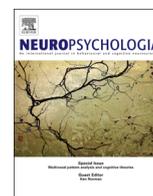




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The role of superior temporal sulcus in the control of irrelevant emotional face processing: A transcranial direct current stimulation study

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ABSTRACT

Emotional faces are often salient cues of threats or other important contexts, and may therefore have a large effect on cognitive processes of the visual environment. Indeed, many behavioral studies have demonstrated that emotional information can modulate visual attention and eye movements. The aim of the present study was to investigate (1) how irrelevant emotional face distractors affect saccadic behaviors and (2) whether such emotional effects reflect a specific neural mechanism or merely biased selective attention. We combined a visual search paradigm that incorporated manipulation of different types of distractor (fearful faces or scrambled faces) and delivered anodal transcranial direct current stimulation (tDCS) over the superior temporal sulcus and the frontal eye field to investigate the functional roles of these areas in processing facial expressions and eye movements. Our behavioral data suggest that irrelevant emotional distractors can modulate saccadic behaviors. The tDCS results showed that while rFEF played a more general role in controlling saccadic behavior, rSTS is mainly involved in facial expression processing. Furthermore, rSTS played a critical role in processing facial expressions even when such expressions were not relevant to the task goal, implying that facial expressions and processing may be automatic irrespective of the task goal.

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1. Introduction

Human beings' information processing system is limited and often deals with an overwhelming amount of stimuli that are competing for attention at the same time. Thus, an important function of attention is to select relevant information and ignore irrelevant information for further processing (Desimone and Duncan, 1995). Attention has been shown to be easily captured by salient signals such as abrupt onset of colorful and emotional stimuli (Vuilleumier, 2005; Yantis and Jonides, 1984). Of these, emotional stimuli are specifically important to attentional orienting because they are often temporally close to dangerous events that may threaten survival. One of the commonly used emotional

stimuli is a face, or facial expressions, that carry biological and social information such as age, gender, identity, and emotion. Facial expressions are also important for guiding social interactions with others in the community.

The use of several paradigms such as the visual search task (Fox et al., 2000, 2001), dot-probe task (Mogg and Bradley, 1999), and RSVP task (Stein et al., 2009) have indicated that emotional faces are detected faster and are more distracting than neutral faces. Moreover, human patients with visual neglect also show less visual extinction for emotional faces (e.g. fearful expression) than neutral faces (Vuilleumier et al., 2001). These studies have shown that participants detect emotional faces faster than neutral faces, suggesting that specific emotional information may modulate human attention.

A range of brain areas have been functionally linked to processing emotional face information depending on the affective significance of the faces, particularly in the case of fearful expressions (for a review see Vuilleumier and Pourtois (2007)). A number of studies

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have demonstrated that the amygdala is specifically involved in emotional processing and is critically associated with fear processing and fear-related learning (LeDoux, 2000; Pessoa, 2008; Phelps, 2006; Vuilleumier et al., 2001; Vuilleumier and Driver, 2007), while orbitofrontal cortex (OFC) and anterior cingulate cortex (ACC) are involved in emotional and social behaviors (Rudebeck et al., 2007, 2008; Rushworth et al., 2007). The amygdala also plays a central role in emotional modulation of face processing. In addition, studies have also begun to uncover other brain regions and their roles in emotional face processing. For example, activity changes are seen in regions such as the visual cortex, superior temporal sulcus, the middle occipital cortex, the fusiform gyri, and the orbitofrontal and parietal cortex (Pessoa and Ungerleider, 2004; Phelps, 2006). Recently evidence from functional brain-imaging studies has also shown that face perception processing is principally associated with three cortical regions, the inferior occipital gyrus, the lateral fusiform gyrus, and the superior temporal sulcus (Haxby et al., 2000). Damage to the ventral occipitotemporal cortex, which includes the above three regions, renders patients unable to recognize faces but other objects are unaffected (McNeil and Warrington, 1993). In particular, the superior temporal sulcus, according to Haxby's face processing model, is associated with the coding of changeable facial cues, i.e. perception of eye gaze; lip movement; and facial expressions. Several nonhuman primates studies have also demonstrated the superior temporal sulcus as a critical region that responds selectively to facial expression processing with single cell recordings data (Hasselmo et al., 1989) and showed activation for emotional body postures and movements with fMRI data (de Gelder and Partan, 2009). Moreover, fMRI studies have demonstrated that selective attention to facial expressions elicit stronger right STS activation (Narumoto et al., 2001), activations in the STS specifically for dynamic fear bodies action (Grezes et al., 2007). A series of TMS pulses over the STS studies causes disturbed facial perception (Pourtois et al., 2004), disrupted trustworthiness judgements (Dzhelyova et al., 2011) and altered accuracy in detecting changes of threatening human body postures (Candidi et al., 2011). Consequently, the STS region has been considered as a crucial region in facial expression and threat related information processing.

There are two main perspectives regarding the relationship between attentional and emotional modulation of visual processing (Pessoa and Ungerleider, 2004; Vuilleumier, 2005; Vuilleumier and Driver, 2007). One viewpoint is that the neural processing of emotional stimuli is not automatic and instead needs some degree of attention (Pessoa et al., 2002). From this point of view, the faster detection of emotional faces and increased activation of the fusiform face area for fearful faces might reflect enhanced attentional bias to emotional stimuli. The hypothesis is that the emotional processing and attention processing are coupled together. Emotional information would serve to rapidly inform attentional control, depending on the allocation of attentional resources. Another view specifies that emotional stimuli enjoy specific neural mechanisms for their processing (such as those involving the amygdala) that boost processing and give emotional stimuli competitive strength against other stimuli (Vuilleumier et al., 2001; Vuilleumier and Driver, 2007). In this hypothesis emotional processing and attention processing are separated and emotional information is processed in a truly automatic pathway that does not depend on attentional resources. Therefore, the emotion modulations reflect a stronger engagement of attention towards the more salient facial stimuli, indirectly mediated by top-down signals from frontal-parietal areas involved in attentional control (Desimone and Duncan, 1995) or the modulation of neuronal responses to facial expressions would be consistent with the existence of direct connections between visual cortex and the amygdala or other emotion-related regions (Amaral et al., 2003), reflecting a limbic region that is crucially involved in rapid emotional processing (LeDoux, 2000).

Although fMRI studies have often used faces in a paradigm where both emotion and attention are manipulated separately (Pessoa et al., 2002; Vuilleumier et al., 2001), it remains unclear whether the relationship between emotion and attention and the modulation of visual processing by emotion might reflect distinct influences. Thus, the present study employed transcranial direct current stimulation (tDCS) to directly compare the emotion related brain regions and attention related brain regions, using a visual search task with emotional faces as distractors.

Emotional stimuli have also been shown to affect eye movements. The eye movement system provides abundant information on cognitive processing for experimental exploration (Liveredge and Findlay, 2000; Van der Stigchel, 2010; Van der Stigchel et al., 2006). One way to measure the effect of emotional distractors is to observe the intervening path that the eyes move across to reach the target destination. Because eye movement trajectories are seldom straight, the magnitude of eye trajectory curvature can be used as an index of the effect of the distractor (e.g. Chao et al., 2011). Specifically, since previous studies have suggested that curvatures represent the dynamic competition between target selection and distractor suppression (McSorley et al., 2006; Van der Stigchel, 2010; Van der Stigchel et al., 2006; Van der Stigchel and Theeuwes, 2005, 2006), saccade curvatures have often been observed to deviate toward or away from the distractor (while traveling to the target location) depending on the paradigm used, as well as the strength of the distractor. For example, saccade curvatures have been used as an index to gauge the effects of affective pictures or facial expression in allocation of attention: Nummenmaa et al. (2009) used emotional scene pictures or neutral pictures as distractors and measured the effects on saccade curvature while participants made vertical saccades to a target location. They found that saccade curvatures deviated away from the distractors when emotional scene pictures were used. This pattern of results suggested that emotional distractors are relatively more salient than neutral scene pictures even if participants never have to make a saccade to the emotional scenes. Recent studies also demonstrated that emotional stimuli were processed more sensitive in oculomotor system than motor system (Bannerman et al., 2009a, 2009b, 2010). Therefore, it is critical to measure emotional effects on saccade programming during performance of a visual search paradigm involving presentation of emotional stimuli.

There is a broad network contributing to attentional modulation. Neuroimaging studies have indicated two separate attentional networks: the dorsal fronto-parietal network and the ventral network (Bressler et al., 2008; Corbetta and Shulman, 2002). The dorsal fronto-parietal network, involving of the intraparietal sulcus (IPS) and frontal eye field (FEF), performs voluntary attentional control such as orienting to a location or object (Hopfinger et al., 2000; Nobre et al., 2004; Rushworth et al., 2001). Similarly, neurophysiological studies have shown a network of brain regions: the superior colliculus (SC), supplementary eye field (SEF), and frontal eye field (FEF) that are associated with pretarget-related neural activity during visual attention (for a review, see Rushworth and Taylor (2006)).

Several studies have shown that transcranial direct current stimulation (tDCS) may induce either facilitatory effects with anodal stimulation or inhibitory effects with cathodal stimulation. This modulation was first shown in animal studies, where subthreshold DC stimulation increased cerebral excitability with anodal stimulation by depolarizing cell membranes and increasing firing rates, while cathodal stimulation resulted in the opposite effect by hyperpolarization and decreasing firing rates (Bindman et al., 1964; Creutzfeldt et al., 1962; Nitsche et al., 2009; Stagg et al., 2009). Several tDCS studies have also demonstrated this bidirectional effects with behavioral measurement (Hsu et al., 2011; Nitsche and Paulus, 2000; Nitsche et al., 2003; for a review, see Dayan et al. (2013)).

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