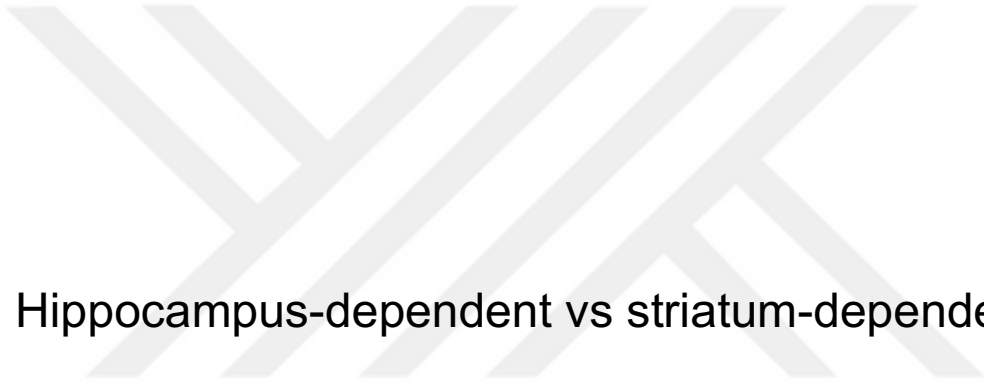


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Hippocampus-dependent vs striatum-dependent learning in the transitive inference task in young and older populations

Master Thesis in Clinical Psychology and Psychopathology

Presented by Hazal Ergüneş

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Abstract

Hippocampus-dependent learning and memory system may contribute to age-related declines in memory abilities for both spatial and non-spatial information. The transitive inference (TI) task is supposed to be a way to assess the hippocampus-dependent learning as suggested by the relational model and supported with neuroimaging studies. However, as revealed by lesion studies, the hippocampus may not be necessarily involved in the TI task and performances could be supported by alternative reinforcement-based learning strategies requiring the critical involvement of the striatum-dependent learning and memory system. Here, I aimed to decipher the learning strategies used in the TI task and test the hypothesis of impaired hippocampus-dependent learning and memory system. Young and older participants were tested on the Visual Discrimination task (VD), Conditional Learning task (CL) and TI task. Performances were analyzed both at the group and the individual levels. In the VD task, older participants performed as well as young participants. In the CL task, they were able to perform as well as young individuals with extended training. However, in the TI task, they performed worse than young participants at the group level and they were not able to learn all premise pairs at the individual level whereas almost all young individuals could learn all of them. Overall, findings revealed that the TI task could be solved by both strategies and the hippocampus-dependent learning might be impaired in aging.

Key words: Multiple memory systems, hippocampus, stimulus-response learning, relational learning, reinforcement-based learning, transitive inference, value transfer theory



1. Introduction

1.1 Multiple memory systems

Multiple learning and memory systems are supported by distinct brain regions including hippocampus and striatum in humans and animals (Milner et al., 1998; O'Keefe & Nadel, 1978; Poldrack et al., 2001; Scoville & Milner, 1957; Squire, 2004, 2009).

The hippocampus-dependent learning and memory system contributes to the rapid acquisition of information and the construction of flexible relational representations between items or events which could be used in novel contexts (Eichenbaum, 2001; O'Keefe & Nadel, 1978; Squire, 2004, 2009). The hippocampus is associated with relational memory establishing arbitrary relations among constituents of an experience, event or scene using spatial, associative or temporal information (Cohen & Eichenbaum, 1993; Eichenbaum, 2001; Konkel & Cohen, 2009). For instance, one could have a memory of a foreign friend's traditional wedding and encode and remember all manner of relations: locations of tables in relation to other objects or decorations (i.e., spatial information), different conversations with specific people (i.e., associative information), gifts and rituals of celebration in the traditional wedding (i.e., associative information) and the order of the occurrence of these rituals (i.e., temporal information). Later on, the same individual could bring a culturally convenient gift while celebrating his/her friend for giving birth to a baby. This example reflects the flexible use of previously constructed relational representations in a novel context based on the memory of the wedding.

On the other hand, the striatum-dependent learning and memory system contributes to the slow and incremental acquisition of information and the construction of fixed stimulus-response representations (Foerde et al., 2006; Knowlton et al., 1996;

Packard et al., 1989; Packard & McGaugh, 1996; O'Keefe & Nadel, 1978; Squire, 2004, 2009). This system is especially involved in habit learning which refers to the acquisition of automatic behavioral responses to encountered stimuli, based on repeated experiences and their outcome (Packard, 2010; Seger & Spiering, 2011). For instance, a student can feel sleepy whenever he studies for an exam (i.e., stimulus) and drink a coffee (i.e. behavioral response) which keeps him awake (i.e., outcome). Thus, the student may begin to drink coffee regularly while studying to keep himself awake and the behavior of drinking coffee may become a habit by gaining an automaticity. This automatic occurrence of the same behavioral response reflects the inflexible nature of striatum-dependent learning and memory system.

In sum, the performance in certain learning and memory tasks may sometimes be supported by different learning and memory systems (Eichenbaum, 1992; Packard et al., 1989; Schacter & Tulving, 1994; Squire, 2004). Thus, the presence of these systems should be considered when designing behavioral tasks and interpreting results accordingly. Interestingly, the potential differential effects of aging on these memory systems on different behavioral tasks were investigated in a number of studies (e.g., Fernandez-Baizan et al., 2019; Lighthall et al., 2018; Mitchell et al., 2000; Ohta et al., 2002; Rapp et al., 1996) and age-related changes were reported in a variety types of memory (Kester et al., 2002; Nilsson, 2003; Nyberg & Pudas, 2019).

1.2 Age-related declines in spatial memory

Consistent with relational memory, allocentric spatial learning and memory refers to the construction of viewpoint-independent representations of the environment based on relations among distal environmental cues, locations or objects (O'Keefe & Nadel, 1978).

Recently, Klencklen et al. (2017a, 2017b) investigated age-related declines in allocentric spatial and color learning and memory. Young (20-30 years) and older (65-75 years) healthy adults were tested following a repeated-trial and trial-unique schedule to evaluate their ability to encode and remember the fixed information (i.e. reference memory) and the changing information between trials (i.e., working memory) respectively (Klencklen et al., 2017a). During the encoding phase of each trial, participants discovered the location of three illuminating disks or three colored rings surrounding illuminating disks (Figure 1). The goal locations or colors were predetermined pseudo-randomly among 18 pads. The goal pads were illuminated when participants touched the foot pads by their foot during the exploration of the testing area but the light disappeared immediately after removal of the foot from the pad. Once all goal pads were identified, participants exited the testing arena. Then, participants performed an interference task by counting back from a predetermined number during a one-minute inter-phase, and they re-entered the testing area for the recall phase. In the recall phase, participants were instructed to touch without any particular order the learned goal locations or colors. In spatial tasks, as all pads were visually identical, participants had to learn and recall the goal locations based on distal environmental cues which were visible in the testing area as well as in the side waiting area. As the entry to the testing area was made always from a different door before and after the interphase, a viewpoint-dependent egocentric strategy (i.e., response learning based on the body position of the subject) was not available to solve the task. Therefore, goal locations could be recalled correctly only by learning the locations of goals in relation to distal environmental cues by constructing the viewpoint-independent representations of the environment (i.e. cognitive map). On the other hand, in the tasks for color information, the locations of goal colors were changed

between encoding and recall phases as well as between trials. Therefore, the spatial information was not relevant to solve the task and participants could recall the goal colors only via visuo-featural information.

Figure 1

Pictures of the Testing Arena During Spatial and Color Tasks



Note. (A) Participant touching the illuminating foot pad during the spatial task. (B) Participant touching the illuminating foot pad during the color task. From Klencklen et al. (2017a, 2017b).

The performance of older individuals was worse than that of young individuals on all memory tasks but especially in working memory tasks. On the one hand, the total number of disks visited to find the goals (i.e., a measure of overall performance), the absolute number of correct choices before erring (i.e., a measure of memory capacity) and the number of errorless trials (i.e., a measure of perfect memory) indicated age-related deficits in working memory performances of older individuals independent of the type of information (color vs spatial). On the other hand, the number of trials with the first choice correct and first two choices correct indicated a greater age-related deficit for spatial information than color information. However, importantly, the number of trials with the first three choices correct did not indicate such a difference in working memory performances for different types of information.

Thus, some measures indicated similar age-related decline in working memory performances for spatial and color information whereas others suggested a greater age-related decline for spatial information than color information. Overall, age-related declines were greater for working memory than for reference memory. However, it remained unclear whether observed age-related declines were specific to the type of information or not.

Klencklen et al. (2017a) suggested that age-related deficits might appear greater for spatial than color information depending on the measure used in the analysis. This was explained by higher representational demands for allocentric spatial memory than color memory (Klencklen et al., 2017a) because it might be qualitatively more demanding, therefore quantitatively might necessitate the encoding of more bits of information (Klencklen et al., 2017b). The immediate memory has a limited capacity in terms of amount of information that could be retained and correctly recalled (Miller, 1956). It suggested that the span of immediate memory might depend on the number of bits of information required to represent a single item (Miller, 1956; see Banta Lavenex et al., 2015 for detailed discussion). Therefore, when such a limited constant capacity was considered with representational demands, it was reasonable to suggest that depending on the measure used, age-related declines might appear similar or not for different types of information. Specifically, if the spatial memory for locations is quantitatively more demanding (i.e., greater bits of information) in comparison to color memory, the decline might appear greater for spatial than color information when the first choice correct and first two choices correct were considered as the capacity limit (i.e., total amount of information that could be retained) might be achieved for spatial but not yet for color information. However, the differences for spatial and color information might disappear when the first three

choices correct were considered because the capacity limit would be achieved also for color information. Altogether, these considerations suggested that both types of information indeed might be similarly affected by aging and they further pointed that the memory load might be an important factor to be considered while interpreting the findings about age-related declines (Klencklen et al., 2017a).

To test these suggestions, Klencklen et al. (2017b) investigated the influence of memory load on age-related changes in working memory performances for allocentric spatial and color information. Participants performed the same spatial and color working memory tasks with one, two or three items. Consistent with previous findings, age-related declines in performance were observed in all working memory tasks, but these declines did not differ depending on the type of information (i.e., spatial vs color). Furthermore, consistent with the hypothesis derived from the previous study, the decline of working memory performance was greater with increasing memory load for older individuals than younger individuals with both type of information. Also, according to an additional analysis of young individuals' results, working memory performance for one spatial location was similar to that for three colors. This remarkable result was also consistent with findings of Banta Lavenex et al. (2015) which demonstrated in spatial domain that the performance for one item might be used in predicting performances for multiple items. Hence, these findings suggested that representational demands of spatial information are greater than those of color information and revealed that age-related declines in working memory performances could be explained by memory load rather than the type of information (Klencklen et al., 2017b).

Therefore, age-related declines in working memory performances for both spatial and non-spatial information could be explained by a dysfunction in a specific

brain region (Klencklen et al., 2017b). Indeed, findings from another study investigating performances on the same tasks of a densely amnesic patient, P9, with bilateral hippocampal damage, were also consistent with this suggestion (Banta Lavenex et al., 2014). Working memory performance of P9 was impaired for both spatial and color information when she had to learn and remember one, two or three items, while performing an interference task between encoding and recall phases. Hence, the age-related declines were observed due to the dysfunctional hippocampus.

Overall, considering findings of Klencklen et al. (2017a, 2017b) and Banta Lavenex et al. (2014) it was proposed that age-related declines observed in working memory performance for both spatial and non-spatial information could be related to impairment of the hippocampus-dependent learning and memory system. Therefore, in my thesis, I aimed to investigate possible age-related declines in hippocampus-dependent learning and memory outside the spatial domain. Specifically, I intended to test young and older populations on the transitive inference task (TI), which is thought to depend on the hippocampus (Eichenbaum, 2001).

1.3 Theories of hippocampus-dependent memories

A number of theoretical models has been proposed to summarize the functional role(s) of the hippocampus (Morris, 2007). One very influential model was proposed by Eichenbaum and colleagues (Eichenbaum et al., 1992), who posited that hippocampal representations of experience are fundamentally relational. Accordingly, the TI task was suggested to be a hippocampus-dependent (Eichenbaum, 2001) as it was traditionally considered to be a relational task (Dusek & Eichenbaum, 1997; Piaget 1928; Vasconcelos, 2008).

1.3.1 Relational model

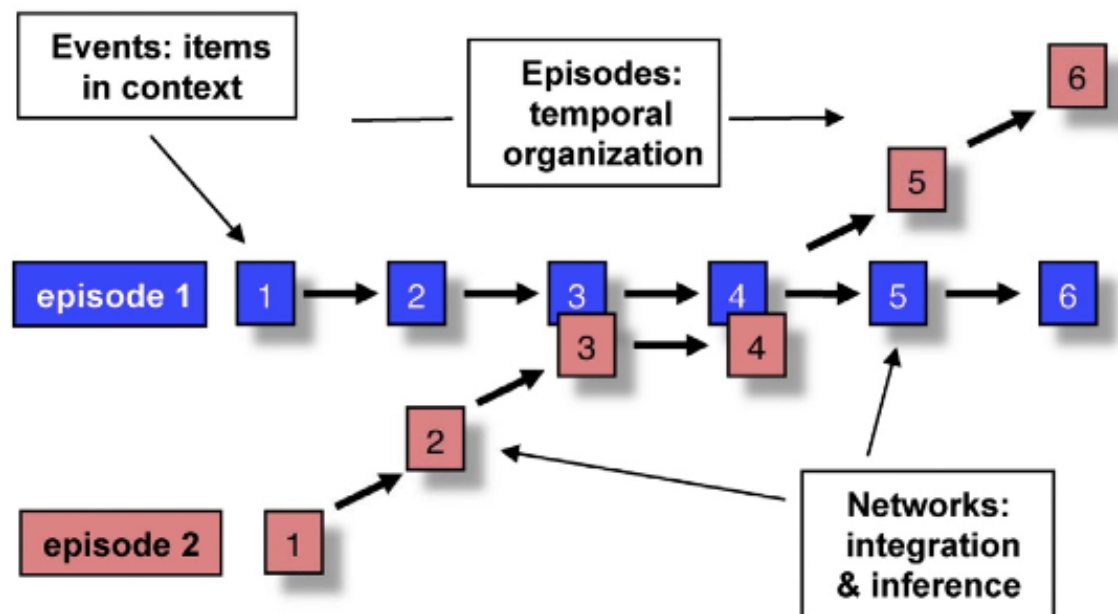
The relational model relies on two basic characterizations of declarative memory, which depends on a functional hippocampus (Eichenbaum, 2001; Milner et al., 1998; Scoville & Milner, 1957; Squire, 2004, 2009). First of all, declarative memory refers to the conscious recollection of facts and events and comprises two components: episodic memory and semantic memory (Eichenbaum, 2001). Episodic memory is the memory for experiences consisting of a sequence of events, which occurs in the course of time in a specific context (e.g., the memory of a car accident while going to a party in a rainy night, or the memory of falling down while running on a wet surface to reach the bus 5 days ago). Semantic memory refers to the general knowledge about the world (e.g., rain soaks). These two types of memories may be related because multiple episodic experiences sharing the same information could be connected to each other and contribute to the previous knowledge and construction of a complex network (e.g., both “car accident” and “falling down” experiences could be linked with each other as both occurred due to the surface getting wet. This linkage could be attributed to the previous knowledge as follows: the surface becomes slippery when it rains. Secondly, declarative memories could be recalled consciously and used in a novel situation to make generalizations (e.g., believing one can be injured if he/she travels whenever it rains) or inferences (e.g., if someone who rides a bike outside in a rainy day, begins suddenly to cry, it could be inferred that he/she got injured because it is known already that if it rains, the surface might be slippery and if the surface is slippery, there might be an accident).

Consistent with these properties of declarative memory, Eichenbaum and colleagues (Eichenbaum, 1992, 2001) argued that the hippocampus is responsible for encoding the relationships between items or events perceived simultaneously or

sequentially, and linking them based on their common features by constructing a network of relational representations (Figure 2). This network represents a flexible organization which allows to make inferences in novel situations. Hence, the hippocampus is suggested to be involved in declarative memory and in the processing of all kind of relational information across different tasks (Eichenbaum, 1992; Eichenbaum & Cohen, 2014).

Figure 2

Conceptual Illustration of Memory Space and Relational Processing



Note. Blue squares represent the sequence of events of episode 1 whereas pink squares represent the sequence of events of episode 2 occurring in specific contexts. Numbers on the squares indicate the temporal organization of events according to their order of occurrence. Altogether, the schema illustrates the relational network with links between episodes and events. This network supports an inference between two events which are indirectly related. Sequence of “Events” illustrated in this figure could be replaced by anything including relational information (e.g., items, objects, behaviors). From Eichenbaum and Cohen (2014).

1.3.2 Transitive inference as a hippocampus-dependent task

Eichenbaum and colleagues (Eichenbaum, 2001) suggested that one method to investigate and illustrate the role of hippocampus outside the spatial domain is the TI task because the role and the functioning of the hippocampus suggested by the relational model, is consistent with the concept of “transitivity”, a.k.a. transitive inference which was introduced by Piaget (1928), as a form of logical reasoning during cognitive development (Breslow, 1981).

TI refers to the ability to make inferences about the relationships between items, that were not presented together before, by relying on previously learnt overlapping premise pairs (Dusek & Eichenbaum, 1997; Greene et al., 2006; Heckers et al., 2004). For instance, one could learn that Ann is taller than Sally, and Sally is taller than Marie, and when the individual is asked about the relationship between Ann and Marie in terms of height, he/she could infer that Ann is taller than Marie based on previous learning. The TI tasks are therefore designed according to the same logic with a higher number of items (Bryant & Trabasso, 1971; Dusek & Eichenbaum, 1997; Greene et al., 2006; Heckers et al., 2004).

During the training phase of the TI tasks, two-item discrimination problems are presented in which one item of each pair is predetermined to be rewarded (A+B-, B+C-, C+D-, D+E, where “+” indicates the winner and “-” indicates the loser). For instance, participants are presented with two images and asked to choose the one which is the “winner” item. Whether a particular item wins or loses depends on the item that it is presented with (e.g., B loses against A, but B wins against C). Therefore, it makes relationships to be learnt conditional and participants are assessed on their ability to learn by trial and error these conditional pairs during the training phase. During the test phase, participants are presented with pairs of items which have not been

presented together before (i.e., AC, AD, AE, BD, BE, CE) and they are evaluated on their ability to make inferential judgments based on previous learning (e.g., if $B > C$ and $C > D$, then $B > D$), which may be possible by determining a hierarchical organization between items ($A > B > C > D > E$) (Dusek & Eichenbaum, 1997). Note that, in the TI task, items B, C and D were predetermined to be the winner and the loser the same number of times, in contrast to items A and E which were predetermined to be always the winner and the loser respectively (as they are end items of the series). Accordingly, the pair BD is considered to be the only true informative comparison to infer the ability to perform a TI task, as other pairs with one of end items (i.e., the item A and the item E) could be solved by using another strategy “A always wins and E always loses”.

Therefore, from the perspective of the relational model of hippocampal function, overlapping premises could be considered as distinct experiences like events, they could be linked to each other and organized into a network like memory space (see Figure 2), as they share a common item (Eichenbaum, 2001). This relational organization could allow a flexible memory expression and inferential judgments between indirectly related items which could justify the use of the TI task for testing the relational model (Eichenbaum, 2001). In sum, the TI task is claimed to be a convenient method to investigate hippocampus-dependent learning and memory when both suggestions of relational model and the nature of the task designed to assess the transitivity were considered.

1.3.3 Testing the relational model with the transitive inference task

1.3.3.1 Neuroimaging Studies. A number of neuroimaging studies tested the relational model of hippocampal function in humans and provided strong evidence for

the implication of the hippocampus in the TI task consistent with the proposal by Eichenbaum and colleagues (2001).

Nagode and Pardo (2002) tested healthy young individuals on a TI and a visual discrimination (VD) task, in which overlapping premise pairs (e.g., A vs B, B vs C) and non-overlapping premise pairs (e.g., A vs B, C vs D) were trained, respectively. The task procedures were similar for the TI and the VD tasks. Therefore, in each pair one item was predetermined to be rewarded. However, in contrast to TI task, there were no common items between pairs and conditional relationships to be learnt between items in the VD task. In the analysis, PET scans of 10 individuals who learned premise pairs and showed the TI ability were used. Findings from PET scans of 4 individuals revealed higher hippocampal activation in the middle of the training in comparison to the beginning of the TI task. PET scans of 10 individuals revealed higher hippocampal activation for overlapping premise pairs than non-overlapping premise pairs during the training phase. This suggested that the hippocampal activation was specific for learning conditional pairs during training in the TI task. Similarly, in a fMRI study, healthy individuals were tested on the TI and VD tasks (Heckers et al., 2004). According to findings, overall behavioral performances did not differ between overlapping and non-overlapping premise pairs which indicated that they were able to learn equally well both non-conditional relationships between items in the VD task (e.g., A wins against B, C wins against D) and conditional relationships between pairs in the TI task (e.g., B loses against A but wins against C). Imaging results showed a significant hippocampal activation during TI. Zalesak and Heckers (2009) focused specifically and in more detail on the inference (test) phase of the TI task and performed both behavioral analysis and imaging analysis for inference pairs including end items referred as ETI (e.g., A vs C, B vs E) and devoid of end items referred as

NETI (e.g., BD) which are informative to determine the ability to perform TI. Accuracy did not differ between NETI and ETI but hippocampal activation was greater for NETI than ETI suggesting that the hippocampus was involved especially for test pairs purely informative about the ability to perform TI (e.g., B vs D). In sum, these studies showed the implication of the hippocampus both during the learning phase and the test phase of the TI task which suggested that the hippocampus is supposed to contribute to learning conditional relationships between overlapping premise pairs and performing inferential judgments.

Furthermore, Greene et al. (2006) combined an imaging analysis with a detailed behavioral analysis for both training and test phases. They provided a very convincing evidence for the relational model suggesting the involvement of the hippocampus both in processing relational information and making inferences based on learnt relationships. At the behavioral level, the performance on inner pairs (i.e., BC and CD) predicted the performance on the inference pair BD which suggested that individuals were able to learn conditional relationships between BC and CD and make inferential judgment based on these relationships (i.e., if $B > C$ and $C > D$ then $B > D$). Specifically, individuals who were able to learn both inner pairs were also successful on the inference pair BD whereas individuals who learnt only one inner pair could not show a successful inference. Hence, learning conditions in which the item C is rewarded or not was critical to correctly choose B over D during testing. In addition, consistent with findings of Zalesak & Heckers (2009), the hippocampus activity was greater for inner pairs than end pairs during training and consistent with behavioral data, imaging results of BD performers indicated a greater hippocampus activity than BD nonperformers. Therefore, it was concluded that the acquisition of premise pairs

is required for a successful inference, and both learning conditional pairs and inferential judgments are hippocampus-dependent.

Altogether imaging studies have shown that the hippocampus is involved both in learning relationships between conditional premise pairs and making inferences supporting the suggestions of the relational model. Therefore, based on these results, it could be concluded that the TI can be used to assess hippocampal-dependent learning and memory capacities.

1.3.3.2 Lesion Studies. Although lesion studies aimed to demonstrate the importance of a functional hippocampus for making inferences by relying on the relational model, they failed to show the critical involvement of the hippocampus during the learning phase of TI tasks (Buckmaster et al., 2004; Bunsey & Eichenbaum, 1996; Dusek & Eichenbaum, 1997). These findings are thus in sharp contrast with the findings of neuroimaging studies (e.g., Greene et al., 2006; Nagode & Pardo, 2002). It worths noting that that the involvement of a brain region in a task could not be interpreted as it is absolutely necessary to solve the task.

Dusek and Eichenbaum (1997) produced hippocampal lesions in rats and tested them with control animals on both premise and test pairs in the TI task, after an initial training on the premise pairs. Overall performance on premise pairs did not differ between lesioned and control animals both during the training and testing phases. In addition, group performance across premise pairs were not different during the testing phase. Performance of both groups indicated a serial position effect which means that their performance was better on end pairs (i.e., AB and DE) than inner pairs (i.e., BC and CD). These findings were thus consistent with the reliance on the strategy “the item A is always rewarded and the item E is never rewarded” for end pairs. Interestingly, during the testing phase, the percentage of correct choices of lesioned

animals on the inner pairs, and on the test pair including end items (i.e., A or E) were above chance level similar to none-lesioned animals. However, their performance on the inference pair BD was below chance level and significantly impaired in comparison to non-lesioned animals.

Buckmaster et al. (2004) obtained similar results in hippocampal-lesioned monkeys. Overall performance on premise pairs during training did not differ between groups, even though the number of correct choices of the lesioned group was higher than that of the control group. During the testing phase, performance on inner premise pairs (i.e., BC and CD), end premise pairs (i.e., AB and DE) and on the test pair including end items (i.e., A or E) did not differ between groups. In contrast, performance of lesioned animals was below chance level and impaired relative to controls on the inference pair BD. Hence, both studies indicated that lesioned animals were able to learn the premise pairs BC and CD and solve the test pair AE despite a dysfunctional hippocampus. However, they were not successful on the inference pair BD. These results suggested that the hippocampus is not absolutely necessary for performances during the training phase but its' involvement is critical for performances in the specific test requiring TIs abilities.

DeVito et al. (2010) investigated the involvement of the hippocampus in the TI task in mice with a slightly different procedure by introducing the task before and after the surgery. They showed that before the surgery, all animals learned all of training pairs and they were performed above chance levels both on the test pairs AE and BD. Interestingly, after surgery hippocampus-lesioned animals outperformed control animals on training pairs, especially on the pairs AB and DE which could be solved by unambiguous reinforcement histories (i.e., the item A is always rewarded and the item E is never rewarded). In contrast, lesioned animals performed significantly worse on

the pair BC than all of other training pairs indicating a U-shaped accuracy curve, whereas performances of controls did not differ across training pairs and thus reflecting a relatively flatter accuracy curve. During testing phase, lesioned animals were impaired on the inference pair BD consistent with previous findings. Moreover, their performance on this pair after surgery was significantly lower than before surgery. Lesioned animals also performed better than controls on the test pair AE, which could be solved by “the item A is always rewarded and the item E is never rewarded”. In sum, the performance of lesioned animals was similar to that of controls before the surgery. However, after the surgery, pattern of performances differed between controls and lesioned groups. Specifically, lesioned group performed better than controls on all pairs including end items, but their performances were impaired on the pair BD. This study therefore suggested that with the repetition of a training phase after surgery, an alternative learning strategy which might not require necessarily the involvement of the hippocampus, allowed lesioned animals to overperform control animals on specific pairs, yet lesioned-animals were unable to perform TI.

Overall, in these studies, the impaired performance on the pair BD in lesioned animals was attributed to a dysfunctional hippocampus and was taken as evidence for the relational model. However, lesion studies failed to show impaired performance on individual premise pairs in the absence of functional hippocampus, as if each training pair was treated independently of the other pairs. In fact, they demonstrated that despite hippocampal dysfunction, performance of lesioned animals on training and test pairs including end items was intact, and with repeated training their performance was even facilitated for all training pairs. Altogether, lesion studies suggested that performances in the TI task could be supported by an alternative learning strategy in a hippocampus-independent manner, possibly with the contribution of reinforcement

histories as evidenced by the amelioration of performance after repeated training (Devito et al., 2010). This strategy could be based on the striatum-dependent learning and memory system which is involved in learning individual fixed stimulus-response associations (Foerde et al., 2006; Knowlton et al., 1996; Packard et al., 1989; Packard & McGaugh, 1996; O'Keefe & Nadel, 1978; Squire, 2004, 2009) and is related with habit memory (Seger & Spiering, 2011, Squire, 2004, 2009).

1.4 Striatum-dependent Learning in the Transitive Inference Task

1.4.1 Reinforcement-based Learning

Consistent with the findings of lesion studies suggesting the presence of an alternative learning strategy in the TI task, some researchers questioned the relational nature of the task and they argued that the performance can rely on a reinforcement-based learning (Frank et al., 2003; Van Elzakker et al. 2003; Von Fersen et al., 1991; Wynne, 1995, 1998).

Reinforcement-based learning, designated also as slow, incremental learning, is closely related to the concept of “habit memory” and is therefore supported by the striatum-dependent learning and memory system (Foerde et al., 2006; Knowlton et al. 1996; Packard et al. 1989; Seger & Spiering, 2011) as both involve stimulus-response associations. Specifically, it refers to the associations between individual stimuli and response (or behavior, action) of which the strength may alter depending on the outcome or the value of the reward received (Eichenbaum, 1992; Seger & Spiering, 2011; Tapp, 1969). According to the Law of Effect, if the outcome is satisfactory for a response given to a stimulus (e.g., reward), the likelihood to produce the same response increases (Tapp, 1969). Conversely, if the outcome is aversive or gives discomfort, the likelihood to produce the same response decreases (Tapp, 1969). For instance, when a homework (stimulus) was given by a teacher, if the student does the

homework (behavior) and consequently gets a bonus point (reward) in the course, the behavior of doing homework can be reinforced. As the rewarding process continues, the likelihood to repeat the same behavior increases and can eventually become a habit. On the contrary, if the teacher shouts at the student because he did not do the homework correctly, then the likelihood to do homework regularly can actually decrease.

The similar logic could also be applied to learning during the TI task and it explains indeed the mechanism of how the strategy “A is always rewarded and E is never rewarded” could be used for pairs including end items with unambiguous reinforcement histories. Specifically, the positive or negative feedbacks (e.g., smiley face vs upset face) received for choosing the item A or E respectively, increases the likelihood to always choose the item A or avoid the item E after enough number of repetitions of trials. However, following the task design, items B, C and D were the winner items or the loser items the same number of time, as their winning or losing depends on the pair that they were paired with. Therefore, as their reinforcement histories are ambiguous, the simple reward-based learning which could explain performances on pairs including end items is not sufficient to explain successful performances of hippocampus-lesioned animals on inner pairs observed in many studies (e.g., Buckmaster et al., 2004; Bunsey & Eichenbaum, 1996; Devito et al., 2010; Dusek & Eichenbaum, 1997). However, the presence of an always rewarded and never rewarded item in pairs, could alter also the strength of individual associations between inner items and rewards (Frank et al., 2003) and this could be explained by a more complex reward-based strategy. In fact, the question of how reinforcement histories could support the performance on all training pairs of the TI

task has been explained by the value transfer theory (VTT), which was supported by data from pigeons trained and tested on the TI tasks (Von Fersen et al., 1991).

1.4.2 Value Transfer Theory

According to the VTT proposed by Von Fersen et al. (1991), each stimulus acquires a strength value based on reinforcement histories via the feedback provided during training. This strength value for individual stimuli indicates the strength of the association of this stimulus with the reward (positive outcome). Therefore, similar to the examples provided above, the strength value of a stimulus increases the likelihood of choosing the same stimulus in a particular pair. A stimulus could gain a value either by being rewarded in a pair, or through the partial transfer of the value from the stimulus paired with it (Von Fersen et al. 1991; Wynne, 1995). The concept of value transfer could be illustrated in real life through generalizations (see Zentall, 2004 for a discussion of value transfer mechanisms). For instance, a child could be afraid of clowns due to a frightening spectacle experienced repeatedly and he/she could develop a fear for any spectacle performer wearing costumes. Here, the value transfer could be represented by the fear developed to a stimulus which was not directly associated with a frightening experience.

Based on the direction of the value transfer, Von Fersen et al. (1991) proposed three different versions of the VTT. Accordingly, value could be transferred (1) always from the rewarded to the non-rewarded stimulus, (2) from the nonrewarded to the rewarded stimulus, or (3) value transfer could occur in both directions, leading to slightly different patterns of performance. Among these models, the first one was the best fitting model for the pigeon data in Von Fersen et al. (1991) and consistent with this model, it was shown that the value transfer occurs always from the rewarded to

non-rewarded item (Clement et al., 1998; Vasconcelos, 2008; Zentall & Sherburne, 1994).

The VTT originally was proposed to explain the reinforcement mechanisms that could support performances in the TI task (Von Fersen et al., 1991). Zentall & Sherburne (1994) tested this theory in pigeons and provided an empirical evidence for the value transfer, specifically from the rewarded stimulus to non-rewarded stimulus by using a simultaneous discrimination task which precluded an explanation by relational learning. Specifically, pigeons were trained with two non-overlapping pairs of items with different hues (e.g., A vs B, C vs D). The item A was always rewarded on all trials whereas the item B was never rewarded (symbolically shown as $A_{100}B_0$). On the other hand, the item C was rewarded on trials with 50% probability whereas the item D was never rewarded (symbolically shown as $C_{50}D_0$). Following the training phase, pigeons were tested on the pair BD. Considering the VTT, the directly acquired strength value of the item A would be higher than the one of the item C due to the probabilities determining their associations with the reward. Therefore, a value transfer from the item A to the item B and from the item C to the item D could be expected. Accordingly, pigeons should be able to choose B over D otherwise they should be unable to discriminate B from D as both were never rewarded. As expected, pigeons chose the stimulus B on 78% of 32 test trials (i.e., B vs D) on the first session and 74.6% of all 32 test trials (i.e., B vs D) on the second session. These findings therefore confirmed the value transfer from the reinforced to non-reinforced stimulus.

Such a value transfer mechanism could be explained by second-order conditioning, a.k.a. higher-order conditioning (Vasconcelos, 2008; Wimmer & Shohamy, 2011; Zentall, 2004) in which the striatum plays a critical role with its connections to amygdala (McDannald et al., 2013; Setlow et al., 2002; Wimmer &

Shohamy, 2011; see Martin-Soelch et al., 2007 for a review). Second-order conditioning refers to the repeated pairing of a stimulus, initially conditioned to elicit a specific response, with a new neutral stimulus (Martin-Soelch et al., 2007). Although the neutral stimulus is not previously associated with the conditioned response, the association between the initially conditioned stimulus and new neutral stimulus allows the new stimulus to elicit the same response. For instance, a tone (i.e., neutral stimulus) could be repeatedly associated with food (i.e. unconditioned stimulus) and when it is presented alone, it could elicit the salivation (i.e., first order conditioning). Then, the tone (i.e, primary conditioned stimulus) eliciting the salivation (i.e., conditioned response) could be repeatedly paired with the light (i.e., new neutral stimulus) and the light alone (i.e., secondary conditioned stimulus) could predict also the salivation (i.e., conditioned response) through its association with the tone although it was never associated with food before.

The same mechanism could be also applied to explain value transfers in the TI (Zentall, 2004). For example, when choosing the stimulus A, is repeatedly followed by a reward, it might become the primary conditioned stimulus and the stimulus B paired with the primary conditioned stimulus A, might become the secondary conditioned stimulus. Therefore, although, the stimulus B is not rewarded when it is chosen against the stimulus A, after enough repetition, it might become the predictor of the reward through its association with the rewarded stimulus A. For this reason, the strength of the association between the item B and the reward could be slightly enhanced with the value transfer from the stimulus A. Therefore, as suggested by the VTT (Von Fersen et al., 1991) when the sequence between items ($A > B > C > D > E$) is considered in the TI task, the value transfer might occur from a stimulus at the higher

end of the sequence to the adjacent stimulus at the lower end when a correct choice was given for an overlapping premise pair (Frank et al., 2003).

When the second-order conditioning is considered as mechanism for all overlapping pairs as explained for the pair AB, a gradient of strength values could be anticipated based on both direct and transferred values. For instance, the stimulus B gains value when it is presented with the stimulus C as it is rewarded item in the pair B+C-, but it also gains a small amount of value from the value of the rewarded stimulus A in the pair A+B- (Wynne, 1995). Similarly, the stimulus C gains a value when it is paired with the stimulus D as the stimulus C is the rewarded item, but the value transfer also occurs from the stimulus B to the stimulus C increasing its strength value slightly when they are paired together (Frank et al., 2003; Vasconcelos, 2008). Therefore, thanks to the value transfer from the stimulus A to B, the strength value of the stimulus B becomes slightly higher than the one of the stimulus C, and thanks to the value transfer from the stimulus B to C, the strength value of the stimulus C becomes slightly higher than the stimulus D (Frank et al., 2003). Therefore, it might be possible to correctly choose the item B in the pair BC and the item C in the pair CD because eventually, during a presentation of a pair, the choice is driven by the difference between values of two stimuli presented as a pair (Von Fersen et al., 1991). Hence, these value transfer mechanisms explained how the inner pairs including items B, C and D could be learned through reinforcement histories despite the fact that they are equal number of presentations where they were rewarded or not rewarded.

1.4.2.1 Pattern of performances predicted by the VTT. Although Von Fersen (1991) et al. did not test empirically the value transfer mechanisms to support their model, they compared the behavioral findings of pigeon data in the TI tasks with the pattern of performances predicted by the VTT.

The pattern of performances was revealed based on a number of computations. The strength value was calculated for each stimulus by including the direct value and the value transferred with the weighing factor between 0 and 0.5 in the equation¹ (Von Fersen et al., 1991). For simplicity, the direct value was considered as equal to 2 if the stimulus is always rewarded (i.e., stimulus A), 1 if the stimulus is rewarded half of the time (i.e., stimuli B, C, D) and 0 if the stimulus is not rewarded at all (i.e., stimulus E). Consistent with the sequence of items, the computations for individual stimuli revealed a ranking of values as follows: $V_A > V_B > V_C > V_D$ (Vasconcelos, 2008; Von Fersen et al. 1991). The difference between strength values of two stimuli for each premise pair was calculated which revealed value difference ranks as follows: $(V_A - V_B) = 2$, $(V_B - V_C) = 3$, $(V_C - V_D) = 4$, $(V_D - V_E) = 1$, where V represents the value of the individual stimuli. In this ranking, the higher number of ranks indicated the smaller differences between strength values of items and higher difficulties to give correct choice for the pair in question (Von Fersen et al. 1991).

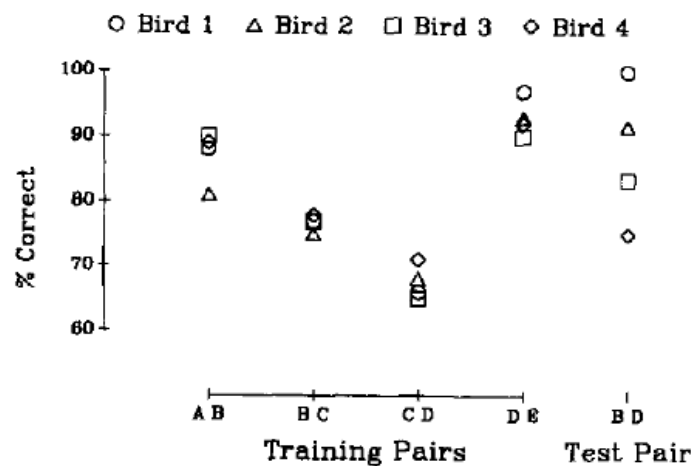
The pigeon data in the TI task with five items supported the VTT by showing the pattern of performance predicted by the model (Von Fersen et al.; 1991). The percentage of correct choices of all pigeons were above 80% on premise pairs during the last session of the training. According to the analysis of performance with premise pairs in the testing phase, the number of correct choices did not differ between the end pairs AB and DE (Figure 3). Similarly, performance with the inner pairs BC and CD did not differ either. However, performance with the end pairs was significantly higher than that with inner pairs, revealing a U-shaped accuracy curve (i.e. serial position effect). This could be explained either by the VTT because AB and DE were

¹ The equation is as follows: $V_i = R_i + a * V_{i+1}$ where V_i : the strength value of the stimulus i , R_i : the direct value component of the stimulus i , a : the weighing factor and V_{i+1} : the value of the stimulus rewarded when presented with the stimulus i (Von Fersen et al., 1991).

the first two pairs indicated to be the best solved pairs or by the use of a simpler reward-based strategy (i.e., A is always rewarded and E is never rewarded). However, the model predicted the best performance on the pair DE (value difference rank = 1) and the worst one on the penultimate pair CD (value difference rank = 4) indicating an asymmetrical form in the curve which was also confirmed by the pigeon data (Figure 3).

Figure 3

Percentage of Correct Responses on Premise Pairs During the Training Phase and the Inference Pair BD in the Testing Phase



Note. Percentage of correct choices on the premise pairs and the test pair BD for each pigeon: Considering the last 10 sessions of training (10 trials for each pair per session) and all of 6 test sessions (2 trials for test pair BD per session). Note the asymmetrical form in the serial position effect predicted by the model. From Von Fersen et al. (1991).

The model also revealed that the strength value of the stimulus B is higher than the strength value of the stimulus D which suggested that the stimulus B can be selected over the stimulus D on the TI pair, although their strength values are relatively closer to each other in comparison to those of items A and E. Von Fersen et al. (1991)

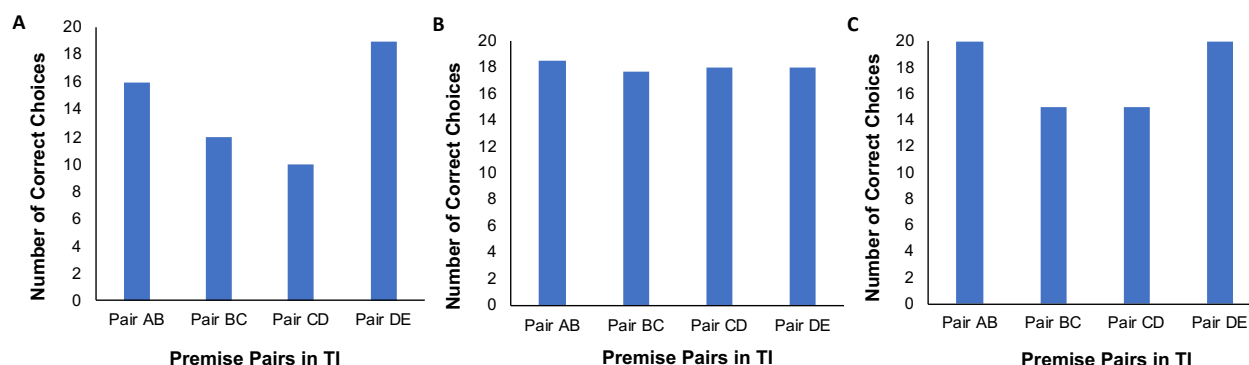
did not test the performances of pigeons on the pair AE. However, the number of correct choices of each pigeon on the inference pair BD was above chance level and therefore this finding was also consistent with the model.

Overall, empirical findings in Von Fersen et al. (1991) supported the theoretical model. They indicated that reinforcement-based learning could explain overall successful performances on premise pairs and lead to “transitive like patterns” at the behavioral level despite the absence of logical reasoning (i.e. if $B > C$ and $C > D$ then $B > D$) (Vasconcelos, 2008; Von Fersen et al., 1991; Wynne, 1995). However, this also indicated that it might be difficult to distinguish one strategy from another if the TI could be solved by both relational learning and reinforcement-based learning.

Nevertheless, some specific patterns of performance could be indicative of one or another. First, the presence of a U-shaped accuracy curve (i.e. serial position effect) could be considered an indicator of the likely use of reinforcement histories, rather than the use of relational representations (Figure 4A). Indeed, according to the relational model a similar performance should be observed for each premise pair. Therefore, a flat accuracy curves should be observed, because individuals should learn all premise pairs and the associated conditional relationships equally well (Figure 4B) (Moses et al., 2006, 2008; Solomon et al., 2011).

Figure 4

Example for Accuracy Curves Indicative of Reinforcement-based Learning and Relational Learning



Note. (A) Reinforcement-based learning: The bar graph illustrates a U-shaped accuracy curve and its asymmetrical form with the best performance on the pair DE and the worst performance on the pair CD. (B) Relational learning: The bar graph illustrates a flat accuracy curve with similar number of correct choices on all of premise pairs. (C) Relational learning with serial position effect: The bar graph illustrates a symmetrical U-shaped accuracy curve, with better performances on pairs AB and DE than BC and CD.

However, still even in relational account, it is possible to observe a serial position effect (Figure 4C) due to the fact that end pairs include the always rewarded item A or the never rewarded item E, in contrast to inner pairs in which the winning or losing of items are conditional (Vasconcelos, 2008; Wynne, 1998). Therefore, performance with the inner pairs and the test pairs without end items (such as the pair BD) are crucial in order to determine the possible reliance on the relational strategy to solve the TI task (Greene et al., 2006; Zalesak & Heckers, 2009). Importantly, the presence of a serial position effect alone may not be sufficiently informative to define unequivocally the strategy used to solve the TI task (Figures 4A and 4C). The

asymmetrical serial position effect (best performance on the end pair DE and worst on the penultimate pair CD) (Figure 4A) could be an additional control to distinguish the possible use of reinforcement histories according to the best fitting version of the VTT (Von Fersen et al., 1991).

In sum, reinforcement-based learning provides an alternative explanation to relational learning for the learning processes supporting performance in the TI task. Accordingly, both theories should be considered and particular attention should be given to a detailed examination of the specific patterns of performance in order to draw clear conclusions about the cognitive mechanisms involved in the TI task.

2. Present Study

Previous studies investigating allocentric spatial and color working memory suggested that the hippocampus-dependent learning and memory system may contribute to age-related declines in memory abilities for both spatial and non-spatial information (Klencklen et al., 2017a, 2017b). Therefore, initially I aimed to further investigate whether hippocampus-dependent learning and memory system is altered in elderly people outside the spatial domain. On the one hand, the TI task could be a convenient method to assess hippocampus-dependent learning and memory outside the spatial domain as suggested by the relational model of hippocampal function (Eichenbaum, 2001), which has been supported by neuroimaging studies (e.g., Greene et al., 2006; Nagode & Pardo, 2002; Zalesak & Heckers, 2009). On the other hand, lesion studies seemingly contrast with neuroimaging studies (e.g., Buckmaster et al., 2004; Devito et al., 2010; Dusek & Eichenbaum, 1997), suggesting that although the hippocampus may be involved in solving a TI task, it may not be necessary. Furthermore, the VTT (Von Fersen et al., 1991) also suggested that the TI task could be solved by relying on reward values of individual items which requires the

involvement of the striatum-dependent learning and memory system as the striatum is critically involved in both simple stimulus-response-outcome (e.g., reward) associations (Foerde et al., 2006; Knowlton et al. 1996; Packard et al. 1989; Seger & Spiering, 2011) and the higher-order conditioning (Martin-Soelch et al., 2007; McDannald et al., 2013; Setlow et al., 2002; Wimmer & Shohamy, 2011) that provided an explanation for the value transfer mechanisms (Vasconcelos, 2008; Wimmer & Shohamy, 2011; Zentall, 2004).

The first aim of my study was to decipher the learning strategy used to perform the TI task by young and older populations. The second aim of my study was to test the hypothesis of an impaired hippocampus-dependent learning and memory system in aging. In order to address these two aims, I performed detailed behavioral analyses both at the group and individual levels, taking in consideration the specific performance and response patterns described above. If the TI task is hippocampus-dependent, as suggested by relational model, and the hippocampus-dependent learning and memory system is impaired in aging, older individuals should perform overall worse than young individuals. Furthermore, depending on the level of impairment of hippocampus-dependent learning, their performances should be either similar across premise pairs or be better with end pairs. Given the known variability in performance observed in older individuals, group analyses need to be supported by statistical analyses at the individual level. Alternatively, older individuals could rely on the complex reward-based strategy (i.e., reward values of individual stimuli) with the contribution of the striatum-dependent learning and memory system, overall performances of young and older populations could be comparable and their pattern of performances across premise pairs could indicate a U-shaped asymmetrical curve.

At the individual level, they could perform above chance level with the end pairs, for which reinforcement histories are unambiguous.

Here, participants were first tested on a VD task shown to be hippocampus-independent (Gaffan, 1974; Malamut et al., 1984; Packard & McGaugh, 1992; Zola-Morgan et al., 1982) to assess whether both populations are able to discriminate visual items with different colors, and to control that motivational and procedural aspects of the task do not affect performance. Second, participants were tested on a conditional learning (CL) task which was designed with two overlapping premise pairs with three items (i.e., A+B-, B+C-). Therefore, task rules were similar for both the CL and TI task as both could be solved by either relational learning (i.e., if $A > B$ and $B > C$ then $A > C$) or reinforcement-based learning (i.e., A always wins C always loses). However, the CL task was more sensitive task than the TI task, for the use of the reinforcement-based strategy due to the absence of pairs without end items with unambiguous reinforcement histories. Hence, the CL task served as an intermediary and a second control task before deciphering the strategy used in the TI task and allowed to investigate how well older population was able to perform with the less stringent task with a greater accessibility to the reinforcement-based strategy. Finally, participants were tested on the TI task with five items.

3. Methods

3.1 Participants

22 healthy young adults (11 females) aged 20-30 years ($M = 25.8$, $SD = 2.5$) and 12 healthy older adults (7 females) aged 67-79 years ($M = 71.9$, $SD = 3.6$) took part in the study. They were recruited via personal connections, email postings on social networks and flyers distributed through local regions. The exclusion criteria were visual perception disabilities (i.e., color blindness), neurological medication and a

history of neurological or psychiatric disease (i.e. Parkinson's disease, Alzheimer disease, dementia). All participants were assessed based on a short health questionnaire and neuropsychological tests (described in section 3.2) prior to testing. One old participant was included in the study despite his vision problem as he performed above chance level on the VD task, which indicated that he was able to discriminate different visual stimuli.

Participants were tested in 4 sessions of approximately 1 hour each on separate days. Sessions were scheduled based on participants' availabilities between Monday and Friday from 8:30 A.M. to 4:00 P.M. All participants gave written informed consent prior to beginning the study and were compensated monetarily for their participation. Human subjects research was approved by the Cantonal Ethics Committee for Human Research and was in accordance with the code of ethics of the World Medical Association (Declaration of Helsinki) for experiments involving human subjects in research.

3.2 Neuropsychological testing

Neuropsychological testing included the following assessments: general cognitive status with the mini Mental State Examination (MMSE) (Folstein et al., 1975); the Progressive Matrice-12 (Raven et al., 2003); the Vocabulary, Digit Spans, Arithmetic and Similitude sub-tests from the Wechsler Adult Intelligence Scale-IV (WAIS-IV) (Wechsler, 2008); color vision with the Ishihara test (Ishihara, 1917); and the Corsi Block-Tapping test Forward and Backward (Corsi, 1972).

3.3 Procedure

Participants were tested on four separate days. On the first day, they first responded to a short health questionnaire. Then, they performed the VD task and half of the neuropsychological tests. On the second day, participants performed the CL

task with 3 items and the rest of the neuropsychological tests. On the third day, participants performed the Probabilistic Classification Learning Task. On the fourth day, they performed the TI task with 5 items. For my Master thesis, the VD, the CL and the TI with 5 items tasks were taken into consideration. As the present study focuses on the investigation of learning strategies in aging in the TI task thought to be hippocampus-dependent (Greene et al., 2006; Nagode & Pardo, 2002; Zalesak & Heckers, 2009), the Probabilistic Classification Learning Task thought to be hippocampus-independent (Knowlton et al. 1996) will be considered in future reports.

All experimental tasks were performed on a transportable touchscreen tablet and responses were automatically recorded by the device. During testing, the screen was filmed with a digital video camera in order to be able to analyze the participants' performance in case of technical problems. During the whole testing procedure, the experimenter remained seated and wore dark sunglasses in order to preclude participants from attending to her eye gaze for clues as to the rewarded items. Experiences took place in a quiet room at the University of Lausanne (young participants) or near the home of older participants.

3.3.1 Visual Discrimination Task

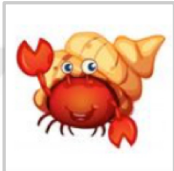
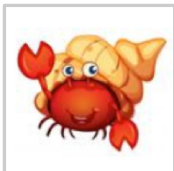
The VD task was used as a control task to measure the participants' ability to use a touchscreen tablet, to distinguish different colored items, and to learn and remember non-conditional relationships between stimuli.

The task included two training phases and two test phases. During the first training phase, participants were repeatedly presented with two non-overlapping pairs of images (A vs B; C vs D). The left/right position of stimuli and the order of pairs to be presented were determined in a pseudo-random manner. For each pair, one item was predetermined to be always the “winner”, whereas the other item was always the

“loser”. For example, in the pair presenting a starfish and a crab, the starfish was always the winner; in the pair presenting a sea horse and an oyster, the sea horse was always the winner (Figure 5).

Figure 5

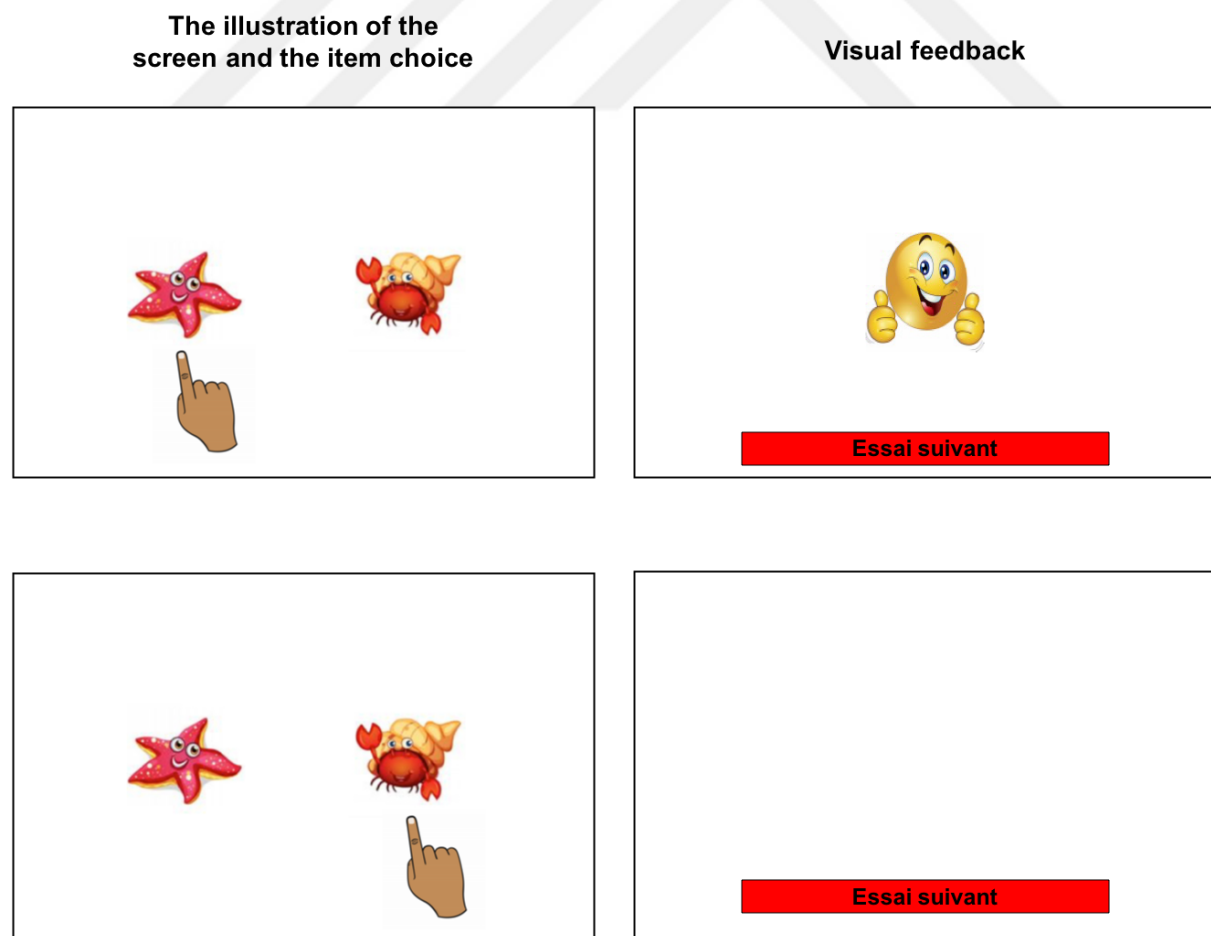
Examples of Pairs of Stimuli Presented in the VD Task

Visual Discrimination task			
Phase	Pairs	Winner	Loser
Training phase	A vs B	 A	 B
	C vs D	 C	 D
Testing phase	A vs D	 A	 D
	C vs B	 C	 B

Participants were instructed to touch the strongest or the winner image, and were provided with an example to facilitate the comprehension of the game. When necessary during the whole training procedure, they were encouraged to try even if they did not think that they knew which image might be the winner. The task was not time limited. Therefore, participants took as much time as they needed to make a choice. When participants chose the correct image, a smiley face appeared on the screen which was accompanied also with verbal feedback such as “*Bravo!*”, “*Yes!*”, “*It’s correct!*”. When the response was wrong, the screen was void of image accompanied again with verbal feedback such as “*No*”, “*It does not matter*” (Figure 6).

Figure 6

Illustration of the Screen and the Choice of Items During the Training Phase of the VD Task; Visual Feedbacks for Correct vs Incorrect Choices



Note. In this illustration, the starfish (item A) was presented against the crab (item B). The item indicated by the finger icon represented the item chosen for this presentation. The smiley face indicated that item A was the correct choice and the screen void of image signified that item B was the incorrect choice for this pair. The button “Essai suivant” appeared on the screen to allow the participants to pass to the following trial after receiving the visual feedback.

During this phase, participants were expected to learn which items were always the winners or losers by trial and error through the given feedbacks. After 10 presentation of each premise pair, the first testing phase was initiated with the single presentation of each test pair (A vs D and C vs B). These pairs consisted of items that were not previously associated with each other (e.g., the sea horse which was always the winner item in the training pair with the oyster, and the crab which was always the loser item in the training pair with the starfish). During this phase, no specific instruction was given, and no visual or verbal feedback was provided. Participants were therefore tested in their ability to use what they have learned during training in novel situations: the starfish and the sea horse always win; the crab and the oyster always lose.

After completion of the initial training and test phases, the second training and test phases were carried out exactly as explained above. All choices given for each pair during all of four phases were automatically recorded.

3.3.2 Conditional Learning Task

The CL task which was designed with two overlapping premise pairs following the similar rules to those of the TI task, served as an intermediate and a second control task before deciphering the strategy used in the TI task. Specifically, it allowed to determine how well older population was able to perform when the reinforcement-based learning strategy is more accessible than relational learning, due to the absence of pairs free of end items with unambiguous reinforcement histories.

The CL task was comprised of two learning phases and two test phases. At the beginning of the task, participants were informed that this task was similar to the previously completed task (VD task) but a little bit different. During the first training phase, participants were repeatedly presented with two overlapping premise pairs (A vs B; B vs C) (Figure 7). The left/right position of stimuli and the order of pairs to be presented were determined in a pseudo-random manner. For each pair, one item was predetermined to be the “winner” item, whereas the other item was the “loser”.

Figure 7

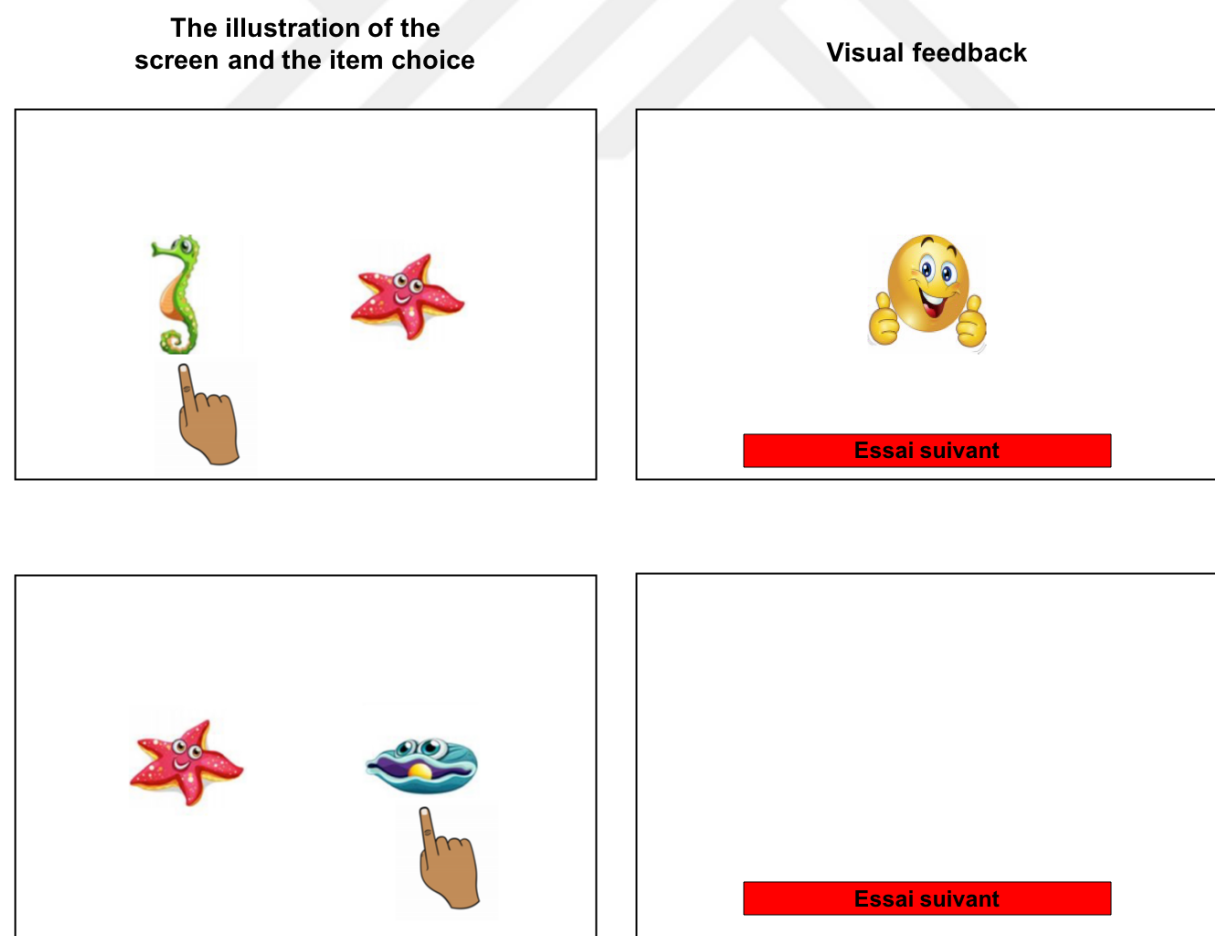
Examples of Pairs of Stimuli Presented in the CL Task

Conditional Learning task			
Phase	Pairs	Winner	Loser
Training phase	A vs B	 A	 B
	B vs C	 B	 C
Testing phase	A vs C	 A	 C

Participants were instructed to choose the strongest or the winner item. They were first presented an example of a trial and when necessary, encouraged to try even if they did not think that they knew which item might be the winner. The task was not time limited. Therefore, they took as much time as they needed to make a choice. When the choice was correct, a smiley face appeared on the screen and was accompanied by a verbal feedback such as “*Bravo!*”, “*Yes!*”, “*It’s correct!*”. When the choice was incorrect, the screen was void of image and accompanied by a verbal feedback such as “*No*”, “*It does not matter*” (Figure 8).

Figure 8

Illustration of the Screen and the Choice of Items During the Training Phase of the CL Task; Visual Feedbacks for Correct vs Incorrect Choices



Note. In this illustration, the sea horse (item A) was presented against the starfish (item B) and then the starfish (item B) was presented against the oyster (item C). For each pair, the item indicated by the finger icon represented the item chosen for the presentation in question. The smiley face indicated that item A was the correct choice for the pair AB and the screen void of image signified that item C was incorrect choice for the pair BC. The button “Essai suivant” appeared on the screen to allow the participants to pass to the following trial after receiving the visual feedback.

After 10 presentations of each premise pair, the first testing phase was initiated with a single presentation of a previously non-trained pair (A vs C) (Figure 7). During testing, participants did not receive any specific instruction, or verbal or visual feedback concerning their responses. After the completion of the first training and test phases, the second training and test phases were carried out exactly as explained above. For older individuals whose performances were exceptionally poor on their first try, the task was repeated once again. All choices given for each pair during all of four phases were automatically recorded.

During the training phases, item A was predetermined to be the winner when paired with item B, while item B was predetermined to be the winner when paired with item C. For instance, the sea horse was the winner when presented against the starfish but the starfish was the winner when presented with the oyster (Figure 7). On the one hand, participants could either pay attention to item B and learn by trial and error when item B would win or lose (Figure 8). On the other hand, they could just learn that “A is always the winner and C is always the loser” by relying on unambiguous reinforcement histories of the items A and C without learning about item B (Figure 8). Thus, both strategies could support the performance on testing phases. Participants could correctly choose item A as the winner, when it was presented against item C by organizing items into a hierarchical order ($A > B > C$) and making inference based on

learned conditional relationships (if $A > B$ and $B > C$, then $A > C$). Alternatively, they could show the same performance by learning that “A is always the winner and C is always the loser”. In sum, both relational learning and reinforcement-based learning could be used in the CL task.

3.3.3 Transitive Inference Task with Five Items

The TI task with five items was used firstly, to decipher the learning strategy used to perform the TI task by young and older populations; secondly, to test the hypothesis of an impaired hippocampus-dependent learning and memory system in aging.

The TI task comprised three parts. The first part included two alternating training and test phases. During the first training phase, participants were repeatedly presented with four overlapping premise pairs (A vs B, B vs C, C vs D, D vs E) (Figure 9). The left/right position of stimuli and the order of pairs to be presented were determined in a pseudo-random manner. For each pair, one of the items was predetermined to be the “winner” and the other item was the “loser”.

Figure 9

Examples of Pairs of Stimuli Presented in the TI Task with Five Items

Transitive Inference task with five items			
Phase	Pairs	Winner	Loser
Training phase	A vs B	 A	 B

	B vs C	 B	 C
	C vs D	 C	 D
	D vs E	 D	 E
Testing phase	A vs C	 A	 C
	A vs D	 A	 D

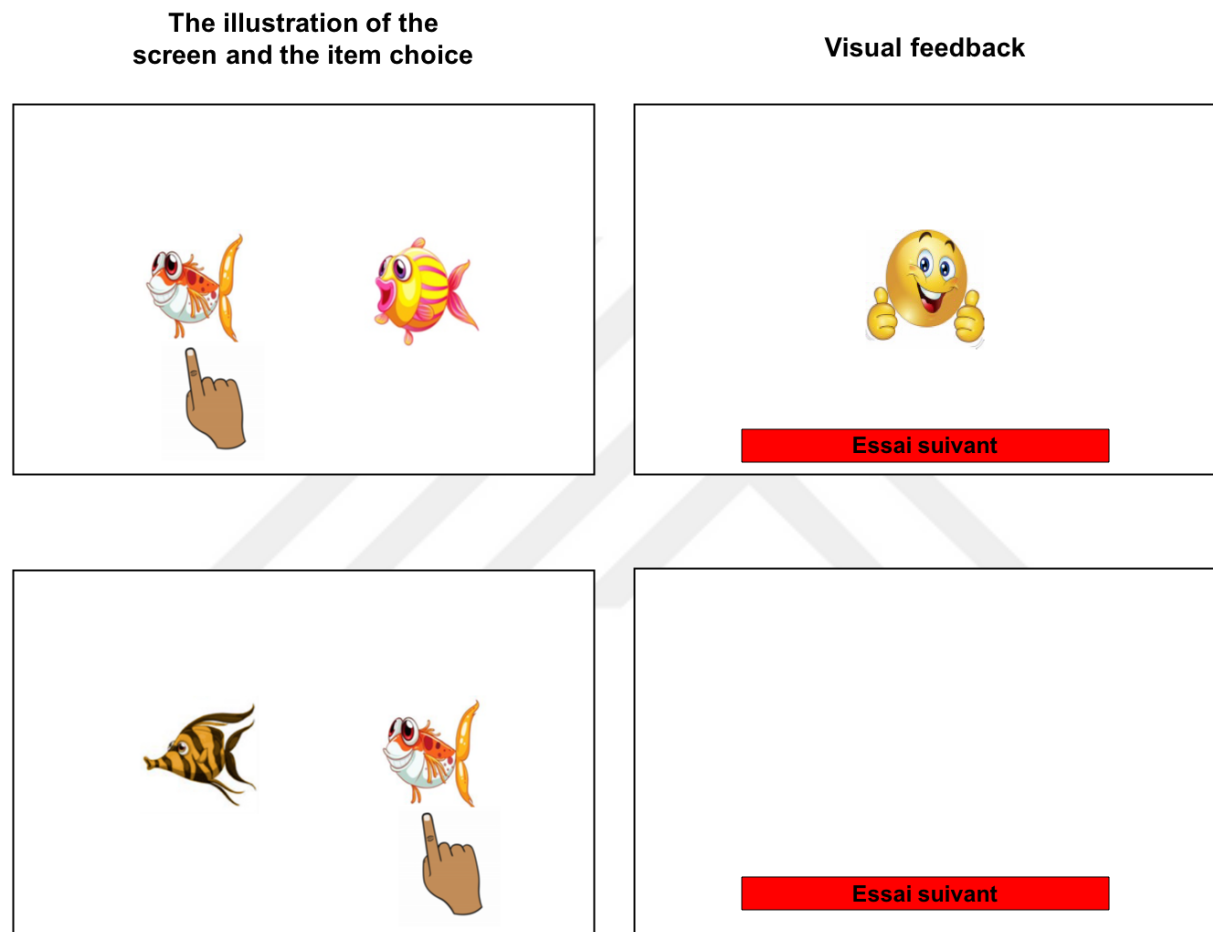
	A vs E	 A	 E
	B vs D	 B	 D
	B vs E	 B	 E
	C vs E	 C	 E

Participants were instructed to choose the strongest or the winner item. They were presented an example of trial and when necessary, encouraged to try even if they did not think that they knew which item may be the winner. The task was not time limited. Therefore, they took as much time as they needed to make a choice. When the choice was correct, a smiley face appeared on the screen and was accompanied with a verbal feedback such as “*Bravo!*”, “*Yes!*”, “*It’s correct!*”. When the choice was

incorrect, the screen was void of image and accompanied again with a verbal feedback such as “No”, “*It does not matter*” (Figure 10).

Figure 10

Illustration of the Screen and the Choice of Items During the Training Phase of the TI Task; Visual Feedbacks for Correct vs Incorrect Choices



Note. The screen at the top illustrates the presentation of item C against item D. The screen at the bottom illustrates the presentation of item B against item C. For each pair, the item indicated by the finger icon represented the item chosen for the presentation in question. The smiley face indicated that item C was the correct choice for the pair CD and the screen void of image signified that item C was the incorrect choice for the pair BC. The button “Essai suivant” appeared on the screen to allow the participants to pass to the following trial after receiving the visual feedback.

After 10 presentation of each premise pair, a single trial of a test pair (B vs D) was presented. As in all test phases of other tasks, this test pair was novel for participants as it included items that had not been presented together before. During testing on this pair, participants did not receive any specific instruction or visual or verbal feedbacks. After this trial, the task continued with the second series of training and test phases as described above. At the end of the first part, participants were told to do the same as before. At the beginning of the third part, participants were informed that they would see the same images (sea animals) on the screen and they had to touch the one which was the strongest but this time the computer would not tell them if their answer was correct or wrong. In this phase, participants were tested on a single trial for all non-overlapping test pairs (A vs C, A vs D, A vs E, B vs D, B vs E, C vs E) (Figure 9). They did not receive any verbal or visual feedback. All choices given for individual training and test pairs were automatically recorded.

During the training phases, items B, C and D were the winners half the time and the losers half the time (Figure 9). Therefore, their reinforcement histories were ambiguous. In addition, their winning or losing were dependent on the item that they were presented with (i.e. C loses in presence of B but wins in presence of D) which made the relationships to be learnt between training pairs “conditional” (Figure 6). Therefore, participants could potentially learn by trial and error the context (i.e., premise pair) in which an item wins or loses (Greene et al., 2006). However, similar to items A and C in the CL, item A was always the winner item and item E was always the loser during training in the TI (Figure 9). Therefore, alternatively, participants could rely on unambiguous reinforcement histories especially when they were presented with the training pairs AB and DE (Vasconcelos, 2008; Von Fersen et al., 1991). Similarly, both learning strategies could support performance on test pairs. After

learning conditional pairs, individuals could further organize items into a hierarchical order ($A > B > C > D > E$) (Dusek & Eichenbaum, 1997; Greene et al., 2006) and they could give correct choices by making inferences based on learned conditional relationships (e.g., if $A > B$, $B > C$, $C > D$, $D > E$, then $B > D$). In particular, the performance on the pair BD could be considered a reliable measure of the ability to perform TI as other test pairs included either item A which was always the winner or item E which was always the loser, while items B and D that were “winners” or “losers” the same number of times (Dusek & Eichenbaum, 1997; Greene et al., 2006). For the same reason, correct choices on other test pairs including items A and E could be made by learning that “A is always the winner and E is always the loser” (Dusek & Eichebaum, 1997).

In sum, similar to the CL, both learning relationships between conditional pairs and learning reinforcement histories could support performances in the TI task. However, contrary to the CL, the TI included training and test pairs free of always rewarded and never rewarded items, which may allow to distinguish different patterns of performance that are indicative of specific learning strategies in the TI.

3.4 Data Analysis

For all the tasks, I first determined whether and how well participants correctly chose the item that was predetermined to be the winner in training and test pairs. The total number of correct choices of each participant was considered separately for the training and test phases of each task. For both the VD and CL tasks, the number of correct choices in the training phase (40 trials in total) and test phases (4 trials for the VD, 2 trials for the CL) were considered. In contrast, the TI comprised two training phases (including 80 trials each, interspersed with two trials of the pair BD) and a single separate test phase (6 trials) at the end. Therefore, total numbers of correct

choices were calculated separately for the first training phase, the second training phase, and the test phase. The number of correct choices for trials with each premise pair was also analyzed separately (20 trials per pair for each phase), in order to inform about the possible cognitive processes supporting task performance, as described in the introduction. Additionally, the number of correct choices on the TI pair (B vs D) included the choices on all trials presented in all of three parts.

As the CL task was repeated for older individuals whose performances were exceptionally poor on their first try, a new variable called “best session” was constructed. If individuals whose total number of correct choices was higher on their second try than their first try, the second session was considered as the best session. Otherwise, the first session was considered as the best session. For all other young and older individuals who did not perform the task twice, the number of correct choices in the only session they performed, was considered as their best session for group comparisons. Therefore, the test and training phases were considered as described above for both the first and the best sessions of the CL task.

In the present study, analyses at the group level were combined with analyses at the individual level. For all these analyses, I first focused on the data from training phases rather than test phases because there was a limited number of test trials precluding a meaningful statistical analysis at the individual level. For the TI task, I focused my analyses on the second phase of testing, which provided more distinctive patterns of performance.

3.4.1 Analysis at the group level

I first aimed to compare overall performance in the training phases of all tasks in order to investigate whether and how the performance of young and older populations may differ in the CL and TI tasks, which are both thought to be

hippocampus-dependent. Second, because hippocampus-independent reinforcement-based strategies may also be used to solve the TI task, I aimed to further investigate the performance of both groups across premise pairs during the training phase of the TI to try to get an initial insight about the possible strategies used to solve the task. If the accuracy curves for the four premise pairs were flat, as is expected from using a hippocampus-dependent relational strategy, or a U-shaped asymmetrical form, as is expected from using a hippocampus-independent reinforcement-based strategy.

Before performing the analyses indicated above, a preliminary analysis was performed to test the assumptions of parametric tests. The Shapiro-Wilk test, that enables to test for the normality of data (Field, 2009), showed that for the majority of measures, data from older individuals were normally distributed whereas data from young individuals were not normal. Specifically, for the older group, only the distribution of the number of correct choices in the training phases of the VD ($W(12) = .842, p = .029$) and the number of correct choices on the pair AB ($W(12) = .753, p = .003$) were non-normal. For the young group, the total number of correct choices in the training phases of the VD ($W(22) = .763, p < .001$), CL ($W(22) = .813, p = .001$) and TI ($W(22) = .474, p < .001$) and the number of correct choices on all premise pairs AB ($W(22) = .238, p < .001$), BC ($W(22) = .670, p < .001$), CD ($W(22) = .556, p < .001$), DE ($W(22) = .313, p < .001$) were non-normally distributed. In addition, The Levene's test indicated unequal variances for the number of correct choices in the first session of the CL ($F(1,32) = 17.07, p < .001$), and in the training phase of the TI, ($F(1,32) = 4.69, p = .038$). Therefore, the homogeneity assumption which is especially important for between-subject designs was also violated (Field, 2009).

Parametric analysis such as independent t-tests and ANOVAs are considered to be robust with nonnormality especially when there are only moderate deviations (Gavin, 2008; McDonald, 2009; Schmider et al., 2010). However, according to recent findings, when the non-normality is combined with the violation of the homogeneity assumption, independent t-test can provide a poor control for Type I error (Kellermann et al., 2013; Nguyen et al., 2016). In addition, under the conditions where the distribution is not relatively symmetrical the use of nonparametric alternative could provide power advantages (Bridge & Sawilowsky, 1999). Moreover, there is evidence showing that one-way repeated measures ANOVA is not robust at all even with higher sample size, which suggested that the robustness against nonnormality mostly mentioned for designs with only between-subject factor is not generalizable to repeated measures designs (Oberfeld & Franke, 2013). Considering altogether the rather small and unequal sample sizes, the presence of nonnormality with relatively severe deviations for the young population and heterogeneous variances, it was reasonable to prefer nonparametric analyses for between group and within-group comparisons.

Therefore, I used the Mann-Whitney test, as a non-parametric alternative to independent t-tests, to compare the performance of older and young individuals. I used Friedman's ANOVA separately for young and older individuals, as an alternative to one-way repeated measures ANOVA, to test differences between performance on different premise pairs. As non-parametric post-hoc analysis, I used Wilcoxon signed-rank tests. All statistical analyses were performed with SPSS 25.0 software. Significance level was set at $p < 0.05$ for all analyses.

3.4.2 Analyses at the individual level

Although the analyses at the group level might be informative about group differences and learning strategies, they cannot be used to determine how individual participants performed or whether individuals whose total number of correct choices in training were above chance level were successful on the premise pairs in the CL and TI tasks. Hence, it is crucial to analyze not only the overall performance of each individual in the CL and TI tasks, but also to determine whether they performed above chance level for each training pair to inform about individual learning strategies. Chance level was calculated for 40 trials, 80 trials, 20 trials and 15 trials by using a chi-square goodness of fit test. Above chance performance was defined by a number of correct choices ≥ 27 over 40 trials ($\chi^2 (1) = 4.90, p = .027$), ≥ 49 correct trials over 80 trials ($\chi^2 (1) = 4.05, p = .044$), ≥ 15 correct trials over 20 trials ($\chi^2 (1) = 5.00, p = .025$), and ≥ 12 correct trials over 15 trials ($\chi^2 (1) = 5.40, p = .020$).

Performance above chance level in the CL was considered as informative about to ability to solve the task under conditions where it could be solved uniquely by the simple reinforcement-based strategy (i.e., A always wins C always loses) without necessarily learning conditional pairs. For the TI task, performance above chance level only on both end pairs was considered as an evidence either for impaired hippocampus-dependent relational learning or the use of simple-reinforcement-based learning which would not sufficient alone to support performances on inner pairs. Performance above chance level for all of four premise pairs were considered either as suggestive of learning all conditional relationships or complex value transfer mechanisms related to reward-based learning as in theory both could explain performances on inner pairs. However, similar performances on each premise pair

and better performances especially on end pairs could be in favor of the relational learning and reinforcement-based learning with value transfers, accordingly.

Finally, despite the absence of a sufficient number of trials to be considered for statistical analyses at the individual level, performance on the test pair BD were nevertheless considered as supportive evidence to interpret the results of the training phase. Individuals who performed above chance level on all premise pairs and gave correct choice for all of last three trials of the TI pair BD could be considered as successful on their ability to make inferences and considered as completely achieved the task. Therefore, their performances could indicate that these individuals were able to learn all the conditional relationships between premise pairs during the training phase, as well as to represent the hierarchical order of items ($A > B > C > D > E$) and making inferential judgments.

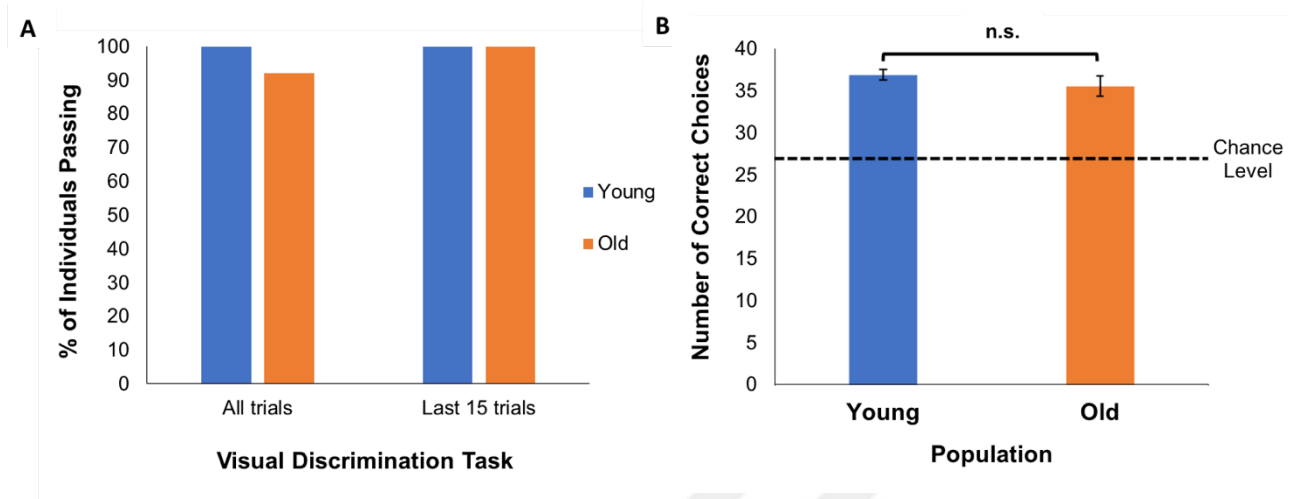
4. Results

4.1 Visual Discrimination Task

The percentages of young and older individuals who performed above chance level in the VD task are presented in Figure 11A. All of 22 young participants (100%) and 11/12 older participants (92%) performed the VD task above chance level when considering all 40 trials. However, the only older participant who was considered to have failed across all trials performed above chance level if we considered his performance within the last 15 trials. Consistently, the number of correct choices did not differ between young ($Mdn = 38.00$, $SD = 2.8$) and older ($Mdn = 37.00$, $SD = 4.2$) participants ($U = 108.00$, $z = -0.88$, $p = .389$, $r = -.15$; Figure 11B). Therefore, all the participants were able to use a touchscreen computer, discriminate different visual stimuli and learn and remember non-conditional relationships (e.g., A is always the winner in the pair AB and C is the winner in the pair CD).

Figure 11

Percentages of Young and Older Populations Passing the VD Task and Number of Correct Choices



Note. (A) Percentage of individuals passing the VD task: calculated considering performances above chance level over all trials and last 15 trials. (B) Number of correct choices in the VD task. Dashed lines indicate the chance level (27 correct choices over 40 trials). n.s.: not significant.

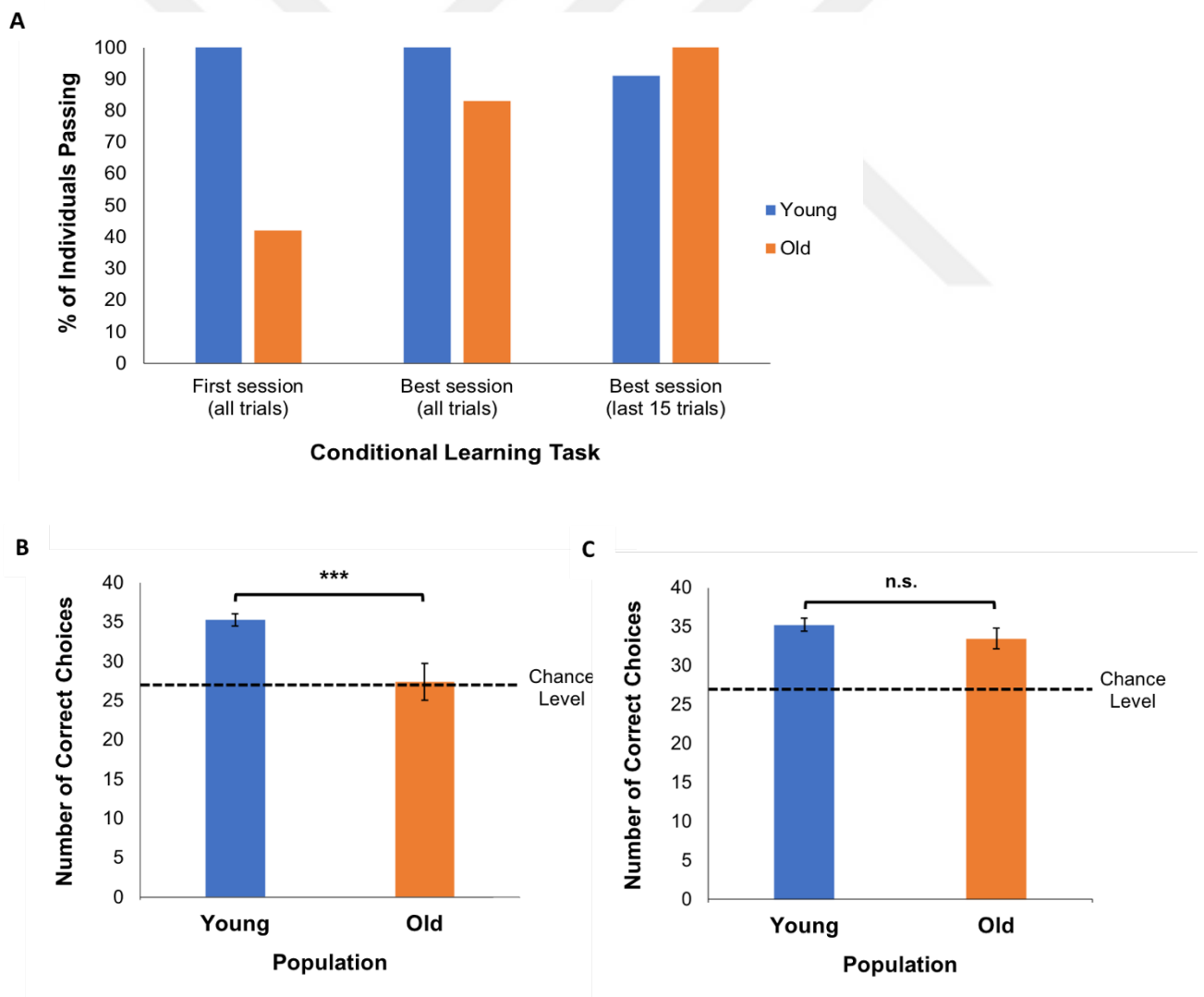
4.2 Conditional Learning Task

The percentages of young and older individuals who performed above chance level in the CL task are presented in Figure 12A. All of 22 young individuals (100%) performed above chance level over all 40 trials, whereas only 5/12 older participants (42%) performed above chance level. However, after a second series of 40 trials presented to some of older individuals, 10/12 older participants (83%) performed above chance level according to their best sessions (Figure 12A, for details see Table 1). When the last 15 trials of the best sessions of the CL tests were considered for all individuals, 12 older participants (100%) performed above chance level, whereas 20/22 young participants (91%) performed above chance level (Figure 12A).

In the first series of tests, the number of correct choices was lower for older participants ($Mdn = 25.50$, $SD = 8.1$) than for young participants ($Mdn = 37.00$, $SD = 3.8$) ($U = 47.00$, $z = -3.09$, $p = .001$, $r = -.53$; Figure 12B). When the best sessions were considered after the second series of tests, the number of correct choices did not differ between young ($Mdn = 37.00$, $SD = 3.8$) and old ($Mdn = 34.50$, $SD = 4.6$) participants ($U = 97.50$, $z = -1.26$, $p = .215$, $r = -.22$; Figure 12C).

Figure 12

Percentages of Young and Older Populations Passing the CL Task and Number of Correct Choices in the First and Best Sessions



Note. (A) Percentage of individuals passing the CL task: calculated considering performances above chance level over all trials of the first session and all trials and last 15 trials of the best session. (B) Number of correct choices in the first session of the CL task. (C) Number of correct choices in the best session of the CL task (i.e., for older population: considering the session with highest scores for each individual among the first and second series of the CL tests, for young population: considering the first series of the CL tests, see table 1 for details). Dashed lines indicate the chance level (27 correct choices over 40 trials). *** $p < .001$. n.s.: not significant.

The number of correct choices at the individual level in the CL task was indicated in Table 1. Among young participants, only S449 and S455 did not perform above chance level over last 15 trials although they were successful over all trials. Among older participants, in the first series of tests, five individuals (S492, S494, S495, S508, S509) who performed above chance level over 40 trials performed also above chance level over last 15 trials. Among other individuals who could not pass the chance level over 40 trials, only S487 and S491 could pass the chance level over last 15 trials. Six older individuals (S486, S488, S490, S491, S506, S507) who failed in the first series of tests, were presented with a second series of tests. Among them, all performed above chance level over 40 trials as well as last 15 trials except S490 who performed above chance only over last 15 trials. Lastly, after second series of tests, as revealed by best sessions all older individuals except two (S487 and S490) performed above chance level over 40 trials and however, their performances were above chance level over last 15 trials as those of other individuals of the group. These individual performances revealed a higher variability in performances and a slower learning for the most of older participants than young participants consistent with analyses at group level.

Table 1*Total Number of Correct Choices of Each Young and Old Individual in the CL Task*

Subjects	First series of tests		Second series of tests		Best session	
	All 40 trials	Last 15 trials	All 40 trials	Last 15 trials	All 40 trials	Last 15 trials
Young population						
S433	34	15	—	—	34	15
S434	28	14	—	—	28	14
S435	30	13	—	—	30	13
S436	37	15	—	—	37	15
S437	39	15	—	—	39	15
S438	36	15	—	—	36	15
S439	38	15	—	—	38	15
S440	39	15	—	—	39	15
S441	38	15	—	—	38	15
S443	35	15	—	—	35	15
S444	31	15	—	—	31	15
S445	38	15	—	—	38	15
S446	37	15	—	—	37	15
S447	36	15	—	—	36	15
S448	38	15	—	—	38	15
S449	29	11	—	—	29	11
S450	35	13	—	—	35	13
S451	38	15	—	—	38	15
S452	38	15	—	—	38	15
S453	38	15	—	—	38	15
S454	37	14	—	—	37	14
S455	27	10	—	—	27	10
Older population						
S486	25	11	33	13	33	13
S487	26	14	—	—	26	14
S488	22	7	29	12	29	12
S490	15	7	26	15	26	15
S491	25	12	40	15	40	15
S492	36	15	—	—	36	15
S494	38	15	—	—	38	15
S495	36	15	—	—	36	15
S506	18	9	38	15	38	15
S507	19	9	31	14	31	14
S508	35	15	—	—	35	15
S509	34	15	—	—	34	15

Note. Pattern of performances in the CL task at the individual level. Green cells: performances above chance level. Red cells: performances below chance level. Grey cells with a dash: individuals who did not receive a second series of tests. Best session for each older individual: the session with individual's highest scores among the first and second series of tests. Best session for each young individual: the

first series of tests (i.e., first session). Above chance performance: number of correct choices ≥ 27 over 40 trials and ≥ 12 correct trials over 15 trials.

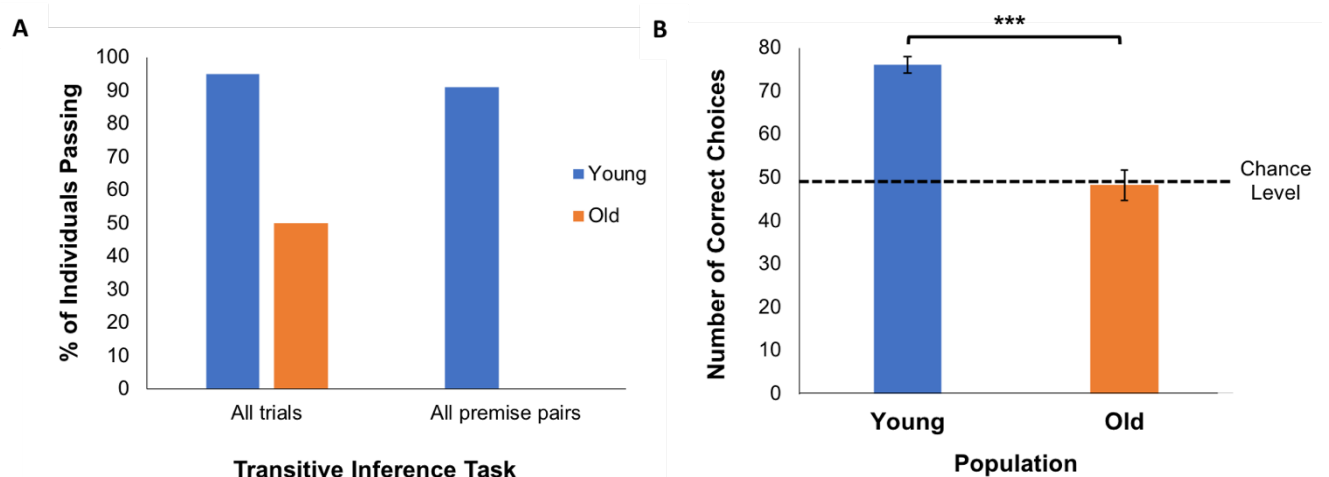
In sum, although age-related performance differences were observed at the beginning, both populations were able to pass the CL task but the learning was slower for older participants in comparison to young participants.

4.3 Transitive Inference Task

The percentages of young and older individuals who performed above chance level in the TI task are presented in Figure 13A. 21/22 young participants (95%) performed the TI task above chance level over all 80 trials, whereas only 6/12 older participants (50%) performed above chance level. However, the number of correct choices was lower for older participants ($Mdn = 47.00$, $SD = 12.1$) than for young participants ($Mdn = 79.00$, $SD = 8.9$) ($U = 8.00$, $z = -4.53$, $p < .001$, $r = -.78$; Figure 13B). Importantly, 20/22 young participants (91%) performed above chance level for each of the four training pairs over 20 trials (Figure 13A, for details see Table 3). In contrast, none of the 12 older participants performed above chance level on all of premise pairs (Figure 13A, for details see Table 3).

Figure 13

Percentages of Young and Older Populations Passing the TI Task and Number of Correct Choices



Note. (A) Percentage of individuals passing the TI task: calculated considering performances above chance level over all trials and on all of four premise pairs (B) Number of correct choices in the TI task. Dashed lines indicate the chance level (49 correct choices over 80 trials). *** $p < .001$.

Within the groups, the number of correct choices differed between premise pairs for older participants ($\chi^2(3) = 11.15, p = .008$), but not for young participants, ($\chi^2(3) = 7.52, p = .054$) although it was very close to being statistically significant. Test results for pair comparisons within each group were given in Table 2 and accordingly, number of correct choices on individual premise pairs was indicated in Graph 14.

For young individuals, the number of correct choices did not differ between pair AB ($Mdn = 20.00, SD = 4.3$) and pairs BC ($Mdn = 20.00, SD = 1.7$) or CD ($Mdn = 20.00, SD = 1.5$). Similarly, the total number of correct choices did not differ between the pair DE ($Mdn = 20.00, SD = 4.2$) and the pairs BC or CD. Lastly, the total number of correct choices were not different either between inner pairs BC and CD or end pairs AB and DE.

In contrast, for older participants, the number of correct choices was higher for the pair AB ($Mdn = 19.00, SD = 6.0$) than the pair BC ($Mdn = 10.00, SD = 3.5; T = 10.00, p = .021, r = -.47$) or the pair CD ($Mdn = 9.50, SD = 3.1; T = 3.00, p = .002, r = -.58$). However, the number of correct choices did not differ between the pair DE ($Mdn = 11.50, SD = 6.2$) and the pair AB or the pair BC or the pair CD. Similarly, the number of correct choices did not differ between the pair BC and the pair CD.

Table 2*Results of Wilcoxon Signed- rank Test for Pair Comparisons Within Each Population*

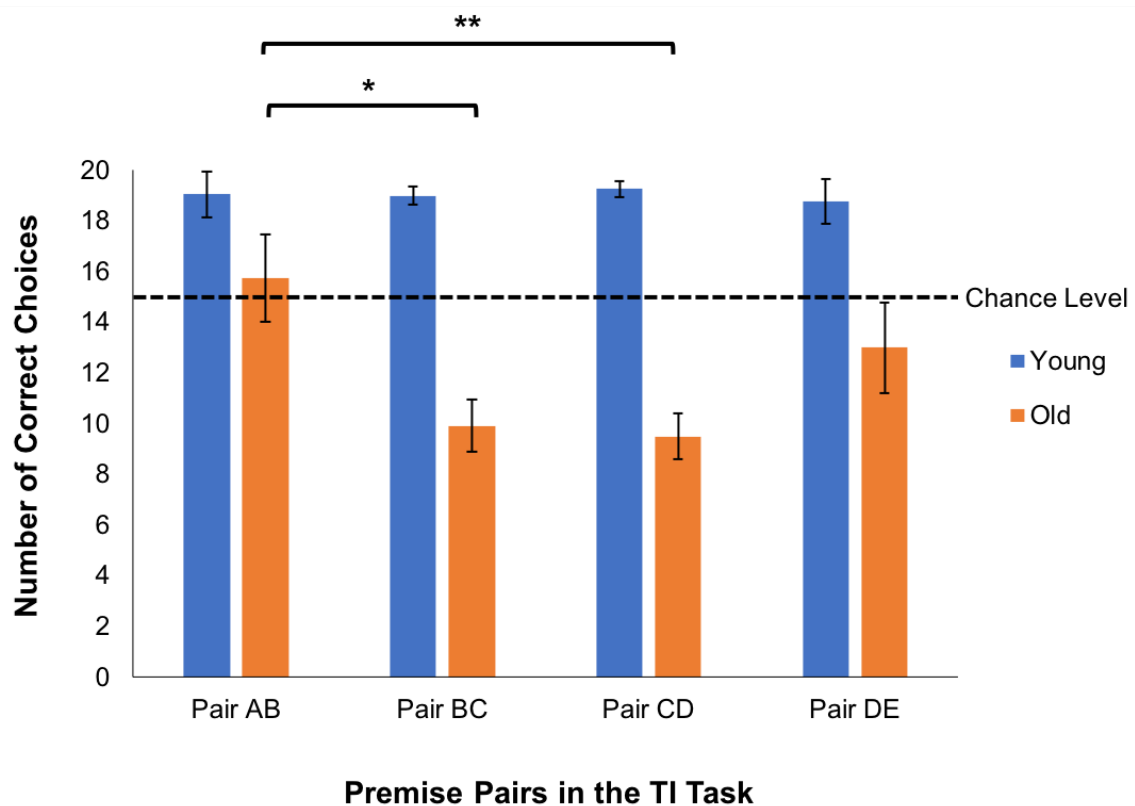
Pair comparisons	Young population			Older population		
	<i>T</i>	<i>p</i>	<i>r</i>	<i>T</i>	<i>p</i>	<i>r</i>
AB-BC	9.00	.125	-.24	10.00	.021*	-.47
AB-CD	12.00	.254	-.19	3.00	.002**	-.58
DE-BC	17.00	.305	-.16	20.50	.158	-.30
DE-CD	17.00	.539	-.10	15.00	.122	-.33
BC-CD	14.00	.336	-.16	35.50	.801	-.06
AB-DE	2.50	.156	-.26	18.50	.389	-.19

* $p < .05$. ** $p < .01$.

Overall these results on individual pairs revealed that young participants performed similarly on all of premise pairs, reflecting a flat accuracy curve (Figure 14) indicative of hippocampus-dependent relational learning (Moses et al., 2006, 2008; Solomon et al., 2011). In contrast, older participants' performance varied based on the premise pairs, reflecting a serial position effect (i.e., U-shaped accuracy) with higher number of correct choices on the pairs AB and DE than the pairs BC and CD (Figure 14). Nevertheless, the best performance of older individuals was on the pair AB and the worst one on the pair CD indicating that there was no an asymmetry as predicted by the best fitting model of the VTT according to which the asymmetry was defined with the best performance on the pair DE and the worst performance on the penultimate pair CD (Von Fersen et al., 1991).

Figure 14

Number of Correct Choices on Individual Premise Pairs in the TI Task



Note. Number of correct choices on training pairs in the TI task. Dashed lines indicate the chance level (15 correct choices over 20 trials). * $p < .05$. ** $p < .01$.

The number of correct choices at the individual level in the TI task was indicated in Table 3. All young individuals except two individuals (S446 and S444) performed above chance level on each individual premise pair. Among them, 11 individuals chose correctly B over D on all of last three trials of the TI pair BD. Thus, for these individuals, it could be suggested that they were able to organize items into a hierarchical order ($A > B > C > D > E$) based on learned conditional pairs and to make inferential judgments (if $B > C$ and $C > D$ then $B > D$). The rest of young individuals might either learn only conditional pairs without inferring the hierarchical relationships between

items or they might rely on reinforcement-based learning with value transfers which could not support the performance on the inference pair. Among two individuals who were not successful in learning all premise pairs, S444 performed above chance level on both of end pairs (i.e., AB and DE) indicating that he/she could use the strategy “A is always the winner and E is always the loser”. However, he/she missed indeed a performance at chance level by just one incorrect choice for both of inner pairs (i.e., BC and CD). However, he/she could not correctly solve all trials of the inference pair BD. Conversely, S446 performed below chance level on both of end pairs but above chance level on both of inner pairs. Importantly, he/she did not make any correct choice on end pairs indicating that he/she chose insistently item B and item E when the pairs AB and DE were presented respectively although these choices were incorrect. Hence, it is likely that he/she only learned the item B as the winner and the item D as the loser by relying on his/her correct choices on the pairs BC and CD and by overgeneralizing it he/she used wrongly the same rule also for end pairs. In addition, this could explain his successful performances on all trials of inference pair BD although it could not be taken as evidence for the ability of inference for this individual.

Although the half of older individuals performed above chance level over 80 trials, none of them was successful in learning all premise pairs. Therefore, depending on pattern of performances, either an impaired hippocampus-dependent relational learning or the use of simple reinforcement-based learning could be suggested. Performances of three individuals (S490, S491, S508) were below chance level on each of premise pairs. The rest of individuals who were considered to have failed in learning all of premise pairs, was above chance level either on one of end pairs (N=5), both end pairs (N=2), one end pair and one inner pair (N=1) or exceptionally on three

premise pairs (N=1). When the specificities of each pairs were considered, performances of the individuals S495 and S509 who were considered to have learned the pairs AB and BC and AB, BC and DE respectively, could be explained by the learning of the conditional relationship between two overlapping pairs (i.e., B loses in presence of A but wins in presence of C). In this case, their inability to perform above chance level on all premise pairs could indicate age-related declines in their performances. On the other hand, the performances of S507 and S494 who were considered to have learned both end pairs, could be explained by simple reinforcement histories (i.e., A always wins and E always loses). However, performances of all other individuals were not entirely consistent with the use of the strategy “A always wins E always loses” as they performed above chance level only on one of end pairs. Lastly, only two individuals (S490 and S509) made correct choices on all of last three trials of the TI pair BD. However, their performances could not be taken as evidence for a successful inference, because performances of S490 were below chance level on all pairs and S509 learned only the pair BC but not the pair CD which is a critical pair to support performances on the pair BD.

In sum, the overall performance of the older population was worse than that of the young population suggesting an overall decline in the task performance with age. Performances of the young population across premise pairs revealed a flat accuracy curve consistent with the relational model and those of older population revealed a U-shaped curve which was inconsistent with the asymmetrical form predicted by the best fitting model of the VTT. At the individual level, almost all young individuals performed equally well on all premise pairs whereas the majority of older individuals was successful in learning only a single end pair.

Table 3*Total Number of Correct Choices of Each Young and Old Individual in the TI Task*

Subjects	Training phase						Test pair BD (/3)
	All 80 trials	Pair AB (/20)	Pair BC (/20)	Pair CD (/20)	Pair DE (/20)	Passing all pairs	
Young population							
S433	80	20	20	20	20	Success	2
S434	77	19	18	20	20	Success	3
S435	78	20	20	20	18	Success	0
S436	80	20	20	20	20	Success	1
S437	80	20	20	20	20	Success	3
S438	80	20	20	20	20	Success	3
S439	79	20	19	20	20	Success	1
S440	74	20	16	18	20	Success	3
S441	79	20	20	19	20	Success	1
S443	80	20	20	20	20	Success	3
S444	66	20	14	14	18	Fail	2
S445	80	20	20	20	20	Success	3
S446	39	0	19	20	0	Fail	3
S447	75	20	16	20	19	Success	0
S448	80	20	20	20	20	Success	3
S449	80	20	20	20	20	Success	3
S450	78	20	20	19	19	Success	2
S451	78	20	19	19	20	Success	2
S452	80	20	20	20	20	Success	3
S453	80	20	20	20	20	Success	3
S454	77	20	18	19	20	Success	3
S455	74	20	19	16	19	Success	0
Older population							
S486	60	20	12	14	14	Fail	1
S487	45	20	6	9	10	Fail	0
S488	49	13	7	9	20	Fail	2
S490	32	7	6	10	9	Fail	3
S491	34	10	7	6	11	Fail	1
S492	45	19	10	4	12	Fail	2
S494	58	20	10	8	20	Fail	0
S495	53	18	15	11	9	Fail	1
S506	38	20	6	12	0	Fail	1
S507	65	20	11	14	20	Fail	2
S508	34	3	14	6	11	Fail	2
S509	65	19	15	11	20	Fail	3

Note. Pattern of performances in the TI task at the individual level. Green cells: performances above chance level. Red cells: performances below chance level for each variable except for “Passing all pairs” and “Test pair BD”. Passing all pairs: Above vs below chance performances on all pairs (success vs fail), coded with green and red colors respectively. Test pair BD: performances with correct choices for all BD trials coded with green, otherwise number of correct choices coded with red. Above chance performance: Number of correct choices ≥ 49 correct trials over 80 trials and ≥ 15 correct trials over 20 trials.

5. Discussion

In the present study, it was aimed to decipher learning strategies used by young and older populations in the TI task and to investigate whether hippocampus-dependent relational learning is impaired in aging. Findings revealed that older participants performed as well as young participants in the VD task indicating that all participants were able to discriminate different visual stimuli and learn and remember non-conditional relationships. In the CL and TI tasks, older participants performed worse than young participants. However, older participants showed similar performance to that of young participants after a second series of trials, implying a slower learning for older participants than young participants. Performances across premise pairs in the TI task indicated a flat and a U-shaped accuracy curve for young and older participants respectively. At the individual level, almost all young individuals performed above chance level on each of premise pair although only half of them was completely successful on last three trials of the inference pair BD. On the other hand, none of older individuals was successful in learning all premise pairs. Importantly, most of them performed above chance level only on one of end pairs (i.e., AB or DE).

5.1 Conditional Learning Task

In the first series of the CL task, older participants performed worse than young participants. However, if given a second series of trials, although they took longer to learn the CL task, their performance level was similar to that of young participants.

Initial performance differences between groups in the CL task could not be explained by anxiety, fatigue and lack of confidence or motivation that might be associated with aging or the unfamiliarity of the older population with the use of electronic devices which is an issue to be considered due to environmental changes including technological advancements (Light, 1993; Salthouse, 1991) since both of the

groups performed equally well the VD control task. In addition, it precludes also an explanation by sensory deficits (e.g., deficit in visual functioning; Lindenberger & Baltes, 1994; Schneider & Pichora-Fuller, 2000) as older participants were able to discriminate distinct visual stimuli with different details, shapes and colors.

As initial performance differences between groups disappeared after the presentation of a second series of trials, the findings in the CL task rather might suggest that the learning of the older population was slower in comparison to the young population. There might be several explanations for this finding. Firstly, one factor that could contribute to slow learning might be declines in the speed of execution of simple processing operations (Salthouse, 1991, 1995, 1996). Such an explanation in general is considered for tasks for which speed is an important factor to be successful on the task (Kester et al., 2002). The CL task was not time limited and therefore did not require fast response times. However, the speed of processing theory provides also an explanation for tasks lacking a speed component by introducing the simultaneity mechanism according to which as the information processing is slow, the relevant information could not be available when it is required to solve the task. When the nature of the CL task was considered, as different pairs were presented randomly, participants could potentially not process the information rapidly enough to use this information efficiently in subsequent presentations. However, with practice, such a constraint might be overcome as more time would be provided to process information and the task familiarity would increase (Light, 1993; Salthouse, 1991).

Alternatively, performances of older participants could be explained by reduced processing or attentional resources (Craig & Byrd, 1982; Craig & Jennings, 1992; Kester et al., 2002). According to this theoretical view, older adults have less attentional resources in comparison to young adults (Craig & Byrd, 1982; Kester et al.,

2002). Therefore; their performances could be impaired in complex tasks which necessitate the allocation of attention (i.e., tasks requiring controlled processes) in comparison to tasks which could be solved with no or less attention and in a more automatic and implicit manner (i.e., tasks requiring automatic processes) (Craik & Byrd, 1982; Kester et al., 2002). From this perspective, it could be asserted that in the VD task, when non-overlapping premise pairs (i.e., A vs B, C vs D) were presented, older participants were able to learn the always rewarded and the never rewarded items as it might require less or no attention. However, as in the CL task, participants were presented with overlapping premise pairs (i.e., A vs B and B vs C), the task might require more attention to the item B to learn in which condition it is the winner or loser item (i.e., B wins against C but loses against A). Therefore, due to the depletion of attentional resources, they might be initially unable to solve the task. However, as underlined by Craik and Byrd (1982) complex tasks might include indeed both controlled and automatic processes and with experience, a shift from the former to the latter might occur. Therefore, older participants might initially rely on controlled processes and then shift to automatic processes with extended training which allowed them to perform as well as young participants as attentional demands were decreased. Specifically, it could be asserted that they reduced attentional demands of the task by not paying attention to the item B. In parallel with this perspective, older participants could potentially rely on the CL strategy at the beginning but could be unable to learn conditional pairs due to the attentional depletion. Then, they could adopt the strategy of “A always wins and C always loses” by solving the task as if there were no conditional pairs like in the VD task. Such an explanation is consistent with the simple reinforcement-based learning which could be adopted in incremental or gradual fashion (Vasconcelos, 2008; Von Fersen et al., 1991, Wynne, 1995) and is reasonable

also as the CL task could be solved uniquely by learning that “A always wins and C always loses” without necessarily requiring the learning of conditional relationships.

5.2 Transitive Inference Task

In the TI task, overall performance of the older population was worse than that of the young population, consistent with findings of other studies which reported overall age-related decline in the TI task (Ryan et al., 2009, Viskontas et al., 2005).

Moses et al. (2006) analyzed the pattern of performances of young adults in the TI task with six items to decipher used learning strategy and suggested that superior performances in the TI task could be associated with the use of relational learning whereas inferior performances could be associated with reinforcement histories of individual items. Specifically, they reported that young participants aware of the hierarchy among items (i.e., $A > B > C > D > E > F$), performed more accurately than unaware young participants. Interestingly, the pattern of performances of young aware participants with high accuracy levels was consistent with patterns indicative of relational learning (e.g., similar performances across all premise pairs and test pairs BD and BE), whereas the pattern of performances of unaware young participants with relatively low accuracy level was as predicted by the use of reinforcement-based learning with value transfers for the version of the TI task with six items (e.g., U-shaped accuracy curve, better performance on the pair BE than BD, better performance on the pair EF than AB). Therefore, considering these findings, the accuracy level might provide an initial insight about the used strategy by young and older populations. However, a detailed discussion of pattern of performances is required to decipher the strategy used by both populations.

5.2.1 Learning Strategy Used by Young Population

At the group level, the number of correct choices of the young population across premise pairs in the TI task revealed a flat accuracy curve as it could be predicted by relational model (Eichenbaum, 2001). Therefore, the shape of the accuracy curve did not support either the VTT or the use of simple reinforcement-based learning (i.e., A always wins and E always loses) as a symmetrical or asymmetrical serial position effect was not observed.

This result was consistent with the findings of Moses et al. (2006) which indicated also a flat accuracy curve for young population who was aware of the hierarchical organization among items (i.e. $A > B > C > D > E > F$) as revealed by the awareness questionnaire. Moreover, they reported also that those participants performed similarly on all test pairs including both end pairs and inner pairs. Altogether, their findings provided evidence for the acquisition of conditional relationships and the reorganization of items into a hierarchy supporting successful inferences. Therefore, they concluded that these individuals used the relational learning to solve the task. Similarly, Moses et al. (2008) examined whether young participants were biased to rely on relational learning or reinforcement histories of individual items to solve the TI task by assessing cognitive abilities associated with medial temporal lobe and frontal lobe, with neuropsychological tests. Consistent with Moses et al. (2006), they reported for young individuals aware of the hierarchy, similar performances across premise pairs, high accuracy levels for inference and training pairs. In addition, their TI performance was predicted by results from neuropsychological tests indicating superior memory for relations for those individuals. Therefore, the flat accuracy curve was an indicator of relational learning as also shown in previous studies (Moses et al., 2006, 2008).

Greene et al. (2006) showed that performances of individuals who were able to learn both inner pairs free of end items and also successful on the inference pair BD, indicated high activation of hippocampus supporting the use of hippocampus-dependent relational learning. Accordingly, at the individual level, almost all young individuals performed above chance level on all premise pairs suggesting that they might learn all conditional pairs which is considered to be the first step of relational learning (Eichenbaum, 2001). However, it does not necessarily imply the ability to infer hierarchical relationships between items. For this reason, despite the absence of a sufficient number of trials to be considered for statistical analyses at the individual level, performances on the test pair BD were considered as supportive evidence to interpret the results of the training phase. Findings revealed that 55% of individuals, successful in learning all premise pairs in the TI task, were also successful on last three trials of the inference pair BD. Therefore, it could be suggested that these individuals were able to learn all conditional relationships between premise pairs, determine the hierarchical organization of items and make inferential judgements although these findings need to be considered cautiously due to the lack of sufficient number of test trials.

Alternatively, performances at the individual level could be explained also by the VTT but unfortunately, it was not possible to distinguish a performance that could be supported by the VTT than the relational model at this level. The only consideration useful to distinguish them might be the presence of discernibly better performances on end pairs that might be predicted by the VTT (Von Fersen et al., 1991). However, almost all young individuals made the same or similar number of correct choices for each pair.

In sum, performances of the young population across premise pair revealed a flat accuracy curve at the group level. Almost all young individuals were able to learn all conditional pairs and more than half of these individuals were also successful on trials of the inference pair BD at the individual level. Therefore, the overall pattern of performances of the young population was compatible with the use of hippocampus-dependent relational learning. However, future studies should consider more test trials to support these findings and design new experiments that would allow to better distinguish the pattern of performances predicted by the VTT from that predicted by the relational model.

5.2.2 *Learning Strategy Used by Older Population*

At the group level, the number of correct choices of the older population across premise pairs in the TI task revealed a U-shaped accuracy curve (i.e., serial position effect) with the best performance on the pair AB and the worst one on the pair CD. Therefore, this finding cannot be explained by the asymmetrical form predicted by the best fitting model of the VTT or other models of the VTT which predict the best performance on the pair AB and the worst one on the pair BC or the best performance on the pair DE and the worst one on the pair BC (Von Fersen et al., 1991). In the present study, it is difficult to determine whether the curve is in a symmetrical U-shaped form or an unusual asymmetrical form as performances differed only between the pair AB and the pair BC or CD whereas none of the comparisons with the pair DE was significant. This finding could be explained either by the use of the strategy “A always wins and E always loses” or by the use of relational learning.

Ryan et al. (2009) compared the performances of young and older populations on the TI task with 6 items and consistent with our findings, they reported that older adults were less accurate than young adults on training and test pairs. Moreover,

although the performances across premise pairs did not differ depending on the age group, their performances also indicated a U-shaped accuracy curve with best performances on the pairs AB and EF. Interestingly, their following analyzes revealed that older participants were less aware of the hierarchy among items than young participants but aware older participants were able to perform similar to young participants on middle inference pairs. Based on these findings, they asserted that age-related differences could be explained by the inability to establish relational representations of premise pairs which might occur due to the dysfunctional medial temporal lobe. However, as the performance on middle pairs remained similar across age groups and awareness-groups, the strategy used by young and older populations remained unclear.

At the individual level, none of the older participants was successful in learning all conditional pairs, which could be considered either as an indicator of an impaired relational learning or an indicator of reinforcement-based learning (with or without value transfers) depending on which particular pairs individuals performed above chance level. Interestingly, individual patterns of performances were not entirely consistent with the predictions of the different models. Firstly, the majority of individuals was successful only on one of end pairs in contrast to the prediction made by simple reinforcement-based learning according to which both end pairs could be learned as their reward histories were not ambiguous (Wynne, 1998; Vasconcelos, 2008; Von Fersen et al. 1991). Secondly, according to the VTT, value transfers could occur from the rewarded stimulus A to non-rewarded stimulus B which might increase slightly the strength value of B and could enable to correctly choose B against C (Wynne, 1988; Von Fersen et al., 1991). However, although 67% of older individuals performed above chance level on the pair AB, only two individuals (S495 and S509)

could perform above chance level on the pair BC but they could not perform above chance level on other adjacent premise pairs. Therefore, these patterns do not seem consistent either with the VTT if it is considered that the mechanism beyond value transfers is striatum-dependent (McDannald et al., 2013; Setlow et al., 2002; Wimmer & Shohamy, 2011; see Martin-Soelch et al., 2007 for a review). Thirdly, if the hypothesis of impaired hippocampus is true, based on the relational model (Eichenbaum, 2001), performances on individual conditional pairs could be expected to be similarly affected by the impairment. Therefore, performances of three individuals (S490, S491, S508) who performed below chance level could be explained by the impaired relational learning and these individuals may represent the most severe cases. However, due to individual differences, the level of impairments might vary too by leading to different pattern of performances. For example, performances of individuals who were able to learn two overlapping premise pairs might represent the cases with slight impairments. Furthermore, performances of individuals who learned a single pair could be still explained by the impaired relational learning as they were not able to learn both end pairs despite the fact that end items had unambiguous reinforcement histories and end pairs could be uniquely solved by using the simple reinforcement-based strategy which is striatum-dependent (Foerde et al., 2006; Knowlton et al. 1996; Packard et al. 1989; Seger & Spiering, 2011).

In sum, at the group level, the form of the U-shaped accuracy curve was not consistent with the asymmetry predicted by the VTT. At the individual level, although patterns of performances were not entirely consistent with the predictions of the models, they could be better explained by the use of an impaired relational learning.

5.3 Inherent Nature and Demands of the Conditional Learning and Transitive Inference Tasks

Overall, findings revealed that older participants were able to perform as well as young participants in the CL task although it required an extended training with the presentation of a second series of 40 trials (20 trials per pair). On the other hand, older participants performed worse than young participants in the TI task in which participants were presented with 40 trials per pair in total. Therefore, the total number of trials presented for each premise pair was the same at the end of the TI task and the second series of the CL task. If 40 trials per pair were sufficient for older participants to perform successfully the CL task, comparable performances between young and older populations could be expected also at the end of the TI task although it was not the case. Therefore, it raises the question of why older individuals could not perform as well as young individuals in the TI task as in the CL task.

The main explanation for these findings is different levels of accessibility of simple reinforcement-based strategy vs relational strategy in the CL and the TI tasks. Specifically, the CL task could be solved uniquely by relying on the strategy “A always wins and C always loses”. On the other hand, the simple reinforcement-based learning remains insufficient to support performances on the TI task without value transfers. Findings discussed above, was consistent with this main difference between tasks and their impact on the accessibility of strategies. Overall, it was hypothesized that the CL task was solved after extended training by relying on the striatum-dependent simple reinforcement-based learning and the TI task could not be solved successfully due to the impairment in hippocampus-dependent relational learning. However, other explanations may also exist and provide an understanding of the factors which might affect performances and the use of different learning strategies.

In the present study, the CL and the TI tasks, overlapping premise pairs were presented in a randomized order and participants were assessed on their ability to learn conditions in which the items are the winner or the loser. Due to the trial and error nature of the task, such a design does not demand only the recall of the correct choice for a pair already learnt but also requires the active maintenance of previous correct or incorrect responses given to pairs and the active manipulation of the previous information based on new information acquired through feedbacks to be able to give correct choice for following premise pairs. Considering the requirement of tasks such as active maintenance and manipulation of information, performances on these tasks could depend on the working memory (Baddeley, 1992, 2012).

Klencklen et al. (2017b) investigating spatial and color working memory in aging, concluded that age-related decline in working memory performances get worse both for spatial and non-spatial information as the number of items to be remembered increased. Similarly, Viskontas et al. (2005) tested young, middle-aged and old groups on the TI task by manipulating the relational complexity which was defined as “number of relations one must simultaneously hold in mind in order to generate the solution”. This manipulation was made to increase demands on working memory processing. In their task version, participants were presented with premises (e.g., Dan is taller than Jane and, Jane is taller than Abe) and asked to arrange cards on which names were written, in order from tallest to shortest. At the lowest level of complexity, participants arranged cards exactly in the order in which premises were presented. As the level of complexity increased, the order of premises varied such that the task required simultaneous integration of premises to arrange cards in the correct order. Findings indicated that as the relational complexity increased, older individuals made more errors and took more time for trials. Consistent with these findings, Eichenbaum (1992)

also reported that when the task has high demands for relational representations, the performance of hippocampal-lesioned animals was impaired, whereas when the task has low demands, they can be able to solve the task. For instance, hippocampal-lesioned and intact rats were tested in two different versions of the odor-discrimination learning paradigm (Eichenbaum, 1992; Eichenbaum et al., 1988). In the simultaneous discrimination task, in each trial, the same two odors were presented at the same time and their left/right position was determined pseudo-randomly. On each trial rats had to choose the odor predetermined to be rewarded. Performances of lesioned animals were severely impaired in this task as it required comparison between odors. On the other hand, in the successive discrimination task, different odors were presented separately by preventing odor comparisons and the rats had to poke their nose into the odor port only for the odor predetermined to be rewarded and avoid the odor predetermined to be not rewarded. Therefore, a factor to be considered for the poorer performances in the TI task in the present study could be the increased memory loads and representational demands as in the TI task there were a higher number of items and pairs to be compared and higher relational complexity in comparison to the CL task.

Furthermore, interference could be also considered to explain different performances of the old population observed in the CL and the TI tasks because the working memory is sensitive to interferences which could decrease the accuracy levels on the tasks (Olton et al., 1979). Indeed, the main source for interferences was considered to be stimulus similarities (Baddeley, 2012; Osgood, 1949). Therefore, as in the TI task, a higher number of items sharing similar features was presented as pairs, the nature of the TI task might cause more interferences in comparison to the CL task leading to a higher number of errors.

Interestingly, consistent with the relational model suggesting the involvement of the hippocampus in the TI task, Banta Lavenex et al. (2014) showed the importance of the hippocampus for the maintenance of memory in presence of interference. A densely amnesic patient (P9) was tested with controls on the color and spatial working memory and reference memory tasks with and without interference task. Findings revealed that the number of correct choices before first error (i.e. CBE, a measure of memory capacity) on the reference memory (i.e., repeated trial procedures) with one color did not differ between P9 and controls. Similarly, P9 was able to perform working memory task (i.e. trial unique procedures) with one color as well as controls in the absence of interference. However, she performed worse than controls in the presence of interference the working memory task with one color. With or without interferences she performed worse than controls on two and three colors. Based on these finding, Banta Lavenex et al. (2014) suggested that extra-hippocampal regions might support the behavior when the information remains constant over repeated trials. However, when the task requires the constant manipulation of the information as in working memory tasks then it could still be efficient to perform the task but its functioning remains restricted when the task includes interference (Banta Lavenex et al., 2014) because they are more susceptible to interferences in comparison to hippocampus (Olton et al. 1979, Schacter & Tulving, 1994).

The similar interpretation could be made also for findings in the present study. The CL included two overlapping premise pairs which could be solved by “the item A is always the winner and the item C is always the loser”. Therefore, this information could be used constantly and therefore the performance could be supported by extra-hippocampal regions. On the other hand, in the TI task as there are higher number of items and also premise pairs free of end items for which reinforcement histories are

not obvious, the task might require more active maintenance and manipulation of the obtained information leading to high levels of interference in comparison to the CL. Accordingly, due to the high levels of interference, the hippocampus might be recruited as it is known to be implicated selectively in presence of interference (Olton et al., 1979).

When initial research questions of whether hippocampus-dependent learning and memory system is impaired in aging and the TI task is solved really in hippocampus dependent manner were considered, it could be deduced that performances in the TI task or in similar tasks like the CL could be supported by both learning and memory systems. Moreover, it could be concluded that hippocampus-dependent learning and memory system could be really affected in aging as suggested by Klencklen et al. (2017a, 2017b) as pattern of performances of the older population could be better explained by the hippocampus-dependent relational learning in comparison to alternative explanations.

6. Conclusion

The present study contributed to the literature about cognitive declines in aging and gave an insight about the learning strategy used to perform the TI task, which may be supported by distinct brain regions. Especially, pattern of performances was found to be consistent either with simple reinforcement-based learning or relational learning and it was not as predicted by the best fitting model of the VTT. Moreover, in some analysis, the patterns indicative of the VTT could not be distinguished from those predicted by the relational model especially for the young population as in theory both could explain successful performances in training. Future studies could aim to investigate further learning strategies and underlying cognitive mechanism by increasing the number of items in the TI task and test trials to better distinguish pattern

of performances predicted by different models. This could allow to better evaluate asymmetrical serial position and end anchor effects and consider other distinctive features of reinforcement-based learning with value transfers such as symbolic distance and first item effects as underlined by the VTT (Von Fersen et al., 1991; Wynne, 1998).

Alternatively, both populations could be tested on the TI task and the transverse patterning task which is also thought to be hippocampus-dependent (Driscoll & Sutherland, 2005; Sutherland & Rudy, 1989) and pattern of performances both at the group level and the individual level could be compared. Similar to the TI task, in the transverse patterning task, overlapping premise pairs are presented. However, according to the task design, there is no a hierarchical relationship between items (e.g., A+B-, B+C-, C+A-) and each item is equally rewarded or not rewarded precluding an explanation of performances by the reinforcement-based learning with value transfers (Von Fersen et al., 1991). Therefore, if pattern of performances of populations on both tasks are similar, it may indicate that reinforcement-based learning with value transfers do not support the performances on the TI task and it could further provide information about the cognitive mechanism involved in the TI task. Otherwise, it might indicate that the TI task and the transverse patterning task might be supported by different strategies and the VTT might explain also performances of the young population. Such comparisons might allow to test also other hippocampal function theories which were not considered in the present study.

Furthermore, future studies also could investigate the impact of memory load and interference in the TI task to determine how pattern of performances were influenced and to what extent the used strategy could be explained by these factors. In addition to the CL task with three items and TI task, populations could be tested on

a version of the CL task with four items which would be in the middle of both tasks in terms of memory load and interference. Overall performances of older population on the version of the CL task with four items might be worse than those on the CL task with three items but better than those on the TI task as it would include three conditional pairs (A+B-, B+C-, C+D-). At the individual level, if older participants rely on simple reinforcement-based learning, they may be successful on test pairs and training pairs AB and CD but they may not be successful on the pair BC. On the other hand, if they rely on reinforcement-based learning with value transfers or relational learning, they could be successful on both end pairs or even on the pair BC as there would be less interference and memory load in this task in comparison to the TI task. Lastly, interference could be separately assessed by an interfering secondary task which could be added to the tasks used in the present study to observe how patterns of performance change in the presence and absence of interference as it was done in Banta Lavenex et al. (2014).

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