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When temporal terms belie conceptual order

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We conceive of time as a sequential order of real-world events, one event following another from past to present to future. This conception colours the way we speak of time ("we look forward to the time") and, as we show here, the way we process written statements referring to the temporal order of events, in real time. Terms such as 'before' and 'after' give us the linguistic freedom to express a series of events (real or imaginary) in any order. However, sentences that present events out of chronological order require additional discourse-level computation. Here we examine how and when these computations are carried out by contrasting brain potentials across two sentence types that differ only in their initial word ('After' X, Y versus 'Before' X, Y). At sites on the left frontal scalp, the responses to 'before' and 'after' sentences diverge within 300 ms; the size of this difference increases over the course of the sentences and is correlated with individual working-memory spans. Thus, we show that there are immediate and lasting consequences for neural processing of the discourse implications of a single word on sentence comprehension.

There is no common agreement of how conceptual knowledge in long-term memory (LTM) is used to create a mental representation of a sentence during online comprehension. However, there is a consensus that we create a temporary representation of a sentence and the situation it refers to[1–3]. In addition, words must activate world knowledge, although when this occurs remains controversial[1–3]. To examine this, we contrasted event-related brain potentials (ERPs) during the reading of two sentence types whose processing we expected to differ based on the linguistic and conceptual knowledge activated by their initial words ('before/after').

Both sentence types consist of an initial subordinate clause and a subsequent main clause, each describing a distinct event that is neither logically nor causally related to the other (for example, 'Before/After' the psychologist submitted the article, the journal changed its policy). In other words, the event in each clause could easily be understood without reference to the other. However, we believe that the first word leads readers to expect some non-arbitrary relationship between the two events. This expectation is based on real-world knowledge of time, and linguistic knowledge of how these notions map onto expressions of time. Our experiences in the real world suggest to us that time unfolds sequentially, with current events sometimes causing future events. Our linguistic knowledge tells us that temporal conjunctions often draw attention to the sequence of events in a discourse[4,5]. Moreover, 'before' and 'after' access such a sequence from different starting points: 'after'

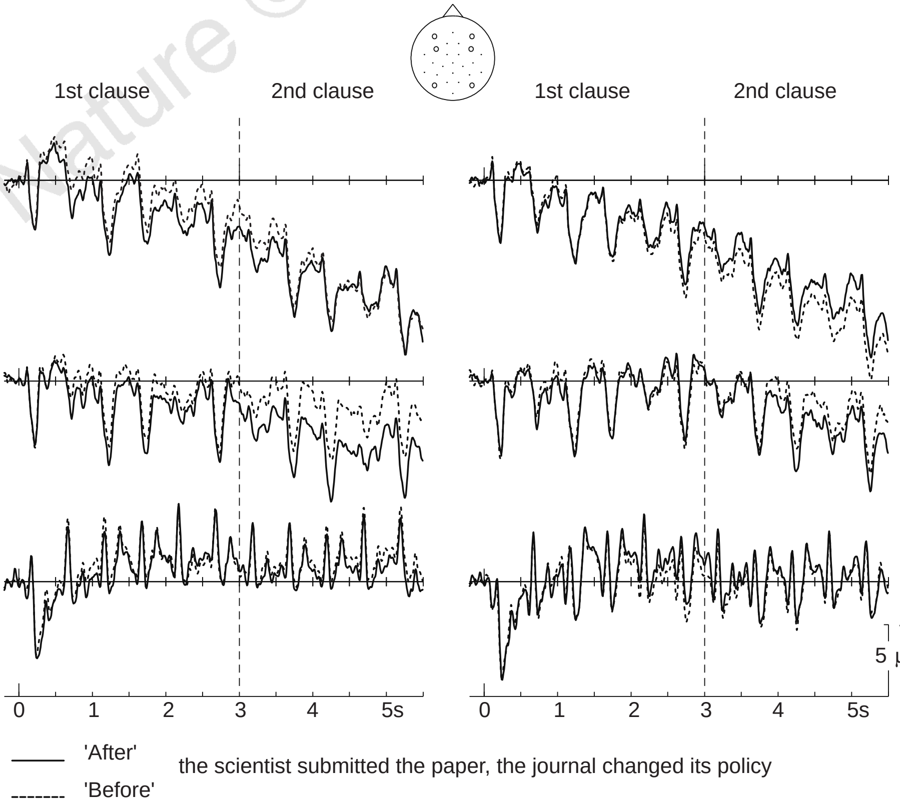


Figure 1 Grand average ($n = 24$) cross-sentence ERPs from prefrontal, frontal and occipital scalp sites (open circles on schematic head) of the left and right hemispheres (left and right sides of the figure, respectively) time-locked to 'before' or 'after'. 'Before' sentences are more negative than 'after' sentences throughout (main effect of sentence type: clause 1, $F_{1,23} = 9.98$, $P < 0.005$; clause 2, $F_{1,23} = 11.23$, $P < 0.003$), especially over the left compared with the right hemisphere sites (sentence type by site by hemisphere interaction: clause 1, $F_{10,230} = 4.63$, $P < 0.001$; clause 2, $F_{10,230} = 5.65$, $P < 0.001$). The difference between sentence types is reliably larger during the second than the first clause (main effect of clause for 'before/after' difference: $F_{1,23} = 4.78$, $P < 0.04$).

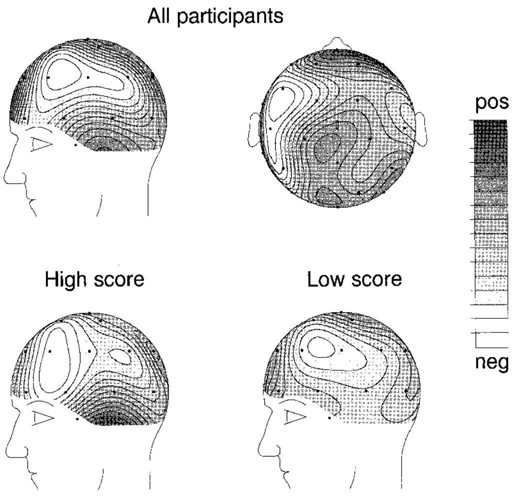


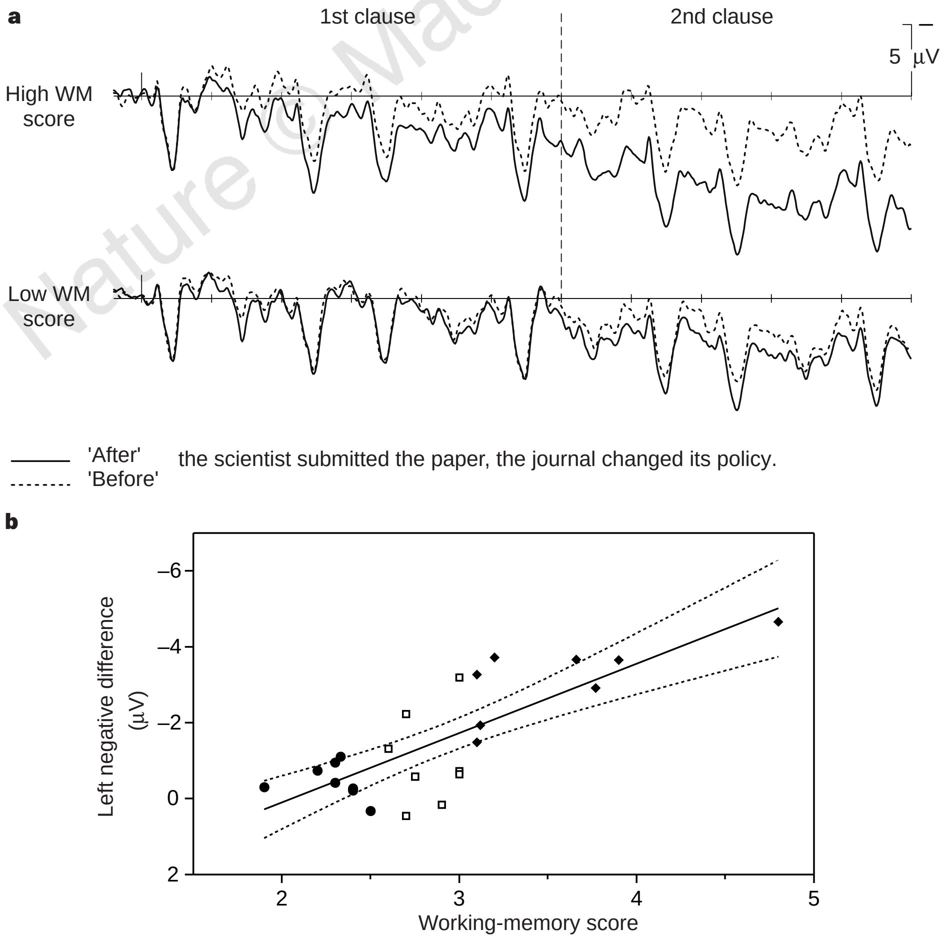
Figure 2 Spline-interpolated isovoltage maps[20] displaying the mean difference between 'before' and 'after' sentences (mean amplitude from 500 to 5500 ms). 'Before' sentences lead to a more negative response that is maximal over the left anterior scalp. Although the effect is different in amplitude for individuals with high versus low working-memory scores, its distribution is very similar (group by site interaction after rescaling according to McCarthy and Wood[21]: $F_{21,294} = 0.81$, not significant). Note that a relative scaling is used (min and max: all participants, –1.7 and 1.0 μV; high score, –3.2 and –0.1 μV; low score, –0.9 and 2.0 μV).

signals that events will be expressed in their actual order of occurrence, whereas 'before' signals that events will be expressed in reverse order. If real-world knowledge has an influence on sentence processing, then the responses to 'before' and 'after' sentences should diverge even though they differ only minimally in their initial lexical item. We suggest that the discourse representations are structured by real-world knowledge of temporal sequence. 'After' sentences adhere to this default model, whereas 'before' sentences do not; as a consequence, 'before' sentences require additional computations.

Consistent with non-interactive models of sentence comprehension, this processing difference could occur relatively late in the second clause, that is, at the point where all of the information relevant for the temporal comparison from each clause is available for integration in a message-level representation[1,2]. However, in line with more interactive models of language comprehension[1,2], we propose that conceptual knowledge is used continuously in real time to build a discourse-level representation of a sentence. Thus, 'before' and 'after' sentences should diverge from their outset.

As shown in Fig. 1, the responses to 'before' and 'after' sentences do diverge as early as 300 ms into the processing of the first word of the sentence; 'before' sentences elicit greater negativity. This difference in brain potential has a left anterior focus (Fig. 2) and grows progressively larger across the sentence. It thus appears that words do access conceptual knowledge as part of the comprehension process almost immediately and this has lasting processing consequences.

These findings also may relate to the possible locus of these effects in the cognitive system, as a similar ERP response has been observed in contrasts of written and spoken sentence types that differ in working-memory demands[6–8]. In several experiments, according to



the scientist submitted the paper, the journal changed its policy.

Figure 3 Relationship of left negative difference and working memory span. **a**, Cross-sentence ERPs from the left frontal recording site for the individuals with the highest ($n = 8$; mean = 3.59, s.d. = 0.59) and lowest ($n = 8$; mean = 2.29, s.d. = 0.18) scores of working-memory (WM) span. Individuals with higher working memory span show a more pronounced difference between 'before' and 'after' sentences (group by sentence type interaction: clause 1, $F_{1,14} = 9.61$, $P < 0.008$; clause 2, $F_{1,14} = 8.37$, $P < 0.015$). **b**, The amplitude of the left frontal negativity (mean difference between 'before' and 'after' sentences across the sentence) is significantly correlated with working memory span scores ($r = 0.783$, $F_{1,22} = 35.4$, $P < 0.0001$). This correlation remains significant even after omission of the subject with the best score ($r = 0.727$, $F_{1,21} = 23.6$, $P < 0.0001$). Filled circles, low score; open squares, medium score; filled diamonds, high score.

psycholinguistic analyses, sentences that are more demanding of working memory are associated with greater negativity over left frontal regions than those that are less demanding[6–8]. These differences have a scalp distribution consistent with the proposed involvement of the frontal regions in working-memory processes and are more pronounced in good than in poor comprehenders[9–13]. If the 'before/after' difference in our data reflects that same process, it too should reflect individual differences. This was indeed found: the largest differences are observed in individuals with high scores for working-memory span (Fig. 3a). In fact, the size of this slow potential difference for 'before' versus 'after' sentences is highly correlated with working-memory span (Fig. 3b).

In previous studies, working-memory load was manipulated by contrasting sentences with different syntactic structures. In some cases, the sentences also differed in the order of the lexical items[7,8]. In our study, the critical sentences differ only in the initial word; their syntactic structure and lexical content are otherwise identical. Thus, the prolonged ERP difference must be due to the different information that 'before' and 'after' activate in long-term memory and the computational consequences of these for the creation of a discourse representation, presumably in working memory. It is this difference that we suggest is reflected in the ERP effect (left frontal negativity) we observe. Our comparison is a purer demonstration of the proposed link between this left frontal negativity and working-memory processes. Working memory also has been implicated in the difficulties that children have in processing temporal terms[14–16], and in the comprehension deficits that adults with Parkinson's disease experience with 'before' compared with 'after' sentences[17].

In summary, these results show the power of a single word not only to express a concept but also to affect sentence processing in real time. To our knowledge, this is the first demonstration that high-level, real-world knowledge has immediate and sustained consequences on neural processing during sentence comprehension. ☐

Methods

Stimuli. Each subject read 120 critical (60 'before', 60 'after') and 480 filler sentences presented in random order, one word at a time (duration 200 ms, with 500 ms between word onsets) in yellow in the middle of a video monitor. The critical sentences had the following structure: Before/After the noun1 verb1-ed the noun2, the noun3 verb2-ed the noun4 .... Word frequency was determined using the CELEX corpus[18] and ranged between 0 and 1474 per million (median = 8.6) for the nouns and between 0 and 2372 per million (median = 27.3) for the verbs, most of which were strongly transitive, with a few having possible ditransitive or intransitive readings. 'Before' and 'after' versions of each sentence were shown to different halves of the 24 right-handed, English-speaking volunteers (11 women; mean age 21.7 years); thus, across subjects the exact same sentences occurred in the 'before' and 'after' conditions. Each critical sentence was followed by a true/false comprehension probe for which the original sentence was rephrased by changing either the temporal conjunction, the order of the clauses, the position of temporal conjunction (sentence initial versus between clauses), or all three. The fillers comprised: 120 sentences containing an embedded object-relative clause; 100 sentences starting with a proper name; 180 two-clause sentences beginning with 'although', 'as' or 'because'; and 80 sentences of varying structures including sentences of one clause.

Assessment of working memory span. Scores on a test of working memory span[19], which assess individuals' capacity to process and store verbal information simultaneously, were used to group subjects (high, medium and low). For this test, subjects read increasingly larger (2, 3, 4, 5 and 6) sets of lengthy sentences aloud; immediately after each set, subjects attempt to recall the last word of each sentence in order (maximum score = 6).

Recording and analysis of biosignals. ERPs (time constant = 8 s) were recorded using standard recording procedures from 26 geodesically spaced sites on the scalp[7,8]. ERPs were obtained for 6144 ms epochs starting 300 ms before onset of the sentence. ERPs were quantified by mean amplitude measures for clause 1 (500–3,000 ms) and clause 2 (3,000–5,500 ms) relative to baseline. Subsequent ANOVA statistics used the Huynh–Feldt correction.

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Spontaneous pinwheel annihilation during visual development

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Neurons in the visual cortex respond preferentially to edge-like stimuli of a particular orientation[1]. It is a long-standing hypothesis that orientation selectivity arises during development through the activity-dependent refinement of cortical circuitry[2–4]. Unambiguous evidence for such a process has, however, remained elusive[5–7]. Here we argue that, if orientation preferences arise through activity-dependent refinement of initially unselective patterns of synaptic connections, this process should leave distinct signatures in the emerging spatial pattern of preferred orientations. Preferred orientations typically change smoothly and progressively across the cortex[1]. This smooth progression is disrupted at the centres of so-called pinwheels[8,9], where neurons exhibiting the whole range of orientation preferences are located in close vicinity[10]. Assuming that orientation selectivity develops through a set of rules that we do not specify, we demonstrate mathematically that the spatial density of pinwheels is rigidly constrained by basic symmetry principles. In particular, the