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Attention modulations on the perception of social hierarchy at distinct temporal stages: An electrophysiological investigation

Chunliang Feng [a], Tengxiang Tian [a], Xue Feng [a], Yue-Jia Luo [b,c,d,*]

[a] State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing, China
[b] National Key Lab of Brain and Cognitive Neuroscience, Shenzhen University, Shenzhen, China
[c] Institute of Affective and Social Neuroscience, Shenzhen University, Shenzhen, China
[d] Research Center of Sport Psychology, Wuhan Sports University, Wuhan, China

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ABSTRACT

Recent behavioral and neuroscientific studies have revealed the preferential processing of superior-hierarchy cues. However, it remains poorly understood whether top-down controlled mechanisms modulate temporal dynamics of neurocognitive substrates underlying the preferential processing of these biologically and socially relevant cues. This was investigated in the current study by recording event-related potentials from participants who were presented with superior or inferior social hierarchy. Participants performed a hierarchy-judgment task that required attention to hierarchy cues or a gender-judgment task that withdrew their attention from these cues. Superior-hierarchy cues evoked stronger neural responses than inferior-hierarchy cues at both early (N170/N200) and late (late positive potential, LPP) temporal stages. Notably, the modulations of top-down attention were identified on the LPP component, such that superior-hierarchy cues evoked larger LPP amplitudes than inferior-hierarchy cues only in the attended condition; whereas the modulations of the N170/N200 component by hierarchy cues were evident in both attended and unattended conditions. These findings suggest that the preferential perception of superior-hierarchy cues involves both relatively automatic attentional bias at the early temporal stage as well as flexible and voluntary cognitive evaluation at the late temporal stage. Finally, these hierarchy-related effects were absent when participants were shown the same stimuli which, however, were not associated with social-hierarchy information in a non-hierarchy task (Experiment 2), suggesting that effects of social hierarchy at early and late temporal stages could not be accounted for by differences in physical attributes between these social cues.

1. Introduction

Social hierarchy permeates organizations and societies of human and other species (Cummins, 2000). Social hierarchy not only is associated with disproportionate distribution of influence and resources (Fiske, 1992; Pusey et al., 1997), but also facilitates functional social interactions among people such that individuals adaptively adjust their behaviors according to the social status of others (Steckler and Tracy, 2014; Tiedens and Fragale, 2003). Therefore, the ability to readily detect and distinguish the social hierarchy of others provides adaptive values for individuals (Deaner et al., 2005; Maner et al., 2008). Unlike extensive investigations on the processing of other biologically and/or socially relevant stimuli (e.g., threatening scenes), however, much fewer studies have focused on the neurocognitive signatures underlying the perception of social hierarchy (Chiao et al., 2008, 2009; Kumaran et al., 2012; Pornpattananangkul et al., 2014; Zink et al., 2008).

Recently, a growing body of behavioral studies has demonstrated that superior-hierarchy targets are preferentially processed relative to inferior-hierarchy targets. For instance, attention systems of humans and nonhuman primates are more attuned to high-status than low-status targets in a gaze-cueing paradigm (Dalmaso et al., 2014, 2012; Shepherd et al., 2006), which probes automatic shifts of attention in response to others' gaze directions (Frischen et al., 2007). Further, previous eye-tracking studies have demonstrated that both humans and nonhuman primates prefer to take more time to view superior-hierarchy targets (DeWall, 2008; Foulsham et al., 2010; Haude et al.,1976; Maner et al., 2008), even at the expense of personal cost (Deaner et al., 2005). Finally, faces associated with high social status are more memorable than

* Corresponding author.
E-mail address: luoyj@szu.edu.cn (Y.-J. Luo).

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those associated with low social status, and perceivers process high-status faces in a more holistic way (Ratcliff et al., 2011). These intriguing findings indicate that superior-hierarchy targets are preferentially processed at multiple cognition stages.

The preferential processing of high-status targets at behavioral level has been supported by recent functional magnetic resonance imaging (fMRI) and event-related potential (ERP) studies. For instance, multiple neural networks are specially recruited in the perception of superior-hierarchy cues, including prefrontal cortex (e.g., ventrolateral and dorsolateral prefrontal cortex) and amygdala (Kumaran et al., 2012; Marsh et al., 2009; Zink et al., 2008). The former brain regions are thought to be associated with adjusting behavior in response to superior-hierarchy targets (Zink et al., 2008), whereas the latter has been associated with initializing rapid and coarse attentional bias to salient events (Öhman, 2005; Pessoa, 2005). Furthermore, although findings are currently not conclusive, preliminary evidence from ERP studies suggests that social hierarchy modulates both rapid attentional bias and sustained processing, which are manifested as more pronounced neural responses evoked by the high-status targets at the early (e.g., N170/N200) and the late (e.g., late positive potential [LPP]) temporal stages, respectively (Breton et al., 2014; Chiao et al., 2008; Pineda et al., 1994).

Although rapid attention bias towards and elaborative processing of superior-hierarchy targets provide essential information for functional social interactions, excessive processing of those high-status cues may also result in negative subjective feelings such as depression, shame and envy (Steckler and Tracy, 2014; Takahashi et al., 2009). For instance, inferior-hierarchy individuals tend to be more fearful than superior-hierarchy individuals (Plutchik and Landau, 1973). Furthermore, social hierarchy information can also preclude empathic feelings to superior-hierarchy targets, such that individuals reported stronger schadenfreude feelings in response to misfortune of those higher in the hierarchy (Takahashi et al., 2009). These findings suggest that hierarchy information does not only impair subjective wellbeing but also hampers prosocial connections among people in some contexts. In these regards, it is important to flexibly respond to superior-hierarchy cues according to specific contexts, such that individuals can voluntarily avoid the preferential processing of these social cues when it is not necessary or even detrimental. This viewpoint is well consistent with numerous studies in the domain of emotion regulation, which have indicated that top-down modulations (e.g., top-down attention, cognitive reappraisal processes) on the biased processing of other biologically salient stimuli (e.g., snakes) are crucial in maintaining psychological health (Gross, 1998; Ochsner et al., 2012). However, it remains unknown whether top-down cognitive processes such as top-down attention modulate the preferential processing of superior-hierarchy targets.

To address this gap, the current study was to investigate the modulations of top-down attention on the processing of superior-hierarchy cues by employing event-related potential (ERP) technique with the aim of elucidating whether top-down attention modulates temporal dynamics of neural responses to social hierarchy. We manipulated social hierarchy based on incidental skill in a game setting (Breton et al., 2014; Zink et al., 2008). Participants performed a simple task prior to ERP recording and were told that social hierarchy was based on their performance in the task. Covertly, participants' social hierarchy was always fixed (two-star players), and targets' hierarchy was either superior (three-star players) or inferior (one-star players) but not equal to participants' (see also Zink et al. (2008)). Notably, top-down attention to hierarchy cues was manipulated by asking participants either to judge hierarchy information or gender of presented targets. The hierarchy-judgment task required attention to hierarchy information whereas gender-judgment task withdrew attention from these social cues. Finally, we conducted Experiment 2 with the same stimuli sets to test whether hierarchy-related effects at multiple temporal stages could be accounted for by differences in physical attributes between the superior (i.e., faces presented together with three stars) and the inferior (i.e., faces presented together with one star) hierarchy. In Experiment 2, number of stars were not associated with social hierarchy but was just employed as classification symbols in a non-hierarchy judgment task. Specifically, participants of Experiment 2 were asked to judge how many stars in the presented stimuli (the attended condition) or gender of presented targets (the unattended condition).

To sum up, with fine-grain temporal resolution provided by the ERP technique, we aimed to distinguish modulations of top-down attention on the preferential processing of superior-hierarchy targets at distinct temporal stages. Both early (P1, N170/N200) and late (LPP) neural responses to social hierarchy were detected in the current study. We hypothesized that modulations of social status would be evident in early temporal stages such as the N170/N200 but not the P1 component (Chiao et al., 2008; Pineda et al., 1994). Importantly, we further hypothesized that modulations of social hierarchy on the N170/N200 would be evident in both attended and unattended conditions, given that salient stimuli evoke enhanced neural responses within such early temporal stages even when attention resources are limited (Carretié et al., 2004; Olofsson et al., 2008). Regarding the LPP component, we predicted that superior-hierarchy targets would evoke more pronounced LPP than inferior-hierarchy targets (Breton et al., 2014), and these effects on the LPP would be sensitive to the manipulations of top-down attention (Hajcak et al., 2009, 2013). Finally, we predicted that these hierarchy-related effects would be absent when the same stimuli were presented but not associated with social-hierarchy information in Experiment 2.

2. Experiment 1

Experiment 1 investigated the temporal dynamics of attention modulations on the perception of social hierarchy, which was conveyed by neutral faces presented together with one star (i.e., inferior hierarchy) or three stars (i.e., superior hierarchy).

3. Methods

3.1. Participants

Seventeen individuals (8 males) (mean age $\pm$ s.d.: 21.65 $\pm$ 2.71 years) participated in the current study for monetary compensation. All participants were right-handed, had normal or corrected-to-normal vision, and had no neurological or psychiatric history. This study was approved by the Institutional Review Board (IRB) at Beijing Normal University (BNU), Beijing, China. Written informed consents were collected from all participants.

3.2. Stimuli

A set of color photographs showing neutral faces from 60 college students (30 males) was employed in the current study. Each photograph was set to the same size of 346 $\times$ 290 pixels (width $\times$ height). Participants were instructed that those photographs were taken from subgroups of players who had performed a dot estimation task (see below).

3.3. Procedure

Prior to electroencephalographic (EEG) recording, all