Robertson, E. M. (2022) Memory leaks: information shared across memory systems. *Trends in Cognitive Sciences*, 26(7), pp. 544-554. (doi: 10.1016/j.tics.2022.03.010)

# Memory Leaks: information shared across memory systems

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*Trends in Cognitive Sciences*
*(TICS-D-21-00266R2)*

*Opinion*

*Revised 22nd of February 2022*

*Further revisions of 25th of March 2022*

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## Abstract

The brain is highly segregated. Multiple mechanisms ensure that different types of memories are processed independently. Nonetheless, information leaks out across these memory systems. Only recently has the diversity of these leaks been revealed. Different memory types (skills vs. facts) can interact in simple ways, either allowing or preventing their further processing, or in more complex ways, allowing the sharing of abstract information between memories. Leaks occur from memories dependent upon hippocampal circuits, which have properties critical for leaks and activity patterns related to memory interactions. This hippocampal contribution is likely achieved in concert with cortical areas. Leaks between memories enable the application of knowledge in novel situations, explain learning dynamics, and solve important problems inherent to memory formation.

## Leaks and the sharing of information

It always leaks. This principle extends from government reports, to military intelligence, and even to our memories. It implies the sharing of information. **Memory leaks** (see Glossary) are highly varied, interfering with memory processing, enhancing memory formation, protecting and linking together different types of memory (facts and skills; [1-8]). The diversity of these leaks is only just being recognized and raises questions about how information, and at times highly complex information, can be transferred between different memory systems in the brain when multiple mechanisms keep memories segregated. Converging evidence is now revealing how this segregation breaks down, and how even complex serial information can be shared between different memory types [9-13]. Perhaps just as important, the growing appreciation for the diversity of leaks provides purchase on the functional contribution they make to cognition. Leaks support the **transfer** of highly complex information, which may act as a teaching signal enabling one memory to drive the formation of another. This explains learning dynamics and provides a solution to key computational and energetic memory problems.

## Leaky memories

A leak is when information escapes from an encapsulated or otherwise sealed system. For example, it occurs when information about a clandestine operation is shared (inadvertently) by one secret service with another nation's security service. The leak could contain quite simple information, such as simply that a cybersecurity attack is planned, or quite complex information, such as providing details of the attack. Similarly, different types of memory leaks contain different amounts of information (low vs. high bandwidth).

## Leaks with a low bandwidth

Leaks occur between memories with very different contents (words vs. actions; [2, 3, 5, 14, 15]). Learning a word-list and then immediately learning a motor skill impairs word-list retention (by approximately 15%; Figure 1). This impairment is specifically due to the motor skill learning. When the motor skill task is replaced with a task requiring the same number and type of movements but lacking any serial structure, thus removing the motor sequence learning aspect from the task, word recall is no longer impaired [2]. The **interference** remains when the order of tasks is reversed.

Learning a motor skill and then immediately learning a word-list impairs subsequent motor skill retention [2]. Importantly, skill impairment can be prevented by disrupting declarative knowledge [3, 4] using different techniques (e.g. transcranial magnetic stimulation (TMS) or exercise [4, 15-19]). Together, these studies provide converging evidence for reciprocal leaks between different types of memory [20].

This kind of leak has two important features. First, the information leaking out is that a memory has or has not been formed (binary information). This is only a small amount of information – it is low-bandwidth. Second, the leak is acting to prevent further processing of the other memory, expressed as interference of that other memory [16]. This interference of the recently formed memory is solely due to the formation or processing of another memory, and is present regardless of whether the motor skill and word-list sequences have any features in common. For example, even different lengths of word-lists and actions sequence can interfere with one another ([2] vs. [6]). Thus, information that a memory is being processed leaks out to prevent processing in another memory system.

A leak may control memory processing [21]. When the leak is present there is a physiological inhibition of neural circuits, which prevents processing, and memory retention is impaired. For example, declarative knowledge leaks inhibit motor cortical excitability, preventing motor skill processing and impairing skill retention. By contrast, when the declarative memory is absent, there is no physiological inhibition, and the skill memory is processed [15-19, 21, 22]. The leak modifies the fate of a different type of memory because there is a finite processing capacity – "a bottleneck" – which once saturated by the leak prevents processing of another different type of memory. This competition for limited resources explains how disrupting one memory system can boost memory performance within another system. For example, disrupting declarative explicit knowledge for a movement sequence enhances performance of that same sequence ([3, 4, 23]; see also [24]). A leak combined with a processing bottleneck provides a mechanism to control memory fate [21]. More recently, work has revealed a qualitatively very different type of leak.

## Leaks with a high bandwidth

Highly complex information can also be shared between memory systems. A sequence can be composed of different types of information, including words or movements. Despite their differences in content, these sequences can be related to one another [25]. For example, a sequence of words could specify a sequence of movements through a simple mapping between the semantic category of a word (clothing, furniture, type of transport, vegetable) and a movement to one of four positions (1 to 4; Figure 1). When this mapping is maintained, the sequences with different content share a common abstract structure; whereas, when this mapping is violated, the sequences have different structures. It is this abstract serial information that can leak between different types of memory. This leak is high-bandwidth because detailed information is being shared.

When a skill and word-list memory are formed in quick succession, the abstract serial structure of a motor skill is shared with, and enhances the formation of a word-list memory ([6], see also [8]; Figure 1). The enhanced rate of word-list learning and improved subsequent recall only occurs when the tasks share a common structure. The enhanced performance is expressed exclusively in serial recall – measured as the longest sequence of words recalled in the correct serial order – while other measures of performance, such as total recall, are not improved by the tasks sharing a common structure. This illustrates that it is specifically the common abstract serial structure of the tasks that is responsible for driving the enhanced performance. A similar pattern emerges when the order of the memory tasks is reversed. The abstract serial structure of a word-list can be transferred to, and so enhance the subsequent immediate learning of a movement sequence [6]. This high-bandwidth leak transmits highly detailed information about the serial structure common between the tasks.

## Leaks may be linked

The enhanced learning due to a high-bandwidth leak of either the word-list or motor skill comes at a cost. When memory tasks with a shared structure are learnt in quick succession (motor skill and word-list task; or vice versa), the enhanced learning of the subsequent memory is (positively) correlated with the impaired retention of the initial memory (Figure 1). The impairment arises from a low-bandwidth leak sharing the simple information that a different type of memory is being formed. Yet, these high and low-bandwidth leaks are not only correlated they are causatively linked. Manipulations that minimize impaired retention of the initial task also substantially reduce the transfer of abstract knowledge from that task to the subsequent memory task [6, 7]. Thus, these observations suggest that leaks are causatively linked, and specifically that a high-bandwidth leak is dependent upon a low-bandwidth leak. However, this may not always be the case.

A low-bandwidth leak is detected by the disruption it causes to a newly formed memory [2, 5, 6]. Following its formation, a memory is unstable [20]. An unstable memory is susceptible to disruption from, for example, learning another memory, which impairs its retention. It becomes stabilised through offline processing during consolidation or through sustained practice [2, 26-30]. However, recent work demonstrates that stability can also be transferred between memories [7]. For example, learning a movement sequence will 6 hours later prevent a newly formed word-list memory from being susceptible to disruption when the memory tasks share a common structure (Figure 1). In this example, the motor skill memory developed stability – during its 6 hours of consolidation – and this property was shared with the word-list memory. The shared stability was dependent upon a high-bandwidth leak of complex information about the serial structure common to the memory tasks. However, this high-bandwidth leak occurred despite the motor skill memory being stable – resistant to interference – and as a consequence, could not be impaired by a low bandwidth leak (i.e., the simple presence of the word-list memory). Potentially, this may demonstrate that high and low-bandwith leaks are independent, and are not critically linked. Alternatively, the stability of the motor skill may have simply prevented a low-bandwidth leak from the word-list from being detected. This pattern is preserved even when the order of the tasks is reversed: a word-list task protects a subsequent motor skill memory formed 6-hours later from disruption [7]. Overall, quite simple information can leak out and affect the processing of another memory (low-bandwidth leak). For example, simply that a memory has been formed impairs the retention of a different memory type. Highly complex information can also leak out (high-bandwidth leak), which leads, for example, to the transfer of stability, protecting memories from disruption, when they have a common abstract structure. Yet, how do these leaks occur within the tightly segregated organization of the brain?

## Leaks in the brain

The brain appears to be designed to prevent interactions, particularly between different types of memory. Different types of memories are predominately processed within different circuits [31]. This minimizes the opportunity for one type of memory, say for a set of skilled actions, to affect the processing of a different type of memory, say for a set of newly learnt facts [20]. According to current estimates, a memory is allocated to between 25% and 3% of the available neurons within a circuit [6, 32-34]. Less than 20 neurons are required to drive the performance of a learnt navigation task [35]. At least in principle, such sparse coding should enable very similar memories to be encoded in quick succession without any need to interact because they are allocated to distinct populations of neurons within a circuit. Furthermore, the activity patterns associated with different memories do not correlate, which enables them to remain distinct, and not interact [36-39]. With these principles as a backdrop, it seems paradoxical for any leak of information to occur between different types of memory. However, some recent studies have shown how this may occur.

An intuitively appealing way for leaks to occur between memories is for them to share the same neuronal population during their formation [20, 40, 41]. This idea has recently been directly tested in snails by imaging neuronal activity during the formation of successive memories. It shows that the sharing of a neuronal population at memory formation explains the interference between memories [42]. Yet could this principle apply to humans, particularly when it appears to contradict sparse coding, which enables different memories to be formed within entirely different circuits? Some recent work shows how this contradiction could be resolved and shows how information can be exchanged between memories.

The population of neurons activated during memory formation remain excitable for several hours (5-6 hours [9, 10]). This increases the probability that these same neurons will be allocated to the formation of another memory in the ensuing hours. It is also during these 5-6 hours that a memory is susceptible to interference [26-28]. Thus, sparse coding no longer applies when memories are acquired in succession. Instead, memories share the same, or at least partially overlapping, neural population and this method of allocation occurs over the time window when memories interact. This principle of memory allocation is played out across cortical and subcortical brain areas, which explains how interactions occur between diverse memories [9, 10, 43, 44]. However, for it to explain the leak between memory systems requires that it operates within circuits capable of supporting the formation of different types of memory.

## Leaks between different memories

The principle that different types of memory are processed within different circuits breaks down in the hippocampus. Memories for events are widely acknowledged to be dependent upon hippocampal circuits [31, 45]. They are dependent upon these circuits not only for their initial formation but also for their subsequent processing [46-50]. These circuits also play a less acknowledged, but no less important role in processing motor skill memories. Damage to the mediotemporal lobe (MTL), which includes the hippocampus, prevents the acquisition of motor skills [51]. Hippocampal activation occurs during the formation of motor skill memories [52]. It also remains active following motor skill formation, continuing to process and modify the skill memory 'offline' while remaining functionally connected to large-scale motor circuits [12, 13]. In this way, hippocampal circuits make a similar contribution to the processing of both declarative and motor skill memories by being critical for their formation and subsequent offline processing [51, 53].

The offline processing of declarative or motor skill memories will maintain the elevated excitability of hippocampal circuits [54]. This will lead those same circuits to also be selected to support the formation of any subsequent memory because neurons with elevated excitability are preferentially allocated to memory formation ([9, 10]; Figure 2). With first one memory and then another being allocated to the same, or at least overlapping circuit, interference occurs between the memories. This explains the correlation between hippocampal activation and memory interference [11]. Overall, by processing different types of memory and allocating these memories to the same circuits when acquired in succession (within ~5-6hrs), the hippocampus enables a recent memory to be disrupted by forming a different type of memory. This is a low bandwidth leak due to a memory being formed. More complex information can also leak out between different types of memory (high bandwidth leak) and here too converging evidence suggests that the hippocampus plays a central role.

Abstract information leaks from memories formed by hippocampal circuits. For example, only motor skill memories that are dependent upon the hippocampus for their formation show performance transfer to a word-list with a shared structure [6]. High-order sequences – where several prior actions are required to predict the subsequent action (n-1 plus n determines n+1) – are dependent upon the hippocampus ([51, 52]; see also [55]). By contrast, low order sequences – where a prior action uniquely predicts the subsequent action (n alone determines n+1) – are not dependent upon the hippocampus and do not show transfer to a word-list, even one with a shared structure [6]. This suggests that hippocampal circuits are required for the sharing of abstract serial information between different types of memory.

Abstract knowledge is learnt by the hippocampus, with highly complex multidimensional learning experiences collapsed onto an abstract regularity [56]. For example, the information available during the performance of a sequence is collapsed, combined in a single representation (low-dimensional manifold), to provide an abstract sequence of state transitions (-2-3-4-; [57, 58]). This abstract relationship is represented within circuits, which are subsequently allocated to the formation of a new memory ([9, 10, 56, 59, 60]; Figure 2). Having this abstract relationship already represented within a circuit will guide and enhance the formation of a new memory with the same abstract structure, albeit with a different content (actions vs. words), which explains how abstract knowledge is shared between different memory types [6]. Overall, abstract information leaks from memories dependent upon the hippocampus because these circuits extract abstract regularities, and then by being subsequently allocated to the formation of a different memory type (action vs. word) share that knowledge. While the hippocampus has a pivotal role to play in the leaks between memories, there is accumulating evidence that cortical circuits also play a role in the leak between memories.

## Leaks across the cortex

Leaks between different types of memories may depend upon the cortex. Lesions to the frontal cortex (in rodents) prevent interference between memories [61]. Similarly, in humans disrupting the function of cortical areas with repetitive transcranial magnetic stimulation (TMS) prevents the leak between different types of memory [5]. For example, disrupting prefrontal function prevents a newly formed word-list memory from being impaired by learning a motor skill memory. Equally, the impairment of a newly formed motor skill memory by learning a word-list can be prevented by disrupting cortical function, in this case, by applying stimulation to the motor cortex. These observations are specifically due to preventing the interaction between the memories because neither of the individual memories is affected by the stimulation. Stimulation was only applied after both memories had been formed [5, 20]. Together, these studies establish the critical importance of cortical circuits for the leak between memories.

Disrupting cortical function modifies brain activity. Specifically, applying TMS to a cortical area affects excitability throughout a network of brain areas. For example, changes in cortical excitability affect hippocampal function due to cortico-hippocampal connectivity following learning [13, 62-65]. By changing excitability there are changes in how memories are allocated to populations of neurons [9, 10]. Rather than memories being allocated to the same population of neurons when they are acquired in quick succession, which leads to interference between the memories, they are instead allocated to distinct neural populations, which prevents interference [5, 20, 40-42]. Artificially modifying excitability makes the pattern of brain activity associated with each memory distinct (decorrelation), which prevents interactions between memories within the hippocampus [38, 39]. The cortico-hippocampal networks that are artificially modulated by stimulation to prevent interference between different memory systems may operate in a similar physiological fashion to mediate the cortical control of memory leaks. Thus, cortico-hippocampal networks may trade-off between accurate retention and the adaptive benefits provided by a leak, for example, enhanced learning (see Figure 1C).

Hippocampal activity can also affect cortical activity [66, 67]. The changes in hippocampal activity due to memory interactions would then lead to cortical changes [11]. This explains the physiological inhibition of the motor cortex when a skill memory interacts with declarative knowledge (for the movement sequence), which prevents further motor skill processing [16]. The leak (low bandwidth) between memories is occurring within the hippocampus but affecting cortical activity. Yet, the relationship between cortical and hippocampal activity may change when the memories acquired in quick succession share the same structure (high bandwidth leak). This common feature may trigger the activation of large-scale cortical circuits associated with the earlier memory [13, 68]. For example, large-scale motor circuits may become activated even during word-list learning, when, and only when, the word-list had the same structure as a motor sequence learnt earlier. This would be an "ectopic" activation, with a memory representation (in this case for motor memories) becoming activated along with the activation of a different memory representation, which is aligned with the task being learnt (in this case for words). Thus, cortical circuits may drive hippocampal activity and so provide information about a common serial structure to enhance learning of the subsequent memory with the same structure [6, 68, 69].

However, how information leaks is shaped by memory state (unstable vs. stable). A memory is stabilized during practice or subsequently offline during consolidation [7, 26, 28, 29, 70-72]. Once in this state a memory leak is no longer expressed as enhanced learning of a different memory type with the same structure; instead, it transfers the stability it has developed to a newly formed different type of memory with the same structure, and so protects this new and otherwise unstable memory from disruption (see Figure 1C vs. Figure 1D; [6] cf. [7]). This change in memory state is due to changes in how a memory is represented within circuits, and how those circuits function [29, 72, 73]. For example, a spatial memory ceases to be dependent upon the hippocampus, and instead becomes dependent upon the frontal cortex [47, 74]. The shift in underlying circuitry alters memory state (unstable vs. stable), how memory leaks are expressed (enhanced learning vs. protection from disruption), and may also alter how they occur. Leaks may become mediated by travelling waves sharing information through upper and lower cortical layers [75, 76]. The state of a memory changes due to awareness for learning, the duration of practice, offline processing, which differs across different brain states (wakefulness and sleep), and at subsequent retrieval [27, 29, 77-81]. Each of these memory state changes alters how a memory is represented, and at least in principle, could therefore modify how leaks occur, develop, and are expressed.

## A leak solves problems

A leak of highly complex information enables the flexible application of knowledge across different situations (**generalization**). For example, a melody may be learnt as a sequence of sounds (auditory memory), which subsequently can guide the skillful playing of the melody on a musical instrument (motor memory). The sequences have a different content (auditory vs. action) but a common structure, which when shared through a leak makes that information available to a different memory type. So even though experience of a task may be lacking, performance will suggest otherwise (i.e., non-naïve; Figure 1; Box 1).

Leaking complex information explains the dynamics of human learning. An initial "fast" performance improvement may develop because what is being learnt has a structure in common with a different memory type formed earlier (action vs. words; [6]). Sharing this critical information will aid learning, enhancing it, and producing "fast" performance improvements. Yet associating the common structure with the unique content of each memory will take time, requiring changes in network strength – dependent upon, for example, synaptic changes and protein synthesis – leading to a subsequent "slow" performance improvement (*fast-slow* learning). Thus, information within one memory helps drive the formation of a different type of memory – when they have a common structure – providing a novel explanation for the dynamics of learning.

Other explanations of learning dynamics are based upon network properties. Hippocampal networks undergo rapid plastic change – explaining the initial "fast" performance changes – while subsequent plastic changes occur more slowly in cortical networks – explaining the subsequent "slow" performance changes [73]. This balances plasticity and stability, ensuring that whilst information from the environment drives the formation of new memories it does not corrupt long-standing memories [82, 83]. A leak between memory systems complements this by providing an explanation for learning dynamics when information that is already available within the brain, for example, the abstract structure of actions, is being used to drive the formation of another memory, such as a word-list with the same serial structure. Thus, both network properties and memory leaks explain learning dynamics, but for different contexts: one when external information alone is responsible for memory formation, and the other when external information is only partially responsible for memory formation.

Leaks may also solve challenging energetic and computational problems of memory formation. A leak allows the network changes that represent a property of an existing memory to be shared with another memory system. This reduces the need for an energetically demanding investment to be made into network changes; for example, in synaptic strength, because they are already present in another memory system [84]. Simultaneously, this reduces the computationally intensive problem of selecting from the vast array of network states (both in activity and synaptic weight space) that can lead to a desired adaptive performance (*ill-posed network problem*; [85, 86]). Instead, the combination of network states has already been solved, and through a leak made available to other memory systems. Thus, the leak between memory systems may overcome some of the toughest problems in memory formation.

## Concluding remarks

Leaks can be quite simple. Binary information about whether a memory has been formed (or not) can leak out and shape the fate of a different memory (i.e. whether it is retained or impaired; [1, 2, 4-6, 9, 10, 21]; Figure 1). This simple information is analogous to a security leak that an attack is planned without any specific details (low-bandwidth leak). Yet, leaks can also transfer detailed information between memories, allowing the same abstract information to be applied to different contents (skills vs. facts, generalization [6, 7]). In this case, the complex information is analogous to a security leak with specific details about a planned attack; such as the time, place and that nature of the attack (high bandwidth leak). These leaks enable different types of contents to merge, and common relational (spatial, temporal) structures to emerge, which could lead to the construction of internal representations (grammar and schemas) and perhaps even concepts (see Outstanding Questions). Leaks rely upon the hippocampus and the cortex, which perhaps contributes by driving hippocampal circuits and controlling the leak (balancing cost vs. benefits). The mechanisms supporting a memory leak will likely change as the state of the memory changes during further practice and offline processing (over wakefulness and sleep), which explains the changed expression of the leak (enhanced learning vs. protection) as memory state changes (unstable vs. stable; [6] vs. [7], see Outstanding Questions). Leaks enable the transmission of information across content boundaries, to enable memories to be linked based upon abstract structure, explaining learning dynamics, allowing the creation of internal representations, and providing solutions to both energetic and computational challenging memory problems.

## Box 1. Different types of transfer

For some types of transfer initial performance is improved. Having practiced a sequence of movements with one hand, subsequent performance with the other hand is skilful despite having never performed the sequence with that hand (i.e., intermanual transfer; [80, 87-89]). During practice the sequence is learnt within multiple co-ordinate frames – external (spatial location or allocentric) plus internal space (finger or egocentric) – and this redundancy allows performance to be transferred between the hands [78, 80]. Yet, this type of transfer occurs within a memory system and relies on redundancy. By contrast, between memory systems, generalization is dependent on different contents (actions vs. words) having a common feature (serial structure), which is a degenerate coding. This may lead to different expressions of generalization. For example, learning a sequence of movements does not improve intial performance, but instead enhances the subsequent learning of a sequence of words when the two sequences (words vs. actions) share a common serial structure ([6]; Figure 1). Alternatively, it can serve to protect a memory from disruption. For example, a newly formed motor skill memory would normally only become resistant to disruption through practice or during consolidation, yet it can be protected from disruption because it shares a structure with a previously learnt word-list ([7, 27]; Figure 1). Thus, information leaking between memory systems can give rise to a variety of different forms of generalization.

## Glossary

**Generalization**: The ability to flexibly apply acquired knowledge or skill across different situations. It is detected by showing performance transfer. For example, intermanual transfer demonstrates that a skill learnt with one hand generalizes between hands. Equally, learning a set of overlapping stimulus pairings (A-B, B-C, C-D, D-E) leads to subsequent recall of the pairings and also the novel pairing (A-E; transitive inference; high-order learning). Learning about different objects including tools and their function leads to subsequently correctly identifying (categorizing) a novel object (chair, desk, hammer). Each of these may rely upon a common core computation (recurrent networks) albeit implemented within different brain circuits to extract common features (across skills, pairings, objects).

**Interference:** The impaired recall of a newly formed memory due to a manipulation. Traditionally, this manipulation has taken the form of learning another memory: one memory task (task A) is immediately followed by another memory task (task B). The subsequent recall of task A is impaired. Other manipulations have also been used, which directly affected brain physiology. For example, brain stimulation techniques (transcranial magnetic stimulation or optogenetics) and protein synthesis inhibitors. These manipulations have a retrograde (retroactive) effect. They interfere with a recently formed memory (retrograde interference) to impair subsequent recall. By contrast, in another type of interference a manipulation affects the subsequent formation of a memory (anterograde interference).

**Memory Leak**: the sharing of information across memory systems. The information leaking can be quite simple (low-bandwidth), e.g. that a memory has or has not been formed. When a memory has been formed this information leaks out and interferes with processing in a different memory system. This interference is due to the formation or processing of another memory, and is observed regardless of whether or not the different memory types have features in common. Highly complex abstract information can also be shared (high-bandwidth leak). Following the formation of a memory the immediate learning of a different type of memory is enhanced, or several hours later it is protected from disruption when the different types of memory have a common structure. In these examples the leak is sharing highly detailed information about the structure common between the tasks.

**Transfer**: When performance acquired in one situation is applied to a novel situation. For example, the skilled performance of a sequence of finger movements acquired with one hand is transferred to the other hand (intermanual transfer). Earlier experience is being used to guide successful performance in a novel situation. Transfer can lead to improved initial performance, or an enhanced ability to learn in the novel situation (please see Box 1).

## Figure Legends

**Figure 1. Different leaks. (A)** Learning one memory (task a), and then immediately learning another different type of memory (word vs. skill; task b) impairs retention of the initial memory. The fate of the initial memory is determined by the simple presence or absence of the other memory (low-bandwidth leak). **(B)** A word sequence and a skilled movement sequence have a common abstract structure when there is a simple mapping between the semantic category of a word (clothing, furniture, type of transport, vegetable), and movement positions (1 to 4). **(C)** Regardless, of any common abstract structure between the memory tasks the impairment in the retention of the intial memory remains (low-bandwidth leak). This impairment is correlated with the enhanced learning that occurs in the subsequent memory task (task b) when the tasks have a common structure, despite having different contents (words vs. skill; see also Box 1). The enhanced learning is due to the sharing of abstract information from one memory (task a) with a subsequently formed memory (task b; high-bandwidth leak). **(D)** Introducing a time interval between the memory tasks (~ 6 hours), stabilises the initial memory preventing its impaired retention, and prevents enhanced learning in the subsequent task. Yet, abstract information still leaks from a stable memory. It protects newly formed memories from disruption, preventing their impaired retention, when they have a common structure. Memory state (unstable vs. stable) modifies the expression of the leak (enhanced learning vs. protection).

**Figure 2. Leaky mechanisms. (A)** Different memory types (skills vs. facts) leak into another when allocated to overlapping neural populations. The hippocampal neurons allocated to a memory remain excitable following its formation (~5-6 hours), which increases the likelihood that these same neurons will be allocated to a subsequent memory, and this overlap restricts the available processing impairing retention of the initial memory [9, 10]. That impairment is related to hippocampal activity [11]. The cost of this impairment (low-bandwidth leak) has a potential benefit. By being allocated to an overlapping population of neurons an abstract feature common to both memories (2-3-1-4) is already encoded within the population, and as a consequence the new memory can be acquired more quickly (high-bandwidth leak; [56]). This enhanced learning is correlated to the impaired retention of the initial memory because both depend upon being allocated to an overlapping neural population [6]. **(B)** Increasing the time interval between forming the memories provides an opportunity for the excitability of the neural population to decline, for the memories to be allocated to distinct populations, and without sharing an overlapping population there is no leak of information between memories (low or high-bandwidth; [6]). Decreasing excitability (prolonged practice) prevents memory leaks – both memory interference and transfer of enhanced performance to a related task are prevented [29, 72, 90-92]; conversely, increasing excitability (brain stimulation) enables performance transfer [92, 93]. Together, these observations link excitability with memory leaks (low and high-bandwidth). Yet, different mechanisms may operate for different expressions of a leak (enhancement vs. protection).

## Acknowledgements

I am very grateful to Karunesh Ganguly (at the University of California; San Francisco), to Michael Kohl (at the University of Glasgow; Centre for Neuroscience), to Mircea Van Der Plas and Alberto Failla (both at the University of Glasgow; Centre for Cognitive Neuroimaging) for thoughtful, engaging and constructive discussions on many of the ideas presented here, and to both the Air Force Office of Scientific Research (AFOSR, FA9550-16-1-0191; Virginia, USA; FA9550-21-1-7057; London, UK), plus the Leverhulme Trust (RPG-2020-124; London, UK) for supporting my work.

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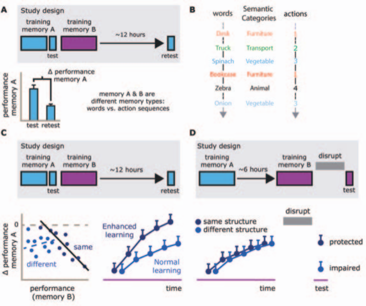
A
Study design
training memory A
test
training memory B
~12 hours
retest
Δ performance memory A
performance memory A
test
retest
memory A & B are different memory types: words vs. action sequences
B
words
Semantic Categories
actions
Desk
Furniture
1
Truck
Transport
2
Spinach
Vegetable
3
Bookcase
Furniture
1
Zebra
Animal
4
Onion
Vegetable
3
C
Study design
training memory A
test
training memory B
~12 hours
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same
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performance (memory B)
Enhanced learning
Normal learning
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D
Study design
training memory A
~6 hours
training memory B
disrupt
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same structure
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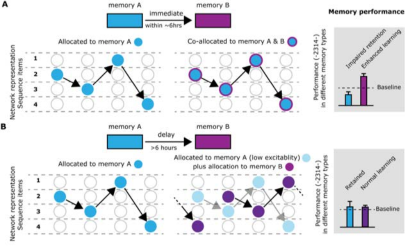
A
memory A
immediate
within ~6hrs
memory B
Memory performance
Allocated to memory A
Co-allocated to memory A & B
Network representation
Sequence items
1
2
3
4
Performance (-2314-)
in different memory types
Impaired retention
Enhanced learning
Baseline
B
memory A
delay
>6 hours
memory B
Allocated to memory A
Allocated to memory A (low excitablity)
plus allocation to memory B
Network representation
Sequence items
1
2
3
4
Performance (-2314-)
in different memory types
Retained
Normal learning
Baseline