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“Consolidação do tempo na memória de longo prazo: fatores facilitadores e interferentes”

Raquel Cocenas da Silva

Tese apresentada à Faculdade de Filosofia, Ciências e
Letras de Ribeirão Preto da USP, como parte das
exigências para a obtenção do título de Doutor em
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Consolidação do tempo na memória de longo prazo: fatores facilitadores e interferentes

Tese apresentada ao Departamento de Psicologia da Universidade de São Paulo, como parte dos requisitos para obtenção do grau de Doutor em Ciências

Área de concentração: Psicobiologia

Orientador: Prof. Dr. José Lino Oliveira Bueno

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A lembrança do tempo que passou

O tempo passou...

E o que dele em mim ficou?

A batida do relógio que na minha lembrança ressoou?

Ou os segundos amedrontados que meu coração captou?

Eu olho o tempo atento se percebo algo que temo,
e tomo tento no julgamento do tempo mesmo após muito tempo.

Um tormento pode alterar o tempo,
porém quando o assunto é armazenamento,
me convenço que o tempo não escapa em nenhum momento.

Raquel Cocenas da Silva

RESUMO

Cocenas-Silva, R. (2013). *Consolidação do tempo na memória de longo prazo: fatores facilitadores e interferentes*. Tese de Doutorado, Departamento de Psicologia, Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, São Paulo.

A consolidação da memória é um processo que ocorre ao longo do tempo, em que memórias recentes são cristalizadas em memória de longo prazo. As memórias recentes são vulneráveis e passíveis de esquecimento, principalmente na presença de fatores interferentes. Entretanto, a consolidação de eventos com conteúdo emocional sofre menos interferências do que o observado com eventos neutros. O objetivo deste estudo foi investigar experimentalmente os efeitos da emoção e de uma tarefa de interferência sobre a consolidação do tempo na memória de longo prazo. Uma série de três experimentos foi conduzida em um procedimento de generalização temporal, no qual os participantes aprenderam uma duração padrão e imediatamente, ou após 24 horas após, julgaram a duração padrão baseada em durações de comparação. No primeiro experimento, os participantes aprenderam uma duração padrão sob o efeito de três condições emocionais: ameaçadora, não ameaçadora e condição neutra, controle. Os julgamentos temporais de longo prazo mostraram que as durações foram melhor recordadas em uma condição emocional do que neutra; isto ocorreu em maior extensão para a condição ameaçadora do que para a condição não ameaçadora. No segundo experimento, foi investigado o processo de consolidação da duração e seus efeitos sobre julgamentos temporais. Uma tarefa de interferência foi introduzida em diferentes atrasos depois da aprendizagem inicial da duração padrão. Os resultados mostraram que os julgamentos temporais de longo prazo foram menos precisos quando a tarefa de interferência foi introduzida 30-45 minutos após a aprendizagem. Esta imprecisão não foi observada quando a memória foi testada imediatamente após a tarefa de interferência sendo encontrado um gradiente temporal do efeito perturbador da interferência dentro da primeira hora após a aprendizagem. O terceiro experimento foi conduzido para examinar o efeito da emoção na memória de longo prazo para duração e sua resistência contra os efeitos da interferência. Os participantes aprenderam uma duração padrão sob duas condições: uma ameaçadora e uma neutra; imediatamente após a aprendizagem, foi introduzida uma tarefa de interferência. Então, 24 horas após, eles julgaram se as durações de comparação eram ou não similares à duração padrão previamente aprendida. Os julgamentos temporais de longo prazo foram mais acurados quando os participantes aprenderam a duração padrão em uma condição emocional. Os resultados desta tese levam a conclusão que as emoções que despertam *arousal* facilitam a retenção do tempo na memória de longo prazo e são também resistentes aos efeitos da interferência. Por outro lado, a interferência perturba a consolidação do tempo e a memória da duração passa por um processo de consolidação que dura pelo menos uma hora.

Palavras chave: Tempo. Percepção de tempo. Memória. Consolidação. Emoção. Interferência

ABSTRACT

Cocenas-Silva, R. (2013). *Time consolidation in long-term memory: facilitators and interfering factors*. Tese de Doutorado, Departamento de Psicologia, Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, São Paulo.

Memory consolidation is a process that occurs over time in which new memories are crystallized in long-term memory. Recent memories are vulnerable and susceptible to forgetfulness, especially in the presence of interfering factors. However, emotional events are better retained in long-term memory than neutral events. The aim of this thesis was to experimentally investigate the effects of emotion and interference task on time consolidation in long-term memory. A set of three experiments were conducted in a temporal generalization procedure, in which participants learned a standard duration and immediately, or 24 hours later, they judged the standard duration based in duration comparisons. In experiment one, participants learned a standard duration under three emotional conditions: a threatening, a nonthreatening and a neutral control condition. The long-term temporal judgments showed that durations were recalled better in the emotional than in the neutral condition; this occurred to a greater extent in the threatening than in the nonthreatening condition. In experiment two, it was investigated the consolidation process for duration and its effect on the time judgment. An interference task was introduced at different delays after the initial learning of the standard duration. Results showed long-term temporal judgments less precise when the interference task was introduced 30-45 min after the learning. Disruption was not observed when the memory was tested immediately after the interference task and there was a temporal gradient of the disruptive interference effect within the first hour after learning. The experiment three was conducted to examine the effect of emotion on the long-term memory for duration and its resistance against interference effects. Participants learned a standard duration under two conditions: a threatening and a neutral condition; immediately after the learning, it was introduced an interference task. Then, 24 hours later, they judged whether or not comparison durations were similar to the previously learned standard duration. The long-term temporal judgments were more accurate when participants learned the standard duration in an emotional condition. The findings of this thesis led to the conclusion that arousing emotions facilitate the retention time in long-term memory and are also resistant against interference effects. Instead, the interference disrupts time consolidation, and memory duration undergoes a consolidation process that lasts at least one hour.

Key words: Time. Time Perception. Memory. Consolidation. Emotion. Interference

SUMÁRIO

1 INTRODUCTION.....	9
1.1 Memory and the consolidation mechanism.....	9
1.2 How to study time perception.....	12
1.3 The effects of emotion on memory consolidation and time perception.....	16
1.4 The effect of interference on memory consolidation and time perception.....	21
2 OBJECTIVE.....	23
3 CHAPTER 1 - Temporal memory of emotional experience.....	25
4 CHAPTER 2 - Memory consolidation for duration.....	41
5 CHAPTER 3 - Emotion and long-term memory for duration: Resistance against interference	61
6 GENERAL DISCUSSION.....	79
REFERENCES.....	81
ANNEXE A - Record of interference task	91

1 INTRODUCTION

1.1 Memory and the consolidation mechanism

Memory is essential for everyday life. This cognitive function involves the ability to acquire (acquisition), storage (consolidation) and retrieve (recall) available information. The process of human memory is considered the central motor learning, which enables the new learning and/or to access previous learning. Ebbinghaus (1850-1909) was one of the first researchers to demonstrate that it was possible to study memory experimentally. He focused on the factors and conditions that surround the question of how a new learning interacts with what had been previously acquired. In their investigations on memory, it was applied methods that involved remembering list of words or nonsense syllables, to evaluate the storage time and the recovery of stored material capacities (McGeoch & Irion, 1952). The first memory studies results were interpreted in association terms that were supposed to be formed between previously acquired stimuli and the new stimuli (Baddeley, Anderson & Eysenck, 2009). This pioneering finding about the possibility to investigate memory experimentally, led to an exponential increase to the investigation of memory in the last century. The experimental studies and the development of new imagery technologies as the functional magnetic resonance imaging (fMRI) and the positron emission tomography (PET) in the last decades, has allowed researchers to examine the neurobiological bases of memory and its functioning in living subjects.

The memory literature shows that the hippocampal region has been linked to memory function and the hippocampus itself, has been identified as a critical structure of memory (Zola-Morgan & Squire, 1993). Nevertheless, it is largely known that the multiple memory mechanisms active different brain structures through neurochemical interactions. Izquierdo and Medina (1997) discuss the order that some brain structures involved in consolidation process and the time course are activated. On the first days, the process started at the hippocampus, amygdala, entorhinal and parietal cortex and, after 60 days, the parietal cortex is necessary for retrieval. These authors also report the main neurotransmitters involved in the memory process: glutamate, GABA, dopamine, norepinephrine, serotonin and acetylcholine. There are yet two neural processes from the time required for consolidation described by Dudai (2004): the first one happens in the early minutes or hours, after the encoding or the

end of learning, involving the synaptic consolidation. The second one happens after weeks, months or even years to perform and there is a reorganization of brain circuits or systems that encode memory.

The seminal studies on memory consolidation were conducted by Muller and Pilzecker (1900) and Hebb (1949). Muller and Pilzecker (1900) in their studies on verbal learning and retention in humans found that a memory trace was formed gradually overtime after acquisition. This phenomenon led them to the origin of the perseveration-consolidation hypothesis, which assumes that neural processes are activated by learning of new information and persists over time becoming consolidated in permanent memory. Hebb, in his dual-trace theory (1949), proposed that if the original activity continues for some period, structural changes at the synaptic contacts among cells could form the memory thereafter. These structural changes would correspond to the long-term memory and the previous continued activity might be identified with short-term memory (Crowder, 1993).

This thesis investigated the time consolidation in the long-term memory. To investigate this process, it was used a temporal procedure that allowed to study the memory process involved in the temporal processing. The temporal generalization task is a procedure that enables to examine the acquisition, the storage and the recall of temporal information (Church & Gibbon, 1982, Droit-Volet, Clement & Wearden, 2001; Wearden & Bray, 2001, Lejeune & Wearden, 2008). The temporal generalization procedure and the modulation of memory consolidation will be described and discussed in the next sections of the thesis.

Memory and the multiple mechanisms

Researchers found that people and animals retain learned information through different mechanisms of memory (Cohen 1984; Schacter 1987; Squire 1992). Xavier (1993) reported some several dichotomous distinctions between these mechanisms:

short-term and long-term memory (Baddeley & Warrington, 1970), operational and reference memory (Honig, 1978), dispositional and representational memory (Thomas, 1984), semantic and episodic memory (Tulving, 1972, 1983) semantic and cognitive memory (Warrington & Weiskrantz, 1982), procedural and declarative memory (Cohen & Squire, 1980, Cohen, 1984), recent and remote memory (Schacter & Moscovitch, 1984. (p. 67).

Several mechanisms of memories vary in terms of function, time duration and contents. According to the time duration, the mechanism that stores information for short time intervals as seconds, minutes and hours is classified by short-term memory. This type of

memory stores small amounts of information for limited period of time. The study of short-term memory was initially developed by John Jacobs (1887), which applied the digits span task to evaluate the mental capacity of their students. The short-term memory is related to task performance which involves simple retention of small amounts of information, tested immediately or after a short interval (Baddeley, Anderson & Eysenck, 2009).

Information lasting hours, days, months and years is accessed by the long-term memory, which is the process of formation and file memory consolidation of our childhood memories or knowledge acquired in the past. The information consolidated in the long-term memory affects our environment perception and contributes to making decisions. The long-term memory is formed from the process of memory consolidation that occurs over time, in which recent memories are crystallized in long-term memory. The long-term memory formation involves a set of metabolic processes in the hippocampus and other brain structures. According to Izquierdo and Medina (1997), the long-term memory requires between three and eight hours to be formed.

Regarding to the function of different types of memory, the reference memory has an integrative function between short and long-term memory. The mechanisms of short and long-term memory are connected, transferring information continuously from one to another. It is the temporary mechanism to store and manipulate information associated with learning, reasoning and understanding. It would also be seen as a more generic term for the temporary information storage of the short-term memory. According to Xavier (1993), the reference memory store information applicable to various situations. The stored information is latent and will be activated by the presentation of the appropriate stimuli allowing therefore the recall. On the other hand, the working memory is associated with short-term memory and its function is to maintain, for a few seconds or a few minutes, the information that is being processed. Although there are several models of working memory, the most influent is the multiple components (Baddeley & Hitch, 1974).

The third classification parameter of the different types of memory is the content, in which include the procedural and declarative memory. The procedural memory consists in the memories of perceptual, sensory, cognitive and motor skills; they are activated in learning tasks (Cohen, 1984). The ability to record facts, events or knowledge comes from the declarative memory. The information stored in this memory is evoked by demand (Cohen, 1984) and represent the result of previous experience. The memory of events, in which individual was involved or had some participation, is called episodic memory and the memory of general knowledge is semantic memory; both are part of the declarative memory.

Although there are several memory mechanisms addressed in the memory literature, in this thesis the focus of discussion is directed to the mechanisms of short and long-term memory and reference memory. In the chapter 1, 2 and 3, it will be discussed the involvement of these memory mechanisms on time consolidation.

1.2. How to study time perception

The study of time perception has important contributions to be related to numerous issues of daily behavior. The present and recently past external environment are represented through duration timing and this phenomenon occurs through the perception and estimation of time. These cognitive processes are fundamental to the adaptation of environmental variations that individuals are exposed. According to Fraisse (1984), the notion of time applies to two concepts, which may be clearly recognized from the personal experience change:

(a) the concept of succession, which corresponds to the fact that two or more events can be perceived as different and organized sequentially; it is based on our experience of the continuous changing through which the present becomes the past; (b) the concept of duration, which applies to the interval between two successive events. Duration has no existence in and of itself but is the intrinsic characteristic of that which endures. (p. 2).

To study time, there are some factors that are relevant in the temporal measures (Hicks, Miller, Gaes, & Bierman, 1976): 1) the time estimation method, 2) the time interval to be estimated, 3) the nature of the cognitive process required by the individual during the interval to be estimated and the 4) temporal paradigm. Temporal estimates can be performed through measurement methods; the most used methods are verbal estimation, temporal production, temporal comparison, temporal reproduction, temporal bisection task and temporal generalization. In the verbal estimation, the interval time is estimated verbally in units of time (seconds, minutes, etc.); in time production, individual produces a time interval. In the temporal comparison, two time intervals are shown and participants must judge the longer or the shorter one, and in the temporal reproduction method, subject reproduce the passage of time using a timer or the computer keyboard, for example. In the temporal bisection task, subjects are trained to discriminate between short and long anchor duration. They were then tested with probe durations of intermediate or similar values. In temporal generalization, subject judge the similarity between a standard duration and comparison durations. In this method, subjects are initially presented with a standard duration several times. After this learning phase, they are presented with different durations (shorter, longer or

equal to standard duration) and must compare these comparison durations with the representation of standard duration in reference memory, using e.g. a keyboard computer. In this thesis the temporal generalization method was adapted for the long-term memory study. Thus, the comparison durations test was performed after an interval of 24 hours of learning standard durations, sufficient period for this duration to be consolidated in long-term memory.

Regarding the intervals time to be estimated, Fraisse (1984) identified three orders of duration on the physical continuum, based on the different cognitive processes that are activated during the time estimation. For durations shorter than 100 milliseconds, the perception is instantaneous; “perception of instantaneity corresponds to the non-separation of the on and off components of evoked potentials. The on moment cannot be distinguished from the off moment.” (Fraisse 1984, p. 9). For durations between 100 milliseconds and 5 seconds the perceived duration is considered part of the perceived present. It can be explained through the psychological present which “corresponds to the duration of an experiential process and not to a given period of duration. However, it has an upper limit which hardly exceeds 5 seconds and has an average value of 2 to 3 seconds. Within these limits, one can speak of the duration perception, which thereby becomes a quantity whose beginning has not yet been stored in memory.” (Fraisse, 1984, p.10). And for durations greater than 5 seconds, duration estimation involves memory mechanisms; “to judge durations that cannot be perceived, the memory mechanisms intervenes in the making of a global judgment about the duration.” (Fraisse, 1984, p.19). It may assume against this distinction between the duration on the physical continuum and the different cognitive processes, that duration shorter than 5 seconds are considered experience of time and duration greater than 5 seconds are considered judgment of time.

According to Block and Zakay (1997) attention and memory subserve experienced and remembered duration respectively. Two temporal judgments paradigm allow examining these cognitive processes: prospective and retrospective paradigm. The prospective paradigm is considered experienced duration (Block, 1990), once participant is informed about the temporal estimation task before the presentation stimuli. The retrospective judgments come from tasks of remembered duration (Block, 1990), being the participant informed that will estimate the time only after the end of stimulus presentation. According to Wearden (in press) “this distinction has been instantiated in the often-quoted distinction between “timing-with-a-timer” (prospective timing) and “timing-without-a-timer” (retrospective timing)” (p. 4). The temporal experiments of this thesis was conducted in the prospective paradigm to ensure that

temporal information was really learned and encoded in reference memory and then to be consolidated in long-term memory.

The results from prospective judgments may be explained through attentional model (Hicks et al., 1976; Thomas & Weaver, 1975; Zakay & Block, 1996). Zakay and Block (1997) based on Zakay and Block (1996), proposed that:

a person divides attentional resources between nontemporal (stimulus) and temporal information. Thus, experienced duration should increase if the number of stimuli requiring processing is small, if a processing task is easy, if participants do not need to actively respond to presented information, or if they do not need to divide attention between two sources of stimuli. (p.185).

The retrospective judgments are interpreted through memory storage models (Block & Reed, 1978; Ornstein, 1969). The storage model reported by Ornstein (1969) assigns a predominant role of memory mechanisms in the time estimation. For this model, time estimation is based in storage reserves of memory during a time interval (the stored size). The greater the number and complexity of the information, the larger the required space for memory and consequently the greater is the time estimation. Thus, if more stimuli are presented or if the stimuli are encoded in a complex way, the duration tends to be overestimated. However, as less and more efficient the encoding stimuli, smaller the size and the stored temporal judgment will be perceived as shorter than it was. Block and Reed (1978) proposed a model of remembered duration called contextual-change. According to this model:

remembered duration involves a cognitive reconstruction based on retrieving contextual information that is stored as an integral part of the memory encoding of events, rather than a reconstruction based on retrieving stimulus information. The greater are the encoded and retrievable contextual changes, the longer is the remembered duration of a period time.” (Block, 1990, p. 24-25).

The most prevalent model to study time perception is the internal clock model (Gibbon et al, 1984). It enables to verify the activation of attentional and memory components involved in time judgments. The internal clock model is based on the scalar expectancy theory (SET) proposed by Gibbon (1977). According to this model, time estimations are performed by an information processing system composed by a modular clock, memory and decision-making mechanisms. The internal clock mechanism comprises a pacemaker which emits pulses and a switch that controls the temporal attention (Figure 2). This switch is triggered and paralyzed from the beginning to the end of the stimulus, allowing a buildup of pulses during the presentation of the event to be estimated. The time estimation is based on a number of accumulated pulses, i.e., the greater the number of pulses, the longer the time judged.

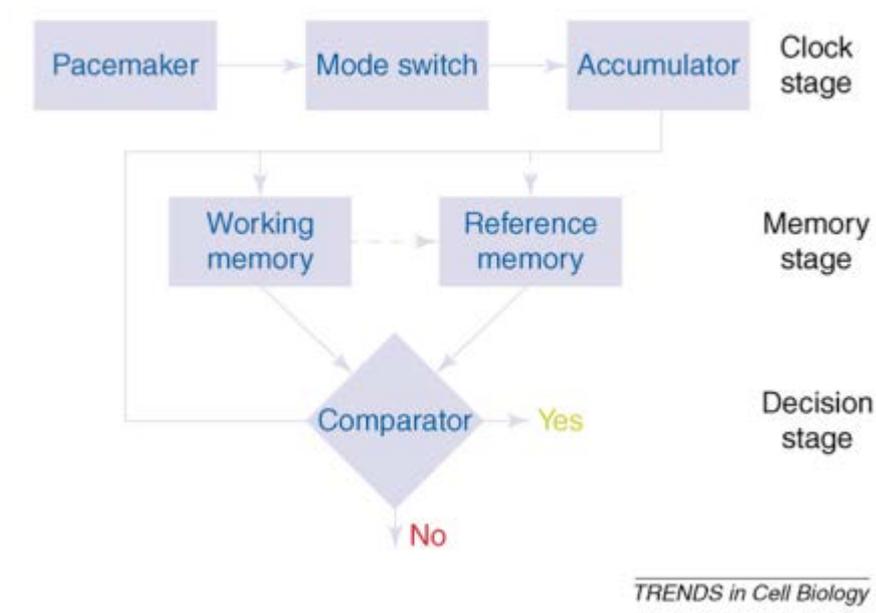


Figure 1. The information-processing model. Adapted, with permission, from Gibbon et al. (1984). This figure was extracted from Droit-Volet & Meck (2007).

According to Droit-Volet (in press), there is a growing consensus about a distributed network of neural areas involved in time processing, extending thus, the previous idea about the existence of a single brain structure involved in the processing of time (pacemaker-accumulator system). Regarding the neurobiological feasibility Matell and Meck (2000, 2004) have proposed a model in which a corticostriatal circuit underlies the processing of time, called the striatal beat frequency (SBF) model. Although this new model is:

currently considered to be the most plausible biological model of the internal clock (Coull et al., 2011). However, it is important to bear in mind that not all scientists agree with this model. Some of them hold that there is no such thing as a specific time processing mechanism, arguing that time measurement emerges from the dynamic activity of a population of neurons that are intrinsically capable of coding time. (Droit-Volet, in press, p.2).

The results of this thesis about time consolidation in long-term memory were interpreted through the internal clock model (Gibbon et al., 1984). Through the mechanism of the internal clock, it is possible to understand the activation of different mechanisms of short-term memory involved in temporal processing, specially the reference memory. This memory plays an important role on temporal processing and on time consolidation in long-term memory. It has a function to store the encoded duration, as a time representation, to determine the long-term temporal judgments.

1.3. The effects of emotion on memory consolidation and time perception

Studying emotions

The studies on emotion have contributed to increase the knowledge of the role that these internal emotional states play in the daily life of humans. Emotions influence thinking, decision-making, actions, social relationships, welfare, physical and mental health (Izard, 2010). A seminal contribution to the science of emotion comes from Paul Ekman (1984, 1992a, 1992b), which classified six independent basic emotions as: anger, disgust, fear, happiness, sadness and surprise. Ekman's classification is based beyond an evolutionary view and grounded on the social constructionist, attributing universal species learning - social learning, regardless of culture (Ekman, 1999).

Many recent findings from behavioral, cognitive neuroscience, neuroimaging, and developmental studies have expanded the theories of basic emotions to explain adequately the vast number of empirical observations from studies in affective neuroscience. They have been used the circumplex model of affect, which assumes a two-dimensional framework, composed of the two motivational and emotional determinants: valence and arousal (Russel, 1980). Each emotion can be understood as a linear combination of these two dimensions, or as varying degrees of both valence (unpleasant/pleasant) and arousal (activation/deactivation).

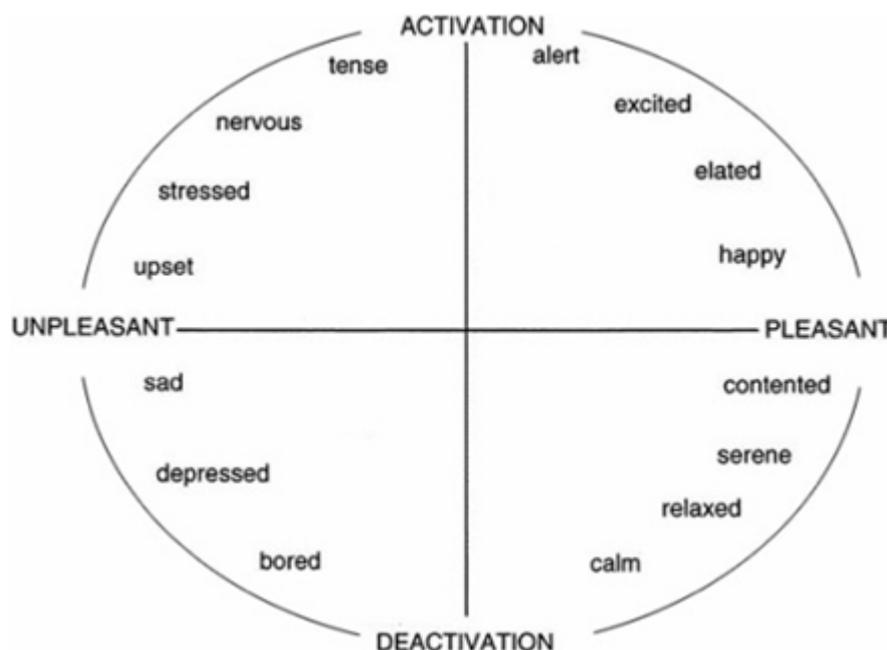


Figure 2. A graphical circumplex model of affect representation, with the horizontal axis representing the valence dimension and the vertical axis representing the arousal or activation dimension (Posner, Russel & Peterson, 2005).

The affective experience is the consequence of a linear combination of these two independent systems, which is then interpreted as representing a particular emotion. According to circumplex theorists, the emotion of fear, for example, is conceptualized by a neurophysiological state typically involving the combination of negative valence and high arousal level in the central nervous system (Posner, Russel & Peterson, 2005).

The subjective emotional experience arises out of cognitive interpretations on these psychological dimension activities that occur in the context of eliciting stimuli, memories of prior experiences, behavioral responses and semantic knowledge. Thus, the measurement of emotions regarding changes in the valence and arousal system are made mostly through physiological indexes, as skin conductance responses and heart rate acceleration (Bradley & Lang, 2000; Droit-Volet, Mermillod, Cocenas-Silva & Gil 2010; Khalfa, Peretz, Blondin & Manon, 2002, Lang, Greenwald, Bradley & Hamm, 1993; Sequeira, Hot, Silvert & Delplanque, 2009), functional magnetic resonance imaging signal intensity in the visual cortex (Bradley, Sabatinelli, Lang, Fitzsimmons, King, & Desai, 2003) and self-assessment reports of arousal, valence, and the emotions that the stimuli induced (Droit-Volet et al., 2010; Katkin & Hoffman, 1976; Walden, Harris, Catron, 2003).

Neurobiology of emotion and memory consolidation

In complex vertebrates and humans, an elaborate neural systems support the varied responses of fear, joy, angry, better facilitating to the environmental adaptation. James Papez (1883-1958) was the first scientist that classified a neural system to understand the neurobiological phenomena related to emotion. Thus, further experimental evidence led to the revision of structures belonging to the circuit proposed by Papez, emerging the concept of the limbic system (Dror, 2001). The limbic system is a group of structures which govern emotions and behavior. Regarding the brain structures in the formation of emotions, there are some of the most important parts of the limbic system involved in the long-term memory formation, the amygdala and the hippocampus. Amygdala is the center of danger, causing fear and anxiety, placing the animal in a state of alert, ready to run or fight. Hippocampus is the main structure related to memory and an important component of the limbic system. This neural structure acts in interaction with the amygdala and is more involved in the recording and deciphering perceptual patterns than in emotional reactions (Squire & Schacter, 2002).

The neurobiology of emotions and memory points a strong relation between them. In the memory consolidation literature, there is evidence that emotions can enhance long-term memory (Buchanan & Lovallo, 2001; Cahil, Gorski & Le, 2003; Kensinger, 2007; LaBar & Phelps, 1998). It's largely known that information encoded under emotional context is more resistant indeed emotions facilitate perceptual processing. The items of emotional relevance are more likely to be noticed than are neutral items and that has been pointed out in studies about stories (Heuer & Reisberg, 1990), film clips (Cahill et al., 1996), words (LaBar & Phelps, 1998), and pictures (Christianson & Fallman, 1990).

During the consolidation period, the memory can be modulated; it appears that emotional arousal, following the learning event, influences the strength of the subsequent memory for that event. Emotionally arousing information can lead to better memory encoding, therefore influencing better retention and retrieval of information. Arousal is related to selective attention during the encoding process and produces better long-term memory results than the encoding of neutral stimuli (Mickley Steinmetz, Schmidt, Zucker & Kensinger, 2012). This enhanced of long-term memory for emotional events, is due to an interaction between amygdala activity and the stress endogenous hormones (McGaugh, 2000). The stress hormone active arousal and produce a physiological and psychological state of being awake or reactive to stimuli. This hormone also increases heart rate and blood pressure, resulting in a condition of sensory alertness, mobility and readiness to respond (Libkuman, Stabler, & Otani, 2004). According to Cahil et al. (2003), the post-learning stress hormone activation does not uniformly modulate memory consolidation for newly information; rather, it interacts with the arousal level associated with initial encoding of stimuli to modulate consolidation of those stimuli.

The effects of arousal on memory have been investigated through several types of stimuli. Visual and acoustic stimuli, i.e., images with contextual information such as color and spatial location (D'Argembeau & Van der Linden, 2005), hedonic tone content (Dunbar & Lishman, 1984), slides with images and sounds with neutral and different arousal level (Christianson, Loftus, Hoffman & Loftus, 1991; Gendron, 2000), film scenes (Kebeck & Lohaus, 1986; Laird, 1982), facial expressions (Nathan, Astell, Reid; Glen & O'Carroll, 2003) and violent events in real life (Christianson & HübINETTE, 1993), are mostly stimuli used.

Christianson and HübINETTE (1993) presented some empirical findings about the effect of arousal on the recall of a threatening event. These researchers surveyed and studied the reports of witnesses to a bank robbery, either as victim or spectator, with regard to emotional reactions and memory for detailed information about the robbery. The consistency of the

witnesses' reports was measured by comparing the information obtained in the police reports and the recall given in the research interview. The results showed high rates of accuracy in reports after a time interval for specific details of the robbery as stocks, weapons and clothing. However, for details like hair and eye color and details of the circumstances, the witnesses presented underperforming. These data can be associated to evolutionary aspects of defensive behavior; after all participants showed an accuracy to recall the actions, weapons and clothing, elements that trigger arousal and are salient for the body in a state of alert and react defensively.

Emotions and time perception

The events that evoke arousal are attractive to signal individuals on needed attitudes in social interactions, in threatening situations, alert and defensive reactions, guiding temporally the individual to defensive and preservation behaviors. Emotions that trigger arousal also affect time perception (Fraisse, 1978).

In the time perception literature there are evidences that durations experienced in an emotional context (high arousal level) are judged as longer than those experienced in a neutral context (Angrilli, Cherubini, Pavese, & Manfredini, 1997; Droit-Volet, Brunot, & Niedenthal, 2004; Droit-Volet, Fayolle, & Gil, 2011; Droit-Volet et al., 2010; Falk & Bindra, 1954; Grommet, Droit-Volet, Gil, Hemmes, Baker & Brown, 2010; Stetson, Fiesta, & Eagleman, 2007).

The effects of arousal on time perception have been investigated using several types of stimuli. The studies that used the administration of drugs, such as cocaine and methamphetamine on time perception, have been showed that these drugs produces an overestimation of durations, once increases the arousal changing the effective levels of dopamine (DA) in the brain. (Buhusi & Meck, 2002; Cheng, Ali & Meck, 2007; Maricq, Roberts & Church, 1981; Meck, 1983; Wittmann, Leland, Churan & Paulus, 2007). In the visual and acoustic stimuli field, Droit-Volet and Gil (2009) and Droit-Volet and Meck (2007) used facial expressions of anger and disgust and found out that the expression of anger produces a lengthening effect on time perception. The images from the International Affective Picture System (IAPS) are frequently used and also have been showed that the effect of high arousal level of the images produce temporal overestimations (Angrilli, Cherubini, Pavas & Manfredini, 1997; Gil & Droit-Volet, 2012; Grommet, Droit-Volet, Gil, Hemmes, Baker &

Brown, 2010). Gil and Droit-Volet (2012) investigated the arousal effect evoked by images exposition from IAPS on time perception. The results from verbal estimations showed that image duration was judged longer for emotional than neutral images. This occurred to a greater extent to images of discrete emotions of disgust and fear. The authors assume that arousal is a fundamental mechanism mediating the effect of emotion on time perception.

The different types of acoustic stimuli as standard sounds stimuli, such as the International Affective Digitized Sounds (IADS), was used by Noulhiane, Samson, Mella, Ragot & Pouthas (2007). The authors found out that among of the 36 sounds used in the study, the sounds duration with emotional content were reproduced and verbally estimated as: 1) longer than the neutral sounds and the negative sounds were judged to be longer than positive. In addition, 2) high-arousing stimuli were perceived to be shorter than low-arousing. These results from standard sounds stimuli on time perception, suggest that both activation and attentional processes modulate the timing of emotional event.

Among the acoustic stimuli, music is also a stimulus largely used to investigate the effect of arousal on temporal processing. The studies have been shown that the music with same duration, but with different emotional content, as high or low arousal level, were perceived as temporally different (Cocenas-Silva, Bueno, Bigand & Molin, 2011, Droit-Volet, Ramos, Bueno & Bigand, 2013). In a multidimensional scaling study Cocenas-Silva et al. (2011) presented 16 excerpts of western music from baroque, classic, romantic and modern repertoires, varying in valence and arousal level. The participants listened and grouped the excerpts according to the similarity time, but they were unaware that all of the stimuli were 20 seconds in length. The multidimensional scaling analysis provided a perceptual representation of musical excerpts on the basis of similarity time duration in a two-dimensional space. In addition, the results showed a lengthening effect on time perception for the high arousal excerpts; the valence had little influence. The findings provided evidence for variability on time perception of musical excerpts of exactly the same duration and in addition, the emotional value of the stimulus determines time estimation.

To test a new acoustic emotional stimulus Droit-Volet et al. (2010) conducted two experiments in a temporal bisection task to investigate the effect of a threatening stimulus on time judgments. There were two acoustic signals: one aversive and one non-aversive. The aversive signal consisted of a 50 ms burst of 95 dB white noise with instantaneous rise time (Hillman, Hsiao-Weckslerb, and Rosengren, 2005). The non-aversive signal was a beep of 50 dB lasting 50 ms. The acoustic signal were pretested to evaluate the arousing nature of the aversive sound by measuring the SCR in a sample of participants. They have also pretested

both subjective affective valence and arousal dimension of this stimulus, using the Self-Assessment Manikin (SAM; Lang, 1980). The expectation of the aversive acoustic signal demonstrated to increase a person's level of arousal and to induce the emotion of fear, because it produces a small scare in participants. Already, the expectation of the non-aversive signal was judged to be low-arousing and pleasant. In experiment 1, two groups of participants performed a bisection task followed by the two acoustic signals (aversive and non-aversive); one signal to each group. Results showed that the expectation of the aversive signal generated a lengthened time perception. In experiment 2, the authors tested the aversive stimulus being presented at the beginning or at the end of the bisection task. They found a temporal overestimation in each condition, compared to the trials in which no aversive stimulus was presented. Furthermore, the temporal overestimation was greater when the expectation for the forthcoming threatening stimulus was longer. The results led the authors to suppose that the anticipation of a forthcoming stimulus increases the arousal level, whatever the nature of this stimulus, thus accelerating the rate of the internal clock. The new acoustic emotional stimulus used in Droit-Volet et al. (2010) was also used in this thesis.

The conclusion of relevant studies on emotions, memory and time perception converge to the same point: emotion affects memory and time perception. In the memory field, researches show that emotional content of an event influences the learning and thus the strength of the subsequent memory for that event. The time perception studies show temporal distortion in the presence of emotional stimuli, more specifically, lengthening effect of time. Although there are several studies that investigated the effect of emotion on memory and time perception, none study investigated the effect of emotion on time consolidation in the long-term memory. One of the aims of this thesis is investigating the emotion of fear effects on time consolidation in the long-term memory in humans.

1.4. The effect of interference in memory consolidation and time perception

Studying interference

In everyday situations of learning or performing tasks, it is common to be exposed to interferences. Interference refers to a disruption in cognitive processes of learning and memory that are activated to perform tasks in which there is interaction between the new material and transfer effects of past learned behavior. Early learned information is vulnerable

2 OBJECTIVE

The goal of this thesis is to experimentally study the factors that contribute to and disrupt the time consolidation in the long-term memory. We search to examine the effect of emotions and interference task at the encoding of temporal information and the implications on the memory consolidation. Everyday events are triggered at a time and this dimension is one of the various attributes automatically associated with an event, when it is stored in memory (Friedman, 2004). The encoding and recall of time information allow the optimization of temporal actions in response to environmental events; the approximate recall of time and the duration of an event, assist future actions and enable the execution of schedules from previous intentions formed (Block & Zakay, 2008).

Three experiments were conducted to examine the effect of emotions and interference task at the encoding of temporal information and, consequently, the implications on the memory consolidation. For all the experiments, we used a temporal generalization task that consists in two phases: learning and testing. In the learning phase, participants encoded a standard duration and immediately, or 24 hours after the encoding, they performed a test. In the test phase, participants discriminated the standard duration previous encoded from the comparison durations (1, 2, 3, 5, 6, 7). Experiment one was conducted to investigate the memory for the duration of emotional events.

In this experiment, the standard duration was encoded under emotional condition, threatening and nonthreatening, and neutral condition. It was used the new acoustic emotional stimuli tested by Droit-Volet et al. (2010). In the threatening condition, the participants expected an aversive sound (a 50-ms burst of 95-dB white noise), in the nonthreatening condition, the participants expected a non-aversive sound (50 ms of a 50-dB beep) and in the neutral condition no signal was delivered. Participants were tested immediately, or 24 hours after learning to examine the effect of emotion on retention time in memory. It was expected that the standard duration would be better retained in memory after a long retention delay (24 hours after learning). Furthermore, it was expected that temporal judgments were more accurate when the standard duration was previously experienced in an emotional, rather than a neutral condition, and that this would occur to a greater extent for the aversive than for the non-aversive emotional condition.

Experiment two was conducted to investigate the consolidation process for duration and its effects on the time judgments. It was used a non-temporal interference task given at

different retention delay between the initial learning of the standard duration and the comparison test, which was performed immediately or 24 hours after learning. The hypothesis was, if a consolidation mechanism was disrupted by interference, the memory duration would be intact if tested immediately after the interference, but distorted 24 hours later. The disruption of consolidation would affect the precision and accuracy of long-term memory, with a stronger disruption when the interference was given closer to the learning phase and a weaker effect when the interference was delayed from the learning phase.

The experiment three was conducted to examine the effect of emotion on the long-term memory for duration and its resistance against interference effects. Participants were divided between two experimental groups: learning of standard duration under effect of expectation of an aversive sound (a 50-ms burst of 95-dB white noise) and learning of standard duration without sound. Both groups were given a non-temporal interference task immediately after the learning phase and they were tested for 24 hours. The hypothesis was that the long-term temporal judgments would be more accurate and precise for the participants which learned the standard duration in an emotional condition than a neutral condition, even under interference effects.

CHAPTER 1

Temporal memory of emotional experience

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Abstract

The few studies that have investigated judgments of time have suggested that the memory of duration is distorted more for emotional events than for neutral events, while in contrast there is abundant evidence that other aspects of memories of emotional events are more accurate. To reconcile this apparent discrepancy, we used a procedure in which the participants learned a standard duration over several trials under three emotional conditions: a threatening, a nonthreatening, and a neutral control condition. They were then tested either immediately or 24 hours after learning. In this test phase, they had to indicate whether presented comparison durations were or were not the same as the previously learned standard duration. We found that durations were recalled better in the emotional than in the neutral condition, and that this occurred to a greater extent in the threatening than in the nonthreatening condition. Arousing emotions thus enhanced temporal memory, just as they enhance memory for other aspects of emotional events.

Keywords: Time, Time perception, Memory, Emotion

Introduction

Life is filled with emotional events, some joyful, others stressful, such as a wedding or a divorce. Consequently, the role of emotion in the memory of past events has been a major focus of interest for studies on autobiographical and episodic memory. However, few studies have examined how we remember the duration of emotional events, even though this dimension is fundamental (D'Argembeau & Van der Linden, 2005). The purpose of the present study was thus to begin to investigate the memory for the duration of emotional events. There is abundant evidence that memories of emotional events are more accurate than those of neutral events (Christianson, 1992). Since the pioneering research conducted by Kleinsmith and Kaplan (1963), several studies have demonstrated that arousing emotions enhances long-term memory for events. For example, after an interval of 24 h, individuals remember arousing words better than neutral words (LaBar & Phelps, 1998; Sharot & Phelps, 2004). Indeed, some evidence suggests that emotions facilitate the consolidation of traces in memory (LaBar & Cabeza, 2006). During a period after encoding, called consolidation, newly learned information is fragile and susceptible to disruption before becoming fixed in memory. Emotional reactions are believed to produce a release of adrenal stress hormones that increases the significance of events and enhances their hippocampus-dependent memory consolidation (McGaugh, 2000). This is consistent with studies that have shown that the administration of stimulant drugs within minutes or hours after training facilitates retention in long-term memory (McGaugh, 1973; McGaugh & Roozendaal, 2002). As a result of changes in the consolidation processes, memories of emotional events are thus more persistent and vivid than those of neutral events (Phelps, 2004).

However, inconsistent with the result that emotional events are remembered better, a small number of studies of memory for temporal aspects of emotional events have suggested a distortion rather than an improvement in memory (for a review, see Droit-Volet, *in press*). For example, individuals who have experienced a traumatic event (e.g., a car accident) report that time appeared to run more slowly than normal during the event (e.g., Anderson, Reis-Costa, & Misanin, 2007; Loftus, Schooler, Boone, & Kline, 1987). Similarly, novice skydivers overestimated the duration of their first jump, and the degree of their overestimation increased with their fear level (Campbell & Bryant, 2007). This raises the question of whether this distortion of the memory for duration of emotional events is specific to time or results from methodological artifacts in the studies that have been conducted to date.

A major problem in the studies on the temporal memory of emotional events is the difficulty of identifying whether the observed time distortions were due to processes of consolidation in memory per se or simply mirrored what was initially encoded. There is now ample evidence that emotions affect the perception of time (e.g., Angrilli, Cherubini, Pavese, & Manfredini, 1997; Droit-Volet, Brunot, & Niedenthal, 2004; Droit-Volet, Fayolle, & Gil, 2011; Droit-Volet, Mermillod, Cocenas-Silva, & Gil, 2010; Falk & Bindra, 1954; Gil & Droit-Volet, in press; Grommet et al., 2010; Stetson, Fiesta, & Eagleman, 2007; Watts & Sharrock, 1984), and it has been demonstrated that durations experienced in a high-arousal emotional context are judged as longer than those experienced in a neutral context. According to internal-clock models of time perception (Gibbon, Church, & Meck, 1984; Treisman, 1963), the increase of arousal occasioned by the emotional event speeds up the internal clock that provides the raw material for the representation of an event's duration. When the pacemaker of the internal clock runs faster, more temporal units occur during the interval timed, and thus its duration is judged to be longer (for reviews, see Droit-Volet & Meck, 2007; Grondin, 2010; Meck, Penney, & Pouthas, 2008). Consequently, the finding of distorted time judgments in long-term memory for emotional events may result from the encoding of time under emotion-provoking conditions rather than from a specific problem of consolidation in memory. To be able to experimentally examine whether time distortions take place due to consolidation processes, it is thus necessary to verify that the duration has been correctly encoded and stored in long-term memory in the first place, irrespective of different emotional contexts. Therefore, in the present study, we used an original procedure in which the participants learned a standard duration in different emotional contexts and then were tested either immediately or after a long-term retention interval.

In addition, most previous studies of temporal memory have used the "retrospective judgment of time" paradigm (Hicks, Miller, & Kinsbourne, 1976). In this paradigm, participants are instructed that they have to estimate the duration of an event only after having experienced it. According to theories that seek to explain retrospective time judgments, there is no guarantee in this situation that participants have paid attention to time or have encoded it. Consequently, temporal judgment is considered to be reconstructed using nontemporal information stored in memory (Block, 1992; Hicks et al., 1976). To avoid such a reconstructive process, we used a "prospective timing" paradigm, in which people were explicitly instructed to pay attention to the stimulus duration that they would experience, and later to estimate it.

The aim of the present study was therefore to try to reconcile the apparent discrepancy between results of enhanced memory for emotional events and those of time judgments, which have suggested distortions of temporal memory under emotion-provoking conditions. We used the temporal generalization task (Church & Gibbon, 1982; Wearden, 1992), which has been used to test memory for duration in a number of previous studies (Jones & Wearden, 2004; Ogden, Wearden, & Jones, 2008; Rattat & Droit-Volet, 2010). In this task, participants initially learn a standard duration (learning phase). They are then presented with comparison durations of the same length as the standard or of shorter or longer durations (test phase), and they must judge whether or not these durations have the same duration as the standard in order to make a “same” or “different” response. In our study, the test phase was administered either immediately after the learning phase or after a retention period of 24 hours. Furthermore, three emotional contexts were used during the learning phase: threatening, nonthreatening, and neutral. In the threatening context, the participants expected an aversive sound (a 50 milliseconds burst of 95-dB white noise) at the end of the stimulus to be timed. The expectation of this forthcoming event has been demonstrated to increase a person’s level of arousal and to induce the emotion of fear because it produces a small pain in ears (e.g., Droit-Volet et al., 2010; Hillman, Hsiao-Wecksler, & Rosengren, 2005; Mermillod, Droit-Volet, Devaux, Schaefer, & Vermeulen, 2010). In the nonthreatening context, the participants expected a nonaversive sound (50 milliseconds of a 50-dB beep) judged to be low-arousing and pleasant (Droit-Volet et al., 2010). In the neutral control condition, no sound was expected. Our hypothesis was that the temporal comparison judgment between the comparison durations and the standard duration would be more accurate when the standard duration had been previously experienced in an emotional rather than a neutral context, and that this would occur to a greater extent for the aversive than for the nonaversive emotional condition.

Method

Participants

A total of 120 students from Blaise Pascal University, Clermont-Ferrand, France, participated in the experiment. All gave informed consent and were paid €10 for their participation.

Materials

The participants sat in a quiet room in the laboratory in front of a PC, which controlled the events and recorded the responses via E-Prime (version 1.2; Psychology Software Tools,

Pittsburgh, PA). The stimulus to be timed (i.e., for the standard duration and comparison durations) was always a blue circle, 2.5 cm in diameter, presented in the center of the computer screen. The participants gave their responses by pressing two keys (“k” or “d”) on the computer keyboard. The emotion-provoking stimuli were two acoustic signals: one aversive and one nonaversive. The aversive signal consisted of a 50-ms burst of 95-dB white noise with an instantaneous rise time that produces a startle reflex (Hillman et al., 2005). The nonaversive signal was a 50-dB beep lasting 50 milliseconds. The emotion-provoking nature of these acoustic signals was recently tested in a temporal task by Droit-Volet et al. (2010) using physiological indexes (skin conductance responses) and self-assessment reports of arousal, of valence, and of the emotions that the stimuli induced. In that study, the aversive signal was rated as highly arousing (i.e., $M = 7.25$, $SD = 1.25$, on a 9-point scale), as of negative valence, and as being fear-inducing. In contrast, the nonaversive signal was judged to be less arousing ($M = 3.5$, $SD = 1.5$) and of positive valence, and to produce neutral emotions and emotions of happiness. The acoustic signals were delivered binaurally using calibrated headphones.

Procedure

The participants performed a temporal generalization task that consisted of two phases: learning and test. In the learning phase, the participants were initially instructed to memorize the standard duration (4 seconds) and were presented with this standard duration five times. They were then given at least two training blocks of four trials each: two for the standard duration and two for comparison durations of 0.5 and 7.5 seconds. The standard duration and the comparison durations were always presented in the form of the blue circle. The participants were told to press one key (e.g., “d”) if the comparison had the same duration as the standard (“same” response), and another key (e.g., “k”) if it was different (“different” response). Buttonpress assignments to the “same” and “different” responses were counterbalanced across participants. Each response was immediately followed by informative feedback (“correct” or “wrong”). None of the participants required more than one or two training blocks (16 trials in total) to learn the standard duration - that is, to produce 100% correct responses.

The procedure in the test phase was similar to that used in the learning phase, except for the use of different comparison durations (1, 2, 3, 4, 5, 6, and 7 seconds) that were presented in the absence of feedback. The participants were told “It’s the same game that you played just now/ yesterday, but now you won’t receive any feedback.” After each comparison duration, they responded by making a “same” or “different” response as in the training phase.

The participants completed eight blocks of 9 trials (72 trials) - that is, 3 trials for the standard duration and 1 trial for each of the comparison durations. The durations were presented in random order within each block. Each trial started when the participant pressed the space bar after the word “ready!” To prevent the participants from using a counting strategy, they were explicitly told not to count, and the experimenter added that if they did count, the results would be distorted (for this method, see Rattat & Droit-Volet, 2011).

A between-subjects design was used in which the participants were randomly assigned to six experimental conditions (20 participants per group) as a function of the retention period between the learning and the test phase (immediate and 24 hours) and the emotional condition experienced during the learning phase (aversive, nonaversive, and control). However, 1 participant in the nonaversive/24-hours-delayed testing condition was excluded from the statistical analyses because he produced a totally flat generalization gradient - that is, he pressed the same button for all responses. In the aversive and nonaversive conditions, the aversive and nonaversive sounds were presented 50 milliseconds after the stimulus duration on every trial of the learning phase (i.e., the 5 trials of standard duration presentation and the 16 trials of the training blocks). The acoustic signal was not delivered during the test phase for these two “emotional” conditions. In the control condition, no sound was presented after the stimulus duration in either the learning or the test phase.

Results

Figures 1, 2 and 3 show the temporal generalization gradients as the mean proportions of “same” responses (comparison duration judged to be the same as the standard duration) plotted against the comparison durations for the immediate test and 24-hours delayed test conditions. The upper, middle, and bottom panels show data for the aversive, nonaversive, and control conditions, respectively.

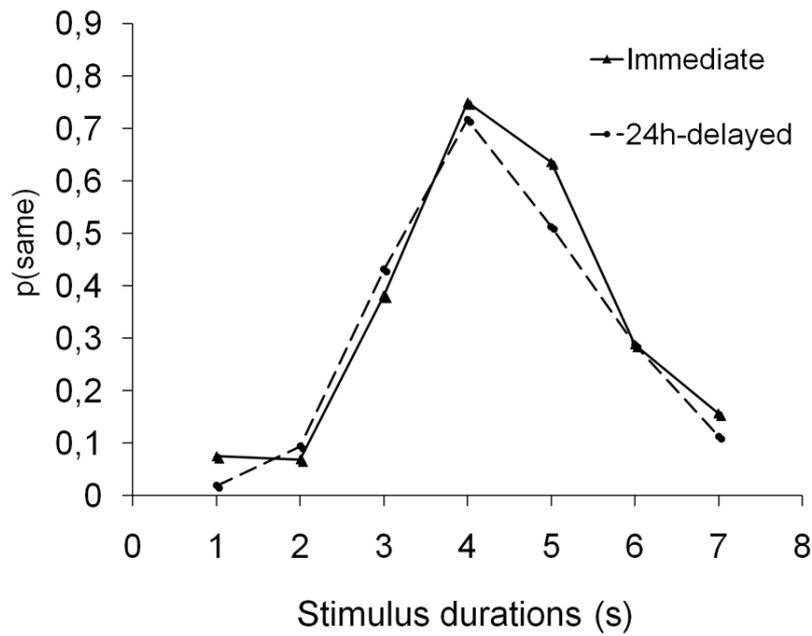


Figure. 1 Temporal generalization gradients (proportions of responses judged as being of the same duration as the standard duration) for the immediate and the 24-hours-delayed tests in the aversive condition.

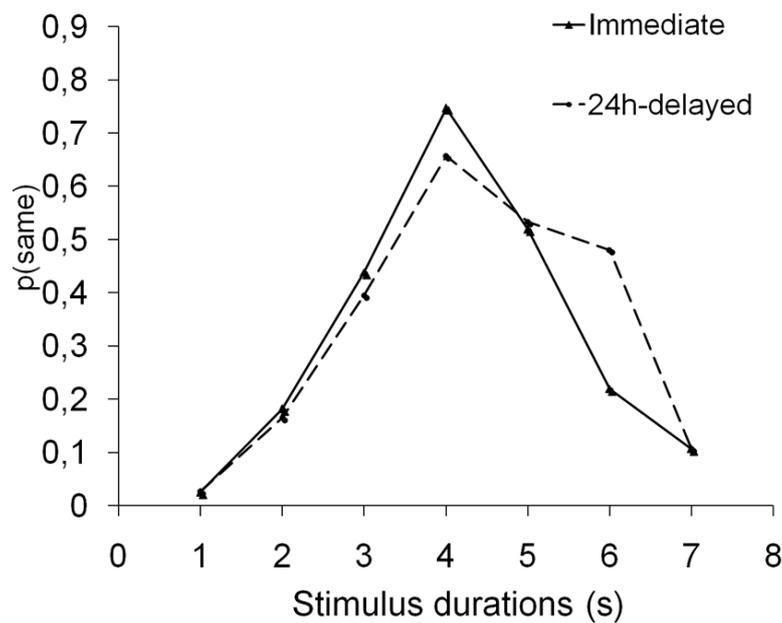


Figure. 2 Temporal generalization gradients (proportions of responses judged as being of the same duration as the standard duration) for the immediate and the 24-hours-delayed tests in the nonaversive condition.

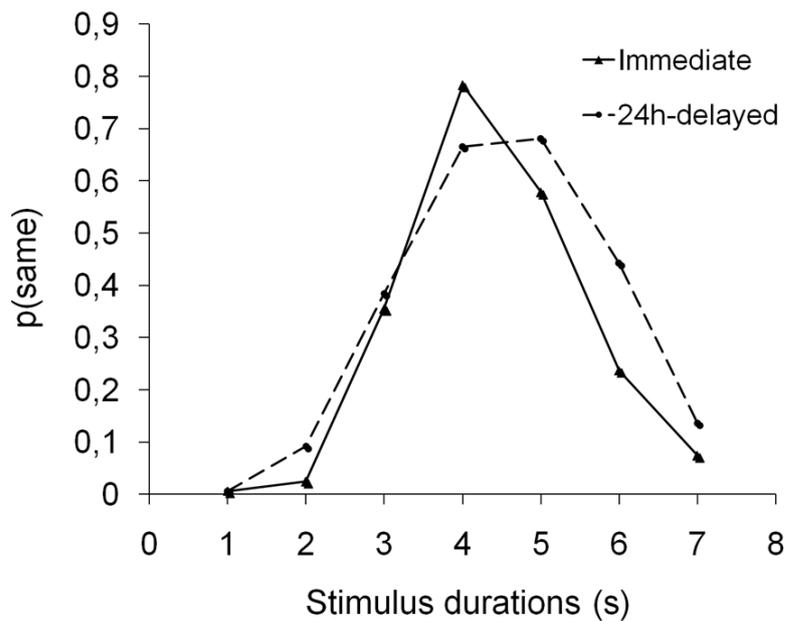


Figure. 3 Temporal generalization gradients (proportions of responses judged as being of the same duration as the standard duration) for the immediate and the 24-hours-delayed tests in the control condition.

To describe the generalization gradients, two measures were calculated: the peak time - that is, the stimulus duration that gave rise to the highest proportion of “same” responses - and the width of the temporal generalization gradient at half of its maximum height (full width at half maximum, or FWHM; as used by Hinton & Rao, 2004; Penney, Holder, & Meck, 1996). These two measures were obtained by fitting each participant’s temporal gradient with the logarithmic curve-fitting algorithms from the PeakFit program. The logarithmic function produced the best fit of temporal gradients for the participants (mean $R^2 = .91$, $SD = .08$).

Figure 4 shows the peak times obtained in this way. An ANOVA was conducted on the peak time measure, with test time (immediate vs. delayed) and emotion condition at training (aversive, nonaversive, and control) as between subjects factors. There was a significant interaction between the test time and the emotion condition at training, $F(2, 113) = 3.52$, $p = .03$, but no main effect of test time, $F(1, 113) = 2.50$, $p = .12$, nor of emotion, $F(2, 113) = 1.76$, $p = .18$. In the immediate test, the peak time seemed to be longer for the aversive than for the other emotional conditions; however, the effect of emotion was not significant, $F(2, 57) = 0.71$, $p = .50$. This suggests that, in the present study, temporal discrimination was accurate in the temporal generalization task when the standard duration was learned across several trials in different emotional conditions. While there was no effect of emotion at the immediate test, the effect of emotion was significant for the delayed test, $F(2, 56) = 4.15$, $p =$

.02. This was due to the fact that, in the control condition, the peak of the generalization gradient was shifted toward a longer duration value in the delayed than in the immediate test, $t(38) = 2.49, p = .02$. The ratio between the peak time and the standard duration (Peak Time - Standard Duration / Standard Duration) was indeed greater than zero in the delayed test, $t(19) = 3.50, p = .002$, whereas it did not significantly differ from zero in the immediate test, $t(19) = 1.06, p = .30$. In sum, durations learned in a neutral condition were distorted (i.e., overestimated) after the long retention interval. In contrast, the difference in the peak time between the delayed and the immediate tests decreased for the durations learned in an emotional context, with a non significant difference in the aversive condition [3.91 vs. 4.19; $t(38) = 1.08, p = .29$] and in the nonaversive condition [4.36 vs. 3.95; $F(1, 113) = 2.50, p = .12$]. In the delayed test, the ratio between the peak time and the standard duration did not differ from zero in the aversive condition, $t(19) = 0.51, p = .62$, whereas it just reached significance in the nonaversive condition [$t(19) = 2.14, p = .047$]; in the immediate test, it always remained close to zero [$t(19) = 1.06$ and $t(19) = 0.38$, respectively; all $ps > .05$]. Overall, these results indicate that the distortion of time following long-term retention of durations was reduced for emotional conditions as compared to the neutral condition, and especially in the case of the aversive condition.

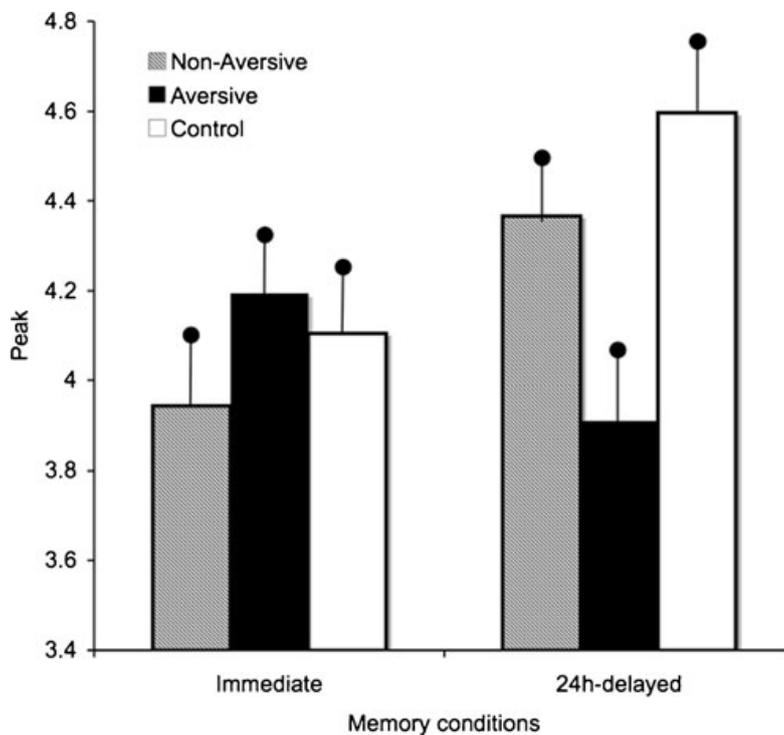


Figure. 4 Mean peak values of the generalization gradient for the immediate and the 24-hours-delayed tests in the nonaversive, aversive, and neutral conditions.

An ANOVA was also run on the measure of variability in time discrimination (i.e., FWHM), using the same between-subjects factors as for the peak time (see Fig. 3). This revealed neither a main effect of test time, $F(1, 113) = 2.81, p = .59$, nor any test time \times emotion interaction, $F(2, 113) = 2.23, p = .11$. There was only a marginally significant effect of emotion, $F(2, 113) = 2.79, p = .06$. However, further statistical analyses revealed that a significant effect of emotion appeared in the 24-hours-delayed test condition, $F(2, 56) = 4.24, p = .02$, while this effect was not significant in the immediate test condition, $F(2, 57) = 0.91, p = .41$. For the 24-hours-delayed test, this significant effect was due to an FWHM value that was smaller for the aversive than for the control condition (1.97 vs. 2.52; Scheffé test, $p < .05$). The FWHM value in the nonaversive condition (2.18) was halfway between the value for the aversive condition and that for the control condition, with no significant difference being obtained between these conditions (all $ps > .05$). After a long retention interval, the variability in time discrimination was thus lower in the aversive than in the neutral condition. This result indicates that durations experienced in emotional conditions were recalled better than those experienced in nonemotional contexts.

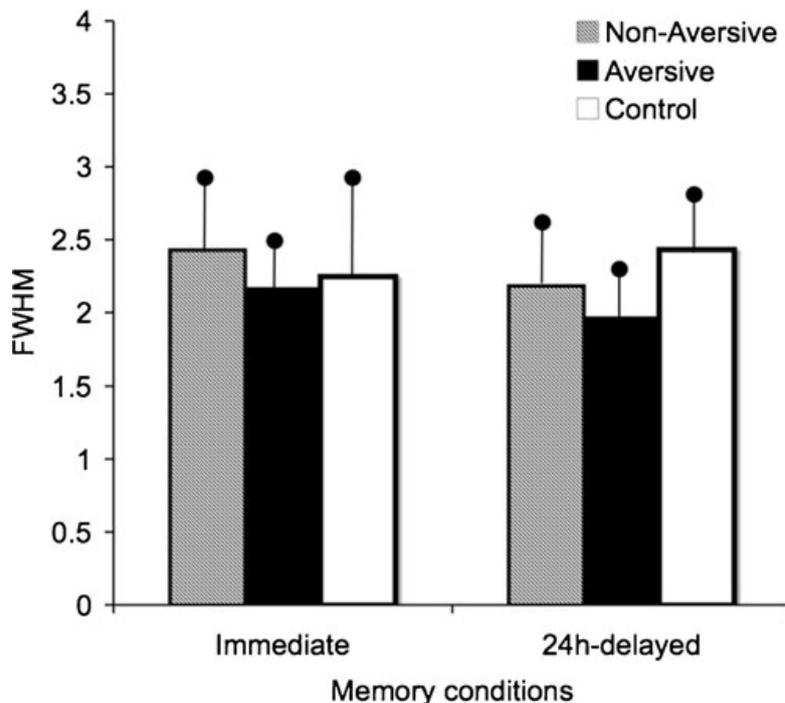


Figure. 5 Mean full widths at half maximum (FWHM) of the generalization gradient for the immediate and the 24-hours-delayed tests in the nonaversive, aversive, and neutral conditions.

Discussion

Our results showed that after a 24-hours retention interval, temporal comparison judgments between the standard duration and other durations were more accurate and less variable when the standard duration had been previously experienced in a context known to evoke emotional responses than when it was experienced in a neutral context. In addition, temporal discrimination was better when the learning of the standard duration was experienced in an aversive rather than a nonaversive condition.

The improvement of the temporal judgment when the standard duration was learned in the emotional context as compared to the neutral context suggests that the emotional responses enhanced the long-term memory of the standard duration. This finding is entirely consistent with the results of studies of long-term memory for emotional events, which have shown that emotions improve the memories of events and of some of their properties (e.g., location) (e.g., D'Argembeau & Van der Linden, 2004; Dunbar & Lishman, 1984). Therefore, contrary to findings in the literature on time distortions in long-term memory for emotional events, our results suggest that durations are remembered better when they are initially experienced in an emotional rather than a neutral context. However, in our study we tested a relative judgment between a current duration and a previously experienced standard duration rather than an absolute judgment of the standard. It will thus be important to further investigate the impact of different types of temporal judgment on the sense of time in long-term memory.

Our results also showed that the accuracy of temporal memories was increased when the standard duration was learned in an aversive rather than a nonaversive context. In the aversive context, the participants expected a threatening sound that is known to induce the emotion of fear and to increase the arousal level during the processing of the standard duration (Droit-Volet et al., 2011). Studies that have used a fear conditioning paradigm have shown that the expectation of this type of threatening stimulus produces arousal responses but also activates the amygdala (Phelps et al., 2001). According to some ideas about the neuroscience of emotion and memory, the amygdala modulates the hippocampus-dependent memory consolidation of emotional events through the production of stress hormones (for reviews, see McGaugh, 2000; Phelps, 2004). Consequently, we can assume that the association between emotional stress reactions induced by the expectation of an aversive sound and the standard duration to be processed would have facilitated the consolidation of the standard in memory and its long-term retrieval.

The processes of consolidation and encoding involve different mechanisms (McGaugh, 2000). However, one can also suppose that the emotional context might have improved the processing of the standard duration, because it has been shown that threatening stimuli automatically attract focused attention for basic survival reasons (Sharot & Phelps, 2004; Öhman & Soares, 1993). In addition, there is a positive correlation between the degree

of activation of the amygdala (for the rapid detection of threatening stimuli) and long-term memory (Cahill et al., 1999). It is thus possible that the amount of attention allocated to the processing of time was higher in the aversive than in the nonaversive or the neutral condition, with the result that the standard duration was encoded better and recalled better 24 hours later. However, our results showed no significant difference in temporal discrimination as a function of the emotional conditions in the immediate test phase as well as during the learning phase. This provides clear support for a consolidation- rather than an encoding related hypothesis.

In the presence of emotional arousal, we would also have expected to observe a lengthening of duration in the aversive as compared to the neutral condition. As we stated in the introduction, numerous studies have shown that time is judged as longer in high-arousal than in low-arousal conditions, because the internal clock speeds up with the increase of arousal (Droit-Volet & Gil, 2009). As far as the memory is concerned, Millar, Styles, and Wastell (1980) proposed that participants reactivate in memory not only the content of past events, but also the emotional state associated with these events. It is thus possible that, in our study, the emotional state experienced during the learning phase was reactivated during the testing phase. In this case, the standard duration and the comparison durations would have been processed with the same internal clock speed, and no lengthening effect would have been observed in the aversive condition. However, Gil and Droit-Volet (2011) have recently observed that the emotion-based lengthening effect is not obtained in the temporal generalization task, but only in tasks in which the participants can compare different emotional stimuli across the same session. In addition, in the present study, the participants learned the standard duration over several training trials, which probably improved timing accuracy in the temporal generalization task. Consequently, methodological factors (the generalization task and learning phase) likely contributed to the absence of a subjective lengthening effect in the aversive condition.

No previous study has experimentally investigated the long-term memory of durations learned in different emotional contexts, and several questions remain unanswered. Nevertheless, our study is the first to provide results that suggest that arousing emotions enhance the long-term memory of stimulus durations, just as they enhance the memory of events and of their nontemporal characteristics.

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CHAPTER 2

Memory Consolidation for Duration

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Abstract

Humans and animals encode and store in memory elapsed intervals as evidenced through their temporal expectancies. However, there are few experimental studies on the long-term memory of duration. The aim of this original study was to examine the consolidation process for duration and its effect on the time judgment. In our study, memory of duration was tested in humans with a temporal generalization task. Consolidation was assessed by means of a 15-min non-temporal interference task introduced at different delays after the initial learning of a 4-s standard duration. The results showed that (1) when tested at 24 h after the learning phase, the memory of the 4-s duration was disrupted (less precision and lengthening effect) if the interference task was introduced 30-45 min after learning, (2) disruption was not observed when the memory was tested immediately after the interference task, and (3) there was a temporal gradient of the disruptive interference effect within the first hour after learning. Overall, these results fulfill the key criteria to infer a synaptic/cellular consolidation process, and thus demonstrate that, as is the case for other memories, memory of duration undergoes a consolidation process that lasts at least one hour.

Keywords: Time, timing, memory, consolidation

Introduction

The memory of durations plays a critical role in time judgments and is fundamental for building temporal expectancy and shaping adaptive behavior. Surprisingly, very few studies have investigated the long-term memory for duration (Lewis, Couch & Walker, 2011). Consequently, whether it involves mechanisms similar to those observed in other memory domains remains unknown.

At the cellular level, one mechanism of long-term memory is the consolidation process. Consolidation is defined as a process of neural plasticity occurring several hours following the learning of new information during which initially fragile memory traces become stabilized in long term memory (Dudai, 2004, 2012; McGaugh, 2000). The memory traces thus consolidate slowly over time. Research in animals, using pharmacological agents, has shown that cellular/synaptic consolidation requires messenger ribonucleic acid (mRNA) translation and synthesis of new proteins, mechanisms which take time to be completed (e.g., Alberini, Milekic & Tronel, 2006; Flexner, Flexner, Stellar, 1963; Gal-Ben-Ari et al., 2012; McGaugh, 1989; Schafe, Nader, Blair & LeDoux, 2001). Thus, two memory systems have been dissociated pharmacologically: (1) a short-term memory, which maintains information from a few seconds to several minutes and which is independent of new protein synthesis, from (2) a long-term memory for hours-to-months maintenance. As a consequence, the studies targeting the consolidation processes showed that memories are intact when tested shortly after infusion of a protein synthesis inhibitor, while they are weakened when tested 24 hours later. This selective process for stabilization at long-term with an intact memory at short-term is therefore one of the hallmarks of cellular/synaptic consolidation. The other hallmark is the temporal gradient of disruption by drugs which delineates the sensitive time window of the consolidation process. This sensitive time window may differ depending upon the type of material to be learned, as well as the disruptive agent, but it is often estimated to last up to 4-6 hours.

Memory consolidation for duration is difficult to assess in animals, as temporal learning often takes several weeks to be behaviorally expressed, even if some data indicate that it may be learned very quickly (Diaz-Mataix, Ruiz Martinez, Schafe, LeDoux & Doyère, 2013; Balsam, Drews & Gallistel, 2010). Temporal learning is thus not easily dissociable from the other learned components. In human adults, studies which have examined the long-term or reference memory of stimulus duration have often used the temporal generalization

task in which the participants compare a current duration to a standard duration stored in “reference” memory (Jones & Wearden, 2003, 2004; Ogden & Jones, 2009; Ogden, Wearden, & Jones, 2008; Rattat & Droit-Volet, 2010). In this temporal generalization task, the participants are initially presented with a standard duration (S) several times. They are then presented with different durations (D) (shorter, longer or equal to S), and must compare these durations with the representation in memory of S to judge whether D is S or not (i.e., “Yes” or “No” response). This task is acquired within a few trials and creates a stable long-term memory up to 24 hours in adults (Rattat & Droit-Volet, 2010), making it particularly suitable for testing whether the memory for duration undergoes a consolidation process.

In memory domains other than time, research on memory consolidation in humans has often used the interference paradigm in which a second task disrupts the memory of a first task if performed within the sensitive consolidating post-learning period (Lechner, Squire & Byrne, 2010; Roberston, 2012). For example, it has been shown that various retroactive interference tasks (cognitive or motor) disrupt the permanent storage in memory of newly learned information (e.g. Brashers-Krug, Shadmehr & Bizzi, 1996; Brown & Robertson, 2007; Keisler & Shadmehr, 2010; Keppel, 1968; Walker, Brakefield, Hobson & Stickgold, 2003). It has been also shown that the interference effect is weakened when the time between the first and the second task is lengthened, and the memories can be consolidated. In the temporal memory domain, two studies have investigated the overnight consolidation of temporal rhythms (Lewis, Couch & Walker, 2011) and of timing in visuomotor tracking (Maquet, Schwartz, Passingham & Frith, 2003), which result in a further improvement in performance due to sleep. However, no studies have examined the initial memory consolidation of duration that happens within the first hours after learning and which is independent of sleep. The few studies on reference memory using interference in the temporal generalization task after the learning of the standard duration have targeted the short-term memory for duration rather than its stabilization in long-term memory (Ogden, Wearden & Jones, 2008; Rattat & Droit-Volet, 2010). In these studies, the interference task was indeed given immediately after the learning phase, and the participants were tested shortly after the interference task. Furthermore, in Ogden et al.’s (2008) study, the participants were asked to repeatedly learn a new duration in successive blocks of trials, which involves a ‘scratch-pad’ type of memory processes rather than a stabilization process in long-term memory. Nevertheless, these studies using short-term memory conditions revealed that the interference task affected the time judgment. In Ogden et al.’s (2008) study, it slightly flattened in some cases displaced the generalization gradient, but more importantly displaced it to the left or to

the right, suggesting that participants tended to remember the standard duration shorter or longer than it really was. In fact, as the interference task was also a temporal generalization task with new standards being either shorter or longer than in the first task, it dictated the direction of the displacement and suggested that both memories for duration had interfered with one another producing a mixing in memory between reference values. In Rattat and Droit-Volet's (2010) study, however, although the interference task (a parlor game) was not in the temporal domain, it made the generalization gradient shift toward the left (shortening effect) compared to the generalization gradient found without interference, which peaks at the standard duration with a right asymmetry (e.g., Droit-Volet, 2002; Droit-Volet, Clément, & Wearden, 2001; Wearden, 1992; Wearden & Towse, 1994). Thus, a non-temporal interference task can disrupt the memory for duration, at least at short term. Whether the disruption of consolidation in long-term memory would have produced a similar effect on the representation of the learned duration is not known.

The present study was thus specifically designed to assess long-term memory of durations in human adults, and to test whether it involves a consolidation process for its stabilization in a long-term form. If so, when an interference task is given within a definite time window after the acquisition phase, a disrupted memory is expected when tested at long-term, but not immediately after the interference. As reported above and in other studies using various temporal tasks, when the interference task is a temporal one, there are potential mixing in memory between the different durations used for the primary and the interference tasks. However, as mentioned above, Rattat and Droit-Volet (2010) showed that it was possible to disrupt the memory for duration with a non-temporal interference task (a parlor game), that was a cognitive load task which required both to maintain information in short-term memory and to manipulate verbal information in working memory. Indeed, some studies have demonstrated with the dual-task paradigm, when the participants simultaneously performed a temporal task and a competing non-temporal task, that the duration processing requires the central executive system of the working memory (e.g., Brown, 1997, 2006; Champagne & Fortin, 2008; Fortin, Rousseau, Bourque, & Kirouac, 1993; Rattat, 2010). In Baddeley's working model, the central executive system is responsible for the control and regulation of cognitive resources (e.g., Baddeley, 2012; Baddeley & Della Sala, 1996; Baddeley & Hitch, 1974). Thus, Rattat and Droit-Volet's (2010) results suggest that a task that involves the central executive system may interfere with the memory system for duration even after the online temporal processing phase. This may be due to the fact that both processes (i.e. memory for duration and working memory) implicate common neural

networks, as discussed later. Consequently, to isolate the specific effect on memory consolidation without temporal reference memory mixing risks, we decided to use as an interference task a standardized working memory task, which calls on the central executive system of the working memory, i.e., the backward digit recall test of the Wechsler Memory Scale (WMS-II, Wechsler, 1998), a test is indeed currently employed to assess individuals working memory abilities.

The purpose of the present study was to assess the stabilization in long-term memory for duration, independently of the potential disruption of the short-term memory. For this purpose, we modified the paradigm of Rattat and Droit-Volet (2010) by introducing the interference task 30 minutes after the learning phase, instead of immediately, thus potentially targeting a time beyond the involvement of the short-term memory system. If a consolidation mechanism was disrupted, then the memory of duration was expected to be intact if tested immediately after the interference (short-term memory test, STM), but modified (e.g. perhaps less precise) at long-term, i.e. 24 hours later (long-term memory test, LTM). Furthermore, a temporal gradient of the disruption should be observed at long-term (i.e., testing 24 hours later), with a stronger disruption, when the interference was given closer to the learning phase and a weaker effect when the interference was delayed from the learning phase. Given the previous studies reported above, it was expected that the disruption of consolidation would possibly affect the precision of memory, as well as its accuracy.

Method

Participants

A total of 103 undergraduate students (Mean age = 19 years; 75 females and 28 males) at Blaise Pascal University (Clermont-Ferrand, France) took part in this experiment for course credit.

Materials

Participants were tested individually in an acoustically isolated room and were seated 50 cm from the screen of a PC computer. An E-prime program (1.2. Psychology Software Tools, Pittsburg, PA) controlled the experiment and recorded the data. The stimulus to be timed was always a blue circle (2.5 cm in diameter) presented in the center of the computer screen. Participants gave their responses by pressing two keys on the computer keyboard, “d” (response ‘yes’) and “k” (response ‘no’), the button-press assignment being counterbalanced across subjects. During the learning phase, each response was followed by the feedback “correct” or “wrong” presented visually in the center of the computer screen for 2 seconds.

The interference task, that lasted 15 minutes, was the backward digit recall task used in the Wechsler Memory Scale (WMS-II, Wechsler, 1998) that is a high cognitive load task, which call on the attention-executive functions of working memory (Baddeley & Hitch, 1994). In the present study, the participants were thus presented with a sequence of digits that they must immediately recall in the reverse order. The number of digits per sequence progressively increased from 2 to 8 digits (i.e., 7 sequences), with two trials per sequence. There were thus a total of 14 trials and the participants were repeatedly given these 14 trials (with new digits sequence) during a 15 minutes period.

Procedure

Each participant was given a temporal generalization task with a learning phase and a testing phase. In the learning phase, the participant was instructed that he/she will be presented with a stimulus duration that he/she must memorize. The participant was explicitly told not to count during this stimulus duration because this would distort the scientific results (this method has been shown to successfully prevent subjects from counting; see Rattat & Droit-Volet, 2012). In the learning phase, the subject was initially presented with the 4 seconds standard stimulus duration 5 times. She/he was then given two learning blocks of 4 trials each in which two trials with the standard duration and two with other durations (0.5 and 7.5 seconds) for comparison were presented. In this learning phase, the participant had to judge if the comparison duration was or not the standard duration by pressing the corresponding ('d' or 'k' key). Each response was immediately followed by the feedback "correct" or "wrong". None of the participants required more than one or two training blocks (8 trials in total) to learn the standard duration, i.e., to exhibit 100% correct responses.

In the testing phase, the participant was told that it was the same game as during the previous (learning) phase. He/she had thus to judge for each comparison stimulus duration if it was or not the standard stimulus duration that he/she had to memorize previously, but now there was no feedback. In the testing phase, the participant completed 8 blocks of 9 trials (72 trials), i.e. 3 trials for the comparison duration identical to the standard duration (4 s) and 1 trial for each of the other comparison durations (1, 2, 3, 5, 6, 7 seconds). The trials were presented in random order within each trial block. Each trial started when the participant pressed the bar-space after the word "ready!" appeared on the screen.

As reported in introduction, there are 2 hallmarks of the consolidation for the standard duration in memory: (1) an effect seen at long-term different from that seen at short-term, and (2), a gradient in the disruption of time judgment at long term that decreased as the time interval between the learning and the interference task increased. Therefore, we examined

these two specific criteria of memory consolidation for duration in two sets of experiments. First, to examine the LTM vs. STM effect, the participants were assigned to one of 4 experimental groups: 2 groups with the testing phase given 45 minutes after the learning phase (STM test), and 2 groups with the testing phase given 24 hours after the learning phase (LTM test). For each retention condition (STM vs. LTM), one group received the 15 minutes interference task (interference) 30 minutes after the learning phase, while the other group did not receive any interference task (control). Following the interference task, during the 24 hours retention delay, the participants did not perform any specific task and simply engaged in their day-to-day activities.

In the second set of experiments, we examined whether the interference task produced a time-dependent graded effect after the initial learning phase (i.e., a control for asserting the disruption of a consolidation process). Two additional experimental groups were used with the testing phase was given 24 hours after the learning phase (LTM test). However, the 15 minutes interference task was given either immediately after the learning phase for the first group (immediate) or 1 hour after the learning phase for the second group (1 hour). This design allowed us to compare the amplitude of the disruption in the temporal judgment at long-term with an interference task given at different time points during the retention interval, at an early and later point.

Results

A long-term memory consolidation for duration different from a short-term memory for duration. Figure 1 shows the mean proportion of “yes” responses ($p(\text{yes})$) plotted against the comparison durations when the participants were tested 45 minutes (STM) or 24 hours (LTM) after the learning of the standard duration, in a condition with or without an interference task given 30 minutes after the memorization of a 4 seconds standard duration.

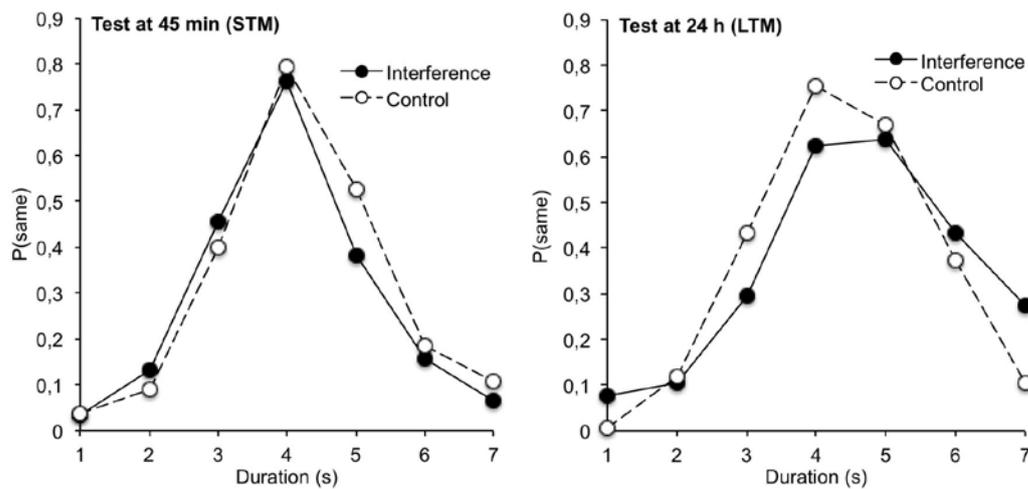


Figure 1. Proportions of ‘same’ responses (comparison duration = standard duration) plotted against comparison stimulus durations in the Short-Term and the Long-Term Memory test (45 min vs. 24 h after the learning of the standard duration), with or without interference task given 30 min after the learning.

An initial ANOVA was performed on $p(\text{yes})$ with one within-subjects factor (comparison duration) and two between-subjects factors (interference and LTM/STM test). The ANOVA1 showed a significant main effect of comparison durations ($F(6, 390) = 94.19$, $p = .0001$), as well as a significant main effect of test ($F(1, 65) = 7.18$, $p = .009$), indicating that the participants responded more often “yes” in the LTM ($M = .35$, $SD = .014$) than in the STM test ($M = .29$, $SD = .02$). However, there was a significant comparison duration \times test interaction ($F(6, 390) = 5.75$, $p = .0001$), indicating that the generalization gradients were different after a long than after a short retention interval. The main effect of comparison duration was nevertheless significant for both the LTM and the STM test condition ($F(6, 228) = 52.64$, $F(6, 162) = 50.11$, $p = .0001$, respectively), indicating that the proportion of “yes” responses differed as a function of stimulus durations in these two testing conditions. The main effect of interference was not significant ($F(1, 65) = 0.30$, $p = .59$), nor the interactions involving the interference factor (all $p > .05$). However, based on our a priori hypothesis, planned comparisons revealed a significant comparison duration \times interference interaction in the LTM test ($F(2.67, 101.56) = 2.52$, $p = .02$), but not in the STM test ($F(2.94, 79.51) = 0.75$, $p = .61$), suggesting a disruption selectively in long-term memory.

To further analyze the curves of the generalization gradients and characterize the impact of the interference on the precision and accuracy of the memory, we calculated for each individual gradient two measures: (1) the peak time, which is the stimulus duration corresponding to the highest proportion of “yes” responses, and (2) the width of the temporal

generalization gradient at half of its maximum height (full width at half maximum, FWHM) (see Cocenas-Silva, Bueno, & Droit-Volet, 2012, 2013; Hinton & Rao, 2004; Penney, Holder, & Meck, 1996). The FWHM is an index of the temporal variability, a high value indicating a high variability in time judgments. These two measures were obtained by approximating each participant's generalization gradient using the 'Log Normal (Amplitude)' function from the PeakFit program (PeakFit version 4.12 for Windows). This procedure produced best fits of temporal gradients for most of the participants (mean $R^2 = .87$, $SD = .09$). Figure 2 shows the mean peak times and FWHM obtained.

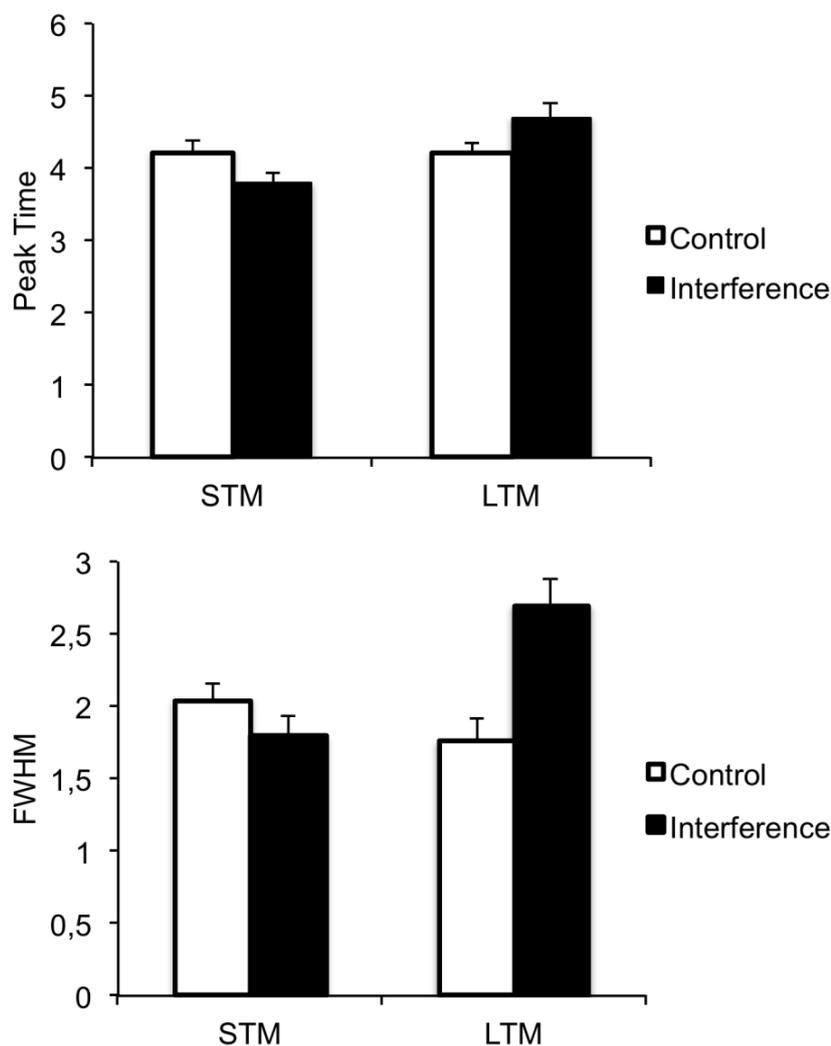


Figure 2. Mean Peak Time (A) and mean Full Widths at Half Maximum (FWHM) (B) of the generalization gradient in the Short-Term and the Long-Term Memory testing (45 min vs. 24 h after the learning of the standard duration), with or without interference task given 30 min after the learning.

The ANOVA performed on the peak time with two between-subject factors (interference, test) showed a significant main effect of test (STM vs. LTM) ($F(1, 65) = 7.26$, $p = .009$), suggesting that the generalization gradient peaked at a longer value in the LTM than in the STM testing condition (4.46 vs. 4.01). However, there was a significant test x interference interaction ($F(1, 65) = 7.58$, $p = .008$), while the main effect of interference was not significant ($F(1, 65) = 0.04$, $p = .84$). Planned comparisons based on the a priori hypothesis that the interference task will disrupt selectively the performances at LTM, and not at STM, showed that the interference task given 30 minutes after the learning phase produced a lengthening effect when memory was tested 24 hours later, with a generalization gradient peaking at a longer value relative to the control no-interference condition ($t(38) = 2.07$, $p = .045$; Figure 2A). In contrast, the interference task tended to produce a shortening effect when memory was tested shortly after the interference (STM test), as indicated by an effect which just failed to reach significance ($t(27) = -2.01$, $p = .055$).

For the FWHM, there was also a significant interaction between the test and the interference ($F(1, 65) = 13.55$, $p = .0001$) with a significant main effect of interference ($F(1, 65) = 4.46$, $p = .038$), whereas the main effect of test failed to reach significance ($F(1, 65) = 3.57$, $p = .06$). The main effect of interference indicated that the width of generalization gradient was greater with than without interference (2.24 vs. 1.9). The significant interaction revealed that the interference task given 30 min after the learning phase produced an increase in the width of generalization gradient when memory for duration was tested at 24 hours (LTM test, $t(38) = 4.04$, $p = .0001$). In contrast, the interference task had no significant impact on the width of the generalization gradient when the memory was tested shortly after (STM test, $t(27) = 1.25$, $p = .22$).

In sum, the present results revealed that the effect of the same interference task on time judgments was observed differentially as a function of the period of testing, with a disruption in long-term memory, and no, or even opposite when present, effects immediately after the interference. Consequently, our results suggest that the interference task produced a disruption of the consolidation process which stabilizes the memory into a long-term form. The disruption of consolidation both increased the variability of the representation of the standard duration stored in long-term memory, and produced a lengthening effect, such that this duration was remembered as longer than in the control condition.

Temporal gradient of the interference effect on time judgment in long-term memory. Figure 3 shows the generalization gradients obtained 24 hours after learning (LTM test) as a function of the interval between the learning phase and the interference task, when it was

given either early, i.e., immediately after the learning phase, or latter, 1 hour after the learning phase. The results from the group with the LTM test and the interference task given 30 minutes after the learning phase (see Figures 1 and 2) are also reported in Figure 3 (empty circles), for comparison only. Figure 3 reveals a temporal gradient of the impact of the interference task, with a progressive decrease in the lengthening effect when the delay between the learning phase and the interference task was increased. The ANOVA1-2 on $p(\text{yes})$ on the 2 extreme interference conditions (immediate vs. 1 hour) indicated that there was no main effect of interference ($F(1, 32) = 1.59, p = .22$), but a significant main effect of comparison durations ($F(6, 192) = 24.91, p = .0001$), and more importantly a significant interaction between the comparison durations and the interference ($F(6, 192) = 2.99, p = .008$). This latter result, indicates that the generalization gradients differed, depending on the time at which the interference task was given (immediately or 1 hour) after the learning phase.

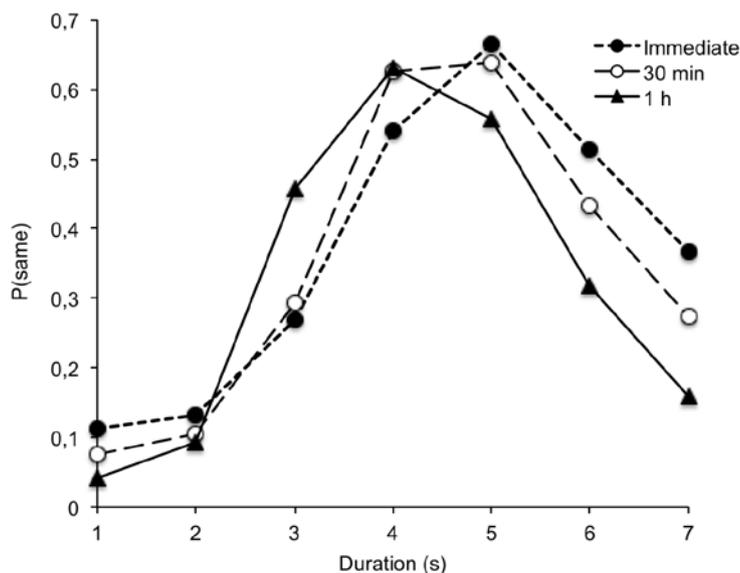


Figure 3. Proportions of ‘same’ responses plotted against comparison stimulus durations in the Long-Term Memory test with an interference task given immediately, 30 min (taken from Figure 1) or 1 h.

The analyses of the peak time (Figure 4) clearly illustrate this temporal gradient suggesting a reduction of the lengthening effect when the interference task was delayed from the learning phase. The peak time value was indeed significantly higher for the immediate interference than for the 1hour interference ($t(31) = 2.30, p = .028$). For the width of the temporal generalization gradient, the same trend was observed with a larger FWHM when the interference task was given immediately after the learning phase. This trend was, however,

not confirmed statistically as there was no significant difference between the immediate and the 1 hour interference condition ($t(31) = 1.25, p = .22$).

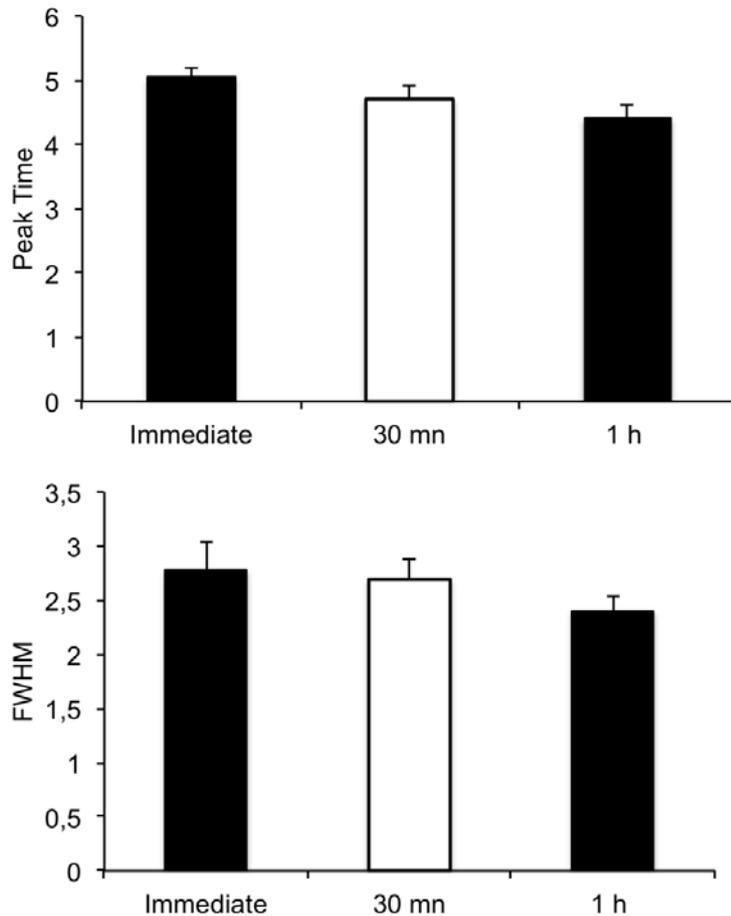


Figure 4. Mean peak Time (A) and mean Full Widths at Half Maximum (FWHM) (B) of the generalization gradient in the Long-Term Memory test with an interference task given immediately, 30 min (taken from Figure 1, in white) or 1 h after the learning of the standard duration.

Discussion

The present study investigated whether the memory of a newly learned duration undergoes a time-limited consolidation process, by testing the impact of a non-temporal interference task on the shape of the generalization gradient 24 hours after learning. Our results showed that the interference task reduced the precision of memories of the standard duration, as indicated by the flattening of the generalization gradient at the long-term memory test for the interference condition compared to the no-interference condition. Our results also showed that the interference task used in the present study produced a lengthening effect of the duration in memory as revealed by a rightward shift of the generalization gradient that peaked at longer comparison durations relative to the control (no-interference) condition.

Importantly, these effects (1) were not observed when the memory was tested immediately after the interference (STM test), and (2) progressively decreased when the interference task was delayed after the temporal learning phase (temporal gradient of the disruptive effect). These two observations fulfill the key criteria to infer a synaptic/cellular consolidation process (Dudai, 2012; McGaugh, 2000; McGaugh & Roozendaal, 2009; Schafe et al., 2001).

One of the critical elements to claim a synaptic consolidation process is the demonstration that the disruptive tool affects the trace stabilization in long-term memory, while leaving intact the memory trace at short-term. This is based on the fact that synaptic and cellular mechanisms involved in the local storage of a memory trace include several cascades of molecular events, such as the synthesis of new proteins, that take time (from minutes to hours). This has been now well described in animals for a number of memory tasks (see Agranoff, Davis, & Brink, 1965; Barondes & Cohen, 1966; Gal-Ben-Ari et al., 2012; Lechner et al., 2010). In our study, we observed this dissociation between long-term and short-term effects for memory of duration in humans. Consequently, our study is the first to describe in human observers a specific long-term consolidation process of memory traces for stimulus durations, within the hour following learning. Thus, memory of time may undergo both synaptic/cellular consolidation (the present study) and overnight consolidation processes (Lewis et al., 2011; Maquet et al., 2003).

To date, there are few studies which have examined the exact nature of temporal reference memory in a temporal generalization task and its resistance to interference effects. In addition, the few studies on this topic investigated the short-term memory rather than the long-term memory for time (Jones & Wearden, 2003, 2004; Ogden, et al., 2008, 2010; Rattat & Droit-Volet, 2010; Filippopoulos, Hallworth, Lee & Wearden, 2012). With regard to short-term memory, consistently with our data, Jones and Wearden (2004) suggested that the manipulation at short-term of the reference memory has minor effect on the temporal generalization judgment. However, Rattat and Droit-Volet (2010) found an immediate disruption of memory of duration by the insertion of a non-temporal interference task shortly after learning. It is possible that the different tasks used as interference tools (a parlor game in Rattat and Droit-Volet (2010); backward digit recall in the present study) may have tackled different memory brain systems. Indeed, data suggest that interference mechanisms may have different temporal dynamics, which may in part be related to the memory systems involved (Been, Jans, & De Weerd, 2011; Robertson, 2012). The temporal studies using interference tasks during the encoding of time in a dual-task paradigm showed that the interference tasks systematically affected the time processing when they required cognitive resources (for a

recent book on this topic see Nobre & Coull, 2011). Indeed, as suggested by the attentional models of timing (Thomas & Weaver, 1975; Zakay & Block, 1996, 1998), the processing of temporal information and that of non-temporal information compete for the same pool of attentional resources. Although this account cannot be applied to our present situation, as the interference is given after and not during the online encoding phase, it may suggest that both procedures unravel competing processes in shared neural networks. Interestingly, the analyses of bidirectional interference effects on the temporal and non-temporal performance in dual-task situations suggested that the interference effect on time judgment was more important for the visuo-spatial than for the auditory information (e.g., Brown, 2006; Rattat, 2010). It would thus be important to examine in future studies the variation of interference effects on the dynamic of memory consolidation processes for duration as a function of the type of interference task. Nevertheless, Rattat and Droit-Volet (2010) found that the impact on peak time when the interference was given immediately after learning and tested shortly after was a shortening effect. This effect was similar to the shortening effect that tended to be observed in our experiment in the STM test condition with the interference task given 30-45 minutes after learning. However, this shortening effect obtained in the STM testing conditions was opposite to the lengthening effect found in the LTM test, i.e., 24 hours after the initial learning. These opposite (shortening and lengthening) effects may be related to different memory systems that are disrupted by the interference task, i.e. a shortening when the short-term memory is affected, and a lengthening when the consolidation process is affected. Thus, with regard to memory for duration, the sparse studies so far open the intriguing possibilities that different mechanisms may be at play during the stabilization of memory into a long-term form, and call for more investigations.

In the present study, we observed a lengthening effect in the time judgments when memory was tested 24 hours after the temporal learning, and the disruption effect followed a gradient consistent with the time-limited consolidation process. This suggests that the participants remembered the standard duration longer than it really was, consistently with a distortion of the representation of time in reference memory (see Wearden & Jones, 2013). The question is how to explain this lengthening effect which suggests that duration has expanded in long-term memory? According to the information processing model of the scalar timing theory (Gibbon, 1977; Gibbon & Church, 1984; Gibbon et al., 1984), three processing modules are involved in the judgment of time: clock, memory and decisional. The clock module consists of a pacemaker that emits pulses that are gated by a controllable mode switch into an accumulator. The reference memory module stores relevant time intervals in long-term

memory in the form of a distribution of values with a mean and coefficient of variation. The decision module compares the current time in the accumulator with a remembered time that is sampled from the reference memory. If the difference between the current accumulator value and the value of the sample from memory is close enough, the judgment 'yes' is made. This model proposed therefore an "exemplar memory" that contains separate representation for each past example (Church, Guilhardi, Keen, MacInnis & Kirkpatrick, 2003). In this way, one can assume that each stimulus duration presented in the learning phase, even the non-relevant stimulus durations (i.e., 0.5 and 7.5 seconds) were encoded and stored in memory. A mixing in memory of different durations could thus occur when the memory representation of durations presented in the learning phase becomes fuzzier. In other words, there would be some sort of confusion between the standard duration and the other stimulus durations (especially the longer one) presented during the learning phase. This is consistent with the results of previous studies showing that the content of the reference memory for a standard duration was influenced by the other durations presented at the same time (Odgen et al., 2008; Odgen & Jones, 2009; Penney, Gibbon & Meck, 2000). Another hypothesis may be that this lengthening effect would arise from decision processes. However this hypothesis is difficult to reconcile with the temporal gradient observed in the interference effects, which would then imply that the decision processes would change with the increase of the time between the learning phase and the interference task. An interpretation in terms of mixing in memory the representation of durations that the subject has been exposed to is therefore more likely to account for the lengthening effect observed here.

Our results also showed that the interference task produced a flattening of the generalization gradient. This is in agreement with the leading scalar timing theory (Gibbon, 1977; Gibbon & Church, 1984; Gibbon et al., 1984) for which the main source of variances in temporal judgments results from storage mechanisms of time intervals in long-term memory. An increased variability in remembered duration due to tasks interference has been reported previously (Rattat & Droit-Volet, 2001; 2005; 2010). Modeling their data, Rattat and Droit-Volet (2010) suggested that the major cause of this flatter generalization pattern was due to the coefficient of variation of the representation of the standard duration in reference memory, which was greater with than without interference. Thus, the variability of the representation of the standard duration is more important in long-term memory than in short-term memory when the memory consolidation process is disrupted by an interference task. However, in the present study, although the flattened generalization gradient was observed with the LTM and not the STM testing demonstrating a consolidation process, no significant time-limited

window was observed within 1 hour after the learning phase (in contrast to the temporal gradient observed for the lengthening effect). It is likely that an increased variability may be a more sensitive measure of altered long-term memory. Thus, the memory for duration may have required more than one hour to be consolidated and stabilized. In summary, we can assume that, in our study, the interference task has disrupted the consolidation over time of the representation of the standard duration in long-term memory, thus making the duration remembered longer and with less precision.

In conclusion, using a methodology derived from animal studies, we have specifically asked whether memory for duration in humans undergoes a consolidation process similar to the synaptic/cellular consolidation mechanisms (e.g. depending upon protein syntheses) observed in other types of memory in animals (Dudai, 2012; Schafe et al., 2001; Alberini et al., 2006; Gal-Ben-Ari et al., 2012). Our study showing time-limited lability of the memory trace and specific impact on long-term memory (in contrast to short-term memory) demonstrates that it is the case. Noticeably, the effect was obtained with an interference task that was not using temporal information. Nevertheless, it has been shown that interferences may be observed when the processing of both tasks share common neural mechanisms within the same neural network (Cohen & Robertson, 2011; Robertson, 2012). In particular, research in animals has shown that a common neural mechanism in the medial prefrontal cortex is involved in memory consolidation of an inhibitory avoidance task and working memory (Barsegyan Mackenzieb, Kuroseb, McGaughb & Roozendaala, 2010). As prefrontal networks have been also involved in temporal processing (see for a recent review Coull, Cheng & Meck, 2010), it is quite possible that the non-temporal working memory interference task we have chosen may have disrupted prefrontal mechanisms when they were required during the consolidation process. Further investigations are needed to search more precisely for the mechanisms and neural networks subserving the long-term memory of time by testing different interference tasks.

FOOTNOTES

1. When Mauchly's sphericity test indicated that the assumption of sphericity had been violated for stimulus duration, the degrees of freedom were adjusted using the Greenhouse-Geisser correction, in order to take this violation into account in the statistical analysis.
2. One participant in the "Immediate interference/test at 24 h" group was excluded from the results because, unlike the other participants, he produced a generalization gradient that was flat.

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CHAPTER 3

Emotion and long-term memory for duration: Resistance against interference

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Abstract

The aim of this study was to examine the effect of emotion on the long-term memory for duration. On day 1, participants learned a temporal task in a high-arousing or neutral control condition that was followed by a 15-min interference task. Then, 24 h later, on day 2, they were given a recall test. In this recall test, they judged whether or not comparison durations were similar to the previously learned standard duration. The results showed that temporal discrimination was more accurate in the emotional than in the neutral condition. Emotion thus strengthened memory traces of time by increasing their resistance against interference effects.

Keywords: Time, Memory, Emotion, Memory consolidation

Introduction

Studies of long-term memory conducted in animals and humans have shown that a new memory of a stimulus or an event is fragile and needs time to become stabilized in long-term memory (Dudai, 2004; Lechner et al., 1999; McGaugh, 2000). During 24 a period after encoding, called consolidation, the memory traces of newly acquired information are therefore susceptible to disruption by interference before becoming fixed in memory. Indeed, there is extensive evidence that, during this period of fragility of memory traces, the injection of drugs that block hippocampus dependent protein synthesis or the introduction of interference tasks impair long-term memory retrieval (e.g., Been et al., 2011; Hatfield & McGaugh, 1999; McIntyre et al., 2012; Robertson, 2012). These interference effects decrease as consolidation progresses and the memory traces become more robust and stable. There are various types of evidence indicating that emotion also plays an important role in memory by facilitating memory consolidation (e.g., Buchanan & Lovallo, 2001; Cahil et al., 2003; Kensinger, 2007; LaBar & Cabeza, 2006; LaBar & Phelps, 1998). As explained by McIntyre et al. (2012), in the context of a highly adaptive function, emotional arousal ensures that significant signals are stored effectively in long-term memory and consequently enables the organism to react appropriately in the future. In threatening situations, emotion results in the release of stress hormones (adrenaline and glucocorticoids) that, through actions involving the noradrenergic activity in the amygdala, facilitate protein synthesis in the hippocampus and persistent changes in synaptic connectivity (Roosendaal et al., 2009; McGaugh, 2002). Stress or emotionally arousing events therefore transform transient plasticity into long lasting synaptic plasticity. In sum, the effect of emotion on brain plasticity enhances the long-term retention of information and increases its resistance against interference effects.

To date, few studies have examined the impact of interference tasks on the long-term retention of duration in human adults and, even less so, on the effect of emotion on this phenomenon. Indeed, studies investigating interference effects on temporal reference memory have focused on the short-term retention of neutral stimuli (e.g., Neath & Fortin, 2005; Jones & Wearden, 2003, 2004; Ogden & Jones, 2009; Ogden et al., 2008, 2010; Rattat & Droit-Volet, 2010). Most of these studies have used a temporal generalization paradigm in which the participants judge the similarity between the memory representation of a standard duration and comparison durations (shorter, longer or equal to the standard duration) and have introduced interference between the presentation of the standard duration and the comparison

durations. In these conditions, the experimental manipulation of temporal reference memory has been found to have little influence on temporal generalization judgments (Jones & Wearden, 2004; Rattat & Droit-Volet, 2010). Nevertheless, temporal judgments appear to be more variable when interference is present than when it is not, with the generalization gradient (i.e., proportion of same responses plotted against comparison durations) being flatter. In addition, although not systematic found, the generalization gradients often tend to peak toward the left (Ogden et al., 2008; Rattat and Droit-Volet, 2010). This finding is consistent with a shortening effect and suggests that the standard duration is judged shorter with than without an interference task. This shortening effect, which has been observed in both animals and humans when a second stimulus duration in short-term memory has been compared with a first stimulus duration, has been explained in terms of a loss of temporal information during the rehearsal of this information in working memory (e.g., Droit-Volet et al., 2007; Spetch & Wilkie, 1983; Spetch & Grant, 1993; Wearden & Ferrara, 1993; Wearden et al., 2002).

The aim of the present study was therefore to use a temporal generalization task to investigate the effect on temporal judgments of an interference task administered immediately after the learning of a standard duration when the retention interval was not short but long, i.e., greater than 24 h at a point where memory consolidation was already well advanced. In addition, we wanted to find out whether the learning of the standard duration would be more resistant to interference when it had been learned in an emotional condition than in a neutral condition. To date, only one study run by Cocenas-Silva et al. (2012) has used a temporal generalization task (without an interference task) to test whether the long-term retention of the standard duration is better when it has been learned in an emotional context. In this emotional context, the participants expected a threatening stimulus after each standard duration. This stimulus, which took the form of an aversive sound, has been demonstrated to be highly arousing and to produce the emotion of fear (see Droit-Volet et al., 2010). In line with the results of studies of emotion, the results suggested that the standard duration was remembered better when it was learned in this emotional context. The authors therefore concluded that the emotional stress reactions induced by the aversive signal facilitated the consolidation of the standard duration in memory and its long-term retrieval. To further test this hypothesis in the present study, we used the emotional conditions previously employed by Cocenas-Silva et al. (2012) in our generalization task. However, we introduced an interference task after the learning of the standard duration, using a task that is known to load the working memory (Baddeley & Hitch, 1974). We expected that the temporal representation of the standard

duration would be more resistant to the effects of the interference task administered during the period of memory consolidation if this duration had been learned in a context of emotional arousal.

Methods

Participants

Thirty undergraduate students (mean age = 20.23, SD = 1.52, 118 21 women, 9 men) from the first year of psychology at Blaise Pascal University in Clermont-Ferrand, France, participated in this experiment in return for one course credit for a single class in cognitive psychology.

Materials

The participants were tested individually in a soundproofed room where they were seated 50 cm in front of a PC screen. The E-prime program (1.2. Psychology Software Tools, Pittsburg, PA) controlled the experiment and recorded the data. The stimuli to be timed always took the form of a blue circle (2.5 cm in diameter) presented in the center of the computer screen. The participants gave their responses by pressing two keys (“d” for same and “k” for different) on the computer keyboard and the button-press order was counterbalanced across subjects. The emotion-inducing stimulus was an aversive acoustic signal consisting of a 50-milliseconds burst of 95-dB white noise with an instantaneous rise time that is known to produce a startle reflex (Hillman et al., 2005). Some studies that have used both physiological indexes (skin conductance responses) and self-assessment on the 9-point Self-Assessment Manikin scale (SAM; Lang, 1980) have demonstrated that the expectation of this aversive stimulus is judged as unpleasant and increases the arousal level (see Droit-Volet et al., 2010). In the present study, the participants in the emotion group were also presented with this aversive stimulus for its assessment on the SAM scale at the end of the session, and rated it as unpleasant (negative valence) with a mean of 2.13 (SD = 0.8) and highly arousing with a mean of 7.0 (SD = 1.59). In the emotional condition, the aversive signal was delivered binaurally via calibrated headphones after presentation of the stimulus duration in all the trials in the learning phase (i.e., 5 trials for the standard duration presentation and 16 trials for the training blocks). The aversive signal was not delivered during the recall test. In the control condition, no acoustic signal was presented after the stimulus duration in either the learning or the test phase. The interference task was a backward digit task, which calls on the central executive functions of working memory (Baddeley & Hitch, 1974). In this task, the participants were presented with a sequence of

digits that they had to recall immediately in reverse order. The number of digits per sequence increased progressively from 2 to 8 (i.e., 7 sequences), with two trials per sequence. There were a total of 14 trials and the participants were repeatedly given these 14 trials (with new sequences of digits) for a period of 15 minutes.

Procedure

In the present study, on the first day, the participants learned the temporal task (learning phase) with or without the aversive stimulus (emotion versus control condition) followed by a 15 minutes task to create interference, and 24 hours later, they received a recall test (recall test). In the learning, the participants were presented with the 4 seconds standard duration five times. They were told to memorize the duration of this stimulus. They were then given at least two learning blocks of 4 trials each: two for the standard duration and two for the comparison durations (0.5 and 7.5 seconds). The participants had to judge whether the comparison duration was the same as or different from the standard duration by pressing the corresponding button. Each response was followed by the feedback “correct” or “wrong”. None of the participants required more than one or two training blocks (8 trials in total) to learn the standard duration, i.e., to obtain 100% correct responses. Immediately after the learning phase, the participants were given the 15 minutes interference task. Then, exactly 24 hours later (e.g., at 8:00 AM on days 1 and 2), they were given the recall test. During the 24 hours retention interval, the participants did not perform any specific task and simply went about their day-to-day activities. In the recall test, the participants were told that they were to play the same game they had played the day before. They therefore had to judge whether each comparison stimulus duration was the same as or different from the standard stimulus duration which they had seen the day before. However, during this phase, they did not receive any feedback or acoustic signal. In the recall test, the participants were not presented with the standard duration and directly completed 8 blocks of 9 trials each (72 trials), i.e., 3 trials for the comparison duration equal to the standard duration (4 seconds) and 1 trial for each of the other comparison durations (1, 2, 3, 5, 6, 7 seconds). The trials were presented in random order within each trial block. Each trial started when the participant pressed the spacebar after the word “ready!”

In addition, each participant was assigned to one of two experimental groups as a function of learning conditions with or without the aversive stimuli (emotion versus control). In the emotion group, the stimulus duration was followed (after a 50 milliseconds interval) by the aversive acoustic stimulus on every trial in the learning phase. In the control group, no signal was delivered during this learning phase. Furthermore, consistently with the findings of

Rattat and Droit-Volet's (2012) study, which demonstrated that the no counting instructions used in numerous timing studies is an efficient method of preventing subjects from using counting strategies, the participants were explicitly told not to count, and the experimenter added that if they did count, the scientific results would be distorted.

Results

Figure 1 shows the mean proportions of "same" responses (p (same)) plotted against the comparison durations for the emotion and the control groups. The temporal generalization gradient appeared to peak at the standard duration for the emotion group. In contrast, in the control condition, the temporal generalization gradient was not only flatter than that of the emotion group but was also shifted toward the right. This suggests that there was a distortion in the memory representation of the standard duration which is consistent with a lengthening effect. Figure 1 thus suggests that the representation of the standard duration in long-term memory was more accurate when it was encoded in the emotional condition than in the neutral condition and was consequently more resistant to the effects of the interference task on the memory retention.

Statistical analyses confirm this interpretation. An initial ANOVA was run on p (same) with the comparison durations as within subjects factor, and the groups (emotion versus control) as between-subjects factor. This ANOVA revealed no significant effect of emotion, $F(1, 28) = 0.98$, $p = .33$. However, there was a significant main effect of comparison durations, $F(6, 168) = 29.23$, $p = .0001$, and a significant interaction between comparison durations and emotion, $F(6, 168) = 5.73$, $p = .0001$. This indicates that the generalization gradients obtained in the test phase differed as a function of the conditions in which the standard duration was learned.

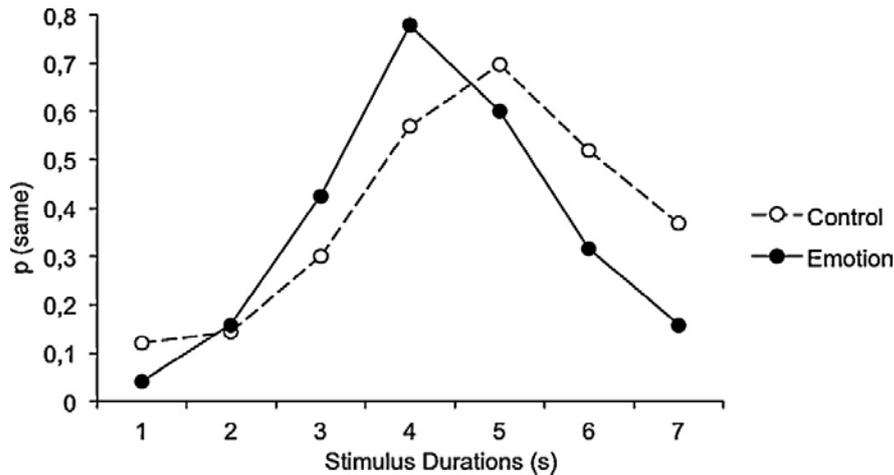


Figure 1. Proportion of same responses plotted against stimulus duration (s) in the recall test, when the standard duration has been learned one day before, in the emotion and the control condition.

To further examine the shape of the generalization gradients as a function of emotion condition, we calculated two measures for each participant's generalization gradient: (1) the peak and (2) the width of the generalization gradient. The peak is the comparison duration that gives rise to the highest proportion of "same" responses. The width is an index of the variability in temporal judgments, i.e., of the sensitivity to time (Cocenas-Silva et al., 2012; Hinton & Rao, 2004; Penney et al., 1996). In the present study, we calculated the width at half of the maximum height (i.e., full width at half maximum, FWHM). These two measures were obtained by approximating each participant's temporal gradient with the "Log Normal (Amplitude)" function from the PeakFit program (PeakFit version of 4.12 for Windows). The logarithmic function produced the best fit of temporal gradients for the participants (mean $R^2 = .88$, $SD = .06$). Figure 2 presents the mean peak and mean FWHM values obtained in this way. The t-test for independent samples showed that the peak time was significantly shorter, and closer to the standard duration value, for the emotion group than for the control group (4.01 versus 5.17, $t(26) = 4.10$, $p = .0001$). This suggests that the memory distortion of the standard duration was smaller in the emotion group than in the control group. Similarly, the fact that the FWHM value was significantly lower for the emotion than for the control group ($t(26) = 3.20$, $252 p = .004$) indicates that sensitivity to time was higher when the standard duration was learned in the emotional condition than in the neutral condition.

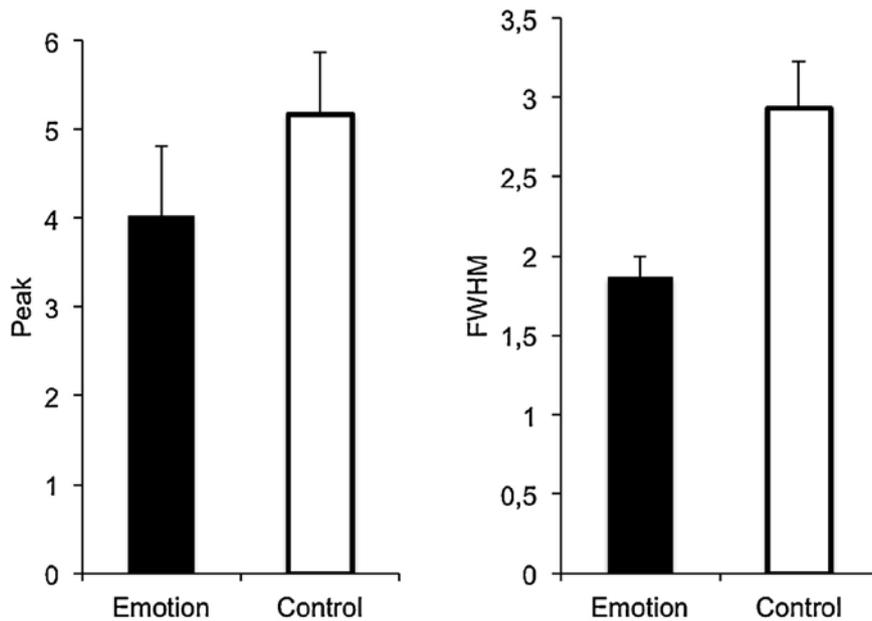


Figure 2. Means and standard errors for the peak value and FWHM (full width at half maximum) of individual generalization gradients in the recall test when the standard duration has been learned one day before, in the emotion and the control condition.

Discussion

In the present study, which used a generalization task, we tested whether memory traces of a standard duration learned in an emotional condition were more resistant to interference effects during the memory consolidation period. Our results showed that, after a retention interval of 24 hours and an interference task administered after temporal learning, the generalization gradient was steeper and peaked at a value closer to the standard duration when the standard duration had been learned in the highly arousing condition than in the neutral condition. In other words, the duration was recalled better after an extended interval when it had been experienced in an emotional rather than in a neutral context, thus suggesting a greater resistance to interference effects.

The results of the present study are consistent with those previously obtained by Cocenas-Silva et al. (2012) in a temporal generalization task without any interference task between the learning and test phases. This earlier study had shown that emotional contexts improve the memorization of durations. Our data thus provided additional data suggesting that emotion improves the long-term retention of the temporal properties of events in the same way as has been demonstrated for the temporal order (D'Argembeau & Van der Linden,

2005) or other non-temporal properties of events (e.g., Dunbar & Lishman, 1984; LaBar & Phelps, 1998; Phelps, 2004). However, they also showed that the memory retention of duration experienced in a high-arousing context was less impaired by an interference task given immediately after the temporal learning. Numerous studies have showed that interfering tasks disrupt memory consolidation when administered post-training, i.e., when memory traces are unstable (Robertson, 2012; Robertson et al., 2004). It has also been shown that emotional arousal enhances the stabilization of memory traces (McIntyre et al., 2012; Roozendaal et al., 2009). Indeed, as suggested in the Introduction, aversive experiences result in the release of adrenaline and glucocorticoids from the adrenal glands. These stress hormones stimulate the release of noradrenaline in the amygdala. This interacts with the hippocampus and facilitates the protein synthesis that potentiates the synapses. The results of our study showing the better resistance in memory of durations learned in a highly arousing context are therefore consistent with studies suggesting that emotion enhances the long-lasting plasticity of the brain by improving memory consolidation.

However, it is also possible that the participants paid more attention to the processing of time in the emotional than in the neutral condition, with the result that time was encoded better and the memory traces strengthened. Indeed, arousing stimuli are more likely to attract focused attention (Mather, 2007; Sharot & Phelps, 2004; Vuilleumier, 2005). However, in our study, we took the methodological precaution of using a training phase with several trials to ensure that the standard duration was acquired equally well in both the emotional and the neutral conditions. In addition, Cocenas-Silva et al. (2012) found that the generalization gradients were no better in the emotional condition than in the neutral condition when testing took place immediately after the learning of the standard duration. Our results concerning the resistance of time judgments to the effects of the post-training interference task therefore suggest that emotion felt during the learning of the standard duration accelerates its consolidation in memory. However, attention and memory consolidation processes might combine to contribute to the improvement in the long-term retention of duration in the presence of emotion. It also possible that the stress had prompted participants to more often use counting strategies in the emotional condition than in the neutral condition, despite the instructions given by the experimenter not to count because this may distort the scientific

results. This was nevertheless unlikely, as indicated the shape of the generalization gradients found in this emotional condition that clearly differ from the steeper generalization gradients obtained when the participants count time (for a comparison with or without counting strategy in the generalization task see Rattat & Droit-Volet, 2012, Figure 1, p. 70). In addition, Rattat and Droit-Volet (2012) have demonstrated that the non-counting instruction is a simple method as efficient as the other methods of preventing counting (articulatory suppression, dual-counting task), e.g. producing no violation of the fundamental scalar properties, a violation characteristic of performance when counting is used.

The results of the present study also showed that, in the neutral condition, an interference task administered immediately after the newly acquired standard duration impaired temporal judgment, thus flattening the generalization gradient and shifting its peak toward the right (i.e., a lengthening effect). These findings are to some extent consistent with the results of temporal generalization studies that have shown an increase in the variability of time judgments when there is interference between the learning and test phases (e.g., Ogden et al., 2008, 2010; Rattat & Droit-Volet, 2010). However, in these studies, the peak of the generalization gradient more often tended to shift toward the left (shortening effect) rather than toward the right. However, these studies did not use a long-term but a short-term retention interval between the learning and the test phase and this type of shorter interval has only a minor effect on temporal reference memory (Jones & Wearden, 2004). Finally, the lengthening effect observed in our study may be linked to a greater degradation of the representation of the standard duration in long-term memory. If this is indeed the case, then we can assume that the temporal degradation produced by the retroactive interference task made the long-term memory representation of the standard duration fuzzier. Consequently, confusion might have occurred in memory between the representation of the standard duration (4 seconds) and that of the comparison durations presented during the learning phase. It is nevertheless also possible that this confusion was greater for the long (7.5 seconds) than for the short comparison duration (0.5 seconds). However, further studies must now be conducted in order to investigate this temporal lengthening effect in the case of the forgetting in long-term memory for duration.

In conclusion, our results show that emotion enhances the long-term retention of stimulus durations, or at least when participants are required to make explicit time judgments. One current debate focuses on the mechanisms underlying the effect of emotion (negative-high arousing) on the perception of time (for a recent review, see Droit-Volet, in press). Some researchers have suggested that emotions increase the arousal level which, in turn, speeds up the internal clock (e.g., Bar-Haim et al., 2010; Droit-Volet & Meck, 2007; Droit-Volet et al., 2004; Gil & Droit-Volet, 2012; Tipples, 2011; Mella et al., 2010). Other researchers have suggested that emotion increases the amount of attention allocated to the processing of time (Lui et al., 2011; Meck & Macdonald, 2007; Smith et al., 2011). However, at a behavioral level, it is very difficult to distinguish between these two closely interrelated processes (attention and arousal) (see Paus, 2000; Robertson & Garavan, 2004). Indeed, in threatening situations, the organism mobilizes attentional resources to detect forthcoming stimuli (vigilant attention system) (e.g., Ledoux, 1996, 2012; Vuilleumier et al., 2003). However, this state of alarm triggers an array of changes in the autonomic (cardiovascular, respiratory) and somatic (facial and bodily motor expression) nervous systems that help prepare the organism to act as quickly as possible, i.e., to fight or to flee (Cannon, 1929). Anyway, whatever the mechanisms underlying the emotional effect obtained, our study provided additional data showing an improvement in the memorization of the duration of significant events when they were learned under highly arousing conditions.

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6 GENERAL DISCUSSION

This thesis investigated the facilitators and interfering factors on time consolidation in long-term memory, using acoustic signal, which induced emotional responses and non-temporal interference task. The results showed that emotion facilitates time consolidation and are resistant to the disruptive impact of interference on time consolidation in the long-term memory. The results of both one and two experiments showed that the time consolidation, in long-term memory, is affected by facilitators and interfering factors. Aversive signal, that evoked emotional arousal responses, improves the retention of standard duration in long-term memory; instead, the interference task, immediately after learning, disrupts time consolidation. Thus, the third experiment of this thesis was conducted to examine the effect of interaction between the facilitator and interfering factors on time retention in long-term memory. It was investigated the long-term memory durations learned in arousing condition followed by an immediate interference task. Results pointed out that, when the standard duration was learned under effect of emotion, even being applied an immediate interference task, the temporal judgments were accurate after 24 hours of learning. This data brings a new perspective leading to the conclusion that emotion is resistant against interference.

The findings of experiment one allow the conclusion that time is better consolidate in long-term memory when temporal information was encoded in an emotional than in neutral condition. It was observed through the temporal generalization task, that emotion, more specifically the arousing emotions at the encoding of the standard duration, had a significant role to facilitate the time consolidation in the long-term memory. It was found that, when participants learned standard duration under effect of the aversive signal, the temporal judgments were more accurate and less variable 24 hours than those in which no arousing responses was evoked. This result converges with studies on memory consolidation literature, which have been showed the positive effects of emotion on memory consolidation for different types of researches (Buchanan & Lovallo, 2001; Cahil, Gorski & Le, 2003; Kensinger, 2007; LaBar & Phelps, 1998).

One of the goals of this thesis was to examine the effect of arousal, not only in the time encoding, but also in time consolidation. Thus, to investigate the different memory processes related to temporal processing, i.e., acquisition, consolidation and recall, it was used two retention intervals (immediate and 24 hours) between the learning phase and the

comparison test in the temporal generalization task. It was found more accurate temporal judgments when participants were tested 24 hours after encoding than immediately after that.

The results provide support for a relevant effect of emotion on consolidation process rather than an encoding related hypothesis. No significant difference was observed in temporal discrimination as an aversive signal effect function in the immediate test phase, as well as during the learning phase, but mainly in consolidation (24 hours test). The results lead to the conclusion that arousing emotion has a robust effect at encoding, and increasing time, the arousing emotions improve the storage of temporal event in long-term memory enabling an accurate recall.

The seminal findings of Kleinsmith and Kaplan (1963) which conducted behavioral studies in healthy adults showed that information with arousing content have some advantages in memory retention with increasing time. LaBar and Phelps (1998) and Sharot and Phelps (2004) found that retention is greater for words with high arousal levels compared to neutral words, when memory is tested after a long time period, intervals of 1-24 hours compared with short intervals, immediate testing. Such observations provide evidence that arousal benefits memory in part by facilitating consolidation processes, which take time to emerge (LaBar & Cabeza, 2006). These findings converge with the results of this thesis. The retention of standard duration was greater to healthy adults who learned in an aversive condition than those which learned in a neutral condition. Furthermore, the long-term temporal judgment was more accurate after 24 hours retention delay between the learning of standard duration and comparison test, rather than those for short-term temporal judgments (comparison test performed immediately after learning).

The fact that events with high arousal level produce effects on the initial encoding process and result a more effective consolidation, may be interpreted as a reflection of attentional influences on memory mechanisms. Attention focusing ensures that emotionally salient features of complex events are preferentially retained in memory, providing evolutionary advantages (LaBar & Cabeza, 2006). The results of experiment one, showed that temporal generalization gradients for the learning phase were precise when participants learned the standard duration under effect of the threatening condition. It may assume that the emotional response, evoked by the aversive signal activated attentional sources, leading participants to pay more attention in time and thus standard duration was correctly stored in reference memory. The temporal generalization gradients of 24 hours delayed test were also precise, confirming that high arousal level produced effects on the initial encoding time a more effective time consolidation.

However, the data about the effect of high arousal level on time perception have showed that time is judged as longer in emotional condition (Angrilli, Cherubini, Pavese, & Manfredini, 1997; Droit-Volet, Brunot, & Niedenthal, 2004; Droit-Volet, Fayolle, & Gil, 2011; Droit-Volet et al., 2010; Falk & Bindra, 1954; Grommet, Droit-Volet, Gil, Hemmes, Baker & Brown, 2010; Stetson, Fiesta, & Eagleman, 2007). According to Droit-Volet and Gil (2009), the lengthening effect occurs due to the internal clock that speeds up with the increase of arousal. Nevertheless, some findings showed overestimation of the 2 seconds duration of fearful faces (Bar-Haim, Kerem, Lamy & Zakay, 2010) and 2 seconds exposure of negative high-arousal picture (Angrilli et al., 1997), but did not occur for longer exposures of the same stimuli (6 or 8 seconds). As these authors explained, arousal mechanisms may lead us on a way to other mechanisms (attention or decision based) over time (Droit-Volet, in press). In this way, the results of experiment one, in which was found accurate long-term temporal judgments of 4 seconds, could also be interpreted through this explanation. The arousal evoked by the aversive signal in the learning of standard duration should give way to attention on the 24 hours test.

The studies on the retention time in memory have been investigated the interference impacts on short-term memory (Jones & Wearden, 2004; Ogden, Weaden & Jones, 2008, 2010; Rattat & Droit-Volet, 2010; Filippopoulos, et al., 2012). No studies were conducted to investigate the effect of interference on time consolidation and retention in long-term memory. It is therefore not know the time course, in which the impact of interference decreases the disruption on consolidation process. Thus, in the experiment two, these questions were investigated. The temporal generalization gradients showed that interference task disrupt the processes of time retention. The temporal judgments after 24 hours of interference task were not accurate, but instead, they were recalled longer than really were. These effects were not observed to short- term memory (immediate test) and decreased with time course of consolidation. Results can be explained according to the synaptic/cellular consolidation, which affects long- term memory but preserves short-term memory, once the synthesis of new proteins take time. This hypothesis have been examined with animals using memory tasks (Agranoff, Davis, & Brink, 1965; Barondes & Cohen, 1966; Gal-Ben-Ari et al., 2012; Lechner, Squire & Byrne, 2010; Michel, Green, Gardner, Organ & Lyons, 2012).

Regarding yet the effect of interference task on the different memory processes, the results showed an opposite effect in short and long-term memory when an immediate interference task was applied after learning. The short-term memory was tested when the interference was given 30-45 min after learning; the judgments of temporal memory were

shortened. Nevertheless a lengthening effect was found to the temporal gradients when interference was applied immediately and memory tested 24 hours after. Data from experiment two converges with Rattat and Droit-Volet (2010) which found also a shortening effect, when the interference was given immediately after learning and tested shortly after.

The data in this thesis has provided additional data to memory consolidation field, once it expands the investigation of the effects of interference task in long-term memory for time. The results showed that immediate interference task has a disruptive effect in long-term memory for time. Participants recalled the standard duration longer than it really was. However, this lengthening effect tends to disappear when the interval time between learning and interference increase. According to internal clock model, (Gibbon, 1977; Gibbon & Church, 1984; Gibbon et al., 1984) the reference memory module stores relevant time intervals in long-term memory. Thus, the immediate interference may disrupt the modulation function of reference memory impairing the storage of time in short-term memory. However, increasing the interval time between the learning and interference task in one hour, this disruptive effect of interference disappears.

The interference task also produced a flattening of the temporal generalization gradients. This effect may be explained, due to the variability of the representation of the standard duration in reference memory (Rattat & Droit-Volet, 2010; Wearden & Jones, 2013). This variability is greater under effect of interference (Rattat & Droit-Volet, 2001, 2010) and thus, the retention impairment is more important in long-term memory than in short-term memory, as observed in the present study. However, the interference applied one hour after learning, it produced a decrease in the variability of the representation of the standard duration in reference memory, showing that the memory for duration may have required minimum one hour to be stabilized and consolidated in long-term memory.

The results of experiments, one and two, therefore, showed that time consolidation in long-term memory is affect by facilitators and interfering factors. Thus, the third experiment of this thesis was conducted to examine the interaction effect between the facilitator and interfering factors on time consolidation in long-term memory. It was tested whether memory traces of a standard duration learned in an emotional condition were more resistant to interference effects during the memory consolidation period. The findings showed that interference did not affect the retention of standard duration in long-term memory when participants encoded the duration in an emotional condition. This result converges with those reported in experiment, one of this thesis, but without interference task.

It has long been known that emotionally arousing events are more likely to be later recollected than similar neutral events. This occurs because emotional reaction, such as arousal and the release of stress hormones follows the event itself. In this way, events that elicit emotional responses, which are likely to be more important for survival, are also more likely to be remembered later. The enhanced memory capability observed for emotional events is due to the amygdala's influence over the encoding and storage of hippocampal-dependent memories (Phelps, 2004). The amygdala plays a crucial part at the memory encoding once facilitates the attention with emotions to create the initial memory representation.

The expectation of the aversive signal followed by the standard duration in the temporal learning activated the amygdala and consequently the attention was directed to standard duration. In this way, the initial memory representation of duration was formed correctly and thus the memory retention of duration was less impaired by an interference task given immediately after the temporal learning. Nevertheless, this finding was not found for participants who learned the standard duration without effect of emotion. Their long-term temporal judgments were less precise and it may assume that less attention was directed to time. The disruptive effect of interference disturbs the time consolidation in long-term memory.

The long-term temporal judgments of standard duration, encoded under effect of emotion may be also explained by post-encoding processes. According to Hamann (2001), after the event, post-encoding processes continue to influence the memory representation. The most important of these post-encoding processes is consolidation, a period of time in which new memories are fragile and prone to disruption. The consolidation process is widely thought to require an extended period to complete, thus, the observed effects of emotion on memory should increase with time, as the gradual process of consolidation proceeds. However, the interference task impaired the post-encoding process for participants which learned the standard duration in a neutral condition. The temporal gradients of these participants were flattened and shifted to the right demonstrating a lengthening effect of long-term temporal judgments. The lengthening effect may be explained due the greater degradation of the representation of the standard duration in long-term memory. It may assume that the temporal degradation, produced by the retroactive interference, task made the long-term memory representation of the standard duration fuzzier.

This thesis allows the conclusion that arousing emotions facilitate time retention in long-term memory while interference task disrupt time consolidation. Nevertheless, the robust

effect of emotion was prevalent and resistant to the effect of interference in long-term memory for time. This benefit of emotion for time in long-term memory make sense within an evolutionary framework once a primary function of emotion is to guide action and to plan for similar future occurrences (Lazarus, 1991). As discuss by Kesinger (2007) it is logical that attention would be focused on potentially threatening information and that memory mechanisms would ensure that details predictive of affective event relevance would be encoded precisely. Therefore, the standard duration which was learned in an emotional condition became relevant for participants and was encoded precisely, resulting in temporal comparison judgments more accurate than those performed in a neutral condition.

This thesis finding contributes to improve the knowledge of temporal memory literature, once expands the investigations for the time consolidation in long- term memory. The previous studies on temporal memory were focused on the short-term memory durations. Furthermore, the present study was the first to investigate experimentally the long-term memory of durations learned in different emotional conditions. Thus, several questions remain unanswered. It will be important to further investigate the impact of different types of temporal judgment on the sense of time in long-term memory.

Regarding the studies conducted to investigate the effect of interference in memory for duration, this thesis is also the first to examine the consolidation process for duration and its effects on the time judgments using interference task. Thus, it would be important conducted other experiments to investigate the temporal lengthening effect found in the present study about the forgetting in long-term memory duration.

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ANNEXE A - Record of interference task

Age	Participant	Condition	Expérience
Item	ESSAI I	ESSAI II	
1. 5-1		3-8	
2. 4-9-3		5-2-6	
3. 3-8-1-4		1-7-9-5	
4. 6-2-9-7-2		4-8-5-2-7	
5. 7-1-5-2-8-6		8-3-1-9-6-4	
6. 4-7-3-9-1-2-8		8-1-2-9-3-6-5	
ESSAI III		ESSAI IV	
8-2		7-9	
3-9-6		6-2-8	
4-5-1-7		9-1-4-2	
8-3-6-2-7		2-7-1-4-8	
9-5-3-8-2-7		4-3-7-1-9-6	
7-4-9-1-6-5-3		8-7-9-6-3-2-5	
ESSAI V		ESSAI VI	
9-6		5-3	
6-7-2		3-8-6	
5-9-7-3		5-7-9-8	
7-1-8-5-3		1-6-4-9-5	
1-6-4-3-7-9		9-2-5-3-1-7	
2-5-3-8-6-7-1		6-2-7-1-9-3-5	