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Neural correlates of control operations in inverse priming with relevant and irrelevant masks

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ABSTRACT

The inverse priming paradigm can be considered one example which demonstrates the operation of control processes in the absence of conscious experience of the inducing stimuli. Inverse priming is generated by a prime that is followed by a mask and a subsequent imperative target stimulus. With "relevant" masks that are composed of the superposition of both prime alternatives, the inverse priming effect is typically larger than with "irrelevant" masks that are free of task-relevant features. We used functional magnetic resonance imaging (fMRI) to examine the neural substrates that are involved in the generation of inverse priming effects with relevant and irrelevant masks. We found a network of brain areas that is accessible to unconscious primes, including supplementary motor area (SMA), anterior insula, middle cingulate cortex, and supramarginal gyrus. Activation of these brain areas were involved in inverse priming when relevant masks were used. With irrelevant masks, however, only SMA activation was involved in inverse priming effects. Activation in SMA correlated with inverse priming effects of individual participants on reaction time, indicating that this brain area reflects the size of inverse priming effects on the behavioral level. Findings are most consistent with the view that a basic inhibitory mechanism contributes to inverse priming with either type of mask and additional processes contribute to the effect with relevant masks. This study provides new evidence showing that cognitive control operations in the human cortex take account of task relevant stimulus information even if this information is not consciously perceived.

Introduction

Cognitive control has been considered one instance which requires conscious processing (e.g., Norman and Shallice, 1986). However, several studies have shown that the processing of a target stimulus can be influenced by a preceding unconscious prime stimulus (e.g., Neumann and Klotz, 1994; Vorberg et al., 2003). Typically, performance benefits are observed when prime and target belong to the same category (congruent condition) as opposed to alternative categories (incongruent condition). On this background, it is a matter of debate whether unconscious stimuli can also modulate cognitive control operations (e.g., Dehaene et al., 2003; Rees et al., 2002). One instance in which cognitive control is required is the inhibition of automatic responses (e.g., Norman and Shallice, 1986). The inhibition of automatic response activation has been assumed to account for the inverse priming effect (e.g., Eimer and Schlaghecken, 1998). Inverse priming is characterized by performance deficits on congruent trials which can result when a separate masking stimulus is presented between prime and target stimuli (e.g., Eimer and Schlaghecken, 1998). The size of inverse priming depends on the stimulus onset asynchrony (SOA) between mask and target stimulus (e.g., Mattler, 2007; Schlaghecken and Eimer, 2000) and the structure of the mask (e.g. Lleras and Enns, 2004). With short mask-target SOAs priming effects tend to be positive, with increasing mask-target SOA inverse priming effects occur. As outlined below, it is assumed that this reversal of priming effects with long SOA is linked to increased automatic control processing on congruent trials. With masks that consist of task-relevant features inverse priming effects are typically larger than with masks that consist of irrelevant features. Here we examined the inverse priming paradigm in a functional magnetic resonance imaging (fMRI) study to determine the automatic control operations in the human cortex which are involved in inverse priming with relevant and irrelevant masks.

To account for the modulation of inverse priming effects by the structure of the mask the literature provides at least three different approaches (Krüger et al., 2011). According to the Co-active Mechanisms approach, an inhibitory mechanism is effective with both types of masks and an additional mechanism contributes to the effect with relevant masks (Lleras and Enns, 2006). According to the Single-Mechanism approach, the inhibitory mechanism generates inverse priming effects with both kinds of masks and it is more productive with relevant masks (Jaśkowski and Verleger, 2007). According to the Separate Mechanisms approach, one mechanism accounts for the entire effect with relevant masks, and a different inhibitory mechanism is only operating with irrelevant masks (Klapp, 2005). Therefore, clear evidence for the

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Separate Mechanisms approach consists in an activation of non-overlapping brain regions with relevant and irrelevant masks. The Single-Mechanism approach predicts that the same brain regions are involved in inverse priming with relevant and irrelevant masks. Shared and specific brain regions in the case of relevant and irrelevant masks, however, would be most consistent with the Co-active Mechanisms approach.

Three previous fMRI studies have addressed the neuronal sources of inverse priming effects (Aron et al., 2003; Boy et al., 2010a, 2010b). Aron et al. (2003) employed arrow stimuli and irrelevant masks and varied the mask-target SOA between 0 and 150 ms. Analyses of priming effects in pre-specified regions-of-interest revealed that inversed priming effects were associated to the activation in subcortical regions of the basal ganglia (thalamus and caudate). Boy et al. (2010b) employed the same paradigm but did not vary the prime target SOA. A special region-of-interest analysis that was based on a selection of the 20% most activated voxels yielded increased activity on congruent trials in regions of the supplementary motor area (SMA). An involvement of SMA in inverse priming was suggested by the absence of inverse priming effects in a patient with a micro-lesion in SMA (Sumner et al., 2007) and by the correlation of the regional concentration of the neurotransmitter GABA in SMA with the magnitude of inverse priming effects as measure in the same paradigm (Boy et al., 2010a). We advance beyond these studies by comparing the effect of mask-target SOAs with relevant and irrelevant masks. This design enabled a model based approach where we compared the effect of SOA on congruent trials to the SOA effect on incongruent trials with either type of mask to examine whether the effect results from common or separate mechanisms in the condition with relevant and irrelevant masks. We used whole-brain analyses to exceed the narrow focus of pre-specified regions-of-interest analyses.

Methods

Participants

28 healthy students from the University of Göttingen were recruited to participate in the four sessions of the experiment. Two of them voluntarily quitted during the first two practice sessions, two subjects did not perform the task correctly, one showed anatomical irregularities, and another subject's data were lost due to technical failure. The remaining 22 subjects constituted the final sample (7 male, mean age 22.6 years, ranging from 19 to 27 years). All had normal or corrected-to-normal vision and were right-handed according to self-report. Before participation, subjects gave written informed consent and completed a questionnaire to ensure MRT safety requirements and to rule out a history of neurological or psychiatric illness. Participants received an allowance of 51 € for their participation. The study was approved by the Ethics Committee of the Medical Faculty of the University of Göttingen.

Stimuli

The trial structure and timing parameters were the same throughout all four sessions of the experiment (see Fig. 1). Prime stimuli were left- or rightward pointing double arrows ($\ll$ or $\gg$) presented at the center of the screen. Each target stimulus consisted of a pair of identical double arrows, pointing towards the left or to the right, presented below and above fixation. Targets pointed to the same side as the primes on half of the trials (congruent condition) and to opposite sides otherwise (incongruent condition). Primes were followed by a masking stimulus presented at the center of the screen. A relevant mask was presented on half of the trials and an irrelevant mask otherwise. The relevant mask consisted of a superposition of both prime alternatives. The irrelevant mask consisted of 130 lines of different length and width each approximately centered on the 13×10 intersections of a virtual grid with a small random spatial jitter. A new irrelevant mask was generated for each trial. All stimuli were presented in black on a white background. Stimulus presentation was realized with a CRT-monitor during the first two practice sessions in the lab, and with MRT-compatible LCD-glasses during the last two sessions in the scanner, both running at 60 Hz. All double arrows subtended $1.5°\times1°$ of visual angle. The two double arrows which constituted the target stimuli were presented 2.3° above and below fixation, respectively. The virtual grid underlying the structure of the irrelevant masks subtended $1.7°\times1.1°$ of visual angle. The color of the fixation point was changed for 1000 ms to give feedback at the end of each trial (green and red following correct and incorrect responses, respectively).

Tasks

(*a*) *Choice-reaction time task*: During the initial two practice sessions and the third session (in the scanner), subjects were required to judge the orientation of the target stimuli as fast as possible avoiding errors. When the target arrows pointed to the left a response with the left index finger was required and otherwise a response with the right index finger. (*b*) *Prime recognition task*: To estimate the visibility of primes on the LCD-glasses of the scanner, we conducted a final prime recognition session with the same setup as in the previous session in the scanner. In this session, subjects were informed about the presence of the prime and they had to report its orientation in the same way as during the first three sessions but without speed stress. Again, a leftward pointing prime required a response with the left index finger and a rightward pointing prime with the right index finger. Trial wise error feedback was given on each task.

Procedure

Prior to the MRT-session participants performed two identical practice sessions outside the scanner because pilot testing suggested that inverse priming effects increased with practice. The temporal structure of the trials was the same in all four sessions of the experiment (Fig. 1). The beginning of each trial was signaled by a large fixation cross presented for 500 ms. The prime followed 300 ms after the offset of the fixation cross for 17 ms. The mask followed 17 ms after prime offset for 100 ms. The mask-target SOA varied randomly between trials with values of 33 or 150 ms. Targets were presented for 100 ms. After target onset, the computer waited 1433 ms or 1317 ms for a response on trials with short or long SOA, respectively. Within this sequence of stimuli a fixation dot was presented when no other stimulus was presented. The intertrial interval was 1033 ms. Thus, in total the duration of each trial was 4333 ms. In the MRT-session, volume acquisition was triggered with a temporal jitter relative to the trial onset because the repetition time of the scanner (TR) was 2 s. Therefore, the jitter varied between 0, 333, 667, 1000, 1333, and 1667 ms. Each experimental condition was realized equally often with each of these jitter conditions.

Design

In each session subjects performed eight runs with 96 trials each. Only the data of the two final sessions in the scanner were analyzed. We used a $2\times2\times2\times2$ repeated measures design with factors Prime Orientation (left vs. right), Target Orientation (left vs. right), SOA (33 vs. 150 ms), and Mask Structure (relevant vs. irrelevant). Each of these 16 conditions occurred six times per run and was combined once per run with each possible jitter between trial onset and the onset of volume acquisition. Thus, we acquired 48 trials in each experimental condition. Apart from the instructed task, choice-RT and prime recognition sessions were identical. Response time (RT), error rate, and the BOLD signal served as dependent measures in the choice-RT session. The analysis of prime recognition performance focused on the effects of independent variables SOA and