

We also disagree with Moscovitch and Nadel's proposal that neurogenesis acts to stabilise and protect some remote memories, given evidence that it preserves hippocampal capacity for new learning by erasing older memories [9].

Moscovitch and Nadel also challenge two other predictions of our proposal. They argue that remote memory is not inaccurate. In support of this, they refer to a study which assessed the change in accuracy of participants' recall over the course of 1 week [10]. We do not consider a 1-week-old memory to be remote, and even across this brief period a marginal drop in accuracy was, in fact, reported.

They also challenge the prediction that the ventromedial prefrontal cortex (vmPFC) drives hippocampal activity during scene construction, referring to an fMRI investigation of future thinking [11]. However, a recent magnetoencephalography (MEG) study has demonstrated, with a high degree of temporal precision, that the vmPFC leads the hippocampus and drives its activity during scene construction [12]. We acknowledge that during the elaboration phase of autobiographical memory retrieval the hippocampus modulates activity in the precuneus [13]. However, further work is needed to characterise the network interactions governing autobiographical memory retrieval during the crucial earliest phase of reconstruction, which is when we predict the vmPFC will 8. lead.

Finally, we did not suggest, as Moscovitch and Nadel claim, that all episodic memories decay over time leaving behind only gist. We maintain that rich, detailed remote episodic memories reconstructed via vmPFC-neocortical-hippocampal interactions can produce a full sense of re-experiencing.

In summary, we argue that the hippocampus is critical for retrieving rich remote episodic memories in perpetuity, but this does not imply its role is one of storage. Letting go of the notion of an enduring hippocampal memory trace will, we believe, provide a more productive way forward for memory research. We thank Moscovitch and Nadel for participating in this debate, and hope that our perspective continues to provoke discussion and, importantly, motivate experiments that will definitively establish the precise roles of the hippocampus and vmPFC in remote memory retrieval.

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### **Forum**

# Perceptual Input Is Not Conceptual Content

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Can we represent number approximately? A seductive reductionist notion is that participants in number tasks rely on continuous extent cues (e.g., area) and therefore that the representations underlying performance lack numerical content. I suggest that this notion embraces a misconception: that perceptual input determines conceptual content.

Nihil est in intellectu quod non prius fuerit in sensu [1].

Nothing is in the intellect that was not first in the senses. In psychology and the cognitive sciences, this medieval dictum still arguably captures the majority view. Here I examine one corollary of the empiricism it espouses: that one should look to sensory input to determine the contents of human concepts. I focus on the representations of the Approximate Number System (ANS) as my example and will argue that for this case, and for the study of concepts quite broadly, we must guard against the 'input misconception': that input determines content.

#### Our Approximate Number Abilities

While only humans, whose cultures teach and use exact mathematics, appear able to think thoughts involving large exact integers (like 47), all humans - including newborns - appear to think thoughts about quantities approximately (e.g., that approximately 16 dots is more than approximately eight) [2].

Despite the diversity of research across species and methodologies implicating an



#### Box 1. Reductionism Across Science

The seductive power of reduction [9] has affected science since well before the modern study of the mind. So has it gone for biology (e.g., the modern synthesis in biology, the fundamental role of DNA) and chemistry (e.g., the reduction of a protein's 3D conformation to its amino acid sequence) and so has it often gone for cognition (e.g., dynamical systems, the prototype theory of concepts, parallel distributed processing; see [10]).

Is reduction always a stride towards truth? There are examples of non-successful reduction attempts in biology (e.g., the modern separation of molecular biology from systems biology) and chemistry (e.g., Levinthal's paradox of the nonreducibility of protein folding to a simple sampling of all possible orientations). P.W. Anderson [11], a Nobel Prize-winning physicist, made the point that one cannot reduce solid state physics to particle physics. More broadly, Jerry Fodor [12] argued that it is not logically possible to reduce the social sciences to neuroscience, biology, chemistry, and ultimately physics - highlighting the importance of functionalism and multiple realizability. So, no, reduction does not always lead us closer to truth.

evolutionarily and developmentally primitive 'number sense' (or ANS), some scholars claim that what looks like a success at representing number might not be one at all. Instead, they suggest that observers solve 'numerical' tasks by relying on nonnumerical cues in the stimulus arrays: cues like cumulative surface area, density, cumulative contour length (perimeters), total envelope of the array, or some combination of these [3]. Infants and adults sometimes do seem to engage non-numerical cues in numerical tasks (but see [4]). Many authors worry that such continuous-magnitude thoughts are first and foremost in the mind and that if one does not control for every physical aspect of stimuli besides number (i.e., all trials controlled for cumulative area, density, contour length, envelope, etc.), one is not entitled to claim that observers are representing number at all.

This is an instance of the classic rationalist/ empiricist dialog. The question is: if humans and other animals rely on evidence from area, density, or other visual cues to make numerical judgements, should we conclude that their judgments are non-numerical? I say no, and argue for a distinction between input and content in three points.

# Point 1: Numbers Are Abstract Entities - They Must Be Inferred

Unlike sunsets, the number 8 does not exist in the physical world. You cannot go out into the physical world and find Ms Eight. A number is an abstract entity. At best, one might concede that objects exist in the world, in which case number is a nonphysical description of an abstract entity (i.e., a property of a set of objects).

I note this to stress that if number is not in the physical world, the mind cannot perceive it directly. Number has to be inferred from evidence that itself is not numerical. I sketch the inferences I have in mind below.

### Point 2: Functional Role Reveals Conceptual Content

The irrelevance of input to determining the content of our conceptual representations becomes clearer when we consider the wider role these representations play throughout cognition; that is, their functional role. Our approximate number representations, on reflection, appear to play the role of numerical representations. The evidence supporting this claim comes from a wide variety of results: brain areas that support the ANS also support explicit, symbolic mathematics [5] and brain damage can affect both approximate and exact mathematics; children with a specific deficit in symbolic mathematics also sometimes show a deficit in approximate mathematics, and throughout the range, from low-achieving, to typically achieving, to high-achieving students [6,7], performance on ANS tasks correlates with performance on symbolic mathematics tests, controlling for other abilities (e.g., symbolic verbal performance, working memory, executive function) [6]; and last, the ANS is multimodal - people, including infants, can compare numbers of sounds to numbers of visual items [8], even at just a few days old - which implicates a common abstract representational currency (number) that crosses modality. Thus, irrespective of what the inputs to the ANS may turn out to be (e.g., area, perimeter, visual texture, amplitude of beeps), the output of the computations performed by the ANS has all of the indicators of being a modality-general approximate number representation.

#### Box 2. The Curious Case of Lilia Rose

Imagine an infant, Lilia, who experiences the scent of a rose each time her attention falls on a collection of visual items or series of sounds. With few items (e.g., four), Lilia experiences only a little bit of rose smell; with many (e. g., 27), she experiences a much more intense rose smell. Gradually Lilia becomes able to estimate the number of items in any collection she sees or hears just from the intensity of rose smell they cause her to experience. The question for the reductionist is: must we say that Lilia's estimates of number are not really numerical because her computations relied on intensity of experienced rose smell along the way to estimating number? When, years later, Lilia becomes able to report that a stimulus 'seems to contain around eight dots,' should we reject her claim as being about rose smell and not number? If you agree that Lilia can make numerical claims based on rose smell evidence, and that infant Lilia also had numerical experiences triggered by rose smell, then I invite you to agree that other creatures also can generate numerical beliefs by relying on area, density, convex hull, or any other non-numerical cue.

## Point 3: Concepts Are Contents Activated by Inference

The antidote to the 'input misconception' is the principle that the input to the representation is not the content of the representation. How do earlier representations relate to later representations? According to empiricism/constructivism, later representations are not inferences or abstractions, but rather are simply



made up of earlier representations (e.g., the representation of BIRD is achieved by combining a representation of something with FEATHERS with something that LAYS EGGS, etc.). Under this understanding of conceptual content, if density and area are used to determine a number judgement in an approximate number task, this would reveal that the representations triggered by that task are not actually numerical, no matter what other thoughts they might correlate with further downstream. On this view, there is no such thing as a 'numerical' thought other than as a relabeling of a DENSITY thought and/or an AREA thought, etc. There is no inference, only re-description (Box 1).

The alternative rationalist view is that minds work the way science works: observations, or experiments, provide evidence for or against a model/hypothesis. The evidence is not the hypothesis. Thus, on the rationalist account, cumulative area and density may provide evidence for a thought about NUMBER, arrived at through inference (Box 2).

So, both views of conceptual content will perfectly well embrace a finding that density and area contribute to performance in approximate number tasks. This is not a scientific disagreement about what evidence would be interesting to have, it is rather a disagreement concerning what the evidence is evidence for.

### The 'Input Misconception' Applies to Many Concepts

Consider sunsets again. Although physical events occur outside our minds, the concept of, for example, a SUNSET, and the property of being-a-sunset, is mind dependent. Such a representation requires an inference from colors in the sky, the time of day, etc. However, a sunset is more than just the sum of these facts, and representing a sunset requires an inference from the evidence much the way it does for EIGHT. So it goes for BALL, AGENT, and EACH, and much more besides.

The 'input misconception' should be replaced with the principle that the input to the representation is not the content of the representation. Especially for the case 3. of an abstract entity like a number, a disconnect between evidence (e.g., density) and content (e.g., EIGHT) will be the rule and not the exception. In such a case, attention to the output side of the computation is necessary to arrive at a proper understanding of conceptual content. Attention to the input side is necessary to guide us towards an understanding of the weighted combination of features engaged by the extraction algorithm evidence that will inform our concepts but will never determine their content.

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