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Comment

"Anything is good that stimulates thought" in the hippocampus Comment on "The quartet theory of human emotions: An integrative and neurofunctional model" by S. Koelsch et al.

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While the emotional trias of brainstem, diencephalon, and orbitofrontal cortex is generally accepted to hold an affective function at its core, fewer researchers would agree that the least common denominator function of the hippocampus is affective [1]. There is a greater consensus on complementary learning systems theory proposing that in contrast to the outer cerebral cortex hosting more stable memories, synaptic associations in the hippocampus create novel knowledge in the context of episodic memories [2]. We chose Oscar Wilde's quote [3, p. 108] as title because we think that the novel hippocampal conjunction of for the most part familiar (long-term) knowledge patterns elicits the positive affect of appreciation [4,5].

Strikingly, Eriksson and colleagues [6] found that new neurons are "born" in the human adult hippocampus. Kumaran and McClelland [5] simulate their function by symbolic conjunction units coding the coincidence of a number of well-known representations. Thus, they represent an entire episode of one's live. If a cognitive system is confronted with the phrase "weapons of mass destruction", actually eliciting negative affect, it represents this in an episodic conjunction unit. The more often the words of this phrase occur together, the more likely their outer cerebral cortex units connect. Such consolidated knowledge can be simulated by co-occurrence statistics [7,8].

When getting a cue at existing knowledge, the hippocampus can reinstate the activation pattern active at encoding [5]. For instance, when later confronted with "weapons of mass…" the hippocampus may complete the pattern by "destruction". This major function of pattern completion generates cued remembering. On the other hand, the hippocampal major function of pattern separation orthogonalizes neural firing patterns. Thereby it creates the distinction between similar but different concepts. For instance, a second conjunction unit might be created for "weapons of women". Finally, hippocampal conjunction units cause generalization when recursively connected to the cortical long-term knowledge. When one conjunction, for instance, codes for "robin is a bird", and another one for "bird can fly", it may generalize the transitive inference of "robin can fly" [5].

Thus, long-term knowledge has a considerable impact on the episodic operations in the hippocampus. When items like 'marriage' and 'widow' are studied to a semantically associated item like 'wedding', for instance, pattern sepa-

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ration may not work properly and 'false memories' are brought forward [8,9]. When participants are maximally sure that this non-studied word was studied, left hippocampal activation decreases as opposed to items with few semantic associations [10]. This type of error is well explained within an interactive activation framework [11], in which the activation of studied items spreads semantic activation to a non-studied item [7,8,12].

We recently discovered that positive words provide more semantic long-term associations than neutral or negative words [8]. Next we tested Phelps and colleague's [13] proposal that much of the variance in recognition memory previously ascribed to valence can actually be explained by the greater amount of associations [8,14]. We found that positive valence does not provide false memory effects independent of the number of associations to the words in the stimulus set [8], thus confirming that associations and positive valence share common variance.

Similarly, Epstein [15] suggests that the positive emotion of aesthetic beauty of literature is elicited when more (long-term) associations become active than can be consciously elaborated [16]. He proposes a 'nucleus' of the information that made it into consciousness, while the remaining information is activated to provide a semantically rich representation in the "fringe". Complementary learning systems theory proposes that when many long-term associations became active, the amount of input to the hippocampus increases. As a consequence, pattern separation becomes active (Fig. 1 in [17]). This likely leads to the generation of novel conjunction units [5]. We propose that the generation of such novel knowledge corresponds to the physical creation of a neuron from its progenitor cells in the hippocampus [6], which is a positively valenced act by itself. This can result from an optimal combination of familiar knowledge that is combined in an optimally innovative way, for instance in the phrase "weapons of mass distraction" [4].

The computation of associations based on pattern completion and pattern separation processes in the hippocampus [18] leads to the stimulation of thought. This is the physical basis of discovering general knowledge principles – which can cause a positive affect figuratively described by the "light of understanding". Thus, beyond attachment-related affects, we propose that the hippocampus is more generally involved in the processing of positive affect. This leads to the observed neural activation patterns when familiar phrases are altered to gain a novel meaning in poetics [19] or music [20].

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References

[1] Koelsch S, Jacobs AM, Menninghaus W, Liebal K, Klann-Delius G, von Scheve C, et al. The quartet theory of human emotions: an integrative and neurofunctional model. Phys Life Rev 2015;13:1–27 [in this issue].
[2] McClelland JL, McNaughton BL, O'Reilly RC. Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory. Psychol Rev 1995;102(3):419–57.
[3] Hyde H. The trials of Oscar Wilde. New York: Dover Publications; 1962.
[4] Giora R, Kronrod A, Elnatan I, Shuval N, Zur A. Weapons of mass distraction: optimal innovation and pleasure ratings. Metaphor Symbol 2004;19(2):115–41.
[5] Kumaran D, McClelland JL. Generalization through the recurrent interaction of episodic memories: a model of the hippocampal system. Psychol Rev 2012;119(3):573–616.
[6] Eriksson PS, Perfilieva E, Björk-Eriksson TB, et al. Neurogenesis in the adult human hippocampus. Nat Med 1998;4(11):1313–7.
[7] Hofmann MJ, Kuchinke L, Biemann C, Tamm S, Jacobs AM. Remembering words in context as predicted by an associative read-out model. Front Psychol 2011;2(252):1–11.
[8] Hofmann MJ, Jacobs AM. Interactive activation and competition models and semantic context: from behavioral to brain data. Neurosci Biobehav Rev 2014;46:85–104.
[9] Roediger HLI, Mcdermott KB. Creating false memories: remembering words not presented in lists. J Exp Psychol Learn Mem Cogn 1995;21(4):803–14.
[10] Kuchinke L, Fritzemeier S, Hofmann MJ, Jacobs AM. Neural correlates of episodic memory: associative memory and confidence drive hippocampus activations. Behav Brain Res 2013;254:92–101.
[11] McClelland JL, Rumelhart DE. An interactive activation model of context effects in letter perception: part 1. An account of basic findings. Psychol Rev 1981;88:375–407.
[12] Collins AM, Loftus EF. A spreading-activation theory of semantic processing. Psychol Rev 1975;82(6):407–28.
[13] Phelphs EA, LaBar KS, Anderson AK, O'Connor KJ, Fullbright RK, Spencer DD. Specifying the contributions of the human emotional memory: a case study amygdala to. Neurocase 1998;4:527–40.

[14] Maratos EJ, Allan K, Rugg MD. Recognition memory for emotionally negative and neutral words: an ERP study. Neuropsychologia 2000;38(11):1452–65.
[15] Epstein R. Consciousness, art, and the brain: lessons from Marcel Proust. Conscious Cogn 2004;13(2):213–40.
[16] Jacobs AM. Neurocognitive poetics: methods and models for investigating the neuronal and cognitive-affective bases of literature reception. Front Human Neurosci 2015;9(186):1–22.
[17] Yassa M, Stark CEL. Pattern separation in the hippocampus. Trends Neurosci 2011;34(10):515–25.
[18] Henson RN, Cansino S, Herron JE, Robb WGK, Rugg MD. A familiarity signal in human anterior medial temporal cortex? Hippocampus 2003;13(2):301–4.
[19] Bohrn IC, Altmann U, Lubrich O, Menninghaus W, Jacobs AM. Old proverbs in new skins – an FMRI study on defamiliarization. Front Psychol 2012;3:204.
[20] Koelsch S, Fritz T, von Cramon DY, Müller K, Friederici AD. Investigating emotion with music: an fMRI study. Hum Brain Mapp 2006;27(3):239–50.