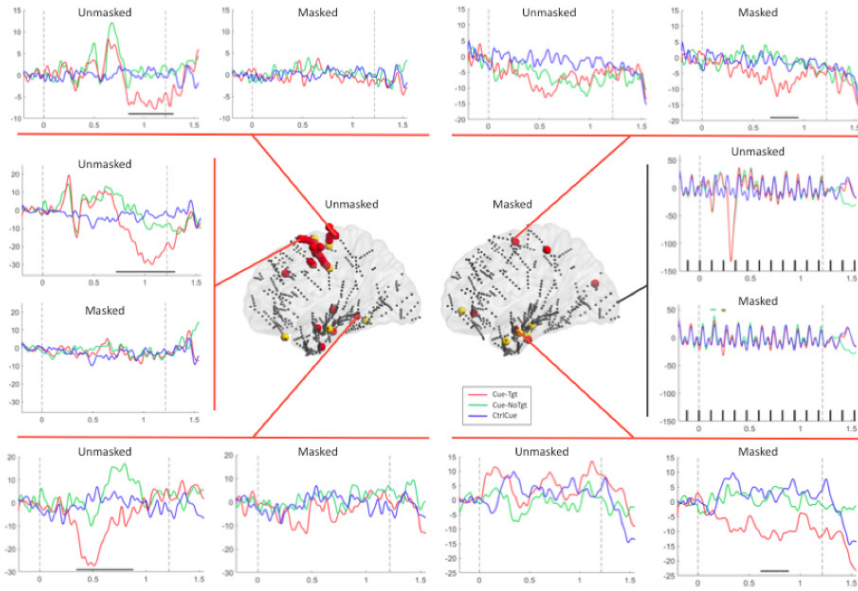


Figure 4.4 Representative electrodes

The central panel replicates the top images of Figure 3.3. For six representative electrodes, we show the time-course of averaged SEEG signal for the 3 conditions (red=Cue-Tgt, green=Cue-NoTgt and blue=CtrlCue), both for unmasked and masked conditions separately. The two dashed line mark the appearance of the cue and target respectively. For 5 of these electrodes, highlighted in red, we also present significant cueing effects by a horizontal black line (Cue-Tgt vs Cue-NoTgt with  $p_{corr} < 0.05$ ). For the occipital electrode, highlighted in black, each vertical bold black bar on the x axis indicates the presentation of a “cue-blank-mask-blank” sequence (8.55Hz frequency). A clear visual entrainment at this visual stimulation frequency is visible on this electrode. Horizontal red and green lines indicate significant differences ( $p < 0.05$ ) between masked Cue-Tgt (green) and masked Cue-NoTgt (red) trials as compared to CtrlCue trials. On this electrode two significant components were found (latency 156ms and 240ms).

Patient Nb	d prime		Unmasked priming effect		Masked priming effect	
	Value	Chi2	Effect size (ms)	p value	Effect size (ms)	p value
1	-0.40	0.11	123.77	1E-10	-2.77	0.86
2	0.30	0.23	-24.98	0.21	-55.31	0.03
3	0.09	0.78	0.53	0.97	-24.57	0.09
4	0.30	0.23	24.74	0.10	-1.89	0.91
5	0.00	1.00	96.81	2E-05	27.35	0.19
6	0.46	0.07	49.94	0.10	46.71	0.09
7	-0.05	0.84	108.11	0.01	24.80	0.56
8	0.20	0.42	-24.53	0.48	-13.53	0.71
9	0.15	0.54	16.17	0.20	-28.64	0.13
10	0.20	0.42	110.96	3E-03	43.99	0.23
11	0.05	0.84	119.33	2E-13	5.90	0.73
12	-0.10	0.69	40.81	0.02	-2.93	0.87
13	-0.11	0.67	-10.85	0.47	-12.08	0.45
14	-0.42	0.10	73.77	3E-09	13.71	0.28

Table 1: Individual behavioral results on numerical decision task

Patient Nb	Nb of electrodes				Nb of electrodes showing an unmasked effect ( $p \leq 0.1$ )				Nb of electrodes showing an unconscious effect ( $p \leq 0.1$ )			
	All	Frontal	Temporal	Other	All	Frontal	Temporal	Other	All	Frontal	Temporal	Other
1	42	42	0	0	4	4	0	0	0	0	0	0
2	50	30	20	0	1	0	1	0	1	0	1	0
3	51	7	44	0	0	0	0	0	1	0	1	0
4	68	7	61	0	0	0	0	0	4	0	4	0
5	37	21	14	2	0	0	0	0	1	1	0	0
6	66	7	59	0	0	0	0	0	1	1	0	0
7	49	49	0	0	3	3	0	0	1	1	0	0
8	48	0	48	0	0	0	0	0	0	0	0	0
9	26	0	9	17	0	0	0	0	0	0	0	0
10	39	0	20	19	1	0	1	0	0	0	0	0
11	45	45	0	0	21	21	0	0	0	0	0	0
12	37	22	6	9	0	0	0	0	1	0	0	1
13	51	0	8	43	1	0	1	0	1	0	0	1
14	65	20	45	0	6	2	4	0	0	0	0	0
All	674	250	334	90	37	30	7	0	11	3	6	2

Table 2: Individual SEEG results



## 4 Discussion

By exploring the initiation of the conscious and unconscious expectancy effect using iEEG, we were able to replicate the results we had previously observed in scalp EEG of an effect of masked cues on the CNV. Most interestingly, iEEG also revealed differences in the neural origins of our effects. Conscious expectancy

effect was recorded majoritarily in the frontal regions classically implicated in the generation of the CNV: the ACC and the SMA but also in temporal regions, this frontal effect was sustained and increasing with time. Unconscious modulations of the CNV seemed limited to temporal regions, the hippocampal gyrus and the inferior temporal gyrus. Indeed, unconscious cues seemed unable to trigger the sustained and amplified effect we observed in frontal regions with conscious cues.

We did not find effects in inferior parietal regions classically described as part of the neural network of attention, one possible explanation could come from the fact that very few patients were implanted in these parietal regions.

Interestingly the visual entrainment effect caused by regularly flashing a sequence of visual stimuli, seemed to follow a postero-frontal gradient, this visual entrainment also seems to be strongest in the attentional network implicating pre-frontal cortex and parietal regions.

We also found several effects of expectancy in the hippocampal gyrus which is interesting considering that recent intracranial recordings in rodent have discovered the existence of time cells similar to place cells that seem to discharge for specific time intervals and might be implicated in trace conditioning learning when learning paired stimuli that are separated by a time interval (Eichenbaum, 2014; MacDonald et al., 2011).

One of the limits of our study, inherent to intracranial recordings, comes from the fact that the position of the electrodes are dependent on patients' implantation sites. By looking at effects at the whole brain level and comparing across regions, we are comparing effects across patients, this limits in part the interpretation of our effects.

This iEEG study allowed us to characterize the spatio-temporal dynamic of the conscious CNV and the modulation induced by cues manipulating expectancy. It also allowed us to replicate the effect of unconscious modulation of expectancy and, moreover, informed us on the distinctions between the conscious and unconscious expectancy processes.





**CHAPTER 5**

**INTROSPECTION OF  
SUBJECTIVE EXPECTANCY**



## 1 Introduction

In our initial behavioral experiment, we assessed the possibility for masked cues to affect expectancy and observed an unconscious priming effect lasting over a second. Following this finding, and using EEG and iEEG recordings, we were able to measure this unconsciously-elicited expectancy effect by observing its effects on the amplitude of the CNV. The EEG experiment confirmed the possibility for masked cues to affect CNV amplitudes over 800ms. Using iEEG, we were then able not only to extend the EEG results in showing unconscious cues affecting neural activity linked to expectancy up to the appearance of the target, more than a second later, but also to localize the origins of this effect more precisely.

One remaining question was however whether these behavioral, scalp EEG, and iEEG evidence of expectancy effect elicited by masked cues were really unconscious, or whether the triggered expectancy processes were accessible to conscious introspection in spite of the absence of conscious perception of the masked cues. Indeed, the possibility to consciously access a process elicited by a cue inaccessible to conscious report has been postulated by several theoretical works (Dehaene and Naccache, 2001; Naccache, 2009). In other terms, in this last experiment, we aimed at probing whether subjects could consciously introspect the level of expectancy elicited by visible and invisible cues in order to fully demonstrate unconscious modulations of expectancy.

We decided to test this conscious maintenance hypothesis using a similar experimental design as in Chapter 1. Thus, we used the same stimuli and defined the following four conditions: unmasked and masked 'Cue-Tgt', and unmasked and masked 'Cue-NoTgt'. To assess the participants' states of expectancy, some trials (16.7%) were interrupted at the precise timing when a target would appear (if present). Participants were then asked to subjectively rate their level of introspected expectancy in this particular trial, on a continuous scale ranging from 'no expectancy' to 'maximal expectancy'.



## 2 Material and methods

### ● 2.1 Participants

Twenty-eight participants were included. Two subjects were excluded for not understanding or respecting the instructions concerning the use of the introspection scale: these two subjects were the only one who did not report subjective expectation for Cue-Tgt unmasked cues trials, that were consciously perceived and instructed to launch a voluntary expectancy process. Therefore, 26 subjects were included in the statistical analysis (age= 25,2  $\pm$ 4.4 ranging from 18 to 38 y.o.; median age 24; 13 females).

### ● 2.2 Stimuli and procedure

We used the same stimuli as in the experiment of Chapter 1 and defined the following four conditions: unmasked Cue-Tgt (144 trials, 100% predictive), unmasked Cue-NoTgt (144 trials, 75% predictive in order to be able to calculate a cueing effect), masked Cue-Tgt (144 trials, 100% predictive), and masked Cue-NoTgt (144 trials, 75% predictive). For each of these four conditions 24 out of the 144 trials were randomly interrupted by presenting an introspection question at the precise timing when the target (or absence of target) should have appeared. Responses were given on a continuous scale ranging from no expectancy to maximal expectancy (see Figure 5.1). Subjects performed one block of 48 trials of training, followed by 12 blocks of 48 trials during the main experiment, and they finally performed two more blocks of 50 trials without probing introspection of expectancy, for the forced-choice discrimination task.



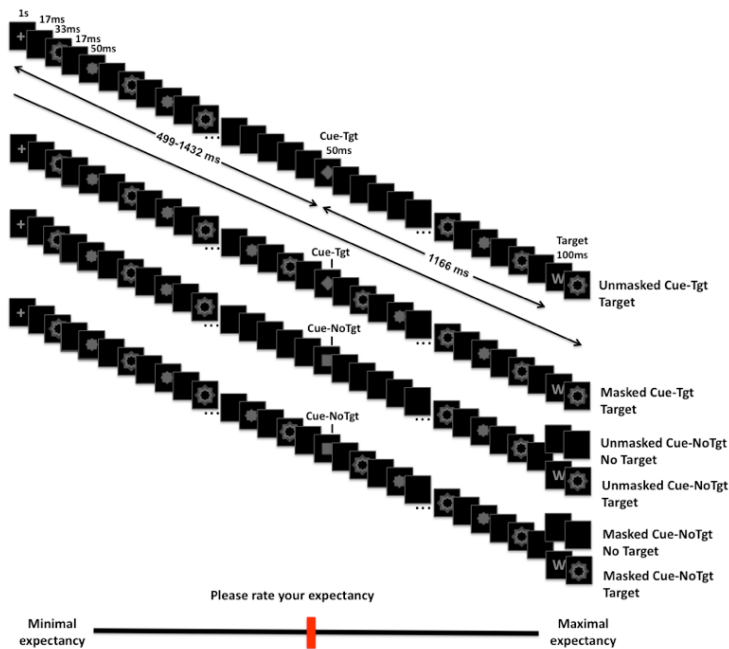


Figure 5.1 : Experimental paradigm

Sequences of visual events are shown for the six type of trials. Each trial begins with a fixation cross presented 1s followed by the repetition of the following pattern: blank (17ms), mask (33ms), blank (17ms) and neutral cue (50ms), interrupted by the presentation of a CueTgt or CueNoTgt followed by a blank or a target (W) according to the 6 possible type of trial. One trial out of six was interrupted at the supposed moment of appearance of the target or blank and subjects were asked to rate their expectancy using a scale like the one presented at the bottom of this Figure.

### ● 2.3 Instructions

The task was similar to the experiment of Chapter 1, subjects were instructed to pay attention to the cues and to answer as fast as possible to the target by pressing a button. They were told that Cue-Tgt cues were always followed by a target, and that Cue-NoTgt cues were not followed by a target in the majority of trials. They were also instructed that in some random trials, we will probe their subjective feeling of expectancy by asking the following question: “Up to which point were you waiting for a target stimulus?”. Subjects were informed that the trial interruption would occur at the precise moment of potential appearance of a target. Subjects reported their introspection by using a cursor on a continuous scale ranging from ‘minima expectancy’ to ‘maximum expectancy’ (See Figure 5.1).



### 3 Results

None of the 26 subjects reported conscious perception of masked cues in the subjective reports collected after the main experiment. Moreover, objective performance confirmed these subjective reports by showing a mean  $d'$  value of 0.036 not significantly different from a null  $d'$  prime  $p=0.68$ .

Subjects responded faster on trials with a conscious Cue-Tgt than on trials with a conscious Cue-NoTgt resulting in a conscious priming effect of 151.93ms ( $sd=62.17$ ;  $p<10^{-10}$ ). Note that we did not observe a significant priming effect for masked cues (effect size=0.86ms;  $sd= 23.97$ ;  $p=0.86$ ), most probably due to a lack of power originating from the very limited number of masked trials (24 Cue-NoTgt with a target trials as compared to 128 trials in the experiment of Chapter 1).

Note that the aim of this experiment was not primarily to observe behavioral and neural correlates of the masked cueing effect already described in Chapter one, two and three, but rather to check if expectancy effects elicited by masked cues could be accessible to conscious introspection.

An ANOVA crossing cue type (2) and masking (2) showed a main effect of cue-type with larger introspection of expectancy on 'Cue-Tgt' trials than on Cue-NoTgt trials ( $F(1,25)=72.25$   $p<10^{-8}$ ), and the absence of effect of visibility ( $F(1,25)=0.66$ ;  $p=0.42$ ). Crucially we found a strong interaction between cue type and visibility ( $F(1,25)=54.58$ ;  $p<10^{-7}$ ; see Figure 5.2). Post-hoc tests showed that cue-type had a strong impact in unmasked trials: introspection of expectancy was increased by 41% after an unmasked 'Cue-Tgt' as compared to an unmasked Cue-NoTgt ( $F(1,25)=66.08$   $p<10^{-7}$ ). In sharp contrast, the same test conducted on masked cues trials did not show any difference of introspection (expectancy rate difference = 1.09% ;  $F(1,25)=0.85$  ;  $p=0.37$ ). Given the importance of this negative result, we ran a Bayesian statistical analysis using an 'ultra-wide' prior regarding the directionality of expected effect. This analyses yielded a Bayesian factor supporting the null-effect with moderate evidence ( $BF_{0+}=3.712$ ).

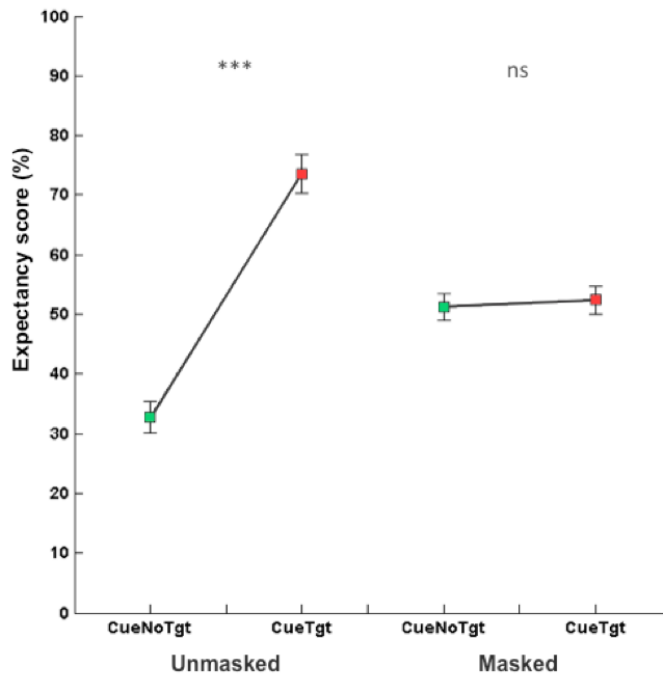


Figure 5.2 : Introspection of subjective expectancy

Mean expectancy score is shown as a function of masking and of cue type (green and red for Cue-NoTgt and Cue-Tgt respectively). Subjects presented a strong expectancy effect for unmasked cues ( $p < 0.001$  \*\*\*) but did not display any significant expectancy effect for masked cues (ns).



## 4 Discussion

We used predictive and non-predictive cues to manipulate on a trial-by-trial basis subjects' expectancy towards a target. These cues can trigger behavioral and neural expectancy effects, as supported by the previous experiments. In this study, we interrupted some of the trials to explicitly investigate the subjective state of expectancy of participants. Conscious cues elicited modulations in the state of expectancy, whereas unconscious cues did not modify subjectively reported expectancy.

We were not able to replicate the behavioral effects of Chapter 2. However, this was probably due to a lack of power given the small number of trials available to calculate this effect.

Regarding the interpretation of the unconscious effect, we cannot completely rule out the possibility for a conscious maintenance of expectancy especially since the introspection task was different from that in the experiments in which we measured the expectancy effects. However most of the evidence point towards the absence of such a conscious maintenance effect.





## CHAPTER 6

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### GENERAL DISCUSSION



## 1 Summary of results

In a series of masked priming experiments, we explored the possibility of initiating consciously and unconsciously sustained expectancy effects, which we assessed using behavioral measures as well as EEG and iEEG recordings. Our experiments allowed us to probe the existence of these effects and to qualify their temporal dynamics and neural underpinnings.

### ● 1.1 Behavioral expectancy effects

In a first experiment, we explored the possibility for masked and unmasked cues to manipulate subject's expectancy and preparation towards the upcoming of a target. Subjects were faster at responding to predictably cued targets, rather than to targets preceded by non-predictive cues. Interestingly when the cues were masked, a small but significant facilitation effect induced by predictive cues was also observed. This constitutes evidence of an unconscious modulation of expectancy.

It is most important to note that this unconscious expectancy effect consisted in the acceleration of the responses to targets appearing more than a second after the masked cues. To our knowledge, this result is the first demonstration of a facilitation effect initiated unconsciously and that lasts over a second. The masked priming effects reported in the literature rarely exceed a few hundred of milliseconds with no reports of priming effects beyond 800ms (Dehaene et al., 2001; Dupoux et al., 2008; Ferrand, 1996; Greenwald et al., 1996). Most studies probing the influences of masked cues on RTs, do so by using priming experiments where a cue activates a semantic category congruent or incongruent with the semantic category of the target, thus facilitating the response to the upcoming target. However, in our study, the cues did not prime a semantic category but provided temporal information about the upcoming of a target, therefore creating expectancy towards the moment of occurrence of that target. As a consequence, the effects we observe might be sustained attentional effects that are different in nature from semantic priming effects. This could explain the reason we found influences of masked cues on RTs lasting longer than what had previously been

reported. Another important aspect is that subjects were instructed to do a simple detection task: they were required to press a button at the appearance of the target. Because the response was a simple motor command, subjects could prepare the desired motor command as soon as the cues appeared. It is therefore possible that our observed cueing effect might be explained by a stronger motor preparation than in the usual masked priming tasks.

### ● 1.2 Electrophysiological assessment of expectancy

Our manipulation of expectancy was reflected behaviorally by improved performances. We also explored the electrophysiological signature of this expectancy effect and found that both masked and unmasked cueing modulated CNV amplitude. Measured in EEG, this effect was initiated at common onset time for conscious and unconscious cues around 600ms, showing overall close topographies centered around the vertex with a more focal Cz aspect for the unconscious CNV effect. This first electrophysiological experiment reported measures of subliminally induced changes in activity lasting up to 1.1s.

By exploring the influence of these cues on the CNV of patients implanted with intracranial electrodes (using iEEG), we also found similar evidence of unconscious influences lasting over a second. Additionally, we described a more precise localization of the origin of these conscious and unconscious modulations of expectancy. The iEEG results indicate a striking dissociation between conscious and unconscious effects. We report comparable early effects in temporal regions for conscious and unconscious cues particularly in the hippocampal gyrus and inferior temporal gyrus, followed by late and sustained frontal effects for the conscious cues. SMA and ACC regions were notably affected by conscious cues. Crucially these were the regions where the sustained effects lasted more than a second. Indeed the rare frontal effects elicited unconsciously disappeared after one second.

### ● 1.3 Introspected expectancy

Our final experiment explored subjects' introspected state of expectancy induced by unmasked and masked cues. In this experiment, we noted that conscious cues induced a strong modulation of the consciously reported state of expectancy, whereas unconscious cues did not seem to modulate the conscious

feeling of expectancy within trials. This finding suggests that the unconscious effect we reported behaviorally and electrophysiologically may not result from masked cues eliciting conscious changes in the state of expectancy as posited by the conscious maintenance hypothesis.



## 2 Unconscious expectancy effect

### ● 2.1 Defining the nature of the effect

#### 2.1.1 Effect manipulated by our paradigm

Overall, we found evidence of an effect of unconscious cues on the state of expectancy reflected by shorter RTs and modulations in CNV amplitude measured in EEG and SEEG. Both behaviorally and electrophysiologically, these unconscious influences seem to exceed one second.

In order to better understand the nature of our effect, it is important to dissect the cognitive processes that could have been modulated by the design of our paradigm.

The main aim of our paradigm was to test whether, and for how long, unconscious processes could modulate subjects' expectancy. However the concept of "expectancy" encompasses several underlying cognitive mechanisms. Indeed "expecting" an event orients attention in time, but also triggers several types of preparatory processes. To explore solely "temporal expectancy"; scientists use the classic temporal-cueing paradigm in which different cues predict shorter or longer intervals before the appearance of the targets. Therefore, the cues always induce response preparation and what is explicitly manipulated is the temporal orienting towards short or long time intervals, making it possible to isolate the pure effect of temporal attention. In the case of our paradigm, we used cues predicting both the probability of occurrence and the time of occurrence of targets. As a result, the effects induced by the cues do not allow us to disentangle the effect of pure temporal attention from a more general preparation to respond.



In the study of expectancy, it is important to tease apart temporal attention per se from spatial attention and response preparation, as we reviewed in Chapter 1 the CNV is strongly linked to temporal attention but can also reflect motor preparation. Recently, Faugeras et al (2016) manipulated orthogonally temporal attention and motor preparation, they found additive behavioral effects for temporal attention and motor preparation, they also found contributions of the motor preparation to the late cue elicited P3 components whereas the CNV was mainly affected by temporal attention. Our paradigm could not truly disentangle between motor preparation driven expectancy effects and pure temporal attentional effect. However the results of Faugeras and Naccache (2016) suggest that expectancy effects affecting CNVs most probably reflect majorly temporal attention.

Finally, we could also test more specifically the involvement of temporal attention by using a temporal orienting paradigm with masked cues.

### 2.1.2 Effect reflected by electrophysiological results

Another possible way of disentangling these two interpretations could be found in the analysis of the neural effects and their particular topographies. We notably know from the literature that the neural signatures of temporal attention involve mainly the fronto-parietal network, with a strong recruitment of left parietal cortex (Coull and Nobre, 1998), but also the ACC and SMA, and the right dIPFC - especially in variable foreperiod paradigms. Conversely, pure motor preparation would be expected to result only in electrophysiological effects in motor and pre-motor cortex.

In our data, expectancy effects elicited with conscious cues were mainly located in frontal regions classically associated with the generation of the CNV, including the SMA and the ACC. Hence, our results are consistent with both an amplification of the temporal processing network, and with preparatory processes (Vallesi et al., 2009).

In contrast, we found little to no effect in parietal regions, known to be an important contributor to the temporal attention network (Coull and Nobre, 1998). This lack of effect in parietal cortex might indicate that the motor interpretation should be favored, but could also result from a particularly low coverage of parietal cortex with iEEG electrodes. Interestingly, in EEG we did find topographies of the conscious CNV effect extending to Parietal regions.

Surprisingly, we also found effects of the cues in temporal regions. Some of these temporal effects were located in the hippocampal regions – which can be implicated in unconscious relational encoding (Duss et al., 2014), and in the inferior temporal gyrus – which is involved in the processing of numbers. Moreover Faugeras et. al (2016) also found among their CNV sources reconstructed from scalp EEG data an implication of temporal region in the generation of the CNV.

Overall, the strong implication of the ACC and the SMA is consistent with an anticipatory effect and the involvement of temporal attention and preparation. However the absence of parietal effects usually found in the attentional network is surprising. Testing our paradigm with patients implanted specifically in the left parietal region could better inform us on the implication of the attentional network in our effect.

When inspecting neural correlates of the unconscious cueing effect, we found smaller, less sustained, and more focal effects. Most of the few electrodes showing an unconscious cueing effect were located within the temporal lobe, including hippocampal regions.

## ● 2.2 Differences between conscious and unconscious effects

If the nature of the expectancy we manipulated can have different interpretations it is nonetheless undeniable that this expectancy was manipulated by both conscious and unconscious cues. Moreover, we observed clear distinctions between the conscious and unconscious expectancy effects: conscious cues influenced behavioral responses very strongly with an effect on RTs of more than 100ms, whereas masked cues only elicited a small behavioral effect of 4.5ms. The conscious and unconscious expectancy effects were also different in their temporality and neural origins. Both unmasked and masked cues triggered similar early effects of up to 400ms. Beyond this stage, differences between conscious and unconscious cues emerged, with amplified frontal effects elicited mainly by conscious cues. While masked cues also elicited some scarce frontal effects, only conscious cues induced a ramping up of frontal effects sustained and increasing with time. Masked cues had predominant influences in the temporal lobe. These influences were maximal around 800ms and decayed past one second. Unmasked cues had similar early effects in temporal regions, but more crucially, they elicited sustained increasing with time frontal effects. These common early

conscious and unconscious effects and their divergence in the later part of the expectancy process can somehow be related to the case of conscious and unconscious visual perception: unconscious visual effects produced only focal and transient activations, while conscious information processing induced also late effects that are more widespread.

This difference in the size effect of the CNV but also its location and temporality suggests that consciously and unconsciously processed cues are acting on expectancy processes in different ways.

### ● 2.3 Intentional vs. unintentional expectancy

Recent literature has distinguished different processes that give rise to expectancy: expectancy can be either automatic, unintentional and highly dependent on contextual factors, but it is also sometimes described as a strategic, intentional process driven by top-down influences. Various paradigms have been designed to try to disentangle the relative contributions of these two different types of processes to the observed expectancy effects, but also to understand how they interact.

When a cue delivers information about the upcoming of a stimulus, it orients attention in time in a top-down manner. This type of manipulation of attention is classically explored using foreperiod paradigms, in which attention is manipulated by the cues that predict the time of occurrence of a target. The effect on expectancy is driven by the nature of the cue and the subsequent attentional orienting that it induces intentionally. Apart from this strategic cue-driven manipulation, expectancy also seems to be affected in a more automatic and unintentional manner by specific temporal structures of the contextual information. For example, sequences of contingent events or rhythmic presentation of events can modulate expectancy in an automatic manner. These two types of expectancy processes (automatic vs top down) seem to interact and contribute to general expectancy. Los and Heslenfeld (2005) illustrated their mutual contributions to the CNV in a task that manipulates both temporal cue validity (strategic) and preceding foreperiod (SE/automatic).

In our experiment, we used a paradigm with temporal cues delivering information that manipulate expectancy and temporal orienting. The conscious cues conceivably manipulated attention in a strategic and intentional manner. In regard to unconscious cues, they manipulated expectancy using information carried by

the cues themselves- which is a strategic manipulation of expectancy. Nevertheless it is not clear as to whether these strategic manipulations of expectancy were intentional or not.

One hypothesis could be that the unconscious cues were indeed triggering intentional strategic manipulation of expectancy. However, most of the literature exploring the relationship between consciousness and intention points towards the fact that consciousness is required to generate intentions. The masked cues present in our experiments could not be distinguished, and were processed fully unconsciously, as supported by the lack of changes in subjective reports of expectation. Subjects were unable to introspect a change in their conscious state of expectancy. If the unconscious cues were indeed manipulating intentional expectancy we would expect intention being inseparable from consciousness, we would expect to find modulations in this consciously introspected expectancy. In the absence of such an effect, we tend to discard the hypothesis of unconscious cues triggering an intentional expectancy effect.

The other hypothesis would be that the subliminal cues did in fact exert a manipulation of expectancy but that this manipulation was unintentional. Indeed unintentional modulations of automatic temporal attention have already been elicited by subliminal stimuli. This was shown by using subliminal auditory stimuli that induced entrainment at a specific frequency (Ten Oever et al., 2017). In the case of our experiment it would imply a manipulation of a more strategic form of temporal attention driven by the nature of the cues that would occur without conscious intentions. We could postulate that our observed conscious and unconscious expectancy effects are different in nature regarding the intentionality of the temporal orienting they induce.



### 3 Conscious expectancy effect

These results can help us define expectancy processes, in addition to the conscious intentional expectancy induced by the cues and the conscious unintentional expectancy induced by the context, we can postulate the existence of unconscious and unintentional expectancy.

Given the spatio-temporal occurrence of our conscious and unconscious effects (early common effects, late sustained conscious effects only), we could propose a two-stage model of expectancy: An initial unconscious and unintentional temporal orienting that is then followed by a second stage of sustained intentional conscious temporal orienting. This two-stage model has been previously proposed as an explanation to visual-sensory processing, indeed, visual information when processed consciously and unconsciously elicits the same early effects in sensory regions and only when processed consciously does it activate extended regions in a sustained manner (Gaillard et al., 2009; Marinkovic et al., 2003). Similarly the initiation of an intentional action has been proposed to take place in two stages (Desmurget and Sirigu, 2009), an initial unconscious state, followed by a conscious intentional state. This model is supported by evidences of early RP that do not trigger conscious intentions. The two-stage model was also extended to higher cognitive process such as semantic processing. Indeed, Rohaut et al. (2014) recently proposed a two-stage model of word semantic processing distinguishing between: (i) a first unconscious stage indexed by an early N400 response (~200–600 ms), (ii) followed or not by a second stage indexed by a P3b-like (~600–1000 ms) ERP component corresponding to the classical LPC/P600, which would correspond to the conscious access to word semantic attributes (Rohaut et al., 2014).

The two-stage model explanation of conscious cognitive processes is in line with the global workspace model explaining the neural basis of conscious access. In this model, early information is processed unconsciously in a first step locally. If it is salient enough, or attended to, it gains access to the global workspace – a highly interconnected and distributed network – making it conscious and allowing for more complex and sustained use of the information (Dehaene and Naccache, 2001).

Our measured expectancy effects seem to have a common neural base with the unconscious effects. This commonality in the early stages of expectancy may suggest that early expectancy starts with an initial stage that is automatic, unintentional and perhaps unconscious, and is followed by a sustained deployment of attention over time that is driven by conscious intentions and reflected by increasing activity in ACC and SMA.



## 4 Limits and perspectives

### ● 4.1 Variability of the time interval preceding the cue

In our paradigm, in the aim of limiting a strong temporal orientation effect induced by the fixation cross we varied the inter-stimulus interval between fixation cross and cue onset. As a result of this, trials were of variable length. While this allowed us to control temporal orienting effects caused by the fixation cross, it may have added other automatic temporal orientation modulations that might add variability to the measures. This may have limited the observation of our desired effect. Indeed, the probability of an event's occurrence increases in time within a trial. This phenomenon referred to as hazard rate has been shown to affect RTs and CNV amplitude and cannot be excluded as affecting our results. Similarly expectation within a trial  $n$  is known to be affected by the length of trials  $n-1$  this is known as the sequential effect, it affects RT as well as CNV amplitude (Los and Heslenfeld, 2005; Los and Van Den Heuvel, 2001). In our paradigm the variable length of trials may have induced such an effect, which would add noise to the initial cueing effect. Since we compared effects elicited by the cues this contextual effect cannot account for the effects we found if anything it might have added noise and played against our effect.

Another consequence of this variability in the interval preceding the cue is that participants could not orient their attention in time to the precise moment of appearance of the cue. It is well reported in the literature that attention benefits the treatments of unconscious stimuli and particularly that the treatment of unconscious cues is impaired when they are unattended (Naccache et al., 2002).

### ● 4.2 Length of the foreperiod

In our paradigm we tested possible expectancy effects within foreperiods of 1.1 to 1.2s. However, this was not sufficient to allow us to distinguish the two phases of the CNV: both early and late CNVs, were most probably confounded and influenced by the cues. In the interest of further distinguishing conscious influences from unconscious effects, we could study these influences over a longer foreperiod. This would enable us in the first place to study the evolution of the unconscious behavioral effects beyond 1.2 seconds. Secondly, it would allow for the exploration of the respective effects of masked and unmasked cues on the early and late phase of the CNV. In particular, do conscious and unconscious cues influence the early and late CNV in a similar fashion? Our hypothesis would be that masked cues elicit mostly bottom-up orientation of attention affecting mainly the early phase of the CNV, whereas we could expect conscious cues to influence both the early and the late phase of the CNV, the latter reflecting sustained orientation of attention and preparation.

### ● 4.3 Initiation versus modulation

Another limit of our paradigm comes from the fact that we did not explore the initiation of an expectancy per-se, since the structure in trials itself caused an automatic expectancy to be triggered at the beginning of each trial. Thus, the cues were thus only modulating an already initiated expectancy. This leaves the question of whether masked cues can fully initiate a sustained expectancy. Another interesting question would be to know if masked cues can terminate a CNV, what would occur in the case of the presentation of masked imperative stimulus?

### ● 4.4 Possibility for conscious maintenance

Our introspection experiment showed on a trial-by-trial level that subjects were not conscious of an unconsciously triggered expectancy effect. The absence of an effect in this task does not totally discard the possibility for this effect to have happened in the iEEG and EEG tasks. Indeed, the tasks were slightly different. Furthermore, the introspection trials themselves might have induced an attentional disengagement that could have impaired the processing of the masked cues in this task. This attentional interpretation could also explain why we did not find any unconscious behavioral effect in this task. More generally, it seems important to

explicitly test the conscious maintenance hypothesis when studying long-lasting influences of subliminal cues on behavior, in order to be able to claim that the information is unconsciously maintained.

#### ● 4.5 Spectral analysis and functional connectivity

The future perspectives of our work include the spectral analysis of the data of the SEEG experiment, particularly to explore potential effects of the cues on the alpha power in sensory regions. Knowing that enhanced CNVs are accompanied by a reduction of alpha power preceding the appearance of a target especially in sensory regions. In our experiment, we could expect to observe lower alpha power in the case of cues announcing a target versus cues announcing no target.

We also consider performing functional connectivity analyses. In the case of conscious modulation of expectancy – where we observe lasting frontal influences increasing with time, we expect stronger fronto-parietal connectivity when subjects perceive a cue predicting a target than when the cue predicts no target.

#### ● 4.6 LFP & single unit

Finally, the patients were also implanted with microelectrodes giving us the possibility to measure local field potentials (LFPs). We are currently processing the data of these electrodes to find LFP recordings and maybe single unit recordings of the CNVs. We could then hopefully observe conscious and unconscious modulations in the neural firing linked to different states of expectancy.

We are particularly interested in the hippocampal region which showed expectancy effects measured with the macroelectrodes. Since recent studies of intracranial recordings in rats and humans have revealed the existence of time cells in the hippocampus coding in particular for precise timing of appearance of a learned stimulus (Eichenbaum, 2014), it would be interesting to observe if hippocampal cells are coding for out time interval when expectancies are consciously or unconsciously triggered.





## 5 Conclusion

Every morning in the metro, I observe the well-orchestrated ballet of partially awoken Parisians navigating their routine to work in an automatic fashion. These people are not pre-programmed robots but are merely over-trained at predicting and anticipating the spatio-temporal occurrence of events. In the current thesis, we investigated the behavioral and neural consequences of temporal expectancy processes. The first contribution of this work was the demonstration that expectancy can be triggered unconsciously, or at least modulated by unconscious stimuli. This suggests that expectancy is not necessarily the result of a conscious intention. Crucially, these behavioral and electrophysiological effects extended beyond a second, thus expanding the temporal limits of unconsciously elicited processes. Second, we also contributed to the finer characterization of the deployment of expectancy in the brain and propose a two-stage view of expectancy. First, a stimulus predicting the occurrence of an impending event triggers an increased negativity in the temporal lobe. Following this early time-window, more sustained effects can be observed in frontal regions, including supplementary motor regions and cingulate cortex. This later effect is characterized by a steady increase in its size and amplitude which resolves when the expected event occurs. While both of these stages are observed with conscious cues, unconscious expectancy effects are only transient and restricted to the first stage. Hence, expectancy would unfold with a first unconscious step then followed by a long-lasting conscious intentional process. Future work should help disentangle the respective contributions of attention and motor preparation to the formation of expectancy.



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