

Music, language and meaning: brain signatures of semantic processing

Stefan Koelsch, Elisabeth Kasper, Daniela Sammler, Katrin Schulze, Thomas Gunter & Angela D Friederici

Semantics is a key feature of language, but whether or not music can activate brain mechanisms related to the processing of semantic meaning is not known. We compared processing of semantic meaning in language and music, investigating the semantic priming effect as indexed by behavioral measures and by the N400 component of the event-related brain potential (ERP) measured by electroencephalography (EEG). Human subjects were presented visually with target words after hearing either a spoken sentence or a musical excerpt. Target words that were semantically unrelated to prime sentences elicited a larger N400 than did target words that were preceded by semantically related sentences. In addition, target words that were preceded by semantically unrelated musical primes showed a similar N400 effect, as compared to target words preceded by related musical primes. The N400 priming effect did not differ between language and music with respect to time course, strength or neural generators. Our results indicate that both music and language can prime the meaning of a word, and that music can, as language, determine physiological indices of semantic processing.

The question of whether music can activate brain mechanisms related to the processing of semantic meaning information has remained unanswered¹. The present study investigated semantic priming of words using sentences and music. A sentence such as *She sings a song* facilitates the processing of a semantically related word such as *music*, whereas it does not facilitate processing of a semantically unrelated word such as *sock*. This effect is known as the semantic priming effect; it refers to the highly consistent processing advantage seen for words that are preceded by a semantically related context^{2,3}.

An electrophysiological index of semantic priming is the N400 component of ERP measurements. The N400 is a negative polarity ERP component that is maximal over centro-parietal electrode sites; the N400 usually emerges at about 250 ms after the onset of word stimulation and reaches its maximal amplitude at around 400 ms. The N400 elicited by words is highly sensitive to manipulations of semantic relations, being attenuated for words that are preceded by a semantically congruous context, compared to when preceded by a semantically incongruous context^{3,4}. That is, when a word is preceded by a semantic context, the amplitude of the N400 is inversely related to the degree of semantic fit between the word and its preceding semantic context.

There is ample evidence that the N400 elicited by words is sensitive to ongoing linguistic analysis, and it is assumed that the N400 reflects that readers and listeners immediately relate the word to a semantic representation of the preceding contextual input. It is widely accepted that the N400 elicited by words is particularly sensitive to the processing of semantics, both in prime-target and in sentential contexts^{5,6}. More generally, the processing of almost any type of semantically meaningful information seems to be associated with an N400 effect⁵.

Whereas meaning is clearly a key feature of language, music theorists posit that semantic information is also an important aspect of music^{7–13}. It is assumed that musical meaning is used by composers as a means of expression, although there is some disagreement about how musical meaning might theoretically be considered. Most theorists distinguish at least four different aspects of musical meaning: (i) meaning that emerges from a connection across different frames of reference suggested by common patterns or forms (e.g., sound patterns in terms of pitch, dynamics, tempo, timbre, etc. that resemble features of objects), (ii) meaning that arises from the suggestion of a particular mood, (iii) meaning that results from extramusical associations (e.g., any national anthem) and (iv) meaning that can be attributed to the interplay of formal structures in creating patterns of tension and resolution. Empirically, emotional responses to music and patterns of perceived tension and relaxation during listening to music have been described, both of which may be regarded as aspects of musical meaning^{14,15}.

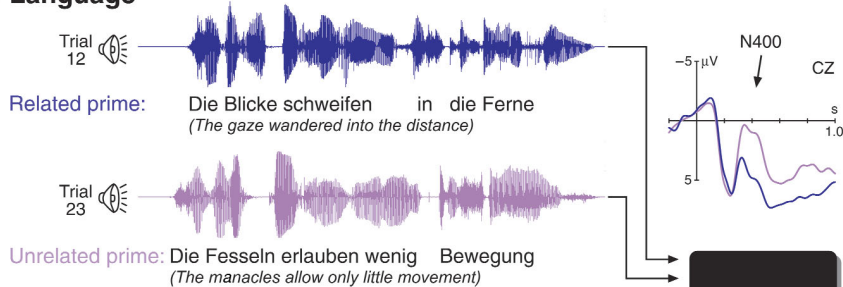
Most linguists, however, would reject the notion that music can transfer specific semantic concepts¹⁶. The aim of the present study is to provide both behavioral and neurophysiological evidence to test this hypothesis. Intuitively, it seems plausible that certain passages of Beethoven's symphonies prime the word *hero*, rather than the word *flea*, but if the underlying cognitive operations are physiologically linked to processing of semantic information has remained unknown.

As primes, we used sentences and musical excerpts (recorded from commercially available CDs) that were, with respect to their meaning, either related or unrelated to a target word (Fig. 1). Target words were 44 German nouns (e.g., *wideness*, *narrowness*, *needle*, *cellar*, *stairs*, *river*, *king*, *illusion*); half of the targets were abstract, and the other

Max Planck Institute of Human Cognitive and Brain Sciences, Stephanstr. 1a, 04103 Leipzig, Germany. Correspondence should be addressed to S.K. (koelsch@cns.mpg.de).

Published online 15 February 2004 ; doi:10.1038/nn1197

a Language



b Music

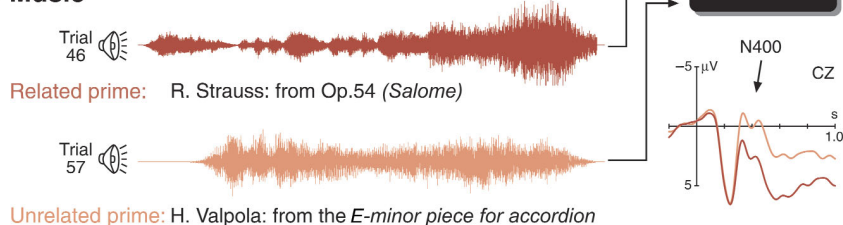


Figure 1 Examples of the four experimental conditions preceding a visually presented target word. (a) Left, prime sentence related to (top, dark blue traces) and unrelated to (bottom, purple traces) the target word *wideness*. Right, grand-averaged ERPs elicited by target words after the presentation of semantically related and unrelated prime sentences, recorded from a central electrode. Unprimed target words elicited a clear N400 component in the ERP. (b) Left, musical excerpt that primed (top, dark brown traces) and did not prime (bottom, light brown traces) the same target word. Right, grand-averaged ERPs elicited by primed and non-primed target words after the presentation of musical excerpts. As after the presentation of sentences, target words presented after unrelated musical excerpts elicited a clear N400 component compared to target words presented after related excerpts. Note that the same target word was used for the four different conditions. Thus, condition-dependent ERP effects elicited by the target words can only be due to the different preceding contexts.

half were concrete words (see Methods). See **Supplementary Methods** online for list of target words, and **Supplementary Audio 1–8** online for musical excerpts.

One-third of the musical primes used in the ERP experiments had been chosen based on self-reports of the composers. For example, the prime for the word *needle* was a passage of Schönberg's *String Terzett* in which he described stitches during his heart attack. The other musical primes had been chosen based on musicological terminology. For example, the prime for the word *narrowness* was an excerpt in which intervals are set in closed position (covering a narrow pitch range in tonal space, and being dissonant), the prime for the word *wideness* was an excerpt in which intervals are set in open position (covering a wide pitch range; see Fig. 1 and excerpts from Strauss and Valpola in **Supplementary Audio 1,2** online). Another example is the Stravinsky excerpt that sounds fervent, and the word *fervent* is semantically related to the word *red*.

Most of the musical stimuli that primed concrete words resembled sounds of objects (e.g., *bird*) or resembled qualities of objects (e.g., low tones associated with *basement*, or ascending pitch steps associated with *staircase*). Some musical stimuli (especially those used as primes for abstract words) resembled prosodic, and possibly gestural cues that can be associated with particular words (e.g., *sigh*, *consolation*). Other stimuli represented stereotypic musical forms or styles that are commonly (that is, even by nonmusicians) associated with particular words (e.g., a church anthem and the word *devotion*; **Supplementary Audio 9** online).

Importantly, participants were not familiar with the musical excerpts, so meaning could not simply be ascribed by extramusical associations that had an explicit, direct link to language (such as title or lyrics). Note that in previous experiments that investigated the N400 effect with pictures, odors and environmental sounds, prime stimuli transferred specific, concrete concepts and were therefore directly linked to language (a picture of Bach, a strawberry

odor, a telephone ringing)⁵. Because participants of the present study did not know the musical excerpts, priming of words could not rely on direct associations between musical primes and target words (especially when targets were abstract words), enabling us to investigate whether the N400 can also be elicited by stimuli that are not directly linked to language.

Stimuli were selected based on data obtained in a behavioral pre-experiment in which a group of subjects rated the semantic fit between primes and target words (see Methods). Primes and target words were presented in two experiments using EEG. In both experiments, target words elicited an N400 when elicited after semantically unrelated sentences. Likewise, an N400 effect was elicited when target words were preceded by semantically unrelated musical excerpts, showing that music can transfer semantically meaningful information by priming representations of meaningful concepts.

RESULTS

In the first ERP experiment, participants judged whether the meaning of the target word was related or unrelated to the meaning of the prime stimulus. Behaviorally, subjects categorized 80% of the target words correctly (that is, congruent with the data of the behavioral pre-experiment) when target words were presented after a musical excerpt (a one-sample *t*-test on the number of correct responses

Table 1 Summary of behaviorally obtained semantic relatedness judgments

	Related		Unrelated	
	Language	Music	Language	Music
Pre-experiment ^a	4.43 (±0.48)	3.51 (±0.74)	-3.51 (±1.39)	-2.93 (±1.20)
ERP experiment ^b	93% (±4.1)	78% (±12.5)	91% (±7.3)	82% (±6.4)
Additional experiment ^c	86% (±9.13)	58% (±8.77)		

^aIn the pre-experiment, subjects rated the semantic relatedness between prime and target words, using a scale ranging from -5 to +5. The corresponding row of the table depicts the mean ratings of items that were selected for the subsequent experiments.

^bIn the first ERP experiment, subjects made a two-alternative relatedness judgment for each target word. The corresponding row of the table depicts mean percentages of correct responses (responses were well above chance, $P < 0.0001$ in each domain, the difference between domains (music, language) was significant, $P < 0.0001$).

^cIn the additional behavioral experiment, a five-word list was presented after each prime stimulus. Subjects were instructed to choose the word from the list that was semantically most closely related to the prime. Shown are mean hit percentages of the words that were used as semantically related targets in the ERP experiments (hit percentages were in both domains well above the 20% chance level, $P < 0.0001$, and higher in the language than in the music domain, $P < 0.0001$).

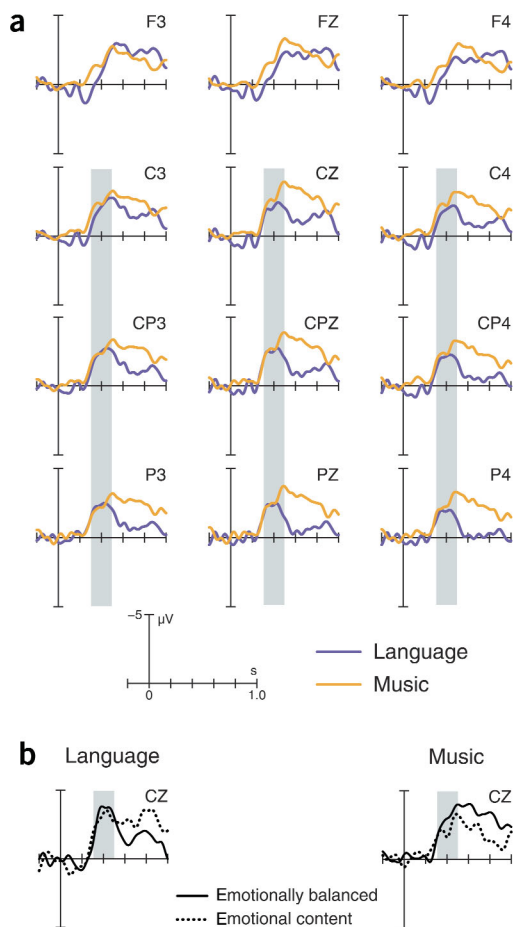


Figure 2 The N400 effect was similar for language and music priming, and did not depend on emotional content. **(a)** Brain effects of semantic relatedness, ERPs elicited by target words (difference potentials, primed targets subtracted from non-primed targets), separately for targets presented after sentences (blue) or music (brown). In both domains, target words elicited the same N400 effect (gray shaded areas indicate electrodes and time window used for statistical analyses). **(b)** Difference waves (primed targets subtracted from nonprimed targets) for emotionally balanced targets (solid line) and for target words with emotional content (dotted line). The potentials demonstrate that the N400 effect was not influenced by the emotional content of target words, neither when preceded by sentences (left) nor when preceded by musical excerpts (right).

showed that subjects performed well above chance, $t = 25.53$, $P < 0.0001$). When target words were preceded by a sentence, 92% of the target words were categorized correctly ($t = 60.28$, $P < 0.0001$). The behavioral data of the ERP experiment replicate the (un)relatedness judgments obtained in the behavioral pre-test (Table 1).

The ERPs of the target words showed, as expected, a larger N400 when presented after semantically unrelated sentences compared to when presented after semantically related sentences (Fig. 1a). This effect is the classical semantic priming effect, reflecting processes related to linguistic analysis that were dependent on the degree of fit between the semantic content of prime sentences and target words. As when preceded by the sentences, the target words also elicited an N400 when presented after an unrelated musical excerpt compared to when presented after a related excerpt (Fig. 1b). The N400 elicited after a musical excerpt that primed the target word was more negative than the N400 elicited after a sentence that primed the word, but like-

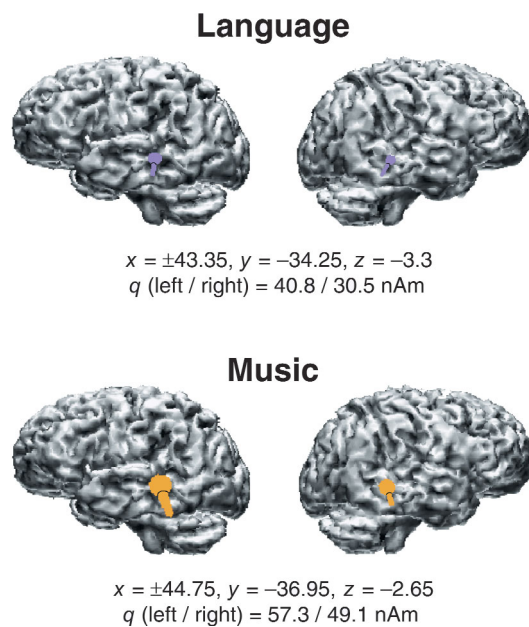


Figure 3 Grand-average source reconstruction of the N400 effect elicited by target words after the presentation of sentences (top) and musical excerpts (bottom). Dipole coordinates are given with reference to standard stereotaxic space³². The mean of explained variance of the data was 90%. Single-subject models were constructed on the time point of maximal explanation of variance (mean time points were in both language and music 413 ms after the onset of the target word). In both domains, dipoles were located in the posterior portion of the middle temporal gyrus (Brodmann's area 21/37), in the close vicinity of the superior temporal sulcus. Locations, strengths and orientations of dipoles did not differ statistically between the language and the music domain.

wise, the N400 elicited after a musical excerpt that did not prime the word was also more negative than the N400 elicited after a sentence that did not prime the word. A two-way ANOVA with factors domain (language, music) and priming (prime, non-prime) revealed a priming effect ($F_{1,23} = 66.31$, $P < 0.0001$), but no interaction ($F_{1,23} = 0.52$, $P > 0.4$), indicating that the N400 effect was present in both domains. A three-way ANOVA with factors domain, priming and concreteness (concrete, abstract target words) did not reveal any two- or three-way interactions. To prove that both abstract and concrete target words elicited N400 effects in both the music and the language domain, ANOVAs with factors priming and concreteness were conducted separately for the music and the language domain. Results of these ANOVAs revealed that in both language and music, both concrete and abstract target words elicited significant N400 effects ($P < 0.0001$ for each noun class in each domain, no two-way interactions).

The N400 effect (that is, the effect of unprimed versus primed target words) did not differ between the language domain (where target words were presented after sentences) and the music domain (where target words were presented after musical excerpts), with respect to latency, amplitude or scalp distribution. In both domains, a bilateral N400 was maximal around 410 ms over centro-parietal electrode sites (Fig. 2a, gray-shaded areas). To test possible differences in scalp distribution of the N400 between the language and the music domain, ten regions of interest (ROIs) were computed, each comprising three adjacent electrode leads. A three-way ANOVA with factors domain, semantic priming and ROI did not reveal a three-way interaction ($F_{9,207} = 1.25$, $P > 0.25$).

The N400 effects did not differ between the prime-target pairs with and without balanced emotional content (see Methods), neither in the language nor in the music domain (Fig. 2b; an ANOVA with factors emotional content (balanced, unbalanced) and domain (language, music) did not reveal any main effects or interaction). This finding rules out the possibility that the musical excerpts merely primed an emotional state that was (in)consistent with the emotional content of the target word.

The sources of electric brain activity underlying the N400 effect did not statistically differ between the language and the music domain, neither with respect to locations, nor with respect to orientations, strengths, time point of maximum or explanation of variance (Fig. 3). To test possible differences between the neural sources underlying the N400 effect in language and music, we used separate *t*-tests (one-sample, two-tailed) for *x*, *y* and *z* coordinates, as well as for orientations, strengths, time point of maximum and explanation of variance of dipoles. One set of tests compared the two left dipoles (one dipole for music and one for language); the other set compared the two right dipoles. No significant difference between language and music was obtained in any test ($P > 0.3$). The source analysis of the N400 effect indicated generators located in the posterior portion of the middle temporal gyrus (MTG, Brodmann's area 21/37), in the close vicinity of the superior temporal sulcus. This localization concurs with numerous studies on the functional neuroanatomy of semantic processes at the level of both words^{17–20} and sentences^{17,21–25}.

To investigate whether the N400 effects observed can also be elicited when participants do not judge the semantic relatedness between prime and target word, we carried out a second ERP experiment using the same stimuli as in the first ERP experiment. Subjects were instructed to attend to the stimuli because they will be given memory tests. Participants were not informed about the semantic (un)relatedness between primes and targets (see Methods, no subject participated in any of the other ERP or behavioral experiments).

As in the first ERP experiment, semantically unrelated target words elicited a clear N400 effect after both linguistic and musical primes (Fig. 4), replicating effects of the first experiment and indicating that the N400 effect can be observed in both domains even when subjects do not make explicit judgments of semantic relatedness (for behavioral data of the memory test, see Methods). Again, a two-way ANOVA with factors domain and priming indicated a clear priming effect ($F_{1,15} = 47.60$, $P < 0.0001$), but no interaction between the two factors ($F_{1,15} = 0.08$, $P > 0.75$). An ANOVA with factors domain, priming and concreteness did not reveal any two- or three-way interaction. The amplitude of the N400 was virtually identical between the first and second experiments. A three-way ANOVA with factors experiment (1,2), domain and priming showed no significant interaction between experiment and priming ($P > 0.1$), nor a three-way-interaction ($P > 0.4$).

To gather further behavioral data, we carried out an additional study in which each prime stimulus was presented, followed by a visual presentation of a five-word list. This list contained the semantically related and unrelated words used in the ERP experiments, as well as three other words that were randomly chosen from the pool of target items used in the ERP experiments. Subjects were instructed to choose the word from the list that had the best semantic fit to the preceding prime stimulus (no subject participated in any of the other experiments). Results replicated data of both the behavioral pre-test, and of the behavioral performance during the first EEG experiment (Table 1). After linguistic primes, subjects chose the correct target word in 86% of the trials (grand-average, a one-sample *t*-test on the number of correct responses showed that subjects performed well

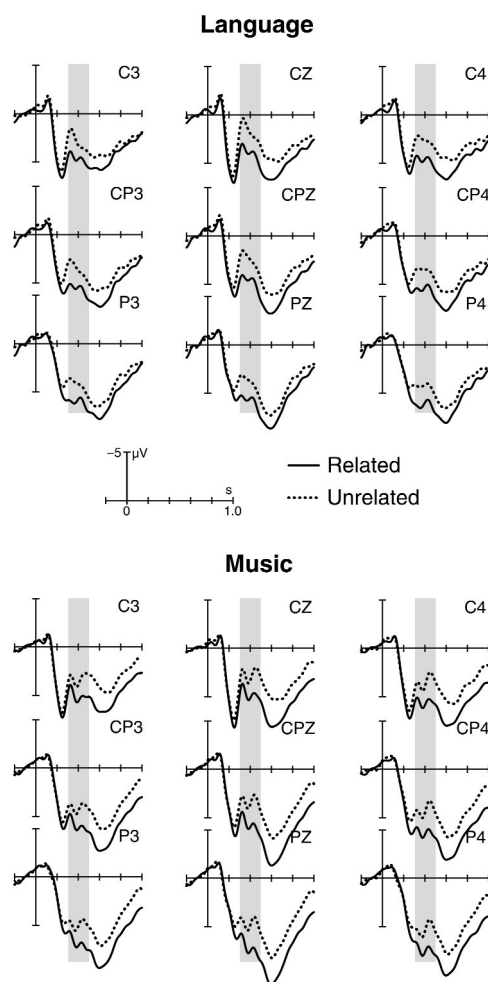


Figure 4 ERPs elicited under a condition in which participants performed a memory test, separately for targets presented after sentences (top) and music (bottom). As in the first ERP experiment, target words elicited an N400 effect in both domains, indicating that ERP effects can be elicited even when participants do not make explicit judgments about semantic relatedness. Gray-shaded areas indicate the time window used for statistical analysis.

above chance (20%), $t = 32.43$, $P < 0.0001$). After musical primes, subjects chose the correct target word in 58% of trials, also well above the 20% chance level ($t = 19.30$, $P < 0.0001$), but less than in the language domain ($P < 0.0001$).

DISCUSSION

Our behavioral data indicated that three independent groups of subjects with no special musical training who are naively presented with particular musical excerpts similarly associate the musical excerpts with particular words. The corresponding ERP results indicated that the N400 priming effect in the music domain did not differ from that in the language domain, with respect to latency, scalp distribution, neural sources or amplitude. The N400 effect was observed regardless of whether or not participants made judgments about the semantic fit of target words. Thus, regarding the N400 priming effect, the auditory perception of music and language primes had the same effect on the processes of semantic analysis during the subsequent visual perception of the target words. In both the language and the music domains,

these processes were dependent on the degree of fit between the meaning of prime and target word. Thus, the present data show that music cannot only influence the processing of words, but it can also prime representations of meaningful concepts, be they abstract or concrete, independent of the emotional content of these concepts.

Our findings do not imply that music and language have the same semantics. Clearly people do not typically have the repertoire to articulate thoughts and intentions musically as well as they do linguistically (but see the whistling languages of shepherds^{26–28} and the musical Solresol language²⁹). However, there is ample evidence that the N400 elicited by words reflects processing of meaning information. The present data show that the influence on the processing of the meaning of the target words (as indexed by the N400 priming effect) can be identical for language and music. Behaviorally, judgment accuracy was higher in the language than in the music domain. A respective difference was not observed in the N400 amplitudes, possibly because the ERP effects are less dependent on conscious judgment.

The present results indicate that music transfers considerably more semantic information than previously believed. The physical parameters of musical information that activate particular associations (and that are, thus, characteristic for the meaning of a musical passage) as well as the cognitive routes by which music primes representations of meaningful concepts remain to be specified. It is possible that participants generated words subvocally during the perception of the musical excerpts, and that these words were subjected to semantic analysis, rather than the musical information itself (although this was not necessary in the second ERP experiment, and although participants reported in the first ERP experiment that they did not vocalize during the presentation of the music). However, it is also possible that at least some musical stimuli directly primed meaningful concepts (that is, without subvocal word generation), and that linguistic labels of musical forms (such as *heroic*, *fervent*, *mischievous*, *ambitious*, etc.) are merely an epiphenomenon of an understanding of musical meaning that could also operate without words. Future studies might catalog stereotypical musical forms that nonmusicians associate with particular meaning information, investigate culture-specificity of stereotypical musical forms, and further investigate which physical characteristics of musical information (e.g., tempo, timbre, duration, pitch range and structural factors such as harmony and key) lead to the priming of particular semantic concepts^{15,30,31}.

METHODS

Subjects. Data were obtained in five experiments from 122 subjects (no subject participated in more than one experiment, all experimental groups of subjects were completely independent, and informed written consent was obtained from all subjects): 26 subjects (aged 19 to 30 years, mean 23.4 years) participated in a behavioral pre-experiment, 24 subjects (aged 18 to 29 years, mean 23.3) in a first ERP experiment, 26 (aged 20 to 29 years, mean 26.5) in a behavioral study in which the emotional content of target words was determined, 16 (aged 20 to 28 years, 22.8) in a second ERP experiment, and 20 (aged 20 to 52 years, mean 25.1) in an additional behavioral study. All participants were nonmusicians (none had participated in extra-curricular music lessons or performances).

Stimuli. In a first step, 248 prime-target items were constructed; primes were sentences and short musical excerpts (recorded from commercially available CDs) and target words were concrete and abstract German nouns (concreteness of words was measured using a questionnaire). For each target word, four primes were chosen: (i) a semantically, or meaningfully, related sentence, (ii) an unrelated sentence, (iii) a related musical excerpt and (iv) an unrelated musical excerpt. Moreover, each prime was used twice: in one trial, the prime was semantically unrelated to a target word, and in another trial it

was semantically related to a target word (the order was pseudo-randomly intermixed in each experiment).

A behavioral pre-experiment was conducted to select items for the ERP experiments by testing which prime-target pairs are judged as semantically (un)related by a larger sample of subjects. Each prime (musical excerpt or sentence) was presented auditorily. Subsequently, the two possible target words for each prime (one related, the other unrelated) were presented simultaneously on a screen. Subjects were asked to rate the degree of semantic fit between the prime and each of the two target words on an 11-point scale (ranging from -5 (semantically strongly unrelated) to $+5$ (semantically strongly related)), leading to two ratings for each prime. For each prime, t -tests were used to analyze whether these two ratings differed significantly from each other. Nonsignificant items were discarded. Average relatedness ratings of the items that were selected for the ERP experiments are listed in Table 1.

A total of 176 significant prime-target pairs were selected for the EEG experiment. As in the pre-experiment, each target word had four primes, and each prime was used twice (see above), resulting in 44 target words (22 abstract, 22 concrete), each with two related primes (one sentence, one musical excerpt) and two unrelated primes. (See Supplementary Audio 1–9 online for examples of musical stimuli and Supplementary Methods online for list of target words. The full set of sound stimuli can be found at www.stefan-koelsch.de.) Duration of musical excerpts was on average 10.5 s, and sentences had an average duration of 2.5 s. Word length and frequency of target words were balanced.

Note that each target word was used for four different prime conditions (see Fig. 1): (i) semantically related sentence, (ii) unrelated sentence, (iii) related music and (iv) unrelated music. Thus, each target was preceded throughout the experiment by four primes (the four different trials for one target word were not presented in direct succession), and differences in the ERPs elicited by a target word (e.g., *wideness*) presented after each of the four primes (see above) can only be due to the different effect of the preceding auditory stimulus on the processing of the (same) word (e.g., *wideness*). Each prime was used twice: in one trial, the prime was semantically related, and in another trial, the prime was unrelated to the target word. The order of types of prime was pseudo-randomly intermixed and counterbalanced for each target word throughout the experiment.

After the first ERP experiment, 26 different subjects rated in a separate behavioral experiment the emotional content of each target word on a 9-point scale, ranging from -4 (strong negative content) to $+4$ (strong positive content), with 0 corresponding to emotionally neutral content. We used t -tests to determine whether the emotional content of the two target words for a prime differed significantly. For 64% of the primes, the two target words (semantically related, unrelated) did not differ in their emotional content, and these items were categorized as emotionally balanced. In this category, the (un)relatedness between the possible emotional content of prime and the emotional content of the target word could not have led to a priming effect because the emotional content did not differ between the semantically related and the semantically unrelated target word.

Procedure. In the first EEG experiment, prime stimuli were presented via loud-speakers with approximately 60 dB SPL. Each trial began with the auditory presentation of a sentence or musical excerpt, followed by the visual presentation of a target word (Fig. 1, presentation time for targets was 2,000 ms). After the target word had disappeared from the screen, participants were asked to indicate whether the prime and the target were meaningfully related or unrelated by pressing one of two response buttons.

Procedure of the second EEG experiment was identical to the first, except that participants were not informed about semantic (un)relatedness between primes and target words. Instead, they were asked to attend to the stimuli in preparation for memory tests. We included 20 additional trials (approximately 10% of all trials) in which a single sentence, musical excerpt or word was presented. After such a presentation, participants were asked to indicate whether or not that stimulus had already been presented in any of the previous trials (ERPs of these trials were not analyzed). Behaviorally, subjects showed on average 71% percent correct responses (9% missed, 20% incorrect responses). A one-sample t -test on the number of correct responses showed that subjects performed well above chance ($t = 6.635$, $P < 0.0001$).

Data analysis. EEG data were recorded from 45 standard scalp locations, referenced off-line to the algebraically mean of left and right mastoid electrodes. Trials were averaged off-line with an epoch length of 1,200 ms, including a prestimulus baseline from -200 to 0 ms (with respect to the onset of the word). Differences in the mean amplitudes of a region of interest (comprising the electrodes C3, Cz, C4, CP3, CPz, CP4, P3, Pz, P4) among the different conditions were tested by repeated-measurement ANOVAs. The time window for statistical analysis was 300 to 500 ms. After statistical evaluation, ERPs were, for presentation purposes only, low-pass filtered at 10 Hz (41 points, FIR).

To localize the neural sources of the N400, for each participant a dipole analysis was performed on the difference ERPs (semantically related subtracted from semantically unrelated ERPs), separately for targets preceded by sentences and musical excerpts. The dipole analysis was conducted using two-dipole models (rotating dipoles; seed points were set for all participants in the same location in the left and right posterior auditory cortex (posterior superior temporal gyrus), maximal distance from seed points was 30 mm, minimal distance between dipoles was 60 mm, mirrored locations). In a first step, dipole localizations were performed for a time window from 380 to 450 ms after stimulus onset. In a second step, for each participant the time point with the best explanation of variance was chosen for a second dipole localization (same method as described above) using the ERP data of this time point. Time points as well as dipole coordinates, strengths and orientations obtained through the second step from each participant were then grand-averaged across subjects (grand-averaged orientations were subsequently normalized).

ACKNOWLEDGMENTS

This work was supported by the German Academic Exchange Service (DAAD).

COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

Received 24 November 2003; accepted 22 January 2004

Published online at <http://www.nature.com/natureneuroscience/>

- Bernstein, L. *The Unanswered Question: Six Talks at Harvard* (Harvard Univ. Press, Cambridge, Massachusetts, 1981).
- Osterhout, L. & Holcomb, P. ERPs and language comprehension. in *Electrophysiology of Mind. Event-Related Potentials and Cognition* (eds. Rugg, M. & Coles, M.) 192–208 (Oxford Univ. Press, Oxford, 1995).
- Kellenbach, M., Wijers, A. & Mulder, G. Visual semantic features are activated during the processing of concrete words: event-related potential evidence for perceptual semantic priming. *Cog. Brain Res.* **10**, 67–75 (2000).
- Kutas, M. & Hillyard, S. Reading senseless sentences: brain potentials reflect semantic incongruity. *Science* **207**, 203–205 (1980).
- Kutas, M. & Federmeier, K. Electrophysiology reveals semantic memory use in language comprehension. *Trends Cogn. Sci.* **4**, 463–470 (2000).
- Friederici, A.D., ed. *Language Comprehension: a Biological Perspective* (Springer, Berlin, 1998).
- Jones, M.R. & Holleran, S., eds. *Cognitive Bases of Musical Communication* (American Psychological Association, Washington, D.C., 1992).
- Swain, J. *Musical Languages* (Norton, New York, 1997).
- Raffmann, D. *Language, Music, and Mind* (MIT Press, Cambridge, Massachusetts, 1993).
- Meyer, L.B. *Emotion and Meaning in Music* (Univ. of Chicago Press, Chicago, 1956).
- Hevner, K. The affective value of pitch and tempo in music. *Am. J. Psych.* **49**, 621–630 (1937).
- Peirce, C. *The Collected Papers of C.S. Peirce* (Harvard Univ. Press, Cambridge, Massachusetts, 1958).
- Zbikowski, L. *Conceptualizing Music: Cognitive Structure, Theory, and Analysis* (Oxford Univ. Press, New York, 2002).
- Krumhansl, C.L. Perceptual analysis of Mozart's piano sonata KV 282: segmentation, tension, and musical ideas. *Mus. Percept.* **13**, 401–432 (1996).
- Krumhansl, C.L. An exploratory study of musical emotions and psychophysiology. *Can. J. Exp. Psychol.* **51**, 336–352 (1997).
- Pinker, S. *How the Mind Works* (Norton, New York, 1997).
- Friederici, A.D. Towards a neural basis of auditory sentence processing. *Trends Cogn. Sci.* **6**, 78–84 (2002).
- Démonet, J. *et al.* The anatomy of phonological and semantic processing in normal subjects. *Brain* **115**, 1753–1768 (1992).
- Price, C., Moore, C., Humphreys, G. & Wise, R. Segregating semantic from phonological processes during reading. *J. Cogn. Neurosci.* **9**, 727–733 (1997).
- Friederici, A.D., Opitz, B. & von Cramon, D.Y. Segregating semantic and syntactic aspects of processing in the human brain: an fmri investigation of different word types. *Cereb. Cortex* **10**, 698–705 (2000).
- Ni, W. *et al.* An even-related neuroimaging study distinguishing form and content in sentence processing. *J. Cogn. Neurosci.* **12**, 120–133 (2000).
- Kuperberg, G. *et al.* Common and distinct neural substrates for pragmatic, semantic and syntactic processing of spoken sentences: an fMRI study. *J. Cogn. Neurosci.* **12**, 321–341 (2000).
- Baumgaertner, A., Weiller, C. & Büchel, C. Even-related fMRI reveals cortical sites involved in contextual sentence integration. *NeuroImage* **16**, 736–345 (2002).
- Halgren, E. *et al.* N400-like magnetoencephalography responses modulated by semantic context, word frequency, and lexical class in sentences. *NeuroImage* **17**, 1101–1116 (2002).
- Helenius, P., Salmelin, R., Service, E. & Connolly, J.F. Distinct time courses of word and context comprehension in the left temporal cortex. *Brain* **121**, 1133–1142 (1998).
- Busnel, R. & Classe, A. *Whistled Languages* (Springer, Berlin, 1976).
- Seboek, T. & Umiker-Seboek, D., eds. *Speech Surrogates: Drum and Whistle Systems* (Mouton, The Hague, Paris, 1976).
- Cowan, G. Mazatco whistle speech. *Language* **24**, 280–286 (1948).
- Crystal, D. *The Cambridge Encyclopedia of Language* (Cambridge Univ. Press, Cambridge, UK, 1995).
- Juslin, P.N. Cue utilization in communication of emotion in music performance: relating performance to perception. *J. Exp. Psychol. Hum. Percept. Perform.* **26**, 1797–1813 (2000).
- Juslin, P.N. & Laukka, P. Communication of emotions in vocal expression and music performance: different channels, same code? *Psychol. Bull.* **129**, 770–814 (2003).
- Talairach, J. & Tournoux, P. *Co-Planar Stereotaxic Atlas of the Human Brain. 3-Dimensional Proportional System: An Approach to Cerebral Imaging* (Thieme, Stuttgart, Germany, 1988).