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Memory consolidation for duration

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Humans and animals encode and store in memory elapsed intervals as evidenced through their temporal expectancies. However, there are very few experimental studies on long-term memory of duration. The aim of this original study was to examine the consolidation process for duration and its effect on time judgement. In our study, memory of duration was tested in humans with a temporal generalization task. Consolidation was assessed by means of a 15-min nontemporal interference task introduced at different delays after the initial learning of a 4-s standard duration. The results showed that (a) when tested 24 hours after the learning phase, memory of the 4-s duration was disrupted (less precision and lengthening effect) if the interference task was introduced 30-45 min after learning; (b) no disruption was observed when memory was tested immediately after the interference task; and (c) there was a temporal gradient of the disruptive interference effect within the first hour after learning. Overall, these results fulfil the key criteria for the inference of 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.

Memory of duration plays a critical role in time judgement, and it is fundamental for building temporal expectancy and shaping adaptive behaviour. Surprisingly, very few studies have investigated 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 learning of new information, during which initially fragile memory traces become stabilized in long-term memory (Dudai, 2004, 2012; McGaugh, 2000). Memory traces thus consolidate slowly over time.

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Research in animals, using pharmacological agents, has shown that cellular/synaptic consolidation require messenger ribonucleic acid (mRNA) translation and synthesis of new proteins, mechanisms that 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: (a) a short-term memory, which maintains information from a few seconds to several minutes, and which is independent of new protein synthesis; and (b) a long-term memory, which is maintained in an hours-to-months range. As a consequence, studies targeting the consolidation processes have shown 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 destabilization at long intervals with an intact memory at short intervals is one of the hallmarks of cellular/synaptic consolidation. Another 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 behaviourally expressed, even if some data indicate that it may be learned very quickly (Balsam, Drew, & Gallistel, 2010; Díaz-Mataix, Ruiz Martinez, Schafe, LeDoux, & Doyère, 2013). Temporal learning is thus not easily dissociable from other learned components. In human adults, studies that have examined reference memory of stimulus duration have often used a temporal generalization task in which 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 the temporal generalization task, 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 they must compare these durations with their representation in memory of S to judge whether D is the same as S or not (i.e., “yes” or “no” response). This task is acquired within a few trials and creates a stable long-term memory of up to 24 hours in adults (Rattat & Droit-Volet, 2010), thus making it particularly suitable for testing whether 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; Robertson, 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 & Shamehr, 2010; Keppel, 1968; Walker, Brakefield, Hobson, & Stickgold, 2003). It has also been shown that the interference effect is weakened when the time between the first and the second task is lengthened, permitting initiation of the consolidation process. In the temporal memory domain, two studies have investigated the overnight consolidation of temporal rhythms (Lewis et al., 2011) and of timing in visuomotor tracking (Maquet, Schwartz, Passingham, & Frith, 2003), which results in a further improvement in performance due to sleep. However, no study has 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 a temporal generalization task after learning of the standard duration have targeted short-term memory for duration rather than its stabilization in long-term memory (Ogden et al., 2008; Rattat & Droit-Volet, 2010). In these studies, the interference task was given immediately after the learning phase, and the participants were tested shortly after the interference task. These studies using short-term memory conditions revealed that the
interference task affected time judgement. In Ogden et al.’s (2008) study, it slightly flattened the generalization gradient in some cases, but more importantly displaced it to the left or to the right, suggesting that participants tended to remember the standard duration as shorter or longer than it was initially judged. However, in Ogden et al., the interference task was also a temporal generalization task with new standard durations, either shorter or longer than in the first task. Consequently, the direction of the displacement of the generalization gradient might have resulted from memories for the new durations that had interfered with those of the previous ones, producing a mixing in memory between reference values. In Rattat and Droit-Volet’s (2010) study, the interference task used (a parlour game) was not in the temporal domain. It nevertheless also made the generalization gradient shift toward the left (shortening effect) compared to the generalization gradient found without interference that 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 nontemporal interference task can disrupt memory for duration, at least in short-term memory. 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 after a long-term period, but not immediately after the interference task. In addition, concerning the interference task, when the task is a temporal one, there is potential mixing in memory between the different durations used for the primary and the interference tasks (Ogden et al., 2008). However, as mentioned above, Rattat and Droit-Volet (2010) showed that it was possible to disrupt the memory for duration with a nontemporal interference task (i.e., a parlour game) when it was a cognitive load task that required both maintaining information in short-term memory and manipulating verbal information in working memory. Indeed, some dual-task paradigm studies have demonstrated that duration processing requires the working memory component of the central executive system (e.g., Brown, 1997, 2006, 2014; Champagne & Fortin, 2008; Fortin, Rousseau, Bourque, & Kirouac, 1993; Ogden, Salominaite, Jones, Fisk, & Montgomery, 2011; Rattat, 2010). In Baddeley’s working memory 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 a common pool of executive resources—that is, common neural networks, as discussed later. Consequently, to isolate a specific effect on memory consolidation, without the involvement of temporal reference memory mixing, we used a standardized working memory task as an interference task that calls upon the central executive system of working memory—that is, the backward digit recall test of the Wechsler Memory Scale (WMS–II; Wechsler, 1998).

The purpose of the present study was to assess the stabilization of long-term memory of duration, which is independent of the potential disruption of short-term memory. For this purpose, we modified the paradigm of Rattat and Droit-Volet (2010) by introducing the interference task 30 min after the learning phase instead of immediately after that phase, thus potentially targeting a time beyond the involvement of the short-term memory system. If a consolidation mechanism was disrupted, then memory of duration was expected to be intact if tested immediately after the interference procedure (memory test at short term, ST), but modified (e.g., perhaps less precise) at long-term testing—that is, 24 hours later (memory test at long term, LT). Furthermore, a temporal gradient
of disruption should be observed at long-term testing (i.e., testing 24 hours later), with a stronger disruption when the interference procedure was given closer to the learning phase and a weaker effect when the interference procedure 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.

**EXPERIMENTAL STUDY**

**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, Pittsburgh, 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 centre 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 feedback, “correct” or “wrong”, presented visually at the centre of the computer screen for 2 seconds.

The interference task, which lasted 15 minutes, was the backward digit recall task used in the Wechsler Memory Scale (WMS–II; Wechsler, 1998), which is a high cognitive load task that calls upon attention–executive functions of working memory (Baddeley & Hitch, 1974). In the present study, the participants were thus presented with a sequence of digits that they had to 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 sequences) during a 15-min 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 or she would be presented with a stimulus duration that he or she had to memorize. The participant was explicitly told not to count during this stimulus duration presentation 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 a 4-second standard stimulus duration 5 times. She or he was then given two learning blocks of four trials each in which two trials with the standard duration and two with other durations (0.5 and 7.5 s) for comparison were presented. In this learning phase, the participant had to judge whether the comparison duration was the standard duration or not by pressing the corresponding “d” (i.e., “yes”) or “k” (i.e., “no”) key. Each response was immediately followed by a feedback word, “correct” or “wrong”. None of the participants required more than one or two training blocks (eight trials in total) to learn the standard duration—that is, to exhibit 100% correct responses.

In the testing phase, the participant was told that it was the same game as that during the previous (learning) phase. He or she had to judge for each comparison stimulus duration whether it was or was not the standard stimulus duration that he or she had to memorize previously, but now there was no feedback. In the testing phase, the participant completed eight blocks of nine trials (72 trials)—that is, three trials for the comparison duration identical to the standard duration (4 s) and one trial for each of the other comparison durations (1, 2, 3, 5, 6, 7 s). The trials were presented in random order within each trial block. Each trial started when the participant pressed the space bar after the word “ready!” appeared on the screen.
As reported in the introduction, there are two hallmarks of consolidation in long-term memory: (a) an effect seen at a long-term (LT) test assessment, while no effect is seen at a short-term (ST) test assessment, and (b) a gradient in the disruption of time judgement at the long-term assessment that decreases as the time interval between the learning phase and the interference task increases. Therefore, we examined these two specific criteria of memory consolidation for the standard duration in two sets of experimental conditions. First, to examine the ST versus LT effect, the participants were assigned to one of four experimental groups: two groups with the testing phase given 45 min after the learning phase (ST test; 15 and 14 participants), and two groups with the testing phase given 24 hours after the learning phase (LT test; 20 and 20 participants). For each retention condition (ST vs. LT), one group received the 15-min interference task (interference) 30 min after the learning phase, whereas the other group did not receive any interference task (control). Following the interference task, during the 24-hour retention delay, the participants did not perform any specific task and simply engaged in their day-to-day activities.

In a second set of experimental conditions, we examined whether the interference task produces a time-dependent graded effect when the task is introduced at different time points after the initial learning phase, in line with the time-dependent disruption of the consolidation process. If memory of duration undergoes a consolidation process, the disruptive effect of interference observed at LT should weaken as the time between learning and the interference task is increased. Two additional experimental groups were thus tested 24 hours after the learning phase (LT test), with the 15-min interference task 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; 19 and 15 participants, respectively). This design allowed us to compare the magnitude of disruption in the temporal judgement observed at long-term when the interference task is given at different time points during the retention interval, at an early and later time point.

Results

* A long-term memory consolidation for duration evidenced by a selective disruption of memory at long term

Figure 1 shows the mean proportion of “yes” responses P(yes) plotted against the comparison durations when the participants were tested 45 min (ST) or 24 hours (LT) after the learning of the standard duration, in a condition with or without an interference task given 30 min after the memorization of a 4-s standard duration. An initial analysis of variance (ANOVA) was performed on P(yes) with one within-subject factor (comparison duration) and two between-subjects factors (interference and LT/ST test). The ANOVA 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 LT (M = .35, SD = .014) than in the ST test (M = .29, SD = .02). However, there was a significant Comparison Duration × Test interaction, F(6, 390) = 5.75, p = .0001, indicating that the generalization gradients were different after a long and a short retention interval. The effect of comparison duration was nevertheless significant for both the LT and the ST test conditions [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 duration in these two testing conditions. The main effect of interference was not significant, F(1, 65) = 0.30, p = .59, nor were the interactions involving the interference factor (all p > .05). However, based on our a priori hypothesis, planned comparisons revealed a significant Comparison Duration × Interference interaction in the LT test, F(6, 228) = 2.52, p = .02, but not in the ST test, F(6, 162) = 0.75, p = .61, suggesting a disruption selectively in long-term memory.

To further analyse the curves of the generalization gradients and characterize the impact of interference on the precision and accuracy of memory, we calculated two measures for each individual gradient: (a) the peak time, which is the
stimulus duration corresponding to the highest proportion of “yes” responses, and (b) 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 temporal variability, a high value indicating a high variability in time judgements. These two measures were obtained by fitting each participant’s generalization gradient with the “log normal (amplitude)” function from the PeakFit programme (PeakFit Version 4.12 for Windows). This procedure produced good 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.

The ANOVA performed on peak time with two between-subjects factors (interference and test) showed a significant main effect of test (ST vs. LT), $F(1, 65) = 7.26$, $p = .009$, suggesting that the generalization gradient peaked at a longer value in the LT than in the ST testing condition (4.46 vs. 4.01). However, there was a significant Test $\times$ 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 LT and not at ST, showed that the interference task given 30 min after the learning phase produced a lengthening effect when memory was tested 24 hours later, with a generalization gradient peaking at a longer value than 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 (ST test), as indicated by an effect that just failed to reach significance, $t(27) = −2.01$, $p = .055$.

For the FWHM (Figure 2B), there was also a significant interaction between test and
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 s). 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: LT test, \(t(38) = 4.04, p = .001\). In contrast, the interference task had no significant impact on the width of the generalization gradient when the memory was tested shortly after the interference task: ST 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 memory testing, with a disruption at long term, and no effect, or even an opposite effect, immediately after the interference task. Consequently, our results suggest that the interference task produced a disruption of the consolidation process that stabilizes memory in 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 that in the control condition.

Temporal gradient of the interference effect on time judgement in long-term memory

Figure 3 shows the generalization gradients obtained 24 hours after learning (LT test) as a function of the interval between the learning phase and the interference task, when it was given either early—that is, immediately after the learning phase—or later, 1 hour after the learning phase. The results from the group tested on LT with the interference task given 30 min after the learning phase (see Figures 1 and 2) are also reported in Figure 3 (empty circle), for comparison only. Figure 3 reveals a temporal gradient in 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 ANOVA\(^1\) on \(P(\text{yes})\) on the two 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 duration, \(F(6, 192) = 24.91, p = .0001\), and more importantly a significant interaction between comparison duration and interference, \(F(6, 192) = 2.99, p = .008\). This latter result indicates that the

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\(^1\)One participant in the “immediate interference/test at 24 hours” group was excluded from the results because, unlike the other participants, he produced a generalization gradient that was flat.
generalization gradients differed, depending on the time at which the interference task was given, immediately or 1 hour after the learning phase.

The analyses of 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 1-hour interference group, 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.

**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 nontemporal interference task on the shape of the generalization gradient 24 hours after learning. Our results showed that the interference
task given during the memory consolidation period reduced the precision of memories of the standard duration, as indicated by a flattening of the generalization gradient during the long-term memory test for the interference condition compared to the no-interference condition. Our results also showed that the interference task produced a lengthening effect on the duration stored in memory, as revealed by a rightward shift of the generalization gradient that peaked at longer comparison durations than those for the control (no-interference) condition. Importantly, these effects (a) were not observed when memory was tested immediately after the interference task (ST test) and (b) 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 for the inference of a synaptic/cellular consolidation process (Dudai, 2012; McGaugh, 2000; McGaugh & Roozendaal, 2009; Schafe et al., 2001).

One of the critical elements in claiming a synaptic consolidation process is the demonstration that the disruptive tool affects 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 takes time (from minutes to hours). This process has now been 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 for memory traces of 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 that 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 short-term memory rather than long-term memory for time (Filippopoulos, Hallworth, Lee, & Wearden, 2013; Jones & Wearden, 2003, 2004; Ogden et al., 2008; Ogden, Wearden, & Jones, 2010; Rattat & Droit-Volet, 2010). With regard to short-term memory, consistent with our data, Jones and Wearden (2004) suggested that the manipulation at short term of reference memory has a minor effect on temporal generalization judgment. However, Rattat and Droit-Volet (2010) found an immediate disruption of memory of duration by the insertion of a nontemporal interference task shortly after learning. It is possible that the different tasks used as interference tools (a parlour game in Rattat & 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). Temporal studies using interference tasks during the encoding of time in a dual-task paradigm have shown that the interference tasks systematically affected temporal processing when they required cognitive resources (e.g., Brown, 2014; Brown, Collier, & Night, 2013; Ogden et al., 2011; for a recent book on this topic see Nobre & Coull, 2011). Indeed, as suggested by attentional models of timing (Thomas & Weaver, 1975; Zakay & Block, 1996, 1998), the processing of temporal information and that of nontemporal 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 nontemporal performance in dual-task situations suggested that the interference effect on time judgement was
more important for visuospatial than for 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 dynamics 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 ST test condition (i.e., test of memory given immediately after the interference task) with the interference task given 30 min after learning. However, the shortening effect obtained in the ST testing conditions was opposite to the lengthening effect found in the LT test—that is, 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—that is, shortening when the short-term or intermediate memory system is affected, and 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 investigation.

In the present study, we observed a lengthening effect in time judgements when memory was tested 24 hours after temporal learning, and the disruption effect followed a gradient consistent with the time-limited consolidation process. This result suggests that participants remembered the standard duration as longer than it was judged initially, consistent 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, Church, & Meck, 1984), three processing modules are involved in the judgement of time: clock, memory, and decisional. The clock module consists of a pacemaker that emits pulses that are gated by a controllable mode switch to an accumulator. A 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 current time in the accumulator with a remembered time that is sampled from reference memory. If the difference between the current accumulator value and the value of the sample from memory is small enough, the judgement "yes" is made. This model proposes 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 nonrelevant stimulus durations (i.e., 0.5 and 7.5 s) 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 other durations presented at the same time (Ogden & Jones, 2009; Ogden et al., 2008; 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 time-dependent graded effect of interference, which would then imply that the decision processes would change with the increase in 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 variance in temporal judgements results from storage mechanisms of time intervals in long-term memory. An increased variability in remembered duration due to task interference has been reported previously (Rattat & Droit-Volet, 2001, 2005, 2010). Modelling their data, Rattat and Droit-Volet (2010) suggested that the major cause of this flatter generalization pattern was the coefficient of variation of the representation of the standard duration in reference memory, which was greater with than without interference. Thus, variability of the representation of the standard duration is more important in long-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 at LT and not at ST tests demonstrating a consolidation process, no significant time-limited window was observed within 1 hour after the learning (in contrast to the temporal gradient observed for the lengthening effect). It is likely that increased variability may be a more sensitive measure of altered long-term memory. Thus, 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 consolidation over time of the representation of the standard duration in long-term memory, thus making the duration remembered longer and less precise.

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 synthesis) observed in other types of memory in animals (Alberini et al., 2006; Dudai, 2012; Gal-Ben-Ari et al., 2012; Schafe et al., 2001). Our study showing time-limited lability of the memory trace and a specific impact on long-term memory demonstrates that this is the case. Notably, the effect was obtained with an interference task that did not involve temporal information. Nevertheless, it has been shown that interference 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 (Barsegyana, Mackenzie, Kuroseb, McGaughb, & Roozendaala, 2010). As prefrontal networks have also been involved in temporal processing (see for a recent review Coull, Cheng, & Meck, 2011), it is quite possible that the nontemporal working memory interference task we chose may have disrupted prefrontal mechanisms when they were required during the consolidation process. Further investigation is needed to research more precisely the mechanisms and neural networks subserving the long-term memory of time by testing different interference tasks.

REFERENCES


