



Mental imagery of face enhances face-sensitive event-related potentials to ambiguous visual stimuli



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ABSTRACT

Visual mental imagery forms mental representations of visual objects when correspondent stimuli are absent and shares some characters with visual perception. Both the vertex-positive-potential (VPP) and N170 components of event-related potentials (ERPs) to visual stimuli have a remarkable preference to faces. This study investigated whether visual mental imagery modulates the face-sensitive VPP and/or N170 components. The results showed that with significantly larger amplitudes under the face-imagery condition than the house-imagery condition, the VPP and P2 responses, but not the N170 component, were elicited by phase-randomized ambiguous stimuli. Thus, the brain substrates underlying VPP are not completely identical to those underlying N170, and the VPP/P2 manifestation of the category selectivity in imagery probably reflects an integration of top-down mental imagery signals (from the prefrontal cortex) and bottom-up perception signals (from the early visual cortex) in the occipito-temporal cortex where VPP and P2 originate.

1. Introduction

The top-down visual processing plays an important role in perceiving visual objects, particularly when optical inputs are weak, ambiguous, or absent, leading to that an observer can “see” an object in an illusory way even when the visibility of the object is low or absent (e.g. see a face in noise). Visual mental imagery is a typical type of top-down processing that forms mental representations of objects when the corresponding visual stimulation is absent (Gosselin & Schyns, 2003; Hansen et al., 2010; Nestor, Vettel, & Tarr, 2013; Smith, Gosselin, & Schyns, 2012; for a review see Ganis & Schendan, 2011). Currently, the mechanism underlying visual mental imagery is largely unknown.

It has been suggested that imagining visual objects in the mind may activate corresponding brain areas for perception of visual objects (O’Craven & Kanwisher, 2000; Klein et al., 2004). For example, some functional magnetic resonance imaging (fMRI) studies have shown that imagery of illusory faces is associated with activation of multiple cortical regions of the visual system, including the fusiform face area (FFA) and the occipital face area (OFA) (Li et al., 2010; Nestor et al., 2013; Righart et al., 2009), which are also the brain areas specific for face perception (Kanwisher, McDermott, & Chun, 1997; Haxby,

Hoffman, & Gobbini, 2000). Extended brain regions for face imagery may also involve the orbitofrontal cortex (Li et al., 2010), inferior frontal gyri (Zhang et al., 2008), and a distributed network between frontal and occipito-temporal areas (Liu et al., 2014).

Among these brain structures, activation of the FFA during mental imagery of faces appears to be the most consistent across different studies using different experimental paradigms, supporting the view that visual mental imagery and perception share some common neural substrates. For example, even when the visual sensory input of a face image is absent, imagery can induce marked activation of the FFA (e.g., observers are instructed to imagine a face with their eyes closed), though the imagery-induced activation is weaker than that induced by a face photograph (O’Craven & Kanwisher, 2000). Also, in both healthy individuals (Li et al., 2010; Nestor et al., 2013) and patients with prosopagnosia (Righart et al., 2010), when the visual input is random noise, the FFA becomes activated as long as an illusory face is reported. The Hadjikhani, Kveraga, Naik and Ahlfors magnetoencephalographic (MEG) study (2009) has further shown that when the visual stimulus containing some schematic clues of a face (e.g., the pattern of one mouth and two eyes) are incidentally perceived as a face, the M165 response occurs both with a similar amplitude to that elicited by a real face stimulus and with an activation source in the ventral FFA. All these

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reports suggest that the FFA is an interface that is involved in functional integration between the top-down imagery process and the bottom-up sensory process. It is important to establish a neurophysiological model of the top-down modulating effect of visual mental imagery of faces.

Numerous electro-encephalographic (EEG) studies have shown that both the vertex positive potential (VPP) component and the N170 component of event-related potentials (ERPs) are markedly face sensitive: both VPP and N170 are enhanced when eliciting stimuli are face-like objects compared to non-face objects (e.g. cars, animals, leaves, flowers, mushrooms, tools, shoes, road signs or words) (for VPP, see Bötzel, Schulze, & Stodieck, 1995; Itier & Taylor, 2004; Jeffreys, 1996; Jeffreys & Tukmachi, 1992; Proverbio & Galli, 2016; Rossion & Jacques, 2008; Rossion, Joyce, Cottrell, & Tarr, 2003; for N170, see Bentin, Allison, Puce, Perez, & McCarthy, 1996; De Haan, Pascalis, & Johnson, 2002; Eimer, 2000; Itier & Taylor, 2004; Proverbio & Galli, 2016; Rossion & Jacques, 2008; Rossion et al., 2000; Taylor, McCarthy, Saliba, & Degiovanni, 1999; for a recent review see Rossion, 2014). It is of interest to know whether these two face-sensitive ERP components (N170, VPP) are sensitive to face mental imagery when any face features in eliciting stimuli are completely eliminated.

The face-responsive N170 component mainly occurs at occipito-temporal recording sites on the scalp, with the amplitude peak near 170 ms following the onset of a face stimulus and manifests the early stage of processing face structural information (Bentin et al., 1996; Rossion et al., 2000). Interestingly, N170 can be elicited by non-face noise images either during the maintenance of the working memory of a real face image (Sreenivasan, Katz, & Jha, 2007) or when a noise image is treated as a human face with a gender (Wild & Busey, 2004). Moreover, N170 can even be elicited by simple schematic or line drawings interpreted as faces or eyes (Bentin & Golland, 2002; Bentin et al., 2002). However, it is not clear whether top-down imagery can still affect N170 when any bottom-up face-signal inputs are substantially limited or even completely eliminated.

The VPP emerges at fronto-central recording sites on the scalp with the peak amplitude between 160 and 200 ms following the onset of a face stimulus and may also represent the stage of structural encoding of a face, because it becomes delayed or sometimes attenuated if the face stimulus is disrupted by an inversion, scramble, or masking treatment (George, Evans, Fiori, Davidoff, & Renault, 1996; Jeffreys, 1989; Joyce & Rossion, 2005; Jemel et al., 2003). It is not clear whether VPP can be used for studying whether a preference to face also occurs in mental imagery.

Some previous studies have suggested that VPP and N170 reflect identical brain processes in face perception (Itier & Taylor, 2002; Joyce & Rossion, 2005; Jemel et al., 2003; Rossion & Jacques, 2008; Rossion, Campanella et al., 1999; Delvenne et al., 1999; Rossion et al., 2003). Particularly, the changing pattern of amplitude of VPP and that of N170 are highly correlated across different reference sites (Joyce & Rossion, 2005), and their latencies also change synchronously either with addition of noise to face pictures (Jemel et al., 2003) or with inversion or contrast reversal of face pictures (Itier & Taylor, 2002). Some studies have also suggested that both VPP and N170 originate from both fusiform gyrus regions and lateral inferior occipital cortex (Rossion, Campanella et al., 1999; Rossion et al., 2003). However, several lines of studies have also suggested that VPP and N170 are based on different brain mechanisms (Itier & Taylor, 2004; Bötzel et al., 1995; George et al., 1996; Taylor et al., 1999; Saavedra et al., 2012): (1) the VPP generator involves a larger network including both infero-temporal cortex and the superior temporal sulcus, but the N170 generator is confined to the parahippocampal place area (PPA) and FFA (George et al., 1996); (2) the hippocampus may be another origin of VPP, indicating that VPP is also associated with memory-related process (Bötzel et al., 1995); (3) a steady age-related change of N170 is observed and VPP is absent in young children, indicating a developmental difference between N170 and VPP (Taylor et al., 1999); (4) cognitive decline affects the VPP and N170 in the opposite direction

(Saavedra et al., 2012); (5) the face-orientation inversion effect is reliable on the amplitude of N170, but not on the amplitude of VPP (Itier & Taylor, 2004).

This study aimed to investigate whether instruction-induced mental imagery of faces can top-down modulate the two face-sensitive ERP components, VPP and N170, when the ERP-eliciting stimuli are completely ambiguous pictures that have no physical features of faces. The controlling condition for face-imagery was mental imagery of houses.

2. Methods

2.1. Participants

Sixteen university students (8 males and 8 females, aged between 20 and 28 years with the mean of 22.9 ± 2.0 years) participated in this study. They were right handed and had either normal or correct-to-normal vision. These participants gave their informed consent before the experiment and were paid a modest stipend for their participation. The experimental procedures were approved by the Committee for Protecting Human and Animal Subjects of the Department of Psychology at Peking University.

2.2. Stimuli

Ten grayscale pictures of faces (5 females and 5 males) and 10 grayscale pictures of houses (5 two-floor ones and 5 three-floor ones) with balanced physical attributes of brightness and contrast were used as the original pictures. The hair and ears of face pictures were removed. The houses were placed into a face-shape contour to reduce the physical interstimulus variance. These original pictures were transferred to completely ambiguous figures using the phase randomization methods of MATLAB 7.0, leading to that all the pixels of a picture were selected and their phases were randomly redistributed to form a new figure. To avoid potential effects of content of original pictures, these ambiguous figures were classified into two categories according to their original content: the ambiguous figures from face pictures and those from house pictures. Each original picture was processed for 15 times. Thus, in total 150 completely ambiguous figures were made from face pictures and 150 completely ambiguous figures were made from house pictures. After the phase-randomization manipulation, these ambiguous figures had neither recognizable face objects nor recognizable house objects. The third category of stimuli were 150 Gaussian noise stimuli, whose brightness was matched to that of completely ambiguous figures.

In addition to the completely ambiguous figures, pictures containing either a real face or a real house were also used. More specifically, 50 face pictures and 50 house pictures (10 original face pictures and 10 original house pictures each submitted to the processing described below 5 times) were processed into half-ambiguous pictures, in which either a face or a house could be easily observed. The half-ambiguous pictures were produced by randomly selecting 50% of the pixels of the original pictures and randomizing the phases of the pixels. In this way, 50 half-ambiguous face pictures and 50 half-ambiguous house pictures were obtained. In each condition with either the face-picture origin or the house-picture origin, 50 original (clear) pictures and 50 half-ambiguous pictures were used (Fig. 1).

2.3. Procedures

During the experiment, participants sat in a dimly-lit and sound-attenuated room (EMI Shielded Audiometric Examination Acoustic Suite), with a distance of 75 cm away from a 15-in. computer screen (resolution, 1024×768 pixels; refresh rate, 60 Hz) that presented the visual stimuli (visual angle, $10.5^\circ \times 7.9^\circ$). There were two blocks (face-imagery block, house-imagery block) of 550 randomly ordered trials, including in each block 150 presentations of ambiguous figures from face pictures, 150 presentations of ambiguous figures from house

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