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Category-selective attention modulates unconscious processes in the middle occipital gyrus

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ABSTRACT

Many studies have revealed the top-down modulation (spatial attention, attentional load, etc.) on unconscious processing. However, there is little research about how category-selective attention could modulate the unconscious processing. In the present study, using functional magnetic resonance imaging (fMRI), the results showed that category-selective attention modulated unconscious face/tool processing in the middle occipital gyrus (MOG). Interestingly, MOG effects were of opposed direction for face and tool processes. During unconscious face processing, activation in MOG decreased under the face-selective attention compared with tool-selective attention. This result was in line with the predictive coding theory. During unconscious tool processing, however, activation in MOG increased under the tool-selective attention compared with face-selective attention. The different effects might be ascribed to an interaction between top-down category-selective processes and bottom-up processes in the partial awareness level as proposed by Kouider, De Gardelle, Sackur, and Dupoux (2010). Specifically, we suppose an "excessive activation" hypothesis.

1. Introduction

Understanding how top-down processes modulate bottom-up processes is a major challenge to reveal the mechanisms of adaptive perception processes in the brain. Based on much evidence, perception processes depend to a large degree on expectations derived from previous experience, and on generalized knowledge (Engel, Fries, & Singer, 2001). Gilbert and Sigman (2007) have advanced the concept of "brain states" to expand the conventional definition of top-down influences which are usually equated with attention (Gilbert & Sigman, 2007). They consider that the role of top-down influences is to set the cortex in a specific working state according to behavioral requirements.

Various previous studies demonstrated that even early visual processes can be modulated by top-down processes across a wide range of experimental paradigms (Rauss, Schwartz, & Pourtois, 2011). For example, Mechelli, Price, Noppeney, and Friston (2003), Mechelli, Price, Friston, and Ishai (2004) used the method of Dynamic Causal Modelling (DCM) and found that supraliminal category-selective (faces, houses and chairs) activations in extrastriate cortex are mediated both by bottom-up connections from early visual areas and by top-down connections from prefrontal cortex (Mechelli, Price, Friston, & Ishai, 2004; Mechelli, Price, Noppeney, & Friston, 2003). In addition, some studies showed that attentional load could modify activity in regions of the visual cortex (Kelley & Lavie, 2011; Rauss, Pourtois, Vuilleumier, & Schwartz, 2009). Other studies

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revealed that conscious visual perception is modulated by spatial attention (Gandhi, Heeger, & Boynton, 1999), feature-selective attention (Müller et al., 2006), and category-selective attention (Gazzaley, Cooney, McEvoy, Knight, & D'esposito, 2005). Moreover, in animal experiments, results showed that top-down processes could modulate the early cortical activity of sensory processes (Ito & Gilbert, 1999; Li, Pi ch, & Gilbert, 2004). Even in the absence of visual stimuli, activity in the visual cortex could be modulated by attention (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999).

Besides the evidences of top-down effects on supraliminal processes, it is an important aspect to understand whether top-down processes can modulate unconscious processes to understand the mechanisms of perception, because we often process the majority of sensory information without consciousness. In addition, because unconscious stimuli can exert effects on motivation (Custers & Aarts, 2010), experience of control (Linser & Goschke, 2007), semantic processing (Dehaene et al., 2001), emotional processing (Luo et al., 2004; Whalen et al., 1998), cognitive control (Lau & Passingham, 2007; van Gaal, Ridderinkhof, Scholte, & Lamme, 2010), and object recognition (Stoerig & Cowey, 1997), top-down effects on unconscious processes might modulate these unconscious influences. In fact, some studies have revealed that unconscious (prime) processes are modulated by conscious top-down factors. For example, spatial attention can influence sensorimotor processes that are entirely separated from conscious perception (Sumner, Tsai, Yu, & Nachev, 2006) and unconscious letter prime effects (Marzouki, Grainger, & Theeuwes, 2007). There is also evidence showing that the effect of unconscious masked priming depends on temporal attention (Kiefer & Brendel, 2006; Naccache, Blandin, & Dehaene, 2002). Using fMRI and a continuous flash suppression paradigm, Bahrami, Lavie, and Rees (2007) observed reduced V1 activity under high attentional load even for invisible stimuli compared with that under low attentional load (Bahrami et al., 2007). Moreover, recent studies measuring event-related brain potentials demonstrated selective top-down influence of task sets on subliminal semantic processing and motor response selection (Kiefer & Martens, 2010; Martens, Ansorge, & Kiefer, 2011).

However, there is little research about how category-selective attention could modulate unconscious visual processes. Category-selective attention is based on discrimination and categorization of features of all the objects around us. Studies showed that feature-based attention is different from other attentional processes such as spatial attention (Kanai, Tsuchiya, & Verstraten, 2006; McMains, Fehd, Emmanouil, & Kastner, 2007). Combined with the evidence that early visual processes can be modulated by top-down factors, in the present study, we aimed at testing the hypothesis that the activity in the early visual cortex elicited by unconsciously perceived categories of pictures (i.e. faces and tools) might be selectively modulated by top-down processes of different types of category cues ("face" and "tool"). Specifically, according to the predictive coding theory (Rao & Ballard, 1999), we postulated that activity in the early visual cortex would decrease under congruent conditions (unconscious pictures with same type of category cues) compared with incongruent conditions (unconscious pictures with different type of category cues).

Furthermore, Kouider et al. assume that the representations at each processing level could be accessed independently from each other and advocated the concept of "partial awareness" (Kouider et al., 2010). In our experiment, the masked tools underlay partial awareness at a low processing level. The participants could sense the changes in contour and orientation of tool pictures but they were unable to recognize them. Therefore, we additionally analyzed the effect of category-selective top-down modulation on unrecognized masked tools with partial awareness.

2. Materials and methods

2.1. Participants

As paid volunteers, 21 adults (10 women, 11 men) aged 18–26 years (mean age 22.7 years) from Southwest University in China participated in this experiment. All participants gave written informed consent, were right-handed, had no history of current or past neurological or psychiatric illness, and had normal or corrected-to-normal vision. This study has been approved by the IRB at Southwest China University. Informed consent was obtained from each participant after the nature of the study was explained.

2.2. Stimuli

A sample consisting of 40 images of neutral facial expressions (20 females, 20 males) from the Chinese Facial Affective Picture System (Luo, Huang, Li, & Li, 2006), 40 pictures of tools and 20 pictures of other categories (e.g. animals, fruits) from the Internet served as stimuli. The mean valence and arousal for neutral faces were 4.31 (SD, 0.58) and 3.61 (SD, 0.51), respectively. In the formal experiment, the pictures were displayed centrally on a uniform gray background (RGB = 192, 192, 192) and subtended approximately 4.3 (height) $\times$ 3.8 (width) degrees of visual angle.

2.3. Procedure

The task programming, stimulus delivery, and recording of behavioral responses were carried out with E-prime 2.0 Software (Psychology Software Tools, Inc. http://www.pstnet.com). Stimuli were displayed on a back-projection screen placed at the back of the scanner bore, which was viewed by the participants via a mirror attached to the head-coil. Manual responses were recorded using an MRI-compatible button box.

There were six conditions concerning the interaction of top-down category cue and subliminal stimuli: face cue with masked face picture (FF), face cue with masked tool picture (FT), face cue with masked blank screen (FB), tool cue with masked face picture (TF), tool cue with masked tool picture (TT), and tool cue with masked blank screen (TB). To avoid any difference in low-level features, masked faces between FF and TF were counterbalanced, as well as masked tools between FT and TT. Thus, top-down effects on unconscious stimuli (see fMRI Data Analysis part) cannot be attributed to low-level stimulus differences.

The stimulus sequence in a trial was as follows (Fig. 1): a cue word ("face" or "tool") was first displayed for 500 ms followed by a scrambled picture which served as forward mask. After 384 ms this mask was replaced by the subliminally presented target (face or tool picture) or a blank screen for 16 ms, which was followed by a backward mask for 384 ms. For the better BOLD signal, masked targets (face, tool or blank screen) and backward masks were repeated 5 times. The last mask was displayed for 400 ms in a trial, followed by another picture (face, tool or other category) for 1600 ms. Participants were asked to decide as quickly and accurately as possible whether the supraliminally presented picture matched the category of the word cue by pressing 1 or 2 on the button box, respectively. The participants were also informed that the stimuli between the cue word and the last picture were distractors. The responses were counterbalanced across subjects. There were 70% consistent and 30% inconsistent trials. Note that no target was displayed twice and masked targets were always of the same category within a trial. In addition, the face targets in a trial were of the same gender. Between trials, a central fixation cross was displayed for a jittered inter-trial interval of 2–6 s. There were 2 runs, each containing 20 trials of each condition, thus 120 trials in total. The different conditions in each run were displayed pseudorandomly.

After fMRI scanning, in order to test the participants' ability to recognize the masked pictures, the participants were asked to report whether or not they saw something apart from the cue words and last pictures. Subsequently a forced-choice discrimination task was performed while still lying in the scanner. Consequently, viewing distance and lightening conditions were identical. Stimuli and trial times were similar to those used in the formal fMRI experiment. However, the same face/tool was repeated five times in a trial. After the presentation of the last mask, a pair of faces/tools, one of which was the same as that presented before, was presented left and right of the fixation. Participants were asked to determine which one was presented previously. The two faces/tools remained on the screen until the participant made a response. There were 60 face and 60 tool trials in the discrimination task. Before performing this task, participants were informed that the face/tool was repeatedly presented in each trial and that only the accuracy was important not the speed of response. Because of the sensed changes of contour and orientation under the condition of masked tool targets, the paired tool pictures were two samples of the same tool. It is reasonable to note that this test is more conservative than the task in the fMRI experiment as a means of visibility test because the same face/tool was repeated in a trial. If this test shows no visibility of masked faces/tools, we can conclude that the participants could not recognize them during scanning.

The fMRI results showed different top-down category-selective attention effects on unconscious face and tool processing (see fMRI Data Analysis part). We thought that the different effects might be due to an interaction between top-down category-selective processes and bottom-up processes. For the tool stimuli early processing stages such as the perception of changes in contour and orientation were susceptible to partial awareness. Because the two samples in the above forced-choice discrimination task had a similar contour, it is theoretically possible that the participants were aware of the tool target but were unable to discriminate the details of the two samples. In order to assure that the participants did not consciously recognize the masked tools, we subsequently recalled 12 available of the 18 participants who joined the fMRI experiment to do an adapted version of the force-choice task. The only difference was asking participants to judge which

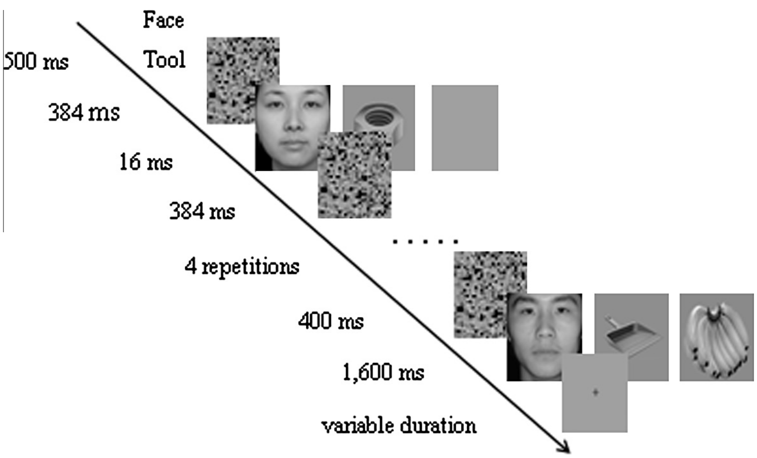

Fig. 1. Schematic illustration of the task. Participants were required to identify whether the last supraliminal picture matched the firstly presented word cue, and also been told that the stimuli between the word cue and supraliminal picture were distractions. For the better blood oxygenation level-dependent (BOLD) signal, the subliminal picture (face/tool/blank) repeated five times. However, there was no face/tool picture displayed twice in a single trial.

type of tool the masked target was. The two options of tool types were displayed in words rather than two sample pictures of the same tool. Using this new forced-choice task would reveal whether the participants were aware the tool but failed to recognize details of it or whether they were completely unaware of the object's identity. In addition, after this behavioral experiment, the participants were asked to report their subjective experience, i.e., whether they could sense the changes of contour and orientation under the two conditions (masked face and tool conditions were tested separately).

fMRI data acquisition: Imaging data were acquired with a 3-T Siemens Trio Scanner (Siemens Medical Systems, Erlangen, Germany) using a 12-channel birdcage headcoil. Two functional scans were acquired using an echo planar imaging (EPI) sequence (TR = 2000 ms, TE = 30 ms, flip angle: 90°; field of view: 220×220 mm^2; matrix size: 64×64). Each functional volume consisted of 32 axial slices of 3 mm thickness with 1 mm gap between slices. Each scan lasted 15 min 2 s and consisted of 456 volumes. Two dummy scans were performed prior to the image acquisition to eliminate signals arising from progressive saturation.

fMRI data analysis: All pre-processing and statistical analyses were carried out using SPM8 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8/). Prior to pre-processing, the first three volumes of each run were discarded. For each participant, functional images were spatially aligned and slice-time corrected to the first volume of the first run, and then normalized to the Montreal Neurological Institute (MNI) template brain. The normalized functional images (re-sampled at 3 mm^3) were spatially smoothed with a Gaussian kernel of fullwidthhalf-maximum of 8 mm^3. A 128 s temporal high pass filter was applied to remove low-frequency scanner artifacts. Using a first-order autoregressive model (AR-1), temporal autocorrelation were estimated using restricted maximum likelihood estimates of variance components, and maximum likelihood estimates of the activations were formed using the previously resulting non-sphericity.

For statistical analysis, we constructed models of six separate regressors coding for onsets and durations (2 s) of FF, FT, FB, TF, TT, and TB. The regressors were convolved with SPM8's canonical hemodynamic response function (HRF) and the models were regressed against the observed BOLD data. For each condition, the fMRI activation consisted of three cognitive processing components: cue, unconscious tool/face picture and modulation of the unconscious picture by the cue. Subsequent analyses focused on effects of top-down modulation on unconscious face processing [(FF–FB)–(TF–TB)] and on unconscious tool processing [(TT–TB) − (FT–FB)] at a small volume FWE corrected threshold of $p < .05$ (cluster size >15 voxels). The same analysis method was used in training-related activation changes (Dahlin, Neely, Larsson, Bäckman, & Nyberg, 2008). In the two analyses of our study, FB and TB were used for excluding the pure top-down effects without the stimuli. The results were later thresholded at a liberal uncorrected threshold of $p < .005$ (cluster size >30 voxels) to see whether the effects were constrained to unilateral visual cortex or not.

3. Results

3.1. Visibility test

The participants reported not recognizing the masked faces/tools. But they could experience the changes of contour and orientation under the condition of masked tools but not under the condition of masked faces. In the conservative measure of stimulus visibility, 18 of 21 participants scored at chance level (binomial test, $p > .05$), suggesting that these individuals were unable to perceive masked faces/tools. The other three participants were excluded from analyses. Also at the group level, discrimination performance did not deviate from chance level (mean percentage correct for face test = 49.00%, SD = 0.08, $t(17) = -0.49$, $p > .05$; mean percentage correct for tool test = 47.00%, SD = 0.07, $t(17) = -1.74$, $p > .05$).

The results of the adapted force-choice task also resulted in performance at chance level (binomial test, $p > .05$). The performance did not deviate from chance level at the group level (mean percentage correct for tool test = 50.33%, SD = 0.09, $t(11) = 0.12$, $p > .05$). Taking the results of both force-choice tasks together, the tool stimuli were only of partial awareness but were not consciously perceived and recognized.

3.2. Behavioral results

The accuracy rates were: 96.2 ± 5.7% (FF), 96.6 ± 6.3% (FT), 97.5 ± 3.7% (FB), 96.7 ± 4.5% (TF), 98.1 ± 3.4% (TT), and 95.4 ± 4.9% (TB) respectively. A two-way repeated-measures ANOVA with cue and target as factors revealed that none of the main effects reached significance, $F(1,17) = .00$, $p > .05$, MSE = .00, $\eta^2 = .00$ for the cue, and $F(2,34) = .62$, $p > .05$, MSE = .00, $\eta^2 = .04$ for the target. Moreover, there was no interaction of both factors $F(2,34) = 1.89$, $p > .05$, MSE = .00, $\eta^2 = .10$.

Because of fewer inconsistent than consistent trials (30% vs. 70%) mean reaction times (RTs) were calculated only for correct consistent trials. The RTs were: 692.1 ± 104.6 ms (FF), 672.7 ± 105.2 ms (FT), 684.8 ± 104.3 ms (FB), 834.1 ± 105.9 ms (TF), 860.2 ± 132.2 ms (TT), and 833.5 ± 128.9 ms (TB) respectively. The two-way repeated-measure ANOVA revealed a the main effect of cue, $F(1,17) = 122.16$, $p < .05$, MSE = 5616.59, $\eta^2 = 0.88$, demonstrating significantly faster RTs to faces than to tools. In contrast the main effect of target did not reach statistical significance, $F(2,34) = 0.36$, $p > .05$, MSE = 1339.71, $\eta^2 = 0.02$. The cue main effect was further qualified by a significant interaction with the factor target, $F(2,34) = 4.56$, $p = <.05$, MSE = 1189.14, $\eta^2 = 0.21$. Post hoc tests showed that this interaction was driven by significantly longer RTs in trials with masked tools as compared to blank screens when the cue was a tool, $t(17) = 2.13$, $p < .05$, Cohen's $d = 1.04$. None of the other t-tests were significant, $p > 0.05$.

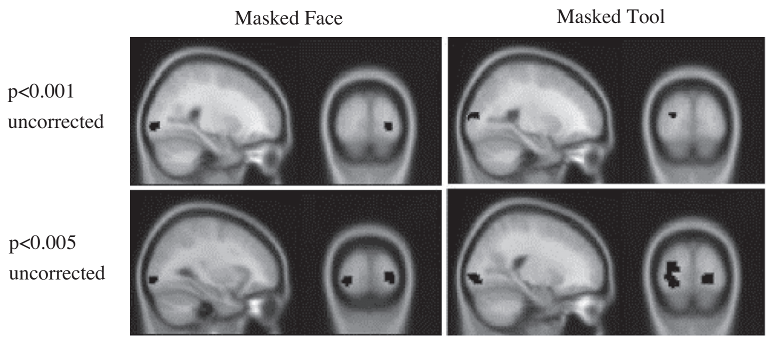

Fig. 2. Left column: (FF–FB) < (TF–TB). Right column: (TT–TB) > (FT–FB). Upper row: Statistical parametric maps were displayed at an uncorrected threshold of $p < .001$, cluster size >15 voxels. However, the activations were all significant at $p < .05$, cluster size >15 voxels (small volume FWE correction). Processing unconscious faces, activation in right MOG (middle occipital gyrus) decreased under face-selective attention compared with tool-selective attention. However, processing unconscious tools, activation in left MOG increased under the tool-selective attention compared with face-selective processes attention. Lower row: Statistical parametric maps were thresholded at $p < .005$, cluster size >30 voxels (uncorrected). Processing both unconscious faces and unconscious tools showed bilateral decrease for unconscious faces and bilateral increase for unconscious tools in lateral visual cortex.

fMRI results: Analyses of top-down modulation on unconscious face processes [(FF–FB)–(TF–TB)] revealed relatively decreased activity in the right MOG (middle occipital gyrus) ($x = 24$, $y = -91$, $z = -2$; and $t = 4.51$) at a small volume (MOG) FWE corrected threshold of $p < .05$ (cluster size > 15 voxels) (Fig. 2) under face-selective attention compared with tool-selective attention. The analyses of top-down modulation on unconscious tool processes [(TT–TB) – (FT–FB)] showed relatively increased activity in the left MOG ($x = -24$, $y = -91$, $z = 13$; and $t = 4.38$) at a small volume (MOG) FWE corrected threshold of $p < .05$ (cluster size >15 voxels) (Fig. 2) under tool-selective attention compared with face-selective attention.

To see whether the effects were constrained to unilateral visual cortex or not, using a liberal uncorrected threshold of $p < .005$ (cluster size >30 voxels), we observed bilateral decrease for unconscious faces and bilateral increase for unconscious tools in the visual cortex under the congruent cue condition compared with the incongruent cue condition (Fig. 2). All results were visualized using xjView toolbox (http://www.alivelearn.net/xjview).

4. Discussion

In the present fMRI study, we investigated how top-down category-selective attention modulates unconscious processes. The results showed that category-selective top-down processes modulated unconscious face/tool processing in the MOG (middle occipital gyrus), but effects for face stimuli differed from effects for tool stimuli. Processing unconsciously perceived faces resulted in decreased activations in MOG under top-down face-selective attention compared with top-down tool-selective attention. However, processing unconsciously perceived tools resulted in increased activations in MOG under top-down tool-selective attention compared with top-down face-selective attention. The different effect might be caused by an interaction between top-down category-selective processes and bottom-up processes that were susceptible to partial awareness in the unconscious tool picture condition, since participants could sense the changes of contour and orientation (see discussion below).

In the experiment, we used a paradigm in which five face/tool pictures were subliminally presented and repeated for a better BOLD signal. Several studies have revealed that visual areas are sensitive to repetition suppression (Weigelt, Muckli, & Kohler, 2008). However, such repetition suppression effects only occur when the same exemplars of an object are repeated, but not for different exemplars (Chouinard, Morrissey, Köhler, & Goodale, 2008). In the present experiment, face stimuli had similar contours but tool stimuli did not. Therefore repeated face stimuli resembled the same exemplar condition, whereas repeated tool stimuli resembled the different exemplar condition. This, however, is an overall effect pattern that should not only influence the conditions in which cue and targets were identical but also the conditions in which cue and target differed. In addition, conditions with cues but without subliminal stimuli were designed to exclude the pure effects of only top-down category-selective attention. Therefore, we assume that the observed effects reflect top-down influences on unconscious processes. The results are consistent with the attentional sensitization model (Kiefer & Martens, 2010), which proposes that processes of unconscious stimuli are susceptible to top-down modulation.

The results of unconscious face processes modulated by the top-down category-selective attention are in line with the predictive coding theory (Rao & Ballard, 1999). The theory proposes that predictions generated by the brain estimate the visual input according to the contextual information from the past. Top-down signals from higher-level areas to lower-level areas carry predictions of lower-level neural activities. The brain aims at reducing the mismatch between top-down signals and the bottom-up inputs. Then feedforward connections carry the unpredictable components of the sensory input from lower-level areas to higher-level areas. In our experiment, in order to make a match/no-match judgment about the supraliminally presented picture, the participants had to maintain the cue in working memory, which is one form of top-down attention (Chun, Golomb, & Turk-Browne, 2011). Alink, Schwiedrzik, Kohler, Singer, and Muckli (2010) found that predictable stimuli reduced activities in primary visual cortex. They concluded that the brain anticipated forthcoming sensory input and that predictable visual stimuli are processed with less neural activation at early processing stages (Alink et al., 2010). Other studies also demonstrated deactivations in lower visual areas with increasing stimulus coherence (Cardin, Friston, & Zeki, 2011; Fang, Kersten, & Murray, 2008; Murray, Kersten, Olshausen, Schrater, & Woods, 2002). Moreover, more abstract property is proposed to be processed in more anterior visual cortex (Dumoulin & Hess, 2007; Fang et al., 2008; Murray et al., 2002). For example, Cardin et al. (2011) showed that activity in V1/V2 reduced with "collinearity" and activity in MOG reduced with "meaning" (Cardin et al., 2011). Therefore, the present observation that the activation of unconscious faces in MOG decreased under top-down face-selective attention compared with top-down tool-selective attention are in accordance with previous studies and the predictive coding theory. We conclude that the unconscious process could also be modulated by the category-selective attention in the earlier visual cortex. This effect may play an important role in our daily life. Given that we often process the majority of information that the brain receives continuously without consciousness, category-selective top-down effects on unconscious processes may activate an unconscious attentional mechanism that directs/modulates unconscious processes.

However, processing tools, that participants were partially aware of, resulted in increased activation of the MOG under the top-down tool-selective attention compared with top-down face-selective attention. Although this effect is opposite to the results under unconscious face condition, we do not think that it is at conflict with the predictive coding theory. In fact, Koch and Tsuchiya (2007) indicated that top-down attention and consciousness could be dissociated and they could have opposite effects (Koch & Tsuchiya, 2007). The different effects in our study might be ascribed to interactions between top-down category-selective attention and bottom-up processes of partial awareness (Kouider et al., 2010). Partial awareness indicates that "representations at each level can be accessed independently from each other". In other words, there are intermediate cases between complete awareness and complete unawareness, i.e. "combing awareness at some levels and unawareness at other levels of representation" (Kouider et al., 2010). In the present experiment, participants could experience the changes of contour and orientation caused by five successive repetitions of different tools, however they did not consciously recognize the presented tool. This describes partial awareness. Moreover, because the faces were completely unconscious and had similar contours, the successive repetitions of faces and tools resulted in different perception of contour changing. Although the participants did not know what was presented under both conditions, they could experience the changes of contour and orientation under condition of masked tool primes but could not under condition of masked face primes. Therefore, the opposite effects of activity in MOG lead us to an "excessive activation" hypothesis. When the unconscious "meaning" of the tool target is consistent with the cue, the incongruity caused by changed contour could result in excessive activation in MOG. An indicative link to that assumption might be the significantly longer RTs in the condition when both cue and target were tools in comparison to tool cue and a blank target screen. However, in order to assure this hypothesis, other conditions should be studied in future. For example, at the stage of partial awareness, category-selective attentional modulation of no-changed contour might show decreased activation in MOG for the same cue compared with the different cue condition. In addition, although it seems to be a small possibility, it needs to be tested whether similar effects could be found with changing contours in a completely unconscious condition. In addition, we do not know whether the (different) unilateral cerebral activation effect can be replicated for the two conditions. Thus, it should be addressed in future studies as well.

To sum, we can conclude that the processing of unconsciously perceived stimuli can be modulated by top-down category selective attention. This modulation might be the results of both top-down sensitization of category-specific processing pathways and bottom-up processing despite unconsciousness.

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