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REMINISCING AND DAYDREAMING Investigating the Similarities Between Episodic Memory Recall and Imagination

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THE POWER OF IMAGINATION HAS LONG BEEN TOUTED AS A DISTINCTIVE PROPERTY OF HUMAN COGNITION AND REMAINS A HEATED TOPIC AMONGST PHILOSOPHERS, SCIENTISTS, AND DAYDREAMERS ALIKE. DESPITE PLAYING A CRITICAL ROLE IN THE MAJORITY OF HUMANITY'S FINEST ACHIEVEMENTS, LITTLE IS KNOWN ABOUT HOW THIS FACULTY ACTUALLY WORKS. RECENT FINDINGS FROM LESION PATIENTS POINT TO THE INVOLVEMENT OF THE HIPPOCAMPUS IN IMAGINING NEW SCENARIOS. THE HIPPOCAMPUS IS HISTORICALLY ASSOCIATED WITH LONG-TERM MEMORY CONSOLIDATION, AND MEMORY MODELS ARISING FROM NEW FINDINGS IN THE MOLECULAR PATHWAYS OF MEMORY ALLOW FOR A MORE FLUID TRANSITION BETWEEN IMAGINATION AND MEMORY. ELIZABETH LOFTUS' FAMOUS STUDIES OF FALSE EPISODIC MEMORY RECOVERY FURTHER DEMONSTRATE OVERLAP BETWEEN IMAGINED AND RECALLED EVENTS. FINALLY, AN FMRI STUDY IS PROPOSED TO COMPARE BRAIN ACTIVITY DURING BOTH EPISODIC MEMORY RECALL AND TASKS THAT REQUIRE IMAGINATION IN ORDER TO PINPOINT REGIONS FOR FURTHER INVESTIGATION. As the field of neuroscience expands, it is increasingly entering uncharted territory; the pieces of human experience that were once major arguments for Cartesian dualism, including morality, foresight, and theory of mind, are quickly finding neural homes. Paradigms and brain imaging technologies are becoming progressively more exacting, allowing cognitive scientists to investigate the brain regions and neural circuitry responsible for abstract and uniquely human traits. One of these traits is imagination, the ability to produce vividly detailed episodic events. Recent studies of hippocampally-lesioned patients have shown that these injuries result in the inability to formulate new imaginative experiences,ⁱ suggesting that these regions, classically linked with memory, are also necessary for imagination. New findings in memory research have offered a modified memory modelⁱⁱ suggesting a fluid continuum between real episodic memories and episodic imaginative experiences. The error-prone nature of episodic memories as evidenced by false memory experimentsⁱⁱⁱ supports the theory of a synonymous relationship between what is currently conceived as episodic memory and imagination. In light of this evidence, we will discuss a possible experimental paradigm that will investigate similarities in brain activity induced by episodic memory recall and the production of an imaginative narrative.

IMAGINING A DRAGON IS A PROCESS WHICH LIKELY OCCURS IN THE HIPPOCAMPUS.



Episodic memory is a uniquely human trait that expresses information in a detailed narrative fashion, coding for who, what, where, when, and why.^{iv,v} When conventional speech refers to 'memories', it is most likely referring to episodic memories. For example, recall a childhood memory, perhaps your first baseball game. You may remember stepping up to home plate, hearing your mom and dad cheer, and striking out in humiliation. Perhaps you may remember the smell of the grass, the warm summer light, or the taste of the snacks back in the dug out. Now imagine a completely fanciful event, perhaps a dragon attacking a ship full of Vikings. Again, you can hear the sea, taste the salt water, and feel the heat of the dragon's breath. As a final exercise, try integrating the two; while stepping up to the plate in your first baseball game, have a dragon stroll out into left field.

Ridiculous, perhaps, but this brief exercise illustrates that as far as the nature of the mental experience is concerned, imagination and episodic memory seem, if only anecdotally, identical. Although some nonhuman animals have displayed episodic-like memories, vi Homo sapiens are the only known species to possess this ability.vii As one might surmise from the previous exercise, classical false memory studies have been able to modify, falsify, and even produce new fictitious memories of fantastic proportions. One of the more classical studies, by Loftus, viii asked participants to recall a series of childhood memories that were given to the researchers by the participants' parents. During these sessions, the investigators would also ask the participants about having been lost in the mall as a child, which the parents of the participants confirmed had never happened to their children. Nonetheless the participants recalled confidently the fictitious event, even creating precise details.ix

The suggested nature of episodic memory supports the fluid model, which integrates imagination and episodic memory, but an understanding of the underlying mechanism of memory production is necessary to further investigate this theory. Memory is comprised of past events, but the function of memory is strictly future-based. An ever-changing environment behooves an organism to record responses in the chance that similar events occur in the future. In humans, the seat of memory is the hippocampus, a bilateral pair of horns that curl in the subcortical region of the brain, ending with the amygdala.^{*} As lesion patient studies have shown, loss of the hippocampus results in profound short-term memory loss, as well as a deficit in the ability to create new long-term memories.^{xi} The findings from these and other memory studies have led to the proposal of a memory model in which short-term memories, lasting from a few seconds to a few hours, are recorded in the hippocampus and are later consolidated to the cortex as long-term memories, where they can remain for a lifetime.^{xii,xiii} synapses. Subsequent co-activation of these two synapses further increases AMPA numbers until these neurons fire swiftly with the smallest synaptic activity.xvi

Behaviorally, the Pavlovian response is observed; if, for example, a rat hears the tone that is followed by an electric shock, it will quickly behave in response to the tone as if it were being shocked. The activation provided by the neurons responding to "tone", after a repeated exposure to the tone-shock pairing that induced long-term potentiation, is enough to elicit a shock response without co-stimulation. The manner in which the hippocampus codes for the information that comprises such memories remains unknown. However, injection of a protein synthesis inhibitor such as anisomycin during training sessions blocks

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Recent neurobiological research has challenged, or at least modified, this long-standing memory dogma. At the neural level, memory encoding begins with a process called long-term potentiation, in which the co-stimulation of a neuron by two separate neurons at the same time molecularly increases the efficiency by which that neuron can later be activated under a similar circumstance.^{xiv} This coincidental strengthening is often referred to as Hebb's Law, expressed as "neurons that fire together, wire together."^{xv} Costimulation leads to molecular changes facilitated by magnesium ions and voltage-gated NMDA channels, which respond to the excitatory neurotransmitter glutamate, causing an influx of calcium ions and, after a short metabolic pathway, protein synthesis that produces AMPA receptors that are inserted specifically in the activated the production of AMPA receptors, long-term potentiation, and subsequent memory of the association between tone and shock.^{xvii} Surprisingly, recent findings from Nader^{xviii} show that if a protein synthesis inhibitor is injected when the learned behavior is recalled at a later date, the presentation of a tone long after the inhibitor has worn off will elicit very little behavioral response. In effect, the memory is erased when it is recalled in the presence of a protein synthesis inhibitor. Nader has proposed that instead of a shortterm and long-term memory system, memories are rather in a labile, active state or an inactive, consolidated state, and the process of consolidation and reconsolidation are practically identical.^{xix} The study has caused much excitement and controversy in the psychology field due to its potential as a therapy to erase or dull traumatic memories, but it also raises questions as to the evolutionary selection of such a memory system. According to the active/inactive state memory model, every time a memory is recalled it is liable to be disrupted. The nature of this model seems very unstable, especially when one considers that those memories that are recalled the most are probably the most important. However the system seems highly evolutionarily conserved, with the same effects of protein synthesis inhibitors dulling or erasing behavioral memory responses in rats, chickens, and crabs.^{xxx}

The positive attribute of this system is that the labile state achieved in recalling a memory allows it to be brought back to the mental drawing board, where it is open to editing. Thus an individual can continually add to several memory scripts; a memory for "tone = shock = freeze" recalled to a labile state can easily have another stimulus added to it, increasing the efficiency of behavioral learning, a trait that could dramatically increase the survival of an individual. For example, a rat that remembers "tone = freeze" will very quickly learn "light flash = freeze" when a light flash is placed directly before the tone/shock training. In humans, lesion patients without the facility of a hippocampus are unable to arrange remembered events in a correct order, supporting the idea of the hippocampus as the region responsible for the assembly of a memory narrative.^{xxi}

It could also be possible that the only memories prone to error in an active/inactive memory model are episodic memories. Memories are split into two categories: declarative and nondeclarative. Declarative memories are further split into episodic and semantic memories, the latter of which deals with facts and certain language skills. Nondeclarative, or implicit memories, record procedural memory, perceptual representation systems, classical conditioning, and nonassociative learning.^{xxii} Few nonhuman animals display semantic memory capabilities, but the majority of cognoscente species have nondeclarative faculties.^{xxiii} In an active/inactive model of memory, the implicit information coded by these types of behavior, like a tone beep or the motions used for riding a bike, are unlikely to be falsely modified as the only equivalent data that can replace the coded information is derived from environmental stimuli. As we have seen from false memory studies, episodic memory seems to have the unique characteristic of being highly susceptible to thought-provoked reconsolidation error.

Interestingly, it wasn't until 2007 that hippocampus lesion patients were tested for their ability to create mental images in response to a verbal prompt.^{xxiv} Episodic memory production is practically nonexistent in these individuals, and if imagination is synonymous with episodic memory recall, one would expect to see retarded imaginative processes. Compared to control individuals of the same age and IQ, the responses of the amnesic patients were severely fragmented, labored, and non-descriptive, leading the research team to conclude that imagining new events was impossible for hippocampally-lesioned patients.

To decisively test whether episodic memory and episodic imagery are the same will require a comparative study of brain activation during both tasks. Before the experiment begins, participants will be asked to send their parents a short questionnaire about events from their child's past. While lying in a function Magnetic Resonance Imaging (fMRI) machine, the participants will be prompted with either one of their childhood memories or an event that never occurred. They will then be asked to recall the event and mentally relive the experience, regardless of its validity. If the prompt is of a familiar event, the participant will be asked to recall the specific memory. If the prompt doesn't ring a bell in the mind of the participant, they will be asked to imagine the event as if it had truly occurred. For the comfort of the participant, the parents will be asked for only positive events. The participants will be told to be as vivid as possible in recalling the memory, and upon finishing the session, lasting only a few minutes, they will need to describe their mental responses. The participants will also be asked to acknowledge which scenarios they recalled and ENCODING OF EPISODIC MEMORIES ACTIVATES NUMEROUS PARTS OF THE BRAIN, AS SEEN HERE IN THIS SERIES OF MRIS.



which they imagined occurring, and brain activities between these two groups will be compared.

Past positron emission tomography (PET) studies have found different activations during the encoding and retrieval of episodic memories,^{xxv} often termed 'hemispheric encoding-retrieval asymmetry'^{xxvi}. Encoding activity has been shown to activate left prefrontal cortex and right hippocampal regions in the majority of individuals. Retrieval has been shown to activate only the left prefrontal cortex, and if imagining and episodic memory retrieval were of the same nature, one would expect similar activations. lize the same brain regions to function, does forcing one function hinder the production of the other? For instance, would accuracy in passive memory tasks decrease while a participant is daydreaming, or vice versa, while hippocampus activity remains the same? What roles do attention areas play in switching classically episodic regions from recording real life to reliving fictions?^{xxix} Do these areas play a role in the dream production of REM sleep? The frontal lobes are known to play a large role in global brain activities, including working memory, novel object recognition, and planning for the future.^{xxx,xxxi} If the frontal lobes are the region associated with Baddeley's central execu-

Despite these illuminating results, the majority of the paradigms that produced these patterns of activation used single still images as cues, which are poor real world examples of episodic memory. The paradigm proposed here uses real autobiographical episodes rather than single images. Also, retrieval required acknowledging familiarity when new and old images were presented to participants, while this proposed

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CHILDREN "USE THEIR IMAGINATIONS."

tive, xxxii is episodic memory one of the processes of a visuospatial sketchpad, the other being creative imagery? What role would the switch between the imagined and the real play in a schizophrenic's notorious misinterpretations of imagined events?

Imagination is one of the cognitive abilities that, until recently, most cognitive neuroscientists would not touch with a long pole; it reminds one too much of the

experiment requires a mental recount of each episodic event. Although the cues used in these past experiments would qualify in content as episodic memories, they are poor examples of the powerfully expressive nature of human episodic memory. That being said, regions of activation could vary widely from these previous results in lateralization, but will most likely still occur within the left prefrontal cortex, hippocampus, and anterior cingulate gyrus.^{xxvii,xxviii}

Other interesting considerations could be applied to further experiments; if imagination and episodic memory utiambiguously defined subsets of the dualist mind. With increased understanding of our species cognitive abilities, research scientists are quickly closing in on subjects once left only to the discussions of philosophers. Some of this research raises questions about the way we perceive imaginative processes. Findings describing the neural basis for memory reconsolidation allow for a more fluid memory model that explains the errors notorious to episodic memory as seen in false memory studies. Hippocampus lesion amnesiacs not only display a loss in short-term memory and long-term memory production, but also the inability to create episodic narratives. As abstract as it may sound at first, imagination is a concise cognitive ability that may be synonymous with episodic memory recall. Understanding the mechanism underlying the similarities and differences between these two cognitive abilities could have implications in attention theories, REM dream theory, and memory models, as well as our perception of reality.

ENDNOTES

i. Hassabis (2007) ii. Nader (2003) iii. Loftus (1997) iv. Sudderdorf (2007) v. Gazzaniga (2002) vi. Gazżaniga (2002) vii. Sudderdorf (2007) viii. Loftus (1997) ix. Loftus (1997) x. Gazzaniga (2002) xi. Gazzaniga (2002) xii. Nader (2003) xiii. Gazzaniga (2002) xiv. Frev & Morris (1997) xv. Gazzaniga (2002) xvi. Frey & Morris (1997) xvii. Frey & Morris (1997) xviii. Nader (2000) xix. Nader (2003) xx. Nader (2003) xxi. Shimamura (1990) xxii. Gazzaniga (2002) xxiii. Tulving (2005) xxiv. Hassabis (2007) xxv. Haxby (1996) xxvi. Gazzaniga (2002) xxvii. Cabeza (2003) xxviii. Gazzaniga (2002) xxix. Cabeza (2003) xxx. Knight (1996) xxxi. Henson (1999) xxxii. Baddeley (1996)

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