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Integration of cognitive and affective networks in humor comprehension

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ABSTRACT

Humor comprehension is a complex process that requires the detection and resolution of the incongruity, eliciting a positive feeling of mirth or reward. We conducted a functional magnetic resonance imaging (fMRI) study to identify the key factors involved in this complex process. To reduce the influence of other factors, we utilized a group of sentences that were nearly identical across conditions (i.e., the first two sentences and the punch line were identical, but the third sentence was different). We found that the punch line (target sentence) in the funny condition induced a perception of funniness and elicited greater activation in language and semantic neural networks, which have been implicated in comprehension processing (i.e., incongruity detection and resolution). We also found increased activation in the mesolimbic reward regions, which have been implicated in the experience of positive rewards in the funny condition. Psycho-physiological interaction analyses revealed that language and semantic regions, such as inferior frontal gyrus (IFG), middle temporal gyrus (MTG), superior temporal gyrus (STG), superior frontal gyrus (SFG), and inferior parietal lobule (IPL) are simultaneously activated during humor comprehension processing. These analyses also revealed that the right MTG, the left IPL, and IFG showed enhanced connectivity with the midbrain. Our findings suggest that these networks play a central role in incongruity detection and resolution, as well as in positive emotional response.

1. Introduction

Humor is a phenomenon that is elicited by particular cognitive processes. The perception of humor is associated with a strong emotional response, laughter, and changes in the brain and body via the autonomic and endocrine systems (Panksepp, 1993). These complex processes in humor comprehension have been investigated by philosophers, psychologists, linguists, and other theorists. Famous theories of humor comprehension propose that humorous stimuli are processed in steps (Coulson and Kutas, 2001; Papousek et al., 2013; Shultz, 1976; Suls, 1972), such that initial information contained in humorous stimuli activates stored expectations or a script. Further information then leads to the detection of incongruence in the relation of the first script to another. To understand the punch line of a joke (either verbal jokes or visual jokes), this incongruity has to be at least partially resolved. For example, the incongruity-resolution model indicates that a joke setup causes the listener to make a prediction about the likely outcome (Suls, 1972). When the punch line does not conform to the prediction, the listener is surprised and looks for a cognitive rule that will make the punch line follow from the material in the joke setup. When this cognitive rule is found, the incongruity is removed, the joke is perceived as funny. Thus, this model suggests that joke comprehension and appreciation is essentially a sort of cognitive problem-solving task. Since humor is context-dependent, funniness results from the insightful integration of contradictory or incongruous ideas (Martin, 2007).

Over the past decade, many neuroimaging studies have examined the neural substrates involved in humor comprehension (Bekinschtein et al., 2011; Chan et al., 2012a, 2012b; Franklin and Adams, 2011; Goel and Dolan, 2001, 2007; Marinkovic et al., 2011; Mobbs et al., 2003, 2005; Moran et al., 2004; Neely et al., 2012; Rapp et al., 2008; Samson et al., 2009, 2008; Vrticka et al., 2013a, 2013c; Watson et al., 2007; Wild et al., 2006). These studies can be classified into two main groups based on the stimulus modalities used in the experiments: visual and verbal. One study utilizing visual stimuli was conducted by Samson and her colleagues, who used incongruity-resolution and nonsense cartoons to investigate the neural basis of

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incongruity-resolution processes. They found that the anterior medial prefrontal cortex, bilateral superior frontal gyri, and the temporo-parietal junctions (TPJ) showed more activation during processing of incongruity-resolution than of nonsense cartoons. Thus, compared with the processing of nonsense cartoons, the processing of incongruity-resolution cartoons appears to require more integration of multi-sensory information, coherence building, and thus more organization of information. Additionally, the temporoparietal junction (TPJ) and prefrontal areas appear to be involved in humor comprehension processes. Neely et al. (2012) conducted an fMRI experiment with typically developing children using video clips. In their experiment, three types of stimuli were used: Funny, Positive (enjoyable but not funny), and Neutral (not intended to evoke any emotional response). The results indicated that the Funny versus Positive contrast showed greater activation in the more superior TOPJ regions (BA 22, 37, and 40). They suggested that TOPJ activation may be specific to humor processing (i.e., involved in the satisfaction of detecting and resolving the incompatible elements of humor).

On the other hand, the study utilizing verbal stimuli demonstrated that semantic jokes induced activation in the bilateral posterior middle temporal gyrus and left inferior temporal gyrus, whereas phonological jokes induced activation in the left inferior temporal gyrus and left inferior frontal gyrus (Goel and Dolan, 2001). The study also suggested that a common component of humor is correlated with activity in the ventromedial prefrontal cortex, which is involved in reward processing. In addition, a recent study utilizing verbal stimuli examined distinct brain regions associated with the detection and resolution of incongruities using unfunny, nonsensical and funny stories (Chan et al., 2012b). They found that detection of incongruities was associated with greater activation in the right middle temporal gyrus and the right medial frontal gyrus. Additionally, the resolution of incongruities was associated with increased activation in the left inferior frontal gyrus, superior frontal gyrus and the left inferior parietal lobule. Based on their results, Chan and colleagues suggested a three-stage neural circuit model for verbal humor processing, which includes incongruity detection and incongruity resolution during humor comprehension, and feelings of amusement during humor elaboration. These findings indicate that humor comprehension entails complex cognitive affective interaction. Several recent studies have investigated the relationship between these cognitive and affective components (Amir et al., 2013; Kohn et al., 2011). To explore gender differences in humor comprehension, Kohn et al. (2011) conducted an fMRI experiment using online subjective funniness ratings for parametric modulation. They found different humor processing styles in men compared to women. The results of the parametric modulation analysis indicated that the amygdala, insula, and precuneus are involved in the affective state of understanding a joke. Amir et al. (2013) conducted fMRI experiment using the drawings that were uninterpretable prior to the presentation of a caption (humorous interpretation or nonhumorous (or insight) interpretation). Their results indicated that humorous versus nonhumorous (insight) contrast showed greater activation in the temporal poles and temporo-occipital junction, TPJ, medial prefrontal cortex and reward regions. Based on their results, they hypothesized that neural activation in association cortex would be greater in response to novel, and surprising experiences, resulting in greater opioid release. Activity in these areas, which may facilitate the release of dopamine through reward pathways, may be experienced as pleasurable (Biederman and Vessel, 2006).

Although the regions involved in the cognitive and affective processes underlying perception of humor have been identified in the studies discussed above, the interaction between these regions is unclear. To elucidate these interaction processes, we conducted a functional magnetic resonance imaging (fMRI) experiment to examine the relationship between these cognitive and affective components of humor. To isolate the key factors that enhance funniness, we used stimuli sentences that were nearly identical across conditions (i.e., the first two sentences and the punch line were identical, but the third sentence was different). As illustrated in Fig. 1, we used the same target sentences across conditions so that any differences between the funny and unfunny condition would be due to the neural mechanisms involved in humor comprehension processing. Based on the incongruity-resolution model (Suls, 1972) and the three-stage neural circuit model (Chan et al., 2012b), we hypothesized that the middle temporal gyrus (MTG), medial prefrontal cortex (MPFC), inferior frontal gyrus (IFG), superior frontal gyrus (SFG), and inferior parietal lobule (IPL) would play a key role in comprehension processing, such as incongruity detection and resolution. We also hypothesized that subcortical regions, including the hippocampus, amygdala, and midbrain play a key role in eliciting feeling of amusement. In addition to contrasting the signals obtained in the funny versus unfunny condition, we used psycho-physiological interaction (PPI) analyses to investigate the functional connectivity between the regions involved in cognitive affective interaction of humor comprehension. PPI analysis is a validated method to explain neural responses in one brain area in terms of the interaction between the influences of another brain region and a task condition (Friston et al., 1997; O'Reilly et al., 2012). Thus, we sought to investigate functional interactions among brain regions during humor comprehension, and to evaluate how humor comprehension elicited activity in the mesolimbic reward system.

2. Methods

2.1. Participants

Twenty graduate and undergraduate students (15 women and five men; mean age = 22.5 years; range: 20–34) participated in this experiment. The participants did not have a history of mental or neurological disorders, and were all right-handed,

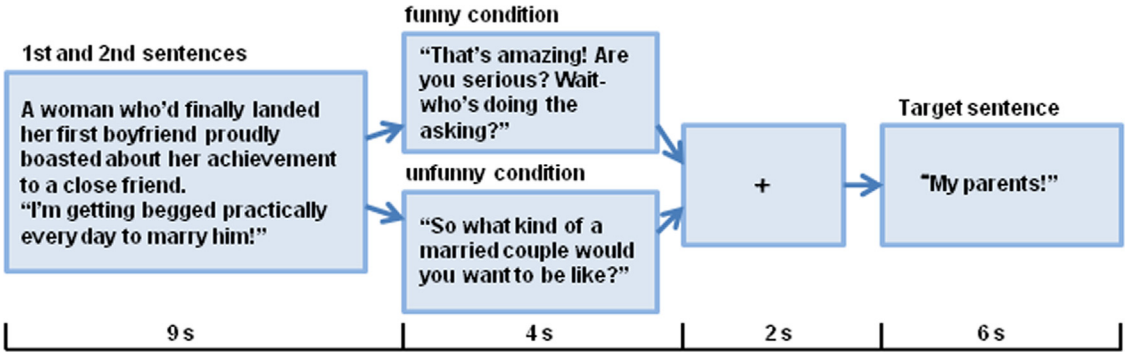

Fig. 1. Experimental paradigm. There were two experimental conditions: the funny and unfunny conditions. The first two sentences and the target sentence (punch line) were identical, while the third sentence differed between conditions. The stimuli were presented in an event-related fMRI paradigm. The analysis was limited to the blood-oxygenation level-dependent (BOLD) signal acquired for each onset point.