

A few questions on the content of the  
previous lecture

# slido



**A critical period reflects ..., after which the individual is ... to fully acquire those abilities.**

ⓘ Start presenting to display the poll results on this slide.

slido



**The arcuate fasciculus ensures a communication pathway between ... and ...**

ⓘ Start presenting to display the poll results on this slide.

# slido



**There are two language processing pathways; a dorsal stream which maps ..., and a ventral stream which maps ...**

ⓘ Start presenting to display the poll results on this slide.



# Cognitive mechanisms of reading and writing

Dr. Lavinia Carmen Uscătescu

April 15<sup>th</sup> , 2024

# Outline

## 1. Reading

- (a) neural substrates

- (b) pure alexia and dyslexia

## 2. Numeracy

- (a) correlates

- (b) dyscalculia

# Reading

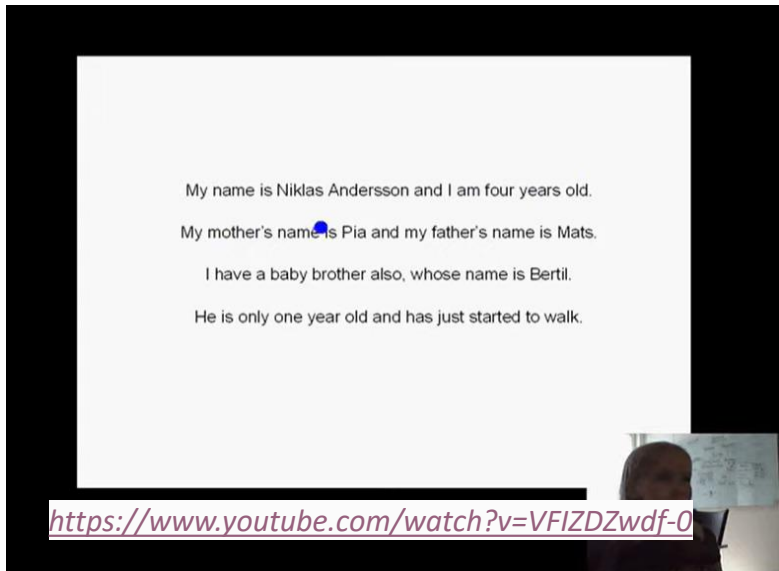
The ability to **read** and **write** is a **cultural invention** of enormous significance => enables humans to exchange ideas without face-to-face contact => our historical knowledge of previous civilizations is derived almost entirely from literate cultures.

Literacy, unlike speaking, requires a considerable amount of **formal training**. It is however **too recent an invention to have evolved specific neural substrates**, having first emerged around 5,000 years ago. Universal literacy has only occurred in western societies over the last 150 years.

A true writing system is one where **symbols** are no longer pictograms of concrete objects, but **represent sounds of words**.



*The earliest writing system (i.e., cuneiform) emerged between 4,000 and 3,000 BC in Sumer (southern Iraq).*



*we consciously process  
 only a very small subset  
 of our visual inputs*

We the pexxxx xx xxx xxxxxxx xxxxxx, xx xxxxx xx  
 ↑  
 Xx xxx people of txx xxxxxxx xxxxxx, xx xxxxx xx  
 ↑  
 Xx xxx xxxxxxx xx xhe United xxxxxx, xx xxxxx xx  
 ↑  
 Xx xxx xxxxxxx xx xxx Xxxxxed States, ix xxxxx xx  
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 Xx xxx xxxxxxx xx xxx Xxxxxx Xxxxxx, in order to  
 ↑

Dehaene, (2009), p. 24, from McConkie & Rayner, (1975)

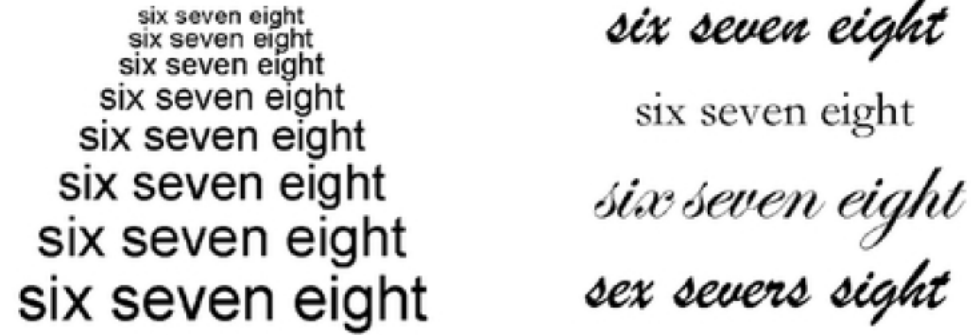
*we can read words presented on the  
 periphery of our visual field if letter  
 size is increased to compensate for the  
 loss of retinal resolution*

**Figure 1.1** The retina stringently filters what we read. In this simulation, a page from Samuel Johnson's *The Adventurer* (1754) was filtered using an algorithm that copies the decreasing acuity of human vision away from the center of the retina. Regardless of size, only letters close to fixation can be identified. This is why we constantly explore pages with jerky eye movements when we read. When our gaze stops, we can only identify one or two words.

Dehaene, (2009), p. 24

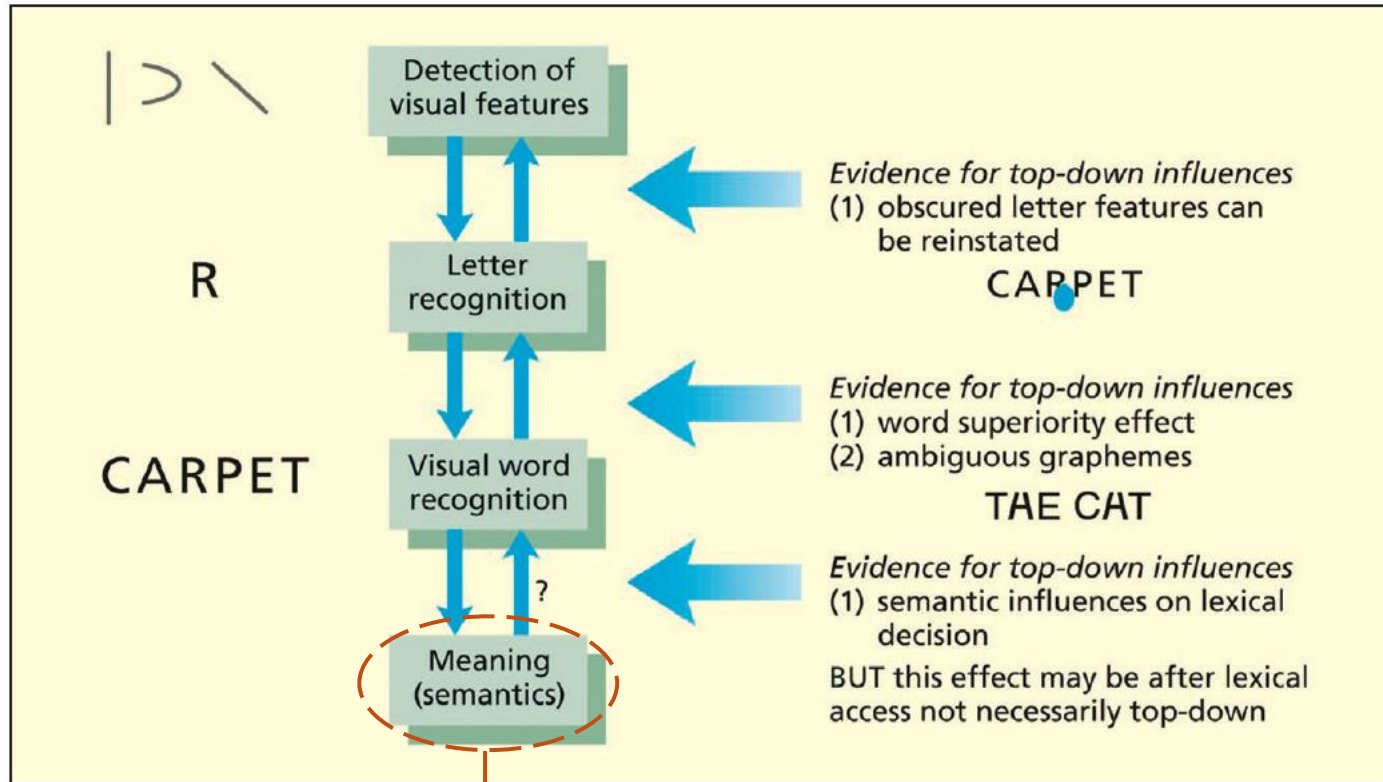
## invariance problem

being able to **identify** words  
**regardless of how they appear**,  
whether in print or handwritten,  
in upper- or lowercase, and  
regardless of their size



**Figure 1.2** Visual invariance is one of the prime features of the human reading system. Our word recognition device meets two seemingly contradictory requirements: it **neglects irrelevant variations** in character shape, even if they are huge, but **amplifies relevant differences**, even if they are tiny. Unbeknownst to us, our visual system automatically compensates for enormous variations in size or font. Yet it also attends to minuscule changes in shape. By turning an “s” into an “e,” and therefore “sight” into “eight,” a single mark drastically reorients the processing chain toward entirely distinct pronunciations and meanings.

*Dehaene, (2009), p. 30*



**FIGURE 13.3:** A basic model of visual word recognition showing evidence in favor of **top-down** influences.

Ward, (2020), p. 335

In a **lexical decision task** (which is a *two-alternative forced choice* type of task) => **Nonwords** (also called **pseudo-words**) are much **faster to reject** if they **do not resemble known words**.

### word superiority effect

we are faster to report the presence of a target **letter** if it is part of a **(pseudo-)word** than part of a **random string** of letters

### bottom-up cognitive mechanisms

when the physical characteristics of a stimulus shape our perception, irrespective of prior knowledge

### top-down cognitive mechanisms

when we use our background knowledge and expectations to interpret what we see

## Lexical Decision Task - demo

### **Lexical Decision Task**

#### **Instructions:**

In this task, you will see two words at the time.  
If both words are REAL ENGLISH words, you press the button "a". If ONE or BOTH words are non-sense words (for example "FLUMMOL"), you press the button "l".  
Respond within 2 seconds.

***Press space bar to start the test***

<https://www.psychtoolkit.org/experiment-library/ldt.html>

DOCTOR  
NURSE

SOAM  
GLOVE

## Neural reuse: a fundamental organizational principle of the brain

**Abstract:** An emerging class of theories concerning the functional structure of the brain takes the reuse of neural circuitry for various cognitive purposes to be a central organizational principle. According to these theories, it is quite common for neural circuits established for one purpose to be exapted (exploited, recycled, redeployed) during evolution or normal development, and be put to different uses, often without losing their original functions. Neural reuse theories thus differ from the usual understanding of the role of neural *plasticity* (which is, after all, a kind of reuse) in brain organization along the following lines: According to neural reuse, circuits can continue to acquire new uses after an initial or original function is established; the acquisition of new uses need not involve unusual circumstances such as injury or loss of established function; and the acquisition of a new use need not involve (much) local change to circuit structure (e.g., it might involve only the establishment of functional connections to new neural partners). Thus, neural reuse theories offer a distinct perspective on several topics of general interest, such as: the evolution and development of the brain, including (for instance) the evolutionary-developmental pathway supporting primate tool use and human language; the degree of modularity in brain organization; the degree of localization of cognitive function; and the cortical parcellation problem and the prospects (and proper methods to employ) for function to structure mapping. The idea also has some practical implications in the areas of rehabilitative medicine and machine interface design.

<https://pubmed.ncbi.nlm.nih.gov/20964882/>

### The neuronal recycling hypothesis (Dehaene & Cohen, 2007)

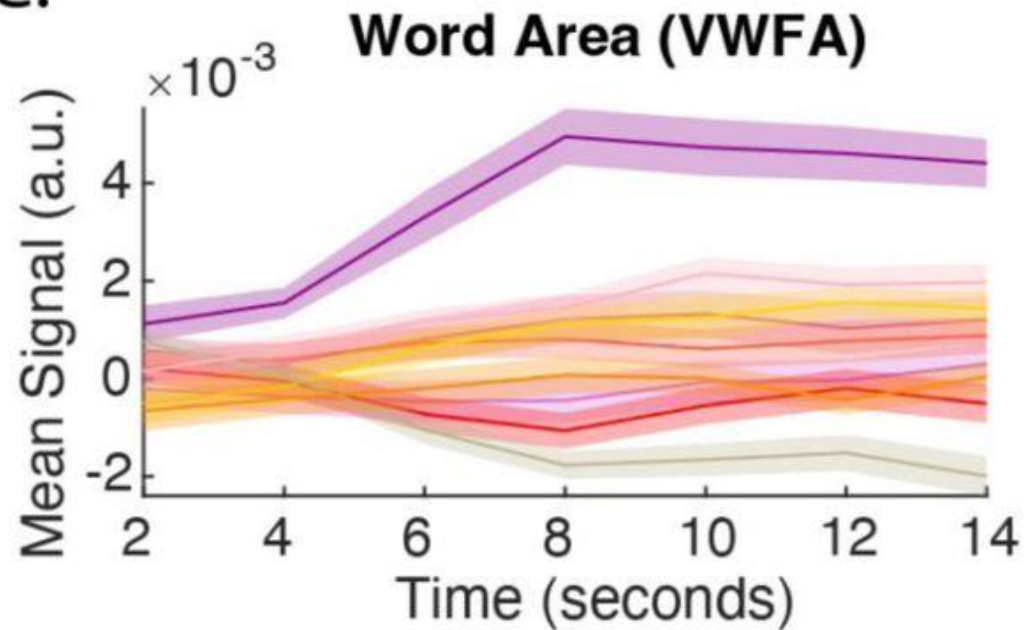
Cognitive capacities such as **reading** and **mathematics** have emerged **too recently** for evolution to have generated specialized cortical circuits . Such **cultural practices** must be **learned**, and the **brain structures** that support them must therefore be assigned and/or **shaped during development**.

## Visual Word Form Area (VWFA)

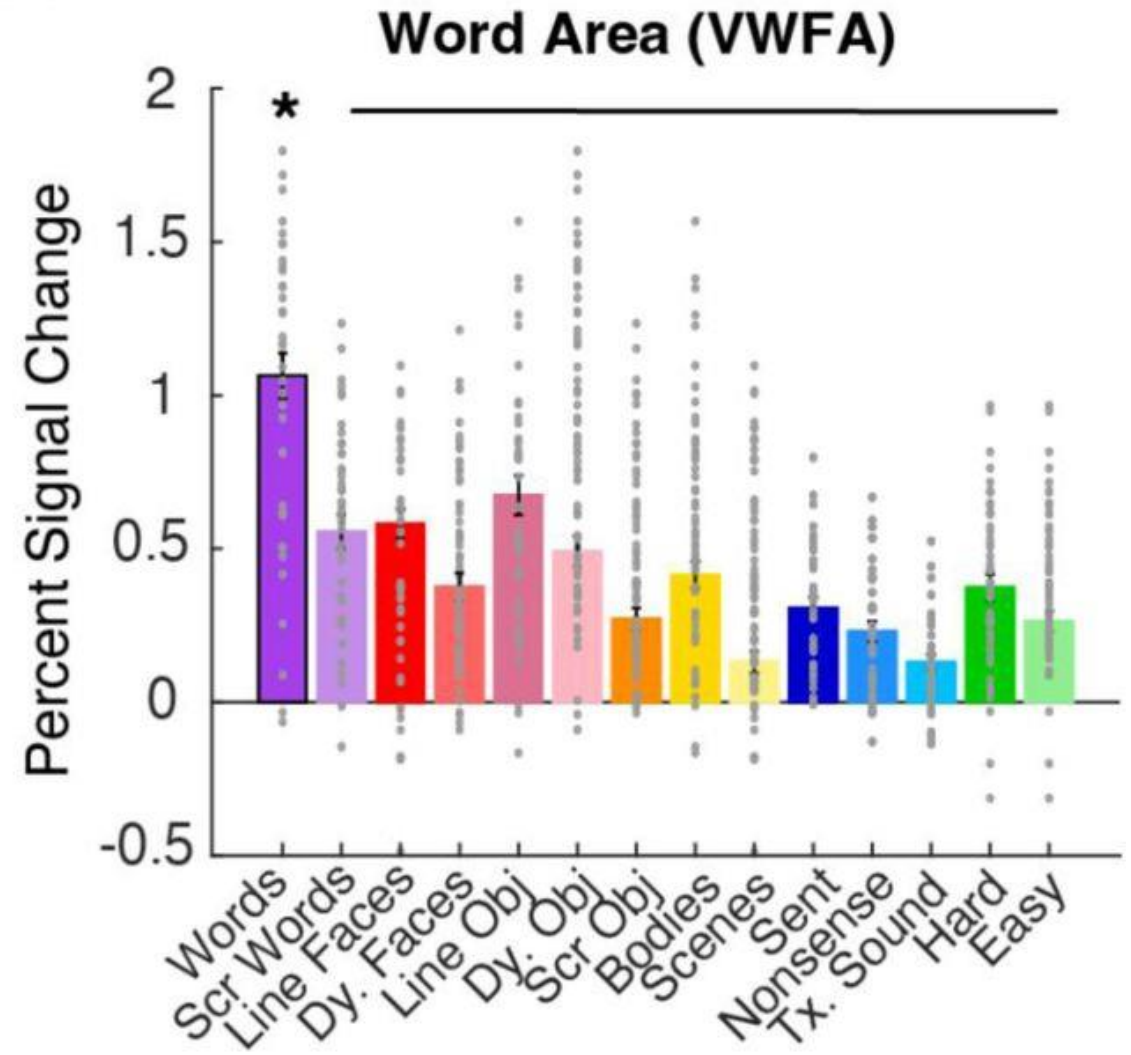
A.



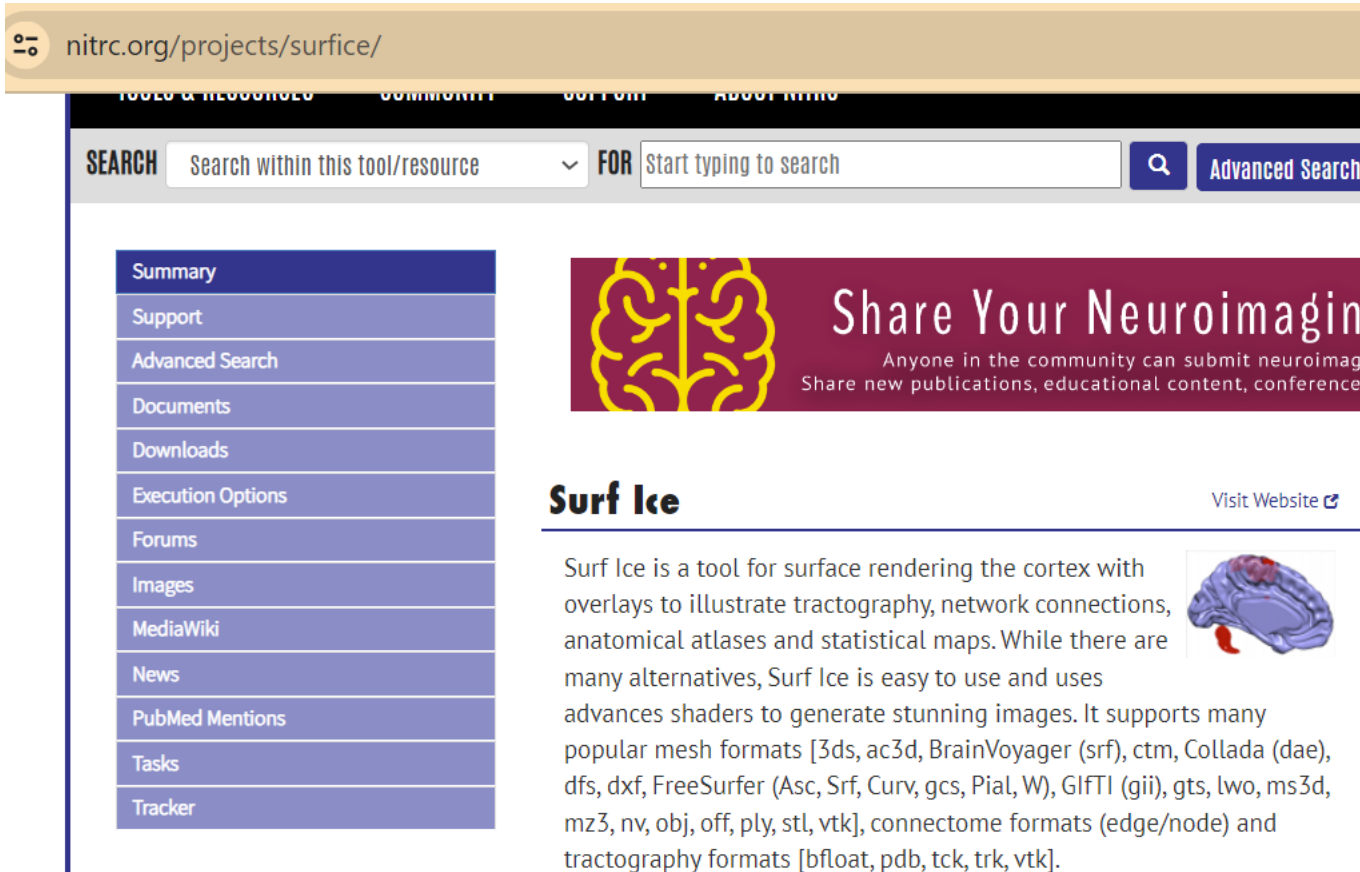
C.




B.

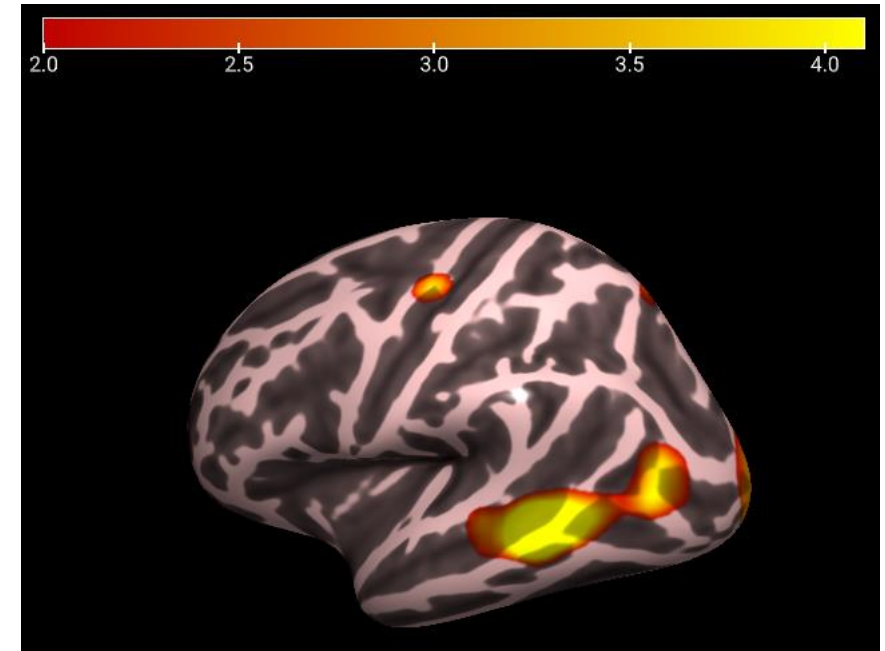


<https://www.nitrc.org/projects/surface/>




The screenshot shows the Nitrc website interface. At the top, there is a navigation bar with links for 'TOOLS & RESOURCES', 'COMMUNITY', 'SURFACE', and 'ABOUT NITRC'. Below this is a search bar with the text 'SEARCH Search within this tool/resource' and a 'FOR' dropdown menu. A sidebar on the left contains a list of links: Summary, Support, Advanced Search, Documents, Downloads, Execution Options, Forums, Images, MediaWiki, News, PubMed Mentions, Tasks, and Tracker. The main content area features a banner for 'Share Your Neuroimaging' with a brain icon and the text 'Anyone in the community can submit neuroimaging. Share new publications, educational content, conference presentations, and more.' Below the banner is the 'Surf Ice' section, which includes a 'Visit Website' link and a description of the tool. The description states: 'Surf Ice is a tool for surface rendering the cortex with overlays to illustrate tractography, network connections, anatomical atlases and statistical maps. While there are many alternatives, Surf Ice is easy to use and uses advanced shaders to generate stunning images. It supports many popular mesh formats [3ds, ac3d, BrainVoyager (srf), ctm, Collada (dae), dfs, dxf, FreeSurfer (Asc, Srf, Curv, gcs, Pial, W), GiftI (gii), gts, lwo, ms3d, mz3, nv, obj, off, ply, stl, vtk], connectome formats (edge/node) and tractography formats [bfloat, pdb, tck, trk, vtk].'

 Use this open-source software to load neuroimaging files for visualization



The screenshot shows the 'Recent Activity - Files' section of the Nitrc website. It displays a list of files with a download icon and a red circle around the file name 'surface\_windows.zip posted by Chris Rorden on Dec 27, 2021'. Other files listed include 'surface: Surf Ice 6-October-2021 release'.

 Scroll to the bottom of the page and download the installer file suitable to your os (e.g., "windows")

## Plot the **VWFA** on an *inflated brain* template in **Surf Ice** - demo

*Use this website to download activation maps (in .nii.gz format; nii = Neuroimaging Informatics Technology; gz = compressed using Gnu Zip (gzip) software)*



NeuroQuery [Dockès et al 2020] Brain maps by querying the neuroscience literature

A query on neuroscience, cognition, or brain pathologies

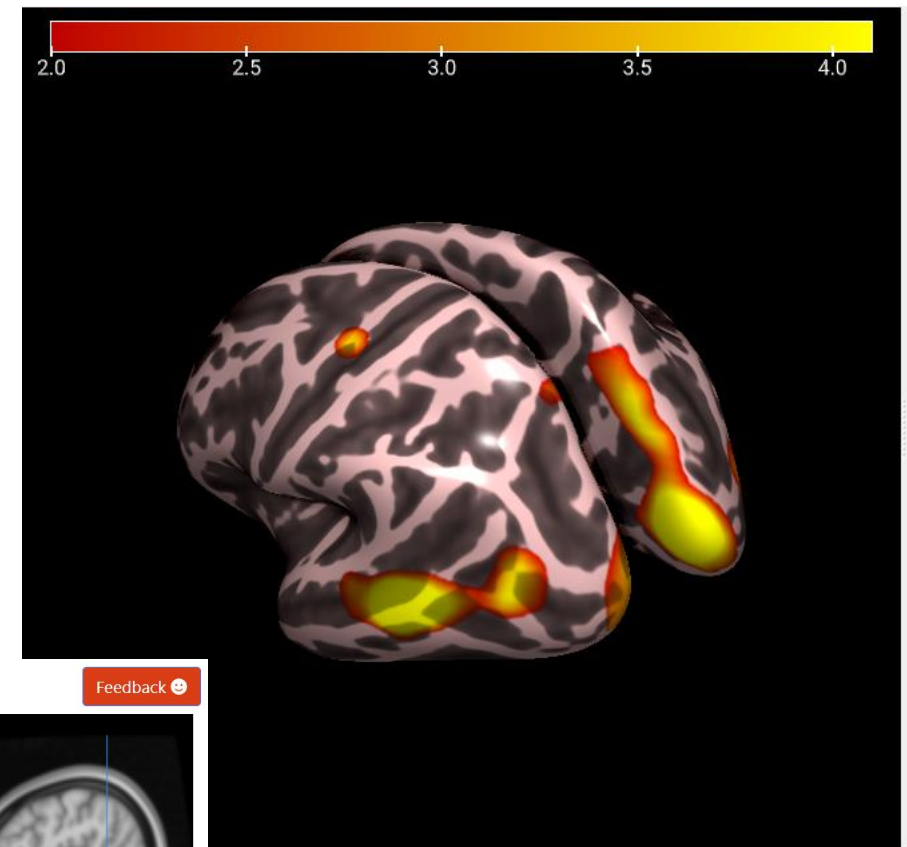
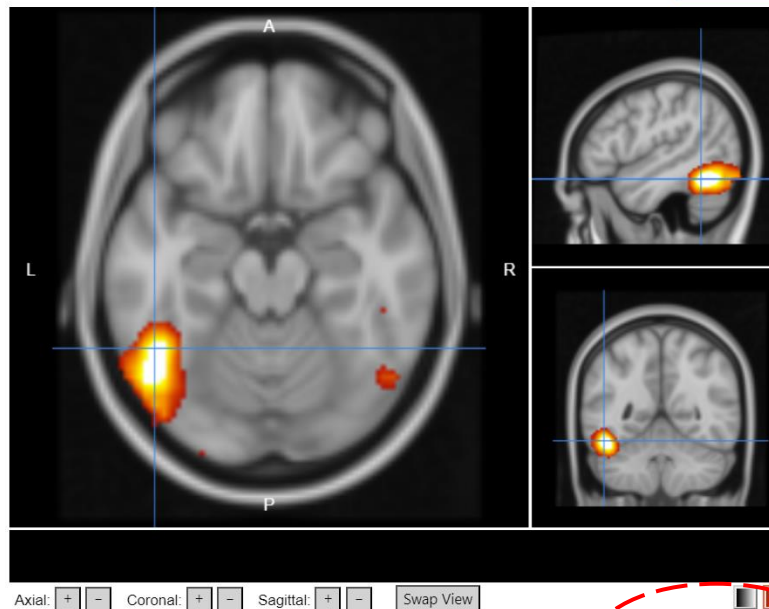
visual word form area

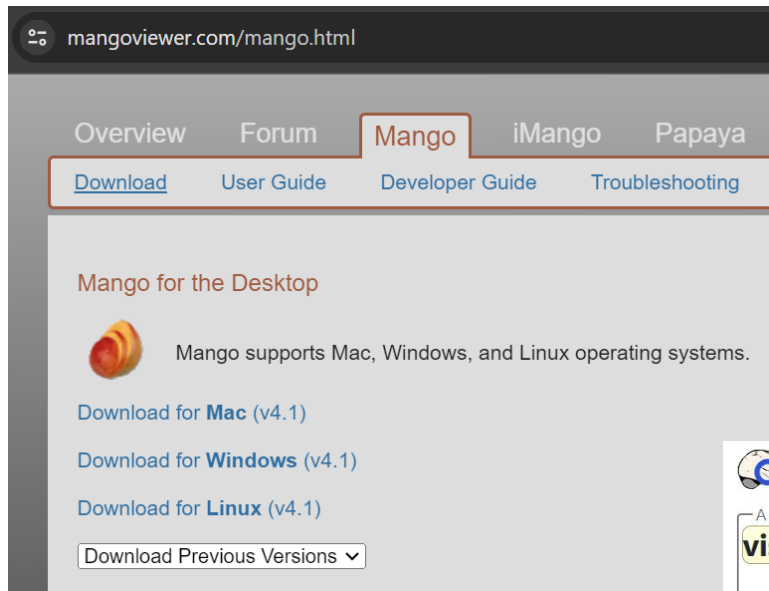
Click to edit. Edit query

Terms related to the query

Term	Similarity	Weight in brain map	N
<b>In query</b>			
visual word			448
area			12598
form			6942
<b>In expansion</b>			
visual			10448
word			6479
motion			9061
fusiform			4278
motor			7928
occipital			6796
insula			7050
parietal			10159
left			12782

Show 12 entries Showing 1 to 12 of 68 entries





*Use this open-source software to load neuroimaging files for visualization*

<https://neuroquery.org/>

*Use this website to download activation maps (in .nii.gz format; nii = Neuroimaging Informatics Technology; gz = compressed using Gnu Zip (gzip) software)*



NeuroQuery [Dockès et al 2020] Brain maps by querying the neuroscience literature

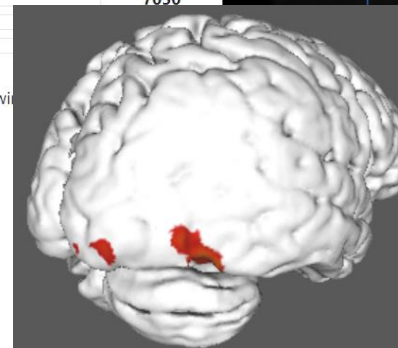
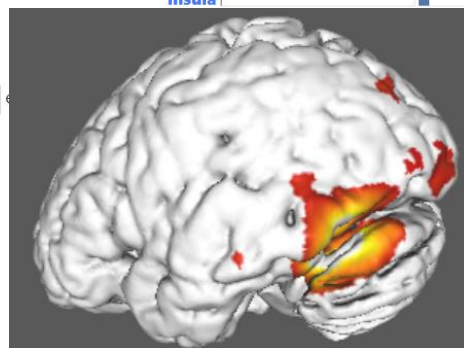
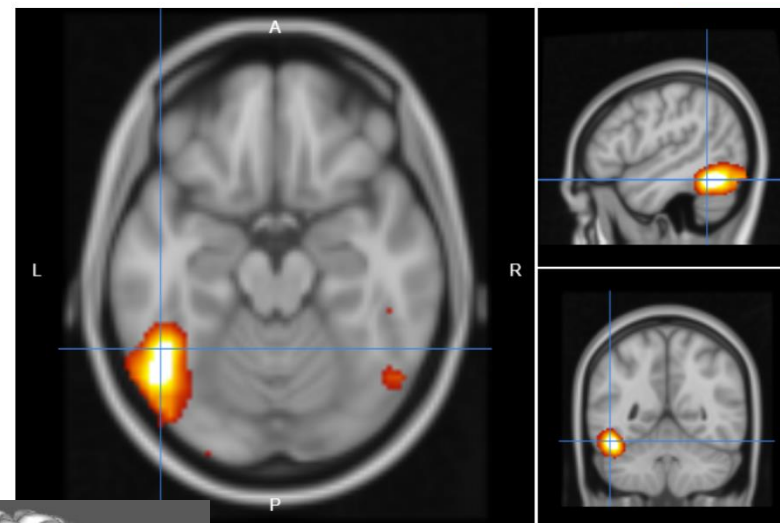
A query on neuroscience, cognition, or brain pathologies

visual word form area

Click to edit. Edit query

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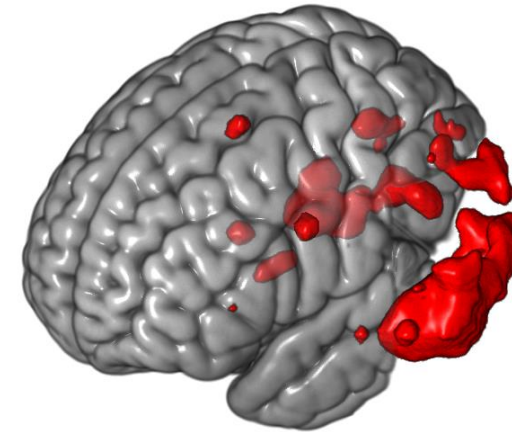
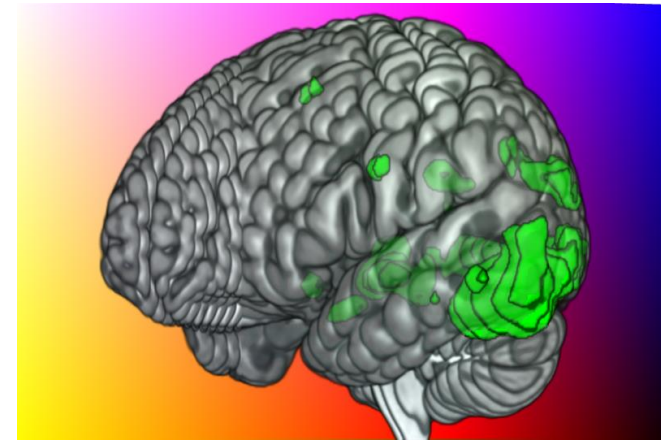


Download map

<https://www.nitrc.org/projects/mricrogl>

The screenshot shows the NITRC website interface. At the top, there's a navigation bar with 'TOOLS & RESOURCES', 'COMMUNITY', 'SUPPORT', and 'ABOUT NITRC'. Below that is a search bar. The main content area features a 'Leave a testimonial' banner and a section for 'MRicroGL'. The MRicroGL section includes a 'Visit Website' link and a description of the software. To the left of the MRicroGL section is a sidebar menu with items like 'Summary', 'Support', 'Advanced Search', 'Documents', 'Downloads', 'Execution Options', 'Forums', 'Images', 'MediaWiki', 'News', 'PubMed Mentions', 'Source Code', and 'Tasks'.


 Use this open-source software to load neuroimaging files for visualization



and more visualization options using scripting

<https://www.nitrc.org/plugins/mwiki/index.php/mricrogl:MainPage#Scripting>

The screenshot shows the 'Recent Activity - Files' section. It lists a file named 'mricrogl: version 20-July-2022 (v1.2.20220720) release'. Below this, there is a download icon and a file named 'MRicroGL\_windows.zip' posted by Chris Rorden on Aug 11, 2022. The file name is circled in red.

 Scroll to the bottom of the page and download the installer file suitable to your os (e.g., "windows")

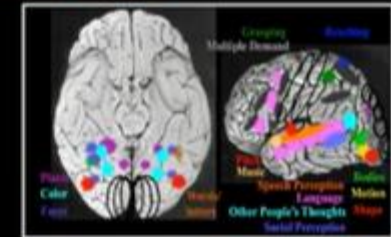


CENTER FOR  
**Brains  
Minds+  
Machines**

March 14, 2018

Does Cortical Function Depend on Experience in Humans?  
And does Connectivity Matter?

Are there any cortical regions  
in humans whose selectivity  
*must* be due to experience?



Experience & connectivity both determine cortical function!  
But this is a *ferret*! What about humans?

The visual word form area:  
a cortical region whose selectivity  
depends on individual experience

---

***Nancy Kanwisher***

Massachusetts Institute of Technology

### **pure alexia** or **letter-by-letter reading**

Reading is often **accurate**, but is far **too slow** and **laborious** to be of much help in everyday life.

Historically, this was the **first type of acquired dyslexia** to be documented and it was termed pure alexia to emphasize the fact that reading was compromised **without impairment of spelling, writing or verbal language**.


### **acquired disorders of reading and writing** or **acquired dyslexia/dysgraphia**

the various patterns of performance exhibited by **previously literate adults** whose literacy abilities are **no longer in the normal range**, in one or more respects, **following brain disease or injury**

### **developmental dyslexia**

problems in **literacy acquisition** (reading and/or spelling) that cannot be attributed to lack of opportunity or other known causes (e.g., deafness, brain injury)

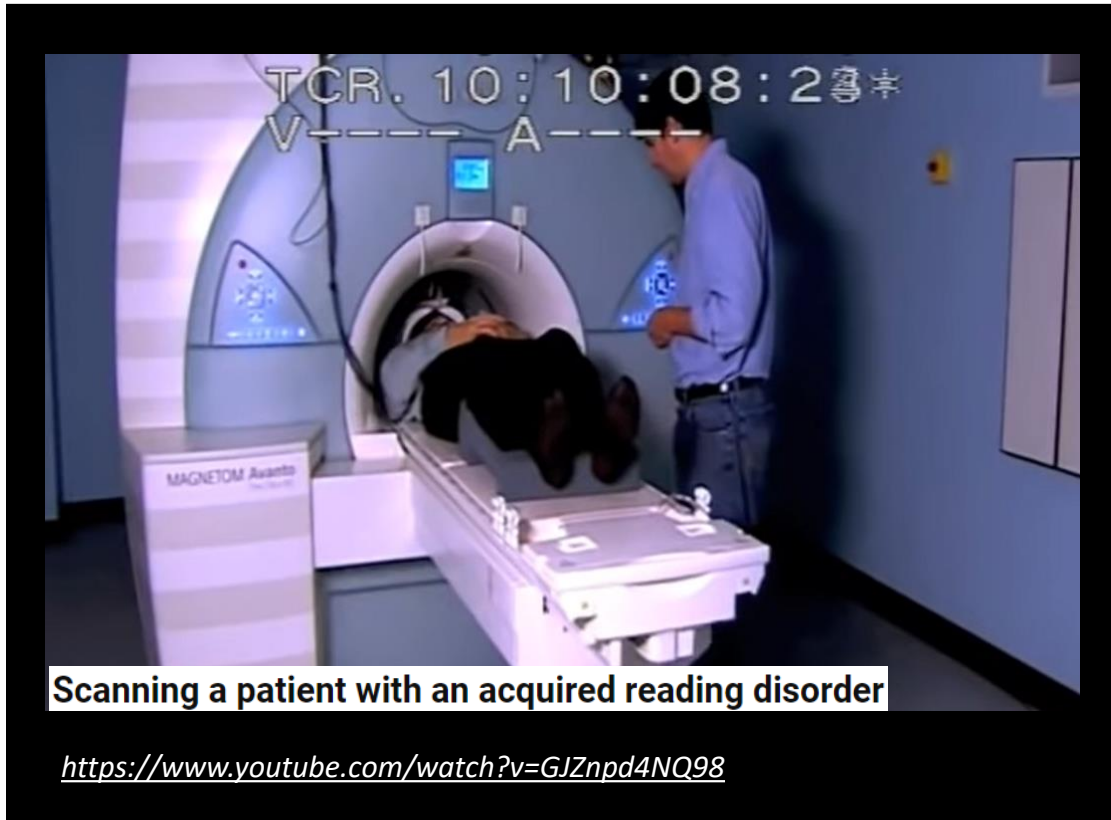
*dominant theory*



### **phonological awareness**

the ability to **explicitly segment** a **speech stream** into **units** such as syllables, rimes and phonemes

## Acquired reading disorders – case studies

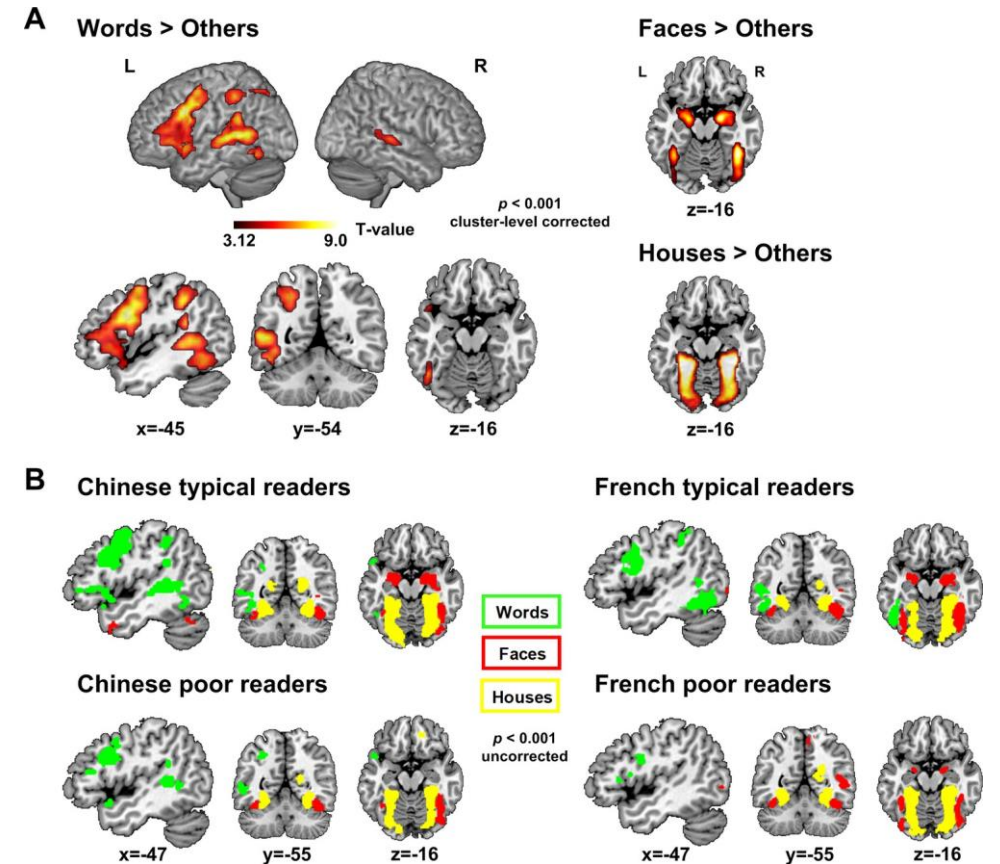


# A universal reading network and its modulation by writing system and reading ability in French and Chinese children

Xiaoxia Feng<sup>1 2</sup>, Irene Altarelli<sup>1 3</sup>, Karla Monzalvo<sup>1</sup>, Guosheng Ding<sup>2</sup>, Franck Ramus<sup>4</sup>, Hua Shu<sup>2</sup>, Stanislas Dehaene<sup>1 5</sup>, Xiangzhi Meng<sup>6 7</sup>, Ghislaine Dehaene-Lambertz<sup>1</sup>

**Abstract** Are the brain mechanisms of reading acquisition similar across writing systems? And do similar brain anomalies underlie reading difficulties in alphabetic and ideographic reading systems? In a cross-cultural paradigm, we measured the fMRI responses to words, faces, and houses in 96 Chinese and French 10-year-old children, half of whom were struggling with reading. We observed a reading circuit which was strikingly similar across languages and consisting of the left fusiform gyrus, superior temporal gyrus/sulcus, precentral and middle frontal gyri. Activations in some of these areas were modulated either by language or by reading ability, but without interaction between those factors. In various regions previously associated with dyslexia, reading difficulty affected activation similarly in Chinese and French readers, including the middle frontal gyrus, a region previously described as specifically altered in Chinese. Our analyses reveal a large degree of cross-cultural invariance in the neural correlates of reading acquisition and reading impairment.

<https://pubmed.ncbi.nlm.nih.gov/33118931/>




## Self-regulation of visual word form area activation with real-time fMRI neurofeedback


[Amelie Haugg](#) , [Nada Frei](#), [Milena Menghini](#), [Felizia Stutz](#), [Sara Steinegger](#), [Martina Röthlisberger](#) & [Silvia Brem](#)

The Visual Word Form Area (VWFA) is a key region of the brain's reading network and its activation has been shown to be strongly associated with reading skills. Here, for the first time, we investigated whether voluntary regulation of VWFA activation is feasible using real-time fMRI neurofeedback. 40 adults with typical reading skills were instructed to either upregulate (UP group, N = 20) or downregulate (DOWN group, N = 20) their own VWFA activation during six neurofeedback training runs. The VWFA target region was individually defined based on a functional localizer task. Before and after training, also regulation runs without feedback ("no-feedback runs") were performed. When comparing the two groups, we found stronger activation across the reading network for the UP than the DOWN group. Further, activation in the VWFA was significantly stronger in the UP group than the DOWN group. Crucially, we observed a significant interaction of group and time (pre, post) for the no-feedback runs: The two groups did not differ significantly in their VWFA activation before neurofeedback training, but the UP group showed significantly stronger activation than the DOWN group after neurofeedback training. Our results indicate that upregulation of VWFA activation is feasible and that, once learned, successful upregulation can even be performed in the absence of feedback. These results are a crucial first step toward the development of a potential therapeutic support to improve reading skills in individuals with reading impairments.

<https://www.nature.com/articles/s41598-023-35932-9>

We can download and visualize their VWFA mask (openly available at <https://osf.io/4qhdb/>) using Surf Ice

 Neurofeedback of the VWFA

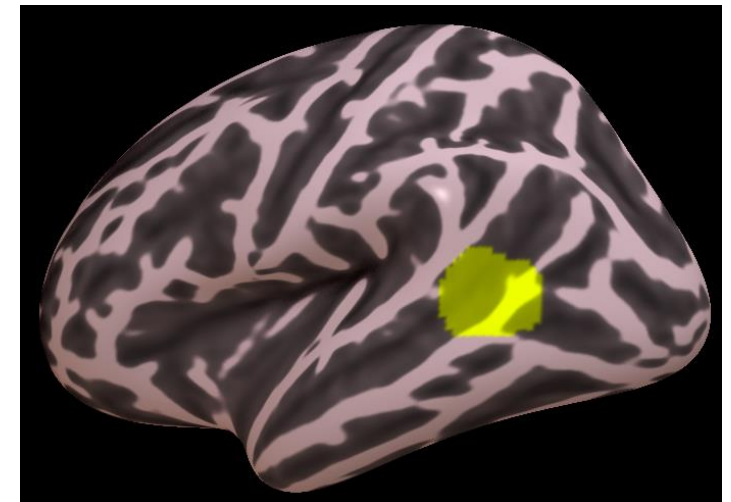
-  OSF Storage (Germany - Frankfurt)

+  exam cards

-  masks

 VWFA\_mask.nii

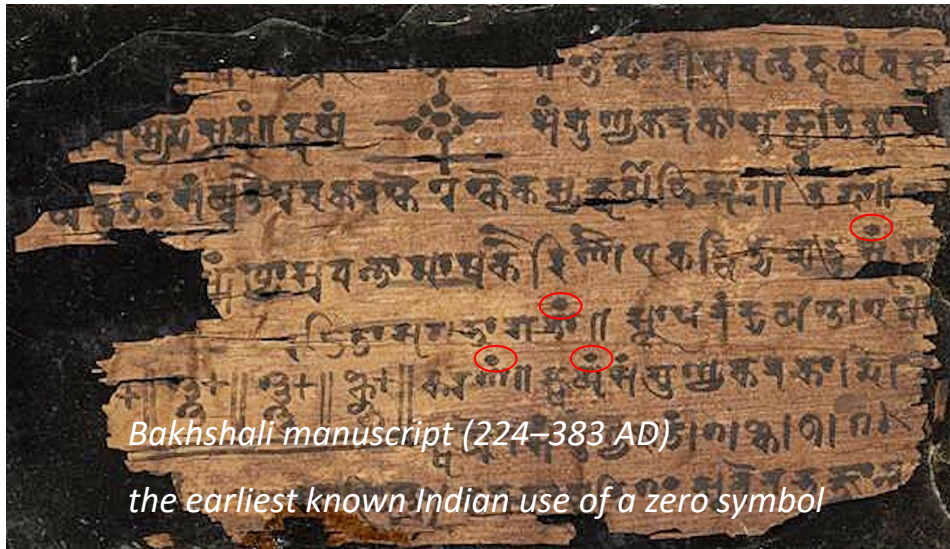
+  scripts



# Numeracy

Becoming skilled at mathematics in the modern world requires **learning of arbitrary notations and their meaning** (e.g., +, −, >), as well as specific **procedures** (e.g., for calculating the circumference of a circle).

Over and above this acquired knowledge, **humans and other species** appear to have a more **basic set of numerical abilities** that enable them to estimate quantity and perform basic calculations. It is in this more fundamental sense that **numeracy** can be said to be **universal**.



The first evidence we have of zero is from the Sumerian culture in Mesopotamia, some 5,000 years ago. There, a slanted double wedge was inserted between cuneiform symbols for numbers, written positionally, to indicate the absence of a number in a place (as we would write 102, the '0' indicating no digit in the tens column).

<https://www.scientificamerican.com/article/what-is-the-origin-of-zero/>

## Animals Count and Use Zero. How Far Does Their Number Sense Go?

Crows recently demonstrated an understanding of the concept of zero. It's only the latest evidence of animals' talents for numerical abstraction — which may still differ from our own grasp of numbers.

<https://www.quantamagazine.org/animals-can-count-and-use-zero-how-far-does-their-number-sense-go-20210809/>

Simple arithmetic in **infants** has been studied using a paradigm called **violation of expectancy**.  
Infants **look longer** at **unexpected events**.



**Evidence of counting in infants**

<https://www.youtube.com/watch?v=2XLe2HFO3ZY>

## BOX

### Typical features of dyscalculia

- **Difficulties in processing numbers and quantities, starting in the preschool years**
  - The connection between a number (e.g., 2) and the quantity it represents (e.g., 2 apples) is made only with difficulty.
  - The relation between numbers and quantities (two apples and one apple =  $2 + 1$ ) is inadequately understood.
  - Ensuing difficulties in counting, comparing two numbers or quantities, rapid assessment and naming of small quantities of dots, determining the position of a number on the number line, understanding the place-value system, and transcoding.
- **Difficulties with basic arithmetic operations and with further mathematical tasks**
  - Computation rules are not understood because the underlying comprehension of numbers and quantities is lacking or insufficiently developed ( $17 + 14 = 1 + 1$  and  $7 + 4 = 13$  or  $211$ ).
  - Deficits in retrieval of math facts (e.g., the multiplication table) with which the answers to simple calculation problems can be recalled directly from memory, rather than needing to be calculated anew each time.
  - Lack of transition from computation by counting ( $8 + 4 = 9, 10, 11, 12 = 12$ ) to non-counting strategies ( $8 + 4 = 8 + 2$  and  $2 = 12$ ).
  - These difficulties become worse with increasing mathematical complexity (larger number range, written computations, multiple calculating operations, word problems).
- **Important:**
  - Finger-counting per se is not a sign of dyscalculia, but rather a normal aid to the memorization of math facts and the learning of efficient calculating strategies. Persistent finger-counting, particularly for frequently repeated, easy calculating tasks, does indeed indicate a problem in calculation.

Not the mere presence of calculating errors, but rather their variety, persistence, and frequency are determinative.

<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6440373/>

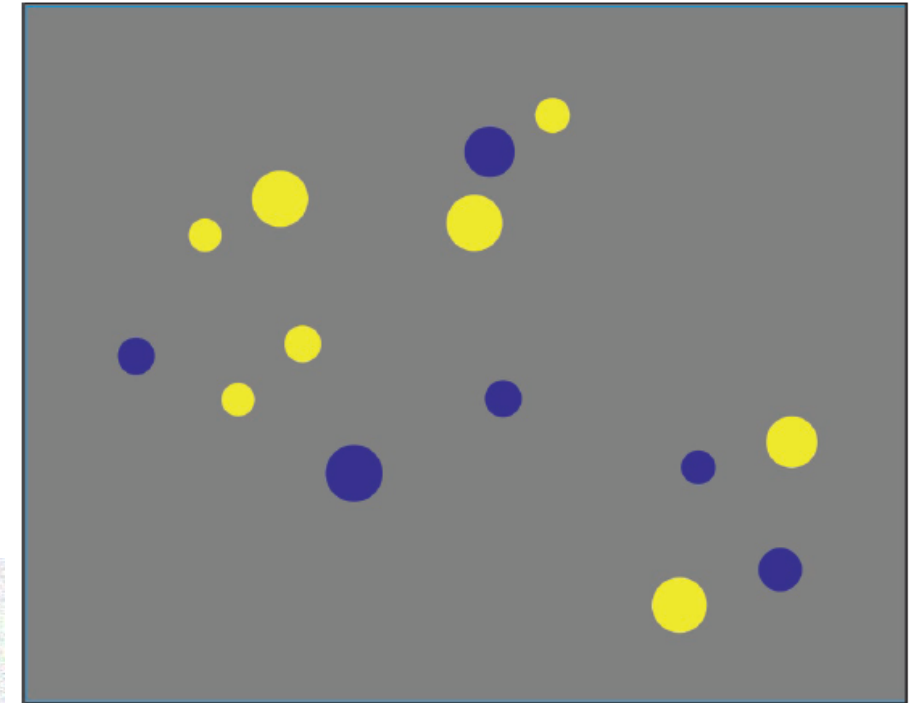
## subitizing

(from Latin: *subitus* = sudden)

the capacity to **enumerate**  
an exact quantity of objects  
**without counting them**

Animals also have demonstrated proficiency in similar quantity discrimination tasks presenting only one food array at a given time. For example, orangutans (Call 2000), chimpanzees (Beran 2001, 2004), and capuchin monkeys (Evans et al. 2009) excelled at selecting the larger of two food quantities even when only one quantity was visible at a given time (either by presenting the subject with one entire array prior to the other or by sequentially adding food items to one array at a time). Performance patterns revealed ratio effects characteristic of the ANS, and importantly, these results suggested that primates could represent numerical information similar to human adults in addition to the use of perceptual mechanisms. Similar performance patterns are evident in work with a variety of nonhuman primate species (e.g., Addessi et al. 2008; Hanus and Call 2007).

The approximate number system (ANS) is a core cognitive system of numerical processing that governs animal and human nonsymbolic numerical representations. Weber's law underlies the ANS, in which performance in discriminating set sizes increases as the ratio between sets also increases.

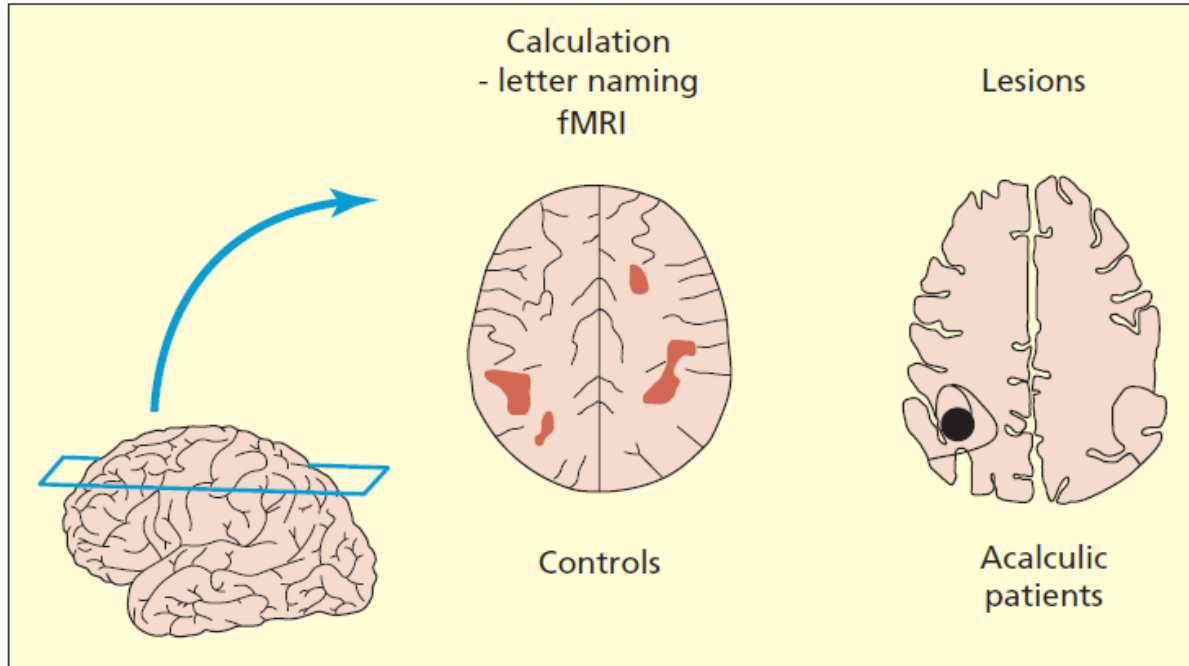


**FIGURE 14.4:** Which set is larger: blues or yellows? When presented too briefly to count (200 ms), then school children differ in their ability to perform the task and this correlates with SAT (Standard Assessment Test) scores in mathematics.

Adapted from Halberda et al., 2008.

Ward, (2020), p. 363

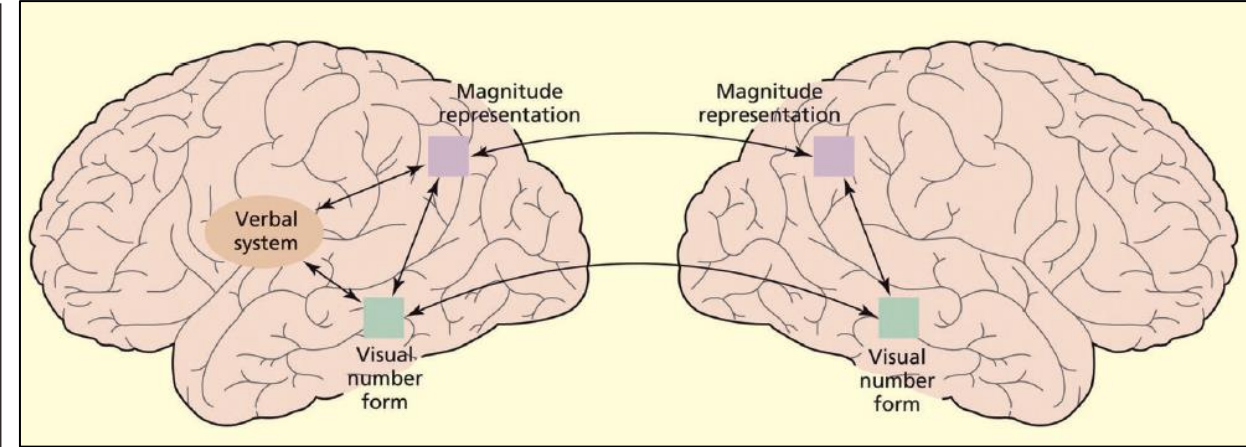
Parrish, A.E., Beran, M.J. (2022). *Approximate Number System (ANS)*. In: Vonk, J., Shackelford, T.K. (eds) *Encyclopedia of Animal Cognition and Behavior*, pp. 381 - 386



**FIGURE 14.9:** There is converging evidence from neuropsychology and functional imaging for the role of the parietal lobes in number meaning (particularly the left parietal lobe).

Left figure from Cochon *et al.*, 1999. © 1999 MIT Press. Reproduced with permission. Right figure reprinted from Dehaene *et al.*, 1998a. © 1998, with permission from Elsevier.

Ward, (2020), p. 368



**FIGURE 14.16:** The three components of Dehaene’s Triple-Code Model are: (a) a semantic magnitude representation; (b) a verbal store of arithmetical facts; and (c) a visual representation for recognizing numerals and a “workbench” for performing certain calculations.

From: Dehaene & Cohen, 1995.

Ward, (2020), p. 376

## Dyscalculia and dyslexia: Different behavioral, yet similar brain activity profiles during arithmetic

Lien Peters,<sup>a,b,c,\*</sup> Jessica Bulthé,<sup>b</sup> Nicky Daniels,<sup>b</sup> Hans Op de Beeck,<sup>b</sup> and Bert De Smedt<sup>a</sup>

### A B S T R A C T

Brain disorders are often investigated in isolation, but very different conclusions might be reached when studies directly contrast multiple disorders. Here, we illustrate this in the context of specific learning disorders, such as dyscalculia and dyslexia. While children with dyscalculia show deficits in arithmetic, children with dyslexia present with reading difficulties. Furthermore, the comorbidity between dyslexia and dyscalculia is surprisingly high. Different hypotheses have been proposed on the origin of these disorders (number processing deficits in dyscalculia, phonological deficits in dyslexia) but these have never been directly contrasted in one brain imaging study. Therefore, we compared the brain activity of children with dyslexia, children with dyscalculia, children with comorbid dyslexia/dyscalculia and healthy controls during arithmetic in a design that allowed us to disentangle various processes that might be associated with the specific or common neural origins of these learning disorders.

Participants were 62 children aged 9 to 12, 39 of whom had been clinically diagnosed with a specific learning disorder (dyscalculia and/or dyslexia). All children underwent fMRI scanning while performing an arithmetic task in different formats (dot arrays, digits and number words). At the behavioral level, children with dyscalculia showed lower accuracy when subtracting dot arrays, and all children with learning disorders were slower in responding compared to typically developing children (especially in symbolic formats). However, at the neural level, analyses pointed towards substantial neural similarity between children with learning disorders: Control children demonstrated higher activation levels in frontal and parietal areas than the three groups of children with learning disorders, regardless of the disorder. A direct comparison between the groups of children with learning disorders revealed similar levels of neural activation throughout the brain across these groups. Multivariate subject generalization analyses were used to statistically test the degree of similarity, and confirmed that the neural activation patterns of children with dyslexia, dyscalculia and dyslexia/dyscalculia were highly similar in how they deviated from neural activation patterns in control children. Collectively, these results suggest that, despite differences at the behavioral level, the brain activity profiles of children with different learning disorders during arithmetic may be more similar than initially thought.

# The World Is Open To Me Now': A Scientist With Dyslexia On How Learning To Read Changed Her Life



*Eventually, she found success by memorizing the shapes of words. It was slow going at first, but around the sixth grade Drennan remembers hitting a tipping point. Her vocabulary had grown large enough to allow her to effectively read.*

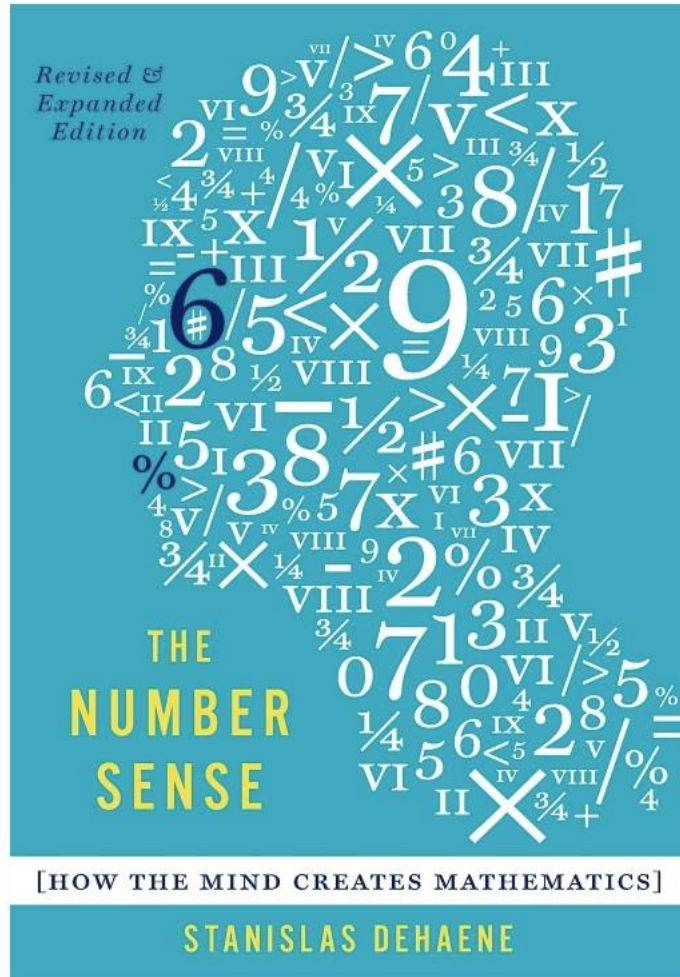
*Drennan eventually went on to earn a Ph.D. from the University of Michigan in 1995. Today, she runs a chemistry lab at MIT exploring how proteins and enzymes in the human body interact with each other using computer generated models of their cellular structure.*

*In a way, Drennan says her dyslexia has been helpful in her research. Because she has become so skilled at recognizing shapes and interpreting what they mean, she's able to notice details that other people in her lab often miss in those cellular pictures.*

*"People say we shouldn't say 'disabled' we should say 'differently abled' and I totally believe that's true for me," she says.*

<https://biology.mit.edu/the-world-is-open-to-me-now-a-scientist-with-dyslexia-on-how-learning-to-read-changed-her-life/>

# Further resources



A WASHINGTON POST BEST SCIENCE BOOK OF THE YEAR

## READING IN THE BRAIN

THE NEW SCIENCE  
OF HOW WE READ



STANISLAS DEHAENE

author of THE NUMBER SENSE



Volume 224, Issue 6

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### ABSTRACT

Many species from diverse and often distantly related animal groups (e.g. monkeys, crows, fish and bees) have a sense of number. This means that they can assess the number of items in a set – its ‘numerosity’. The brains of these phylogenetically distant species are markedly diverse. This Review examines the fundamentally different types of brains and neural mechanisms that give rise to numerical competence across the animal tree of life. Neural correlates of the number sense so far exist only for specific vertebrate species: the richest data concerning explicit and abstract number representations have been collected from the cerebral cortex of mammals, most notably human and nonhuman primates, but also from the pallium of corvid songbirds, which evolved independently of the mammalian cortex. In contrast, the neural data relating to implicit and reflexive numerical representations in amphibians and fish is limited. The neural basis of a number sense has not been explored in any protostome so far. However, promising candidate regions in the brains of insects, spiders and cephalopods – all of which are known to have number skills – are identified in this Review. A comparative neuroscientific approach will be indispensable for identifying evolutionarily stable neuronal circuits and deciphering codes that give rise to a sense of number across phylogeny.

<https://journals.biologists.com/jeb/article/224/6/jeb218289/237916/Neuroethology-of-number-sense-across-the-animal>