($t_{1,7} = 0.88$, $p = 0.41$), but responded significantly less frequently to middle-silence whistles than to unmanipulated whistles ($t_{1,7} = 3.31$, $p = 0.013$, **Fig. 1**, bottom). This either suggests that tamarins amodally complete the whistle unit or respond more to signals with continuous acoustic energy. Condition 2 distinguished between these hypotheses.

We designed two whistle manipulations in condition 2. In the first, white noise began at the onset of the whistle and ended 150 ms before the end of the whistle (begin noise); in the second, white noise began 150 ms after the onset of the whistle and terminated at the end of the syllable (end noise; **Fig. 1**, middle). Antiphonal calling did not differ between sessions ($F_{1,9} = 0.01$, $p = 0.93$), but we found a significant effect of stimulus type ($F_{3,27} = 26.34$, $p < 0.0001$). Subjects responded significantly more often to unmanipulated whistles than to both begin-noise ($t_9 = 3.1$, $p = 0.013$) and end-noise whistles ($t_9 = 6.736$, $p = 0.0001$), but responded at equal rates to both types of manipulated whistles ($t_9 = 0.43$, $p = 0.67$, **Fig. 1**, bottom). These results show that signals with continuous acoustic energy are not sufficient to drive the antiphonal response to whistles. Rather, the placement of white noise must be located in a way that bridges the start and end of the whistle unit. In conclusion, tamarins amodally complete the middle-noise whistle unit, and thus, in the absence of training, are susceptible to this auditory illusion.

Although auditory illusions are rarely investigated[9], such phenomena provide insights into how the brain organizes perceptual information. Given the phylogenetic relatedness of humans and cotton-top tamarins, these results suggest that the neural mechanisms mediating auditory continuity may have evolved in a common ancestor at least 40 million years ago, before the divergence of these two primate clades, and possibly earlier[5]. If true, then similar principles may facilitate the organization of sensory information in human and nonhuman primate brains[10,11,12]. Future work will explore whether cotton-top tamarins and humans use similar principles to organize sensory information in other modalities. Such data are critical to a more complete understanding of brain evolution.

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Category specificity in reading and writing: the case of number words

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In standard models, word meanings contribute to reading words aloud and writing them to dictation[1–3]. It is known that categories of knowledge and the associated word meanings can be spared or impaired selectively[4], but it has not been possible to demonstrate that category-specific effects apply to reading and writing. Here we report the case of a neurodegenerative patient with selectively spared numerical abilities whose brain damage left him able to read and write only number words.

Although reading aloud can be achieved by mapping letters directly on to sounds and sounds directly on to letters[5], there is evidence that word meanings (semantics) interact with these processes[2,3]. When knowledge of letter–sound mappings is lost, and the meaning of the target word is intact, models allow that accurate reading and spelling can be achieved on the basis of the meaning-mediated process alone. This account has been applied specifically to reading and writing numbers, with essentially the same prediction[6]. Under these conditions, selective preservation of a single semantic category should result in the patient being able to read only words in the preserved category.

The patient we describe, I.H., had temporal lobe atrophy mainly on the left with relative sparing of the hippocampus, which resulted in a severe decline in his linguistic abilities and his general knowledge. (Detailed information about the patient's neuroanatomy and references for the standard neuropsychological tests are available on the *Nature Neuroscience* website, http://neurosci.nature.com/web_specials.) Nevertheless, his memory for people and personal events remained relatively good[7]. This combination of focal temporal lobe atrophy and lexical–semantic symptoms has been labeled 'semantic dementia'[8,9].

A first set of experiments showed that I.H.'s mathematical ability was remarkably well preserved, despite his severe impairment in all the other domains of knowledge (**Tables 1** and **2**). A second set of experiments showed that he was still able to read and write almost all number words, despite being severely impaired at reading and writing non-number words matched by frequency, spelling regularity and length (**Table 3**). His performance, unlike other cases of semantic dementia[10], was not affected by spelling regularity. His performance was flawless in reading and spelling regularly spelled (ten) and irregularly spelled (two) number words, but equally impaired in reading and spelling regular and irregular non-number words such as 'table' or 'flat.' This pattern of performance plus his inability to read novel letter strings ('non-words'), is standard evidence that I.H. was unable to use letter-sound knowledge in reading or spelling.

Table 1. Verbal and pictorial semantic memory tasks.

	I.H.	Controls
Verbal tasks		
Graded naming test	0	83
Category naming (*n* = 40)	10	99
Naming real objects (*n* = 15)	0	100
Word classification (*n* = 50)	f.u.i.	100
Name-to-picture matching (*n* = 40)	22	97
Pyramid and palm tree task: verbal version (*n* = 52)	f.u.i.	99
Phonological fluency (FAS)	0	42*
Semantic fluency	0	117*
Verbal definition (*n* = 73)	0	99.5
Pictorial tasks		
Picture classification (*n* = 40)	80	99
Subcategory picture classification (*n* = 9)	66	100
Size judgment task (*n* = 20)	65	99
Object decision task (*n* = 20)	70	88
Pyramid and palm tree task, pictorial version (*n* = 52)	52	99

Percent of correct answers in semantic memory tests. Matched controls for the semantic tests were 7 subjects, mean age ± s.d., 70.7± 5.1 years, of similar education to I.H. The 'category naming task' required naming 40 black-and-white pictures belonging to different living and man-made categories. A different set of items was used in the 'naming real objects' task, in which participants were asked to name a series of common real objects (for example, fork, flower). In the 'word and picture classification tasks,' participants had to assign an item (name or picture) to the appropriate category. The 'pyramid and palm tree task' required selecting one of two same category items (for example, palm tree or pine tree) that goes with the third (pyramid). The size judgment required selecting the larger object in real life from two same-category pictures (for example, bed and chair). (For references for the standard neuropsychological tests used, see the *Nature Neuroscience* web site, http://neurosci.nature.com/web_specials.) f.u.i., failed to understand instructions; *mean items produced.

Table 2. Numerical tasks.

	I.H.	
Controls		
Number tests		
Counting (*n* = 80)	100	100
Magnitude comparison (*n* = 20)	100	100
Selection of chips (*n* = 48)	100	100
Transcoding (up to 4-digit numbers)		
Reading Arabic numerals (*n* = 100)	97	100
Reading number words (*n* = 100)	100	100
Writing Arabic numerals (*n* = 100)	97	100
Written Arabic numbers to written number words (*n* = 20)	100	100
Written number words to Arabic numbers (*n* = 20)	100	100
Transcoding arithmetical signs (*n* = 8)	0	100
Calculation		
Single-digit operations (*n* = 254)	89	98
Oral multidigit operations (untimed) (*n* = 28)	96	
Written multidigit operations (*n* = 96)	80	96
Approximation to correct result (*n* = 100)	f.u.i.	100
Approximation of numbers on a line (*n* = 100)	100	100
Other tests		
Personal and non-personal numerical questions (*n* = 20)	5	100
Definitions of arithmetical operations (*n* = 4)	0	100

Percent of correct answers in numerical tests. I.H. was at or near floor when the task required language production or when the comprehension of relatively complex verbal instructions was needed. For instance, I.H. failed to define the four arithmetical operations, despite being able to use them in performing arithmetical operations. The approximation task consisted of selecting an approximate answer without calculating.

Table 3. Reading and spelling number words and non-number words.

	Reading	Spelling	Controls
Non-number words (*n* = 70)			
Regular	16	0	100
Irregular	12	0	100
Exceptional	0	0	100
Non-words (*n* = 60)	12	Not tested	100
Cardinal number words (*n* = 30)			
Regular	100	100	100
Irregular	100	100	100
Exceptional	100	100	100
Ordinal number words (*n* = 22)	95	95	100
Ambiguous number-related words (*n* = 18)	50	50	100

Percent of correct answers in reading and spelling number and non-number words, and in reading non-words. The experimental set consisted of 140 items composed of regular (for example, flat, ten), irregular (months, four) and exception (juice, two) words matched for frequency, length and number of syllables with cardinal and ordinal number words. Cardinal number words were all the numbers from one to twenty, each tenth number (twenty, thirty, forty, etc.) and the words hundred, thousand and million; the ordinal number words were those corresponding to the cardinals (first, second). The ambiguous number-related words described operations with numbers, but also had non-numerical meanings (division, share). Errors in reading non-number words consisted of 58% fragments (for example, "a..a..r-r..a..arr" for array), 20% visually similar words (for example, "branch" for brand) and 6% phonologically similar words (for example, "south" for sound), 2% omissions and 14% other errors (for example, non-words). There were no regularization errors.

Three years previously he had shown superiority at reading regular words, and an ability to read non-words. This suggests that the course of the disease degraded his ability to use the letter–sound knowledge. However, his knowledge of word sounds and spellings was well preserved, as I.H. was able to repeat heard words (61/70) and discriminate both spoken words from spoken non-words (120/120) and written words from written non-words (180/180).

These findings have two main theoretical implications. First, they provide a new and rigorous test of the role of semantics in reading and spelling. Because I.H. was unable to exploit letter-sound knowledge, semantic mediation was shown to be sufficient for accurate reading and spelling in the only preserved category. However, from these data, we cannot exclude the possibility that additional non-semantic routes may have a role in normal subjects or in other patients[11]. Second, these data reinforce the neuroanatomical and functional independence of the number domain itself. Atrophic processes in I.H. spared the left parietal lobe, which is believed critical for numerical tasks[12,13]. Numerical concepts are defined by relatively few abstract features that are applied recursively—for example, by adding 1 to get larger and larger cardinalities. This account is not consistent with the claim that semantic memory is organized solely in terms of sensory features (such as shape, size, color) and functional features (such as edibility, capacity to be sat on, capacity to cut)[14], as these features are not applicable to the domain of numbers. However, it is consistent with the proposal that semantic memory is organized in terms of distinct categories[15], one of which is number.

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