

Unconscious Automatic Brain Activation of Acoustic and Action-related Conceptual Features during Masked Repetition Priming

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Abstract

■ Classical theories of semantic memory assume that concepts are represented in a unitary amodal memory system. In challenging this classical view, pure or hybrid modality-specific theories propose that conceptual representations are grounded in the sensory–motor brain areas, which typically process sensory and action-related information. Although neuroimaging studies provided evidence for a functional–anatomical link between conceptual processing of sensory or action-related features and the sensory–motor brain systems, it has been argued that aspects of such sensory–motor activation may not directly reflect conceptual processing but rather strategic imagery or postconceptual elaboration. In the present ERP study,

we investigated masked effects of acoustic and action-related conceptual features to probe unconscious automatic conceptual processing in isolation. Subliminal feature-specific ERP effects at frontocentral electrodes were observed, which differed with regard to polarity, topography, and underlying brain electrical sources in congruency with earlier findings under conscious viewing conditions. These findings suggest that conceptual acoustic and action representations can also be unconsciously accessed, thereby excluding any postconceptual strategic processes. This study therefore further substantiates a grounding of conceptual and semantic processing in action and perception. ■

INTRODUCTION

Conceptual representations in human long-term memory play an important role for language, action, and thought because they constitute word meaning and provide the cognitive basis for categorically organized knowledge about the physical and social world (Kiefer & Pulvermüller, 2012; Barsalou, Simmons, Barbey, & Wilson, 2003; Levelt, Roelofs, & Meyer, 1999; Humphreys, Riddoch, & Quinlan, 1988; Rosch, 1975; Tulving, 1972). Although the relevance of concepts for a broad range of cognitive activities is well accepted (Kiefer & Barsalou, 2013), the organization of semantic memory is controversially debated.

Traditionally, concepts are assumed to be represented in a unitary amodal semantic memory system independent of the sensory and motor brain systems (Tyler & Moss, 2001; Pylyshyn, 1984; Anderson, 1983). According to this amodal view, modality-specific sensory and action-related input information is transferred into a common symbolic format irrespective of the type of conceptual information (e.g., action-related, acoustic, visual, etc.). Activation in modality-specific brain regions during conceptual tasks, if any, is ascribed to postconceptual strategic processes, like elaboration or imagery (Chatterjee,

2010; Machery, 2007). This classical view has been challenged by more recent modality-specific approaches to semantic memory: Embodied or, more generally, grounded cognition theories (Kiefer & Barsalou, 2013; Pulvermüller & Fadiga, 2010; Barsalou, 2008; Kiefer, Sim, Liebich, Hauk, & Tanaka, 2007; Martin, 2007; Gallese & Lakoff, 2005) postulate that conceptual representations are rooted in the sensory and motor brain areas, which typically process sensory- and action-related information. According to this view of grounded semantics, access to perceptually and action-related concepts activates cell assemblies in modality-specific cortex leading to a partial reinstatement of brain activity otherwise present during action and perception (Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008; Hauk, Johnsrude, & Pulvermüller, 2004). Modality-specific activation thereby is essential for conceptual processing and thus occurs automatically even when stimuli are only perceived unconsciously. Most approaches to grounded cognition are actually “hybrid models” in the sense that, over and above an essential role of sensory and motor brain systems for conceptual processing, they assume a cross-modality convergence zone (Damasio, 1989) in multimodal association cortex (Kiefer & Pulvermüller, 2012; Pulvermüller et al., 2010; Patterson, Nestor, & Rogers, 2007; Simmons & Barsalou, 2003). Cross-modality semantic convergence zones, for example in anterior temporal, parietal and prefrontal

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areas (Binder & Desai, 2011; Patterson et al., 2007) may help integrating conceptual features from the different modalities into a high-dimensional supramodal semantic space, a function also carried by long-distance connections between modality-specific parts of distributed conceptual circuits. As a discrimination between pure and hybrid grounded cognition theories is not central to the present work, we do not further distinguish between these variants in this manuscript.

In support of grounded cognition theories of conceptual representations behavioral (Boulenger et al., 2006; Helbig, Graf, & Kiefer, 2006), neuropsychological (Trumpp, Kliese, Hoenig, Haarmer, & Kiefer, 2013; Warrington & McCarthy, 1987), electrophysiological (Kiefer, 2005; Pulvermüller, Lutzenberger, & Preissl, 1999), and neuroimaging studies (Hauk et al., 2004; Martin, Wiggs, Ungerleider, & Haxby, 1996) suggest that conceptual processing crucially involves the sensory and motor brain systems. For instance, Hauk et al. (2004) showed in an fMRI study that silently reading of action words, which are related to face, arm, or leg movements (lick, pick, or kick), differentially activate brain areas along the motor strip directly adjacent or overlapping with the somatotopic activations of actual movements of the tongue, fingers, or feet, respectively (see also Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005; Tettamanti et al., 2005; Pulvermüller, Harle, & Hummel, 2000). Furthermore, action-related representations associated with manipulable objects (e.g., “hammer” or “drill”) have been shown to activate a posterior portion of posterior middle temporal gyrus and adjacent areas in STS (Hoenig, Sim, Bochev, Herrnberger, & Kiefer, 2008; Chao, Haxby, & Martin, 1999). Because of its proximity to motion-sensitive areas (Lewis, 2010), it has been suggested that this region codes action-related motion (Martin & Chao, 2001). In ERP recordings, action-related words elicited more positive ERPs at frontocentral electrodes compared with words denoting concepts, for which action is less relevant (Kiefer, Sim, Helbig, & Graf, 2011; Kiefer, 2001, 2005; Pulvermüller et al., 1999).

Whereas action-related conceptual information processing appears to involve motor and motion-sensitive areas, sensory conceptual information seems to draw upon corresponding sensory areas. Several neuroimaging studies observed activation in overlapping brain regions during conceptual and perceptual tasks (e.g., Simmons et al., 2007; Simmons, Martin, & Barsalou, 2005). In a combined fMRI/ERP study, Kiefer et al. (2008) provided evidence for the involvement of auditory brain systems in conceptual processing of sound information: Using a lexical decision task (word/pseudoword decisions), participants were visually presented with words denoting objects for which acoustic features are highly (bell) or less (pillow) semantically relevant (note that a bell is only called a bell if it can give a certain sound; the sound of a pillow is irrelevant for it being a pillow). fMRI scanning revealed activation in left posterior superior and middle

temporal gyri for words with high acoustic feature relevance. This region in auditory association cortex overlaps with the activation pattern during real sound perception. Hence, acoustic conceptual features recruit auditory brain areas even when implicitly presented through visual words. In the ERP recordings, words with high versus low relevance of acoustic conceptual features bilaterally elicited a more negative scalp potential at frontocentral electrodes, where acoustically evoked potentials are typically recorded (Näätänen, 1992). This ERP effect related to acoustic features thus exhibited the opposite polarity of the effect of action features mentioned above. The notion of a distributed but feature-specific representation of acoustic and action-related conceptual information in or close to modality-specific cortex has been further substantiated in an fMRI study, in which sound- and action-related concepts activated different portions of posterior superior and middle temporal gyri close to the modality-specific acoustic and motion-sensitive areas (Kiefer, Trumpp, et al., 2012).

As many of these previous studies used implicit semantic tasks (e.g., lexical decision or silent reading tasks), which minimize strategic processes, and yielded an early onset of sensory–motor activity in the ERP recordings (about 200 msec and earlier), this activity most likely indicates rapid access to conceptual features rather than late strategic postconceptual processes such as imagery (Machery, 2007) or semantic elaboration (Chatterjee, 2010). However, as the time course of imagery may be variable and strategic processes may occur even in implicit semantic tasks, the contribution of strategic postconceptual processes to sensory–motor activity cannot be entirely excluded.

In order to study unconscious automatic word processing without the contribution of strategic processes, conscious perception of the word stimulus can be eliminated by displaying a pattern mask (e.g., a random sequence of letters) before and thereafter (Kiefer, 2012). Unconscious word processing can be then measured via subliminal priming effects (e.g., facilitation) by masked prime words on subsequent processing of visible targets (Kiefer, Adams, & Zovko, 2012; Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003; Greenwald, Draine, & Abrams, 1996). Although masked primes cannot be consciously perceived, there are meanwhile numerous demonstrations that they trigger cognitive processes at several levels of complexity including semantic processing (for reviews, see Kiefer, 2012; Ansorge, Horstmann, & Scharlau, 2011; Kiefer, Ansorge, et al., 2011; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). As stimulus visibility is a prerequisite of controlled stimulus processing (Kiefer, Adams, et al., 2012; Merikle, Joordens, & Stolz, 1995), contributions of strategic processes to masked priming effects can be safely ruled out.

An elegant method to investigate processing of conceptual feature types is to assess word category effects within a masked repetition priming paradigm (Holcomb

& Grainger, 2007; Roediger, Weldon, & Challis, 1989). At a behavioral level, reactions to repeated stimuli are faster and more accurate than to not-repeated stimuli (repetition priming). In neuroimaging studies, repetition priming was most commonly associated with reduced activity (repetition suppression) in visual (Kherif, Josse, & Price, 2012; Buckner et al., 1998) as well as in frontal brain areas related to semantic retrieval (Demb et al., 1995). Occasionally, increased activity (repetition enhancement) to primed versus unprimed stimuli was also observed (Henson, Shallice, & Dolan, 2000; Schacter et al., 1995), particularly in response to unfamiliar visible stimuli.

In electrophysiological recordings, stimulus repetition is associated with characteristic ERP modulations. Several studies have shown that visible repeated words modulate ERPs starting at about 200 msec: an early negative deflection peaking in the time frame of the N250 and a later negative deflection peaking at about 400 msec (N400) as well as a late positive component peaking at about 600 msec (Kiefer, 2005; Schweinberger, Pickering, Burton, & Kaufmann, 2002; Schweinberger, Pfütze, & Sommer, 1995; Rugg, 1985). Typically, N250 and N400 amplitude is attenuated, whereas late positive component amplitude is enhanced. Other studies using masked repetition priming paradigms (Eddy, Schmid, & Holcomb, 2006; Holcomb & Grainger, 2006) found similar priming effects in the same time frames but additionally a negative/positive deflection starting already at about 100 msec (N/P1).

In principle, repetition priming effects may arise from any stage throughout the processing stream (perceptual, semantic, response stage). Hence, a variety of cognitive processes may contribute to repetition effects in general (Rugg & Nieto-Verga, 1999). Given the appropriate experimental design, however, repetition priming effects can be referred to a certain processing stage (Thompson-Schill & Gabrieli, 1999; Lloyd-Jones & Humphreys, 1997; Vriezen, Moscovitch, & Bellos, 1995). When repetition priming effects for words denoting concepts with a differential weighting of features are compared during reading or lexical decision tasks, visual input (visual letter string) and the motor response (reading, lexical decision) are identical for both word categories. If neurophysiological repetition priming effects vary as a function of conceptual feature type, these feature-related differences must arise from differentially activated semantic representations because the other factors are held constant. Differential neurophysiological repetition effects as a function of stimulus categories have been a valuable and highly sensitive tool in the past to identify the nature of underlying stimulus representations (Kiefer, 2005; Henson, 2003). Hence, an interaction between feature type and repetition would substantiate feature-related brain activations as neurophysiological reflections of semantic memory organization and would strengthen modality-specific theories of conceptual representations.

In the aforementioned study, Kiefer (2005) investigated feature-specific effects on visible words denoting action-

related (manipulable artifacts) or visually related concepts (natural kinds) using ERPs. In the unrepeated condition, action-related concepts were associated with a greater positive potential at frontocentral electrodes, whereas visually related concepts elicited a more positive potential at occipitoparietal electrodes. Most importantly, however, stimulus repetition differentially diminished this feature-related ERP activity resulting in feature-specific ERP repetition effects. However, this study as well as other previous work mentioned above used visible stimuli to elicit conceptual processing. The contribution of strategic processes like imagery therefore cannot be entirely excluded. Thus, it is important to investigate conceptual processing under unconscious viewing conditions, because only grounded cognition but not amodal theories predict automatic activation of conceptual features in corresponding modality-specific brain regions (Kiefer & Barsalou, 2013).

In the present ERP study we therefore used masked repetition priming to test the prediction of grounded cognition theory that action- and sound-related concepts are automatically processed in distinct modality-specific neural circuits. Electrophysiological recordings are very suitable to track the time course of subliminal repetition priming, because ERPs, due to their high temporal resolution, are an ideal tool to capture fast decaying unconscious processes (Kiefer, 2002; Kiefer & Spitzer, 2000). We wanted to test whether action- and sound-related concepts would elicit dissociable ERP repetition priming effects under unconscious viewing conditions, in which strategic imagery or semantic elaboration processes can be ruled out. Participants were visually presented with masked prime words and subsequently with visible target words, which either named action- (hammer; action words) or sound-related concepts (helicopter; sound words). In the repetition priming conditions the identical action or sound word was presented as prime and target (e.g., action: hammer–hammer; sound: helicopter–helicopter). In the nonrepetition condition, the action or sound target word was preceded by a matched control word with low relevance for the corresponding feature type (e.g., action: butterfly–screwdriver; acoustic: candle–radio). To exclude that motor activity would compromise ERP effects of conceptual processing participants performed a silent reading task on the target words.

As in previous studies action-related words elicited more positive ERPs (Kiefer, Sim, et al., 2011; Kiefer, 2001, 2005; Pulvermüller et al., 1999) and sound-related words more negative ERPs (Kiefer et al., 2008) at frontocentral electrodes compared with control words, we expected differential subliminal repetition effects as a function of feature type: Repetition of action words should specifically diminish the frontocentral positivity associated with action-related conceptual features, resulting in a relatively less positive potential for repeated action words. Repetition of sound-related words, in contrast, was expected to reduce the frontocentral negativity

associated with sound-related conceptual features, resulting in a relatively more positive potential for repeated sound words. In line with modality-specific theories of conceptual memory, such a differential pattern of ERP repetition effects under unconscious viewing conditions would indicate that feature-specific neural activity during conceptual tasks is automatic and does not depend on strategic imagery or semantic elaboration processes.

METHODS

Participants

Twenty-six (16 women) right-handed (Oldfield, 1971) native German-speaking volunteers (mean age = 21.5 years, ranging from 19 to 25 years) with normal or corrected-to-normal visual acuity and without any history for neurological or psychiatric disorders participated in the ERP study after giving written informed consent. The procedures of the study have been approved by the local ethical committee. Participants were paid for participating.

Stimuli

Three hundred twenty object names, which were selected according to the data of a norming study, served as stimuli. Four independent subject groups ($n = 15$ each), who did not participate in the main experiment, rated a sample of 374 object names in total according to different dimensions (210 names in the first/third group, 164 names in the second/fourth group): The first and second group was asked to rate how strongly they spontaneously associate action, acoustic, and visual features with the named object on a scale from 1 to 6 (1 = *no associations*, 6 = *strong associations*). The third and fourth group had to rate the emotional association (1 = *no associations* to 6 = *strong associations*) and familiarity (1 = *unfamiliar* to 6 = *familiar*) of each object name in the same way. More specifically, participants were asked how strong they associate the named object with actions they can perform with it; how strong they think of typical sounds the object produces; how strong they associate visual features like contour, detailed features, or color with the object; how they associate emotions with the object; and how familiar the object is for them.

Thereafter, two critical word sets referring to concepts with high relevance of action-related (action words) and sound-related features (sound words), respectively, and two corresponding control word sets (action control and sound control) were formed, comprising 80 words each. The selected word sets differed significantly only with regard to the relevance of the critical features (action/sound-related vs. action/sound control, $p < .001$) but were comparable for the other four features (all $p > .05$). Sets were also matched for word length (all $p > .5$) and word frequency (all $p > .5$; according to the

CELEX lexical data base; Baayen, Piepenbrock, & Gulikers, 1995). A pilot study using a lexical decision task ($n = 11$) showed that word sets with high relevance of action/sound features and the corresponding control words showed similar RTs (action: 562 msec vs. 568 msec, $p = .35$; sound: 570 msec vs. 564 msec, $p = .30$) and error rates (action: 4.7 vs. 4.1, $p = .33$; sound: 6.55 vs. 5, $p = .16$). Hence, word sets exhibited a comparable word recognition difficulty.

The 320 stimuli were used to create word pairs consisting of a prime and a target word for the repetition and nonrepetition conditions. Two stimulus lists with different prime–target pairings were created such that the targets of the repetition and nonrepetition conditions were exchanged within each conceptual feature type: In one list a critical word of a given feature type served as target in the repetition priming condition, whereas in the other list it served as target in the nonrepetition condition of the same feature type and vice versa. Stimuli lists were counterbalanced across participants so that overall the same critical words of each feature type appeared in the repetition and in the nonrepetition conditions as targets. To maintain the matching of the stimulus material in important linguistic and conceptual variables across the two lists, we subdivided each of the four initial word sets (action, sound, and corresponding control words with $n = 80$) into two matched subsets ($n = 40$ object names each). Conceptual and linguistic variables for the critical and the corresponding control word subsets as well as the p values of two-tailed t tests are shown in Table 1. When directly comparing action and sound words with each other, they differed significantly with regard to the critical feature dimension in both subsets (all $p < .001$). However, as can be seen from Table 1, sound words showed a relatively high association with noncritical action features, whereas action words exhibited a relatively low association with acoustic features. The relatively high relevance of action features for sound words presumably reflects the fact that sound is frequently produced by specific actions with objects (e.g., ringing a bell). In the two repetition conditions (action, acoustic), the prime and the target words were identical and corresponded to the two subsets of action and sound words, respectively: action repetition (repA, e.g., hammer–hammer; $n = 40$ pairs) and sound repetition (repS, e.g., helicopter–helicopter; $n = 40$ pairs). In the nonrepetition conditions, the target word was either an action or a sound word, whereas the prime word was a corresponding control word: action nonrepetition (nrepA, e.g., pillow–screwdriver; $n = 40$ pairs) and sound nonrepetition (nrepS, e.g., candle–radio; $n = 40$ pairs). When creating the word pairs in the nonrepetition conditions, the length of prime and target words in each trial was equated as much as possible. Furthermore, three independent judges checked associations between prime and target and agreed that word pairs were semantically, phonologically, and orthographically unrelated.

Table 1. Conceptual and Linguistic Variables for the Critical Word Subsets Referring to Action-related and Sound-related Concepts and for the Corresponding Control Word Subsets (Action Control and Sound Control)

	<i>Action</i>	<i>Acoustic</i>	<i>Visual</i>	<i>Familiarity</i>	<i>Emotion</i>	<i>Word Length</i>	<i>Word Frequency</i>
<i>First Subset</i>							
Action-related	4.40	1.74	4.20	4.06	2.61	7.65	29.83
Action control	1.77	1.59	4.24	3.89	2.45	7.55	32.93
<i>p</i>	< .001	.51	.79	.32	.33	.87	.90
Sound-related	3.25	5.13	3.94	3.69	2.80	7.70	29.88
Sound control	3.30	1.11	3.89	3.86	2.57	7.50	28.80
<i>p</i>	.79	< .001	.78	.46	.21	.80	.96
<i>Second Subset</i>							
Action-related	4.39	1.78	4.16	4.06	2.61	7.68	30.00
Action control	1.77	1.61	4.29	3.77	2.54	7.55	33.98
<i>p</i>	< .001	.44	.40	.11	.69	.83	.80
Sound-related	3.24	5.19	3.73	3.54	2.60	7.65	29.48
Sound control	3.30	1.13	4.07	3.88	2.52	7.50	28.35
<i>p</i>	.71	< .001	.09	.08	.65	.83	.92

Procedure

Silent Reading Task

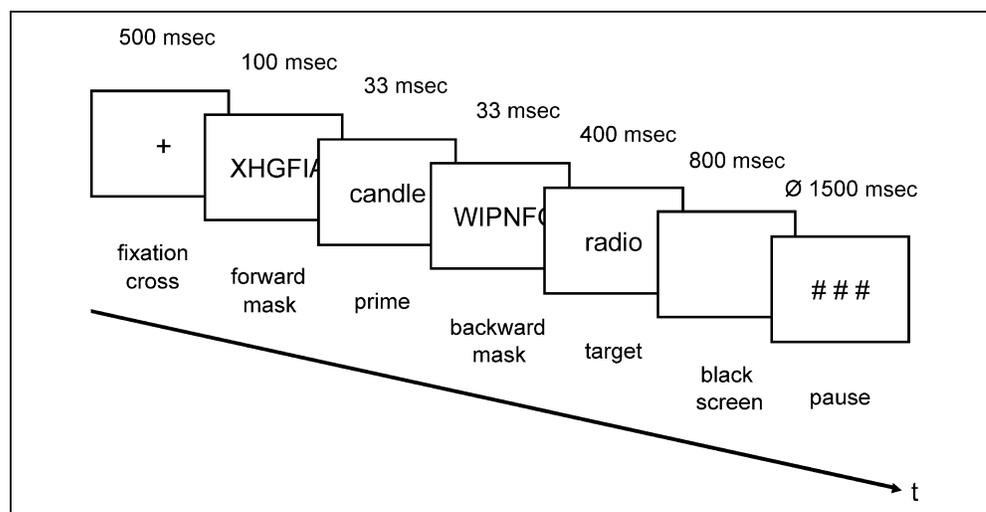
The word pairs were visually presented on a computer screen in white font on a black background synchronously with the screen refresh (16.67 msec). Each trial of the task started with a fixation cross (500 msec; see Figure 1) followed by a forward mask (100 msec), a prime word (33 msec), and a backward mask (33 msec). Each mask consisted of 14 randomly selected capital letters. Immediately after the backward mask, a target word was shown for 400 msec, and the screen went black for 800 msec. At last, three hash marks indicated a break

between trials lasting at an average of 1500 msec (varying randomly from 1000 to 2000 msec). Participants were asked to read the target words silently and attentively. Word pairs ($n = 160$ for each participant; 40 per condition) were randomly presented within four blocks consisting of 40 trials each. These blocks were separated by short breaks.

Masked Prime Identification Test

Directly after the main experiment, participants were informed of the prime words shown between the masks and were asked whether they had recognized these.

Figure 1. Temporal sequence of one trial of the silent reading task. The shown prime–target pairing is an example for the nonrepetition condition of sound words.



None of the participants reported awareness of the primes. For a more objective measurement of prime recognition, a masked prime identification test was administered (Kiefer, 2002). Participants performed a simple visual discrimination task on masked stimuli consisting of 40 words and 40 letter strings. Each letter string comprised seven repetitions of the identical capital letter (e.g., AAAAAAA), which was randomly selected in each trial. Trial sequence in this task was the same as in the silent reading task. Participants' task was to decide whether the masked stimulus was a word or a letter string. Instructions stressed accuracy over response speed. Participants were also requested to make the best guess when they did not feel confident about the correct response. Participants' indicated their response by button presses with the index (word) and the middle finger (letter string), respectively.

ERP Recordings, Signal Extraction, and Data Analysis

ERP recordings were performed in a dimly lit sound-attenuated and electrically shielded booth. Participants were seated upright in front of a computer screen at a distance of 75 cm. The averaged word length of primes and targets was 4.5 cm (7.6 characters), which resulted in an averaged visual angle of 3.4°. Participants were instructed to remain relaxed and restrict their blinks and eye movements to the pauses between trials.

Scalp potentials were recorded using an equidistant montage of 64 sintered Ag/AgCl electrodes mounted in an elastic cap (EasyCap, Munich, Germany). An additional electrode between FPz and Fz was connected to the ground and another one between Cz and FCz was used as recording reference. Eye movements and blinks were recorded with 4 (of the 64) electrodes placed beneath and laterally to the eyes. Impedances of all electrodes were kept below 5 k Ω . EEG signals were amplified with Brainamps amplifiers (BrainProducts, Gilching, Germany; low-pass filter: 70 Hz, 24 dB/octave attenuation; 50 Hz notch filter) and continuously recorded with a digitalization rate of 500 Hz. Starting with a digital bandpass filter (low cutoff: 0.1 Hz, 12 dB/octave; high cutoff: 30 Hz, 24 dB/octave), EEG data were further processed using the BrainVisionAnalyzer (BrainProducts, Gilching, Germany): Electrical signals were corrected for ocular artifacts using independent component analysis (Makeig, Bell, Jung, Ghahremani, & Sejnowski, 1997). Continuous EEG was segmented in epochs starting -320 msec before target stimulus onset to allow for a 153-msec baseline correction before the onset of the forward mask (at -166 msec) and ending 1000 msec after target stimulus onset. Baseline correction was performed before the onset of the forward mask to avoid distortion of the baseline by visually evoked potentials to the mask (Kiefer, 2002). Thereafter, artifact-free EEG segments were averaged separately for each of the four experimental conditions. An averaged reference

transformation (Kiefer, Marzinzik, Weisbrod, Scherg, & Spitzer, 1998; Bertrand, Perrin, & Pernier, 1985) was performed to obtain reference independent estimations of scalp voltages.

Statistical analysis focused on a frontocentral scalp ROI, where action- and sound-related potentials are typically recorded (Kiefer et al., 2008; Kiefer, 2001, 2005; Pulvermüller et al., 1999; Näätänen, 1992), including three pairs of contralateral electrodes: AF3/AF4, F1/F2, and FC1/FC2. Grand-averaged ERPs (averages over all 26 participants) of the four experimental conditions mainly differed in the N1 (100–250 msec), N250 (250–400 msec), and N400 (400–550 msec) time intervals (Eddy et al., 2006; Holcomb & Grainger, 2006; Kiefer, 2005; Schweinberger et al., 1995, 2002; Rugg, 1985). Mean voltages within these time windows were calculated and subjected to repeated-measures ANOVAs with the factors Feature Type (action vs. sound), Priming (repetition vs. nonrepetition), Hemisphere (left vs. right), and Electrode Site. When appropriate, degrees of freedom were adjusted according to the method of Huynh-Feldt (Huynh & Feldt, 1970). To exclude that pretarget activity might have compromised possible priming effects, an additional ANOVA was performed in the time interval between forward mask (at -166 msec) and target word onset (at 0 msec). This analysis did not reveal any significant effects (all $p > .10$).

Neural source estimates for significant repetition priming effects were determined using distributed minimum norm source modeling (Hauk, 2004) implemented in BESA 5.1 (MEGIS). Sources were computed for the grand-averaged ERP difference waves between the action/sound repetition and the action/sound nonrepetition conditions, respectively. Minimum norm source estimates were calculated using the standardized realistic finite element head model. The prestimulus baseline was used to estimate the noise regularization parameters. Minimum norm was computed with depth weighting, spatiotemporal weighting, and noise weighting for individual channels. Brodmann's areas (BA) of peak activity were estimated using the Talairach Daemon (Lancaster et al., 2000). Given the low spatial resolution of EEG BA only provide an approximate location of the neural sources.

RESULTS

Masked Prime Identification

Mean accuracy in the masked prime identification test was 51%. Hence, prime identification performance was very close to the chance level of 50%, which is expected when merely guessing. d' sensitivity measures (Green & Swets, 1966) calculated from participants' hit rates (correct responses to words) and false alarm rates (incorrect responses to series of letters) did not significantly deviate from zero ($d' = .03$, $t(25) = .42$, $p = .68$). Thus, consistent with the participants' reports, participants could not consciously distinguish between words and letter strings.

Electrophysiological Results

Starting at about 100 msec after target stimulus onset, electrophysiological recordings showed that sound words elicited a relatively more negative, action words, in contrast, a relatively more positive scalp potential at frontocentral electrodes. A comparison of the repetition with the nonrepetition condition for each feature type revealed that repetition of sound words led to a positive potential shift, repetition of action words, instead, to a negative potential shift. These effects were statistically analyzed in the three time windows (N1, N250, and N400), determined a priori by previous literature (see Methods section; Figure 2).

N1 Time Window (100–250 msec)

A repeated-measures ANOVA with the factors Feature Type, Priming, Hemisphere, and Electrode Site did not reveal significant main or interaction effects ($p > .05$) in this early time window.

N250 Time Window (250–400 msec)

In the N250 time window, the ANOVA revealed a significant interaction between Feature Type and Priming, $F(1, 25) = 7.14$; $p < .01$. Subsequent separate ANOVAs for each feature type with the factors Priming, Hemisphere, and Electrode Site yielded a significant main effect of Priming only for sound words, $F(1, 25) = 5.17$; $p = .03$, but not for action words. Repeated sound words elicited a more positive scalp potential than nonrepeated ones. Source analysis of this repetition priming effect for sound words suggested neural generators in temporal areas in and close to BA 21 and BA 22 as well as in right parietal (BA 7, BA 40) and frontal areas (BA 6, BA 9, BA 10; see Figure 3A).

N400 Time Window (400–550 msec)

The ANOVA in the N400 time window also revealed a significant interaction between Feature Type and Priming, $F(1, 25) = 4.60$; $p = .04$. Separate analyses for each feature

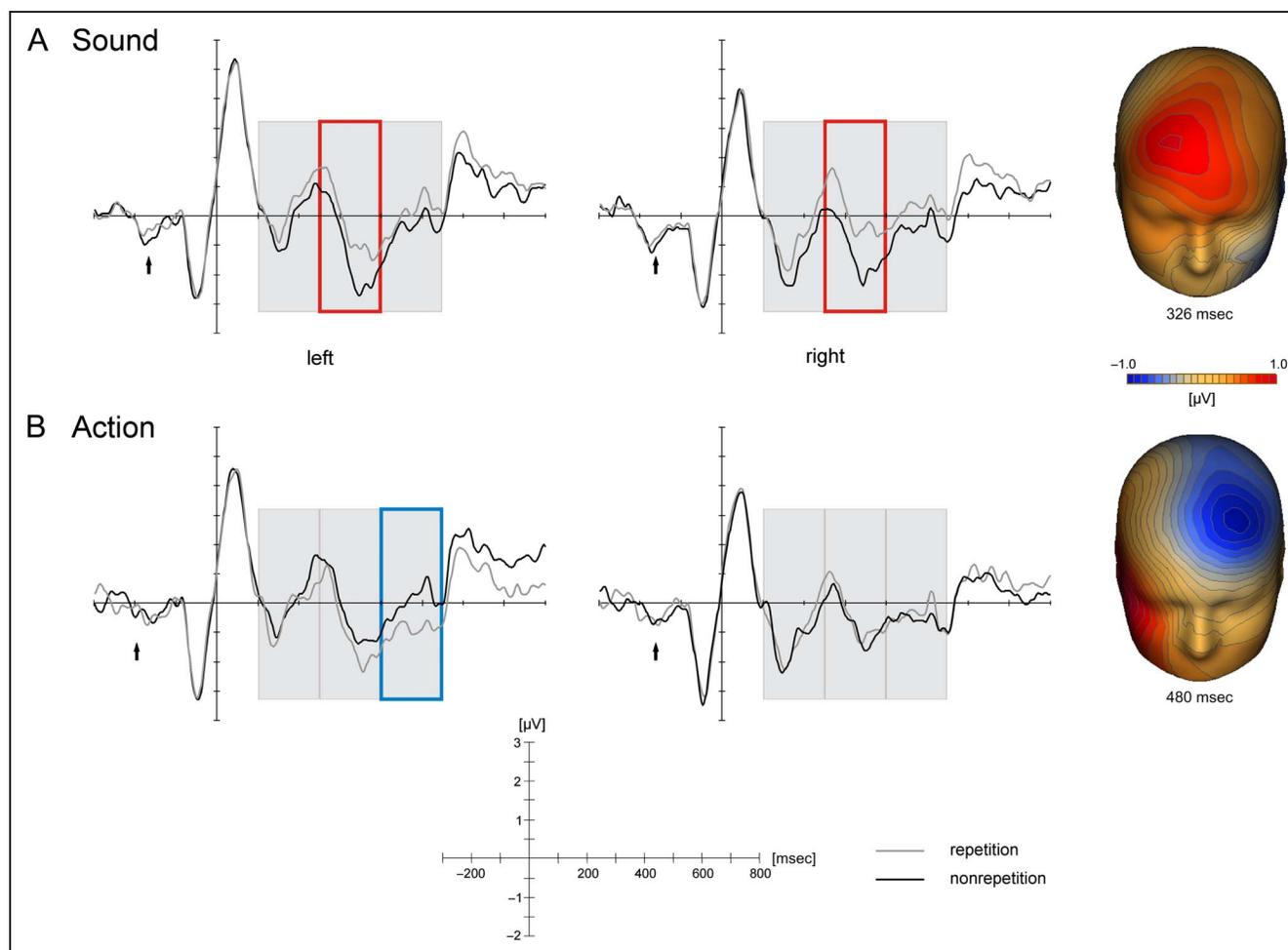
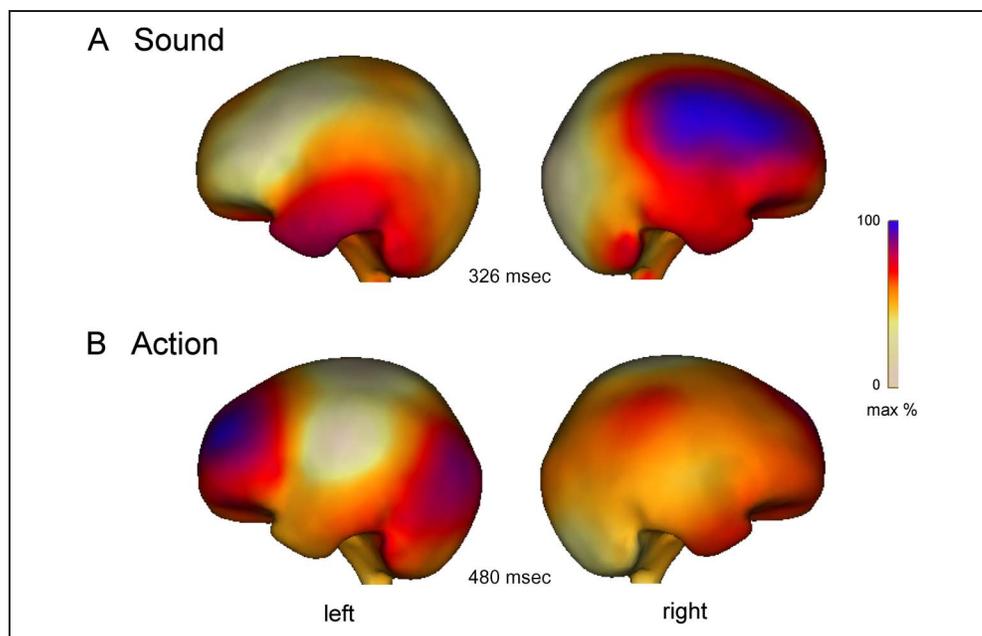


Figure 2. Grand-averaged ERPs from the frontocentral scalp ROI as a function of feature type and prime modality (repetition vs. nonrepetition). Shown are the average ERP waveforms elicited by sound-related (A) and action-related (B) words as well as the corresponding topographic maps recorded at the scalp at its maximum global field power. Gray-shaded areas indicate the critical time windows (100–250 msec, 250–400 msec, and 400–550 msec). Colored rectangles highlight significant priming effects. Little black arrows indicate the beginning of the forward mask followed by prime word presentation.

Figure 3. Neural source estimates of scalp potentials calculated according to the minimum norm algorithm from ERP difference waves as a function of feature type: (A) Source of the significant repetition priming effect in response to sound-related words. (B) Source of the significant repetition priming effect evoked by action-related words. Maps of cortical currents are shown at the respective maxima of global field power.



type revealed significant priming effects only for action words: In this condition, a significant interaction between priming and hemisphere, $F(1, 25) = 4.84; p = .04$, was obtained. Post hoc Scheffé tests showed significant potential differences between the repetition and nonrepetition conditions only over the left hemisphere ($p = .01$), but not over the right: Action words elicited a more negative potential in the repetition than in the nonrepetition condition. Thus, repetition priming effects for action words exhibited the opposite polarity of the effects for sound words. Source analysis of the action word repetition priming effect suggested neural generators in left frontal cortex in and close to BA 6 as well as in parietal cortex (BA 7, BA 40; see Figure 3B).

DISCUSSION

This study investigated processing of action- and sound-related concepts in a masked repetition priming paradigm using ERP recordings. To rule out any influence of processing strategies, including imagery or postconceptual elaboration, on conceptual processing, we thus assessed the electrophysiological correlates of priming effects elicited by unconsciously perceived masked words. Only grounded cognition theories predict automatic feature-specific conceptual processing in or close to modality-specific cortex during unconscious viewing conditions. Amodal theories, in contrast, predict comparable priming effects for both conceptual feature types because they assume an identical abstract representation of all kinds of concepts. In line with our predictions, based on preexisting results from consciously perceived word material, subliminal feature-specific ERP priming effects were obtained at frontocentral electrodes. Priming effects differed between feature types with regard to

polarity, topography, time course, and brain electrical sources: Sound words evoked bilaterally more positive scalp potentials in the repetition than in the nonrepetition condition in an early time window starting already 250 msec posttarget stimulus onset. Source activity was obtained in temporal as well as right parietal and frontal areas. Action words, in contrast, elicited a more negative potential in the repetition compared with the nonrepetition condition, which was specific to the left hemisphere and emerged in a slightly later time window. Neural generators were suggested in left frontal and parietal cortex.

In previous ERP studies, processing of (unrepeated) fully visible and thus consciously perceived action- and sound-related words differentially modulated ERPs at frontocentral electrodes: Action words elicited a relatively more positive potential (Kiefer, Sim, et al., 2011; Kiefer, 2001, 2005; Pulvermüller et al., 1999), whereas sound words evoked a relatively more negative potential (Kiefer et al., 2008) than corresponding matched control words. ERP source analyses revealed neural generators for action words in frontal and parietal motor areas (Boulenger, Shtyrov, & Pulvermüller, 2012; Kiefer, Sim, et al., 2011; Hauk & Pulvermüller, 2004) and generators in auditory association areas of posterior temporal cortex for sound words (Kiefer et al., 2008). For unrepeated action- and sound-related words, we found similar ERP activity patterns at frontocentral electrodes in this study. Most importantly, the subliminal repetition priming effects indicate a reduction of feature-specific activity because of a preactivation of the same concept (see, e.g., Horner & Henson, 2008; Eddy, Schnyer, Schmid, & Holcomb, 2007; Grill-Spector, Henson, & Martin, 2006; Dehaene et al., 2001): For action words, repetition resulted in a less positive potential compared with unrepeated words; for sound words, in contrast, repetition resulted in a less

negative (i.e., more positive) potential. It should be noted at this point that across participants the target words in the repetition and nonrepetition conditions were identical. Thus, as the stimuli were the same, the observed ERP effects cannot reflect any unnoticed stimulus differences because of insufficient word matching. Rather, these differences must arise from unconscious activation of action-related versus sound-related conceptual features of the primes. Source analyses of scalp ERP repetition effects in this study suggested a differential configuration of neural generators for sound and action words: For sound words, source activity was strongest in temporal as well as in right frontal areas. For action words, in contrast, source activity was strongest in left frontal and parietal cortex. The results of these source analyses largely agree with those of the previous studies using visible stimulation mentioned above although the sources were comparably quite extended and somewhat smeared, presumably because of the relatively small amplitude and consequently low signal-to-noise ratio of the subliminal priming effects. The most notable discrepancy to earlier findings was the observation that generators of the repetition priming effect of sound words in the present work not only comprised temporal but also right frontal cortex. Possibly, processing of conceptual features differs in a conscious and unconscious processing mode. Unconscious processing of acoustic conceptual features may activate widespread parts of the conceptual network because of a lack of intentional cognitive control so that processing is more unconstrained. Therefore, as sound words showed relatively strong association with action features (see Table 1), it is conceivable that unconscious processing of sound words activates associated actions in frontal motor areas that typically produce the corresponding sound. Alternatively, activity in right frontal cortex may reflect a modulation of executive processes in dorsolateral prefrontal cortex during the reading task by masked repetition priming. Although these alternative interpretations cannot be decided on the grounds of the present data because of the low spatial resolution of EEG, our source analyses clearly show that the neural substrate of subliminal repetition priming differs as a function of feature type.

Our results are also in accord with previous ERP (Kiefer, 2005) and fMRI studies (Chao, Weisberg, & Martin, 2002) on category-related repetition effects with visible stimuli, in which a reduction of category-related activity in the sensory and motor systems was observed. Our results confirm and extend these findings by demonstrating that feature-specific repetition priming effects can also be observed for subliminally presented masked primes. As masked repetition priming effects reflect unconscious automatic processing (Kiefer, 2012; Kiefer & Martens, 2010), feature-specific conceptual processing cannot be explained by postconceptual strategic mechanisms such as visual imagery or semantic elaboration (Machery, 2007; Noppeney, Price, Penny, & Friston, 2006). In line

with grounded cognition theories of conceptual representation (Kiefer & Barsalou, 2013; Pulvermüller & Fadiga, 2010; Barsalou, 2008; Kiefer et al., 2007; Martin, 2007; Gallese & Lakoff, 2005), these specific repetition priming effects must reflect access to conceptual sound versus action features, most likely stored in or close to corresponding modality-specific cortex as suggested by our source analyses. The present findings are also confirmed by data from a recent masked feature priming experiment, in which prime and target words of the priming condition were of the same feature type (e.g., sound or action), but not identical (Trumpp, Traub, & Kiefer, 2013). In this experiment, we tested whether preactivation of a conceptual feature dimension (action vs. sound) by an unconscious prime word modulates subsequent processing of a target word denoting a concept with high relevance of the same feature dimension. To assess the validity of the priming effects, two different nonpriming conditions were included: In one condition, the prime was an unrelated control word with low feature relevance and the target was a critical action or sound word as in the present experiment. In the second nonpriming condition, the prime was a critical action or sound word and the target an unrelated control word with low feature relevance. Results revealed feature-specific subliminal priming effects, which resembled those of the present repetition priming study with regard to polarity and topography. Furthermore, ERPs to the two nonpriming conditions both significantly differed from the feature-priming condition, but not from each other. Hence, the presently observed feature-specific priming effects are not confined to repetition priming and can be observed with different nonpriming conditions demonstrating their validity.

One characteristic of the present results appears necessary to comment on: the significant left-lateralized repetition effect for action words and the more symmetric effect for sound words. Both effects are seen over frontal scalp regions, which is not surprising, because motor systems are in frontocentral cortex with gyral cortex projecting to the anterior scalp as well as superior-temporal sulcal activity typically seen in auditory areas is well known to project to the frontal lobe (Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001). Consistent with the findings of the current source analysis in this study, the laterality of the action word effect suggests that primarily left-lateral generators carry the semantic representation of action-related words (e.g., Pulvermüller, Shtyrov, & Ilmoniemi, 2005), in particular when unimanual actions are referred to as in this study (Hauk & Pulvermüller, 2011).

A further characteristic of the present results is the beginning of the priming effects. The obtained effects did not reach the short latencies of semantic word category differences in response to visible words that start at around 200 msec (Pulvermüller et al., 1999; Hauk & Pulvermüller, 2004) or occasionally as early as around 100 msec (Hoenig et al., 2011; Kiefer, Sim, et al., 2011; Kiefer et al., 2008; Pulvermüller, Assadollahi, & Elbert,

2001), but they are in good agreement with those reported in previous work describing masked or visible repetition priming effects in the time range of the N250 and N400 (Eddy et al., 2006; Holcomb & Grainger, 2006; Kiefer, 2005). The temporal discrepancy between semantic word category and (masked) repetition priming effects is not entirely surprising. Word category differences arise from a comparison between critical (sound, action, etc.) and control words reflecting direct access to semantic memory. In (masked) repetition priming paradigms, instead, word category differences are only measured indirectly by assessing the influence of a prime word on the processing of a target word. It should be noted that the present timing of unconscious repetition priming effects closely corresponds to the timing of word category-specific repetition priming effects with visible stimuli that also started rather late at about 350 msec posttarget stimulus onset (Kiefer, 2005). Thus, the different time course of masked repetition priming and word category effects is not primarily an issue of unconscious versus conscious processing but can be referred to the experimental method to probe processing of different classes of concepts (repetition priming vs. word category differences). Underlying processes may therefore be slightly different, that is, explicit access to semantics versus unconscious pre-activation, resulting in slightly different time courses. Furthermore, electrophysiological masked priming effects may frequently emerge rather late, presumably because it takes some time until neural activity related to the processing of this relatively weak visual input reaches a critical level to be measured. It should be noted at this place that the relatively late onset of the action word priming effects cannot imply that activation is under the influence of cognitive control. The stimuli (primes) triggering the priming effect were effectively masked and not consciously perceived. We verified invisibility of the primes by means of a rigorous identification test. As a consequence, the present masked priming effects must reflect unconscious automatic stimulus processing, even in the action condition.

The different onset of the priming effects for sound and action words may reflect feature-specific differences in conceptual processing. Studies using more continuous measures of semantic structure found influences of several kinds of semantic features on the time course of word meaning computation (for instance, Amsel, 2011). This dynamic time course may reflect considerable differences in the strength of connections as well as in the speed of information transmission between cortical regions involved in conceptual processing (Pulvermüller, 1999). It is thus possible that masked word repetition influences processing in cell assemblies coding sound features earlier than in cell assemblies coding action features. In addition, it is possible that in the 250–400 msec time window the effect size of the priming effect in the action condition was smaller than in the sound condition thereby resulting in insufficient power to detect earlier

priming effects of action words as well. The precise factors underlying such time course differences have to be elucidated in future investigations.

In conclusion, this study demonstrates specific subliminal repetition priming effects on ERPs for action and sound words. Topography, polarity, and suggested neural generators of these effects were consistent with previously reported ERP responses to fully visible action- and sound-related stimuli. The present findings suggest that conceptual sound and action features can also be activated by subliminally presented words under unconscious viewing conditions, in which postconceptual strategic processes such as imagery or semantic elaboration can be excluded. As only grounded cognition but not amodal theories assume automatic activation of conceptual features in modality-specific cortex, the present research further substantiates the notion of a grounding of concepts in perception and action.

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