Abstract: A humor structure comprises two essential stages: the setup and the punch line. The punch line stage is to provide the incongruity resolution that creates amusement in humor. The current article aimed to look into how humor is amusing and how it differs between the sexes. Functional and effective connectivity analyses in cognitive and affective neuroscience have facilitated the implications of humor comprehension, appreciation, and laughter responses. The processing of incongruity-resolution humor revealed effective connectivity from the amygdala to the precuneus (amygdala → precuneus). Conversely, the processing of nonsense humor demonstrated effective connectivity from the amygdala to the inferior frontal gyrus (amygdala → IFG). During humor appreciation, there was effective connectivity from the ventral tegmental area (VTA) to the amygdala (VTA → amygdala) for incongruity resolution humor and nonsense humor. Interestingly, women exhibited greater activation in the mesolimbic reward system than men.

Keywords: fMRI, humor, verbal jokes, amygdala, functional connectivity, effective connectivity

To Laugh or Not to Laugh: That is the Question of Humor
Techniques and Sex Differences

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Humor may make people laugh and enhance individuals’ mental well-being. Humor facilitates social and interpersonal interactions (Chan et al., 2018b). Nevertheless, the underlying question remains: What is the neural mechanism by which humor elicits amusement and laughter in individuals? The origins of numerous humor techniques can be traced back to the structure and content of humor (Amir & Biederman, 2016; Attardo & Raskin, 1991; Chan & Lavallee, 2015).

Both men and women can understand different forms of humor techniques. Following the understanding of humor, however, there are sex differences in the appreciation of different types (Chan, 2016b). The current article critically reviews functional magnetic resonance imaging (fMRI) studies on humor. The review encompassed an investigation of the structure and content of humor, humor techniques, sex differences in humor, and the implications of humor on education.

1. Humor Structure and Content

1.1 Humor Structure

At the most basic level, the structure of humor consists of two stages: the setup and the punch line (Suls, 1972). In the setup stage, expectations are generated as we listen, based on our store of knowledge about people and things. These expectations are then violated in the punch line stage (Chan, 2023).

Humor processing consists of three components: humor comprehension (cognitive understanding, often denoted as “Aha!”), humor appreciation (affective emotion, amusement) and humor expression (laughter response, signified as “Haha!”) (Chan, 2016b). Neuroscientific studies of humor processing have represented these structures through a limited number of stimuli types (Farkas et al., 2021; Vrticka et al., 2013). Most neuroimaging studies examining humor comprehension and appreciation have used single-panel cartoons (Azim et al., 2005; Chan et al., 2018a, 2022; Kohn et al., 2011; Mobbs et al., 2003; Moran et al., 2004; Samson et al., 2008, 2009; Watson et al., 2007) and two-stage verbal jokes with visual stimuli (Chan et al., 2012, 2013, 2016, 2023a; Chan & Lavallee, 2015; Chan, 2016a, 2016b; Li, 2020). Few studies have used the two-stage structure for cartoons (Bartolo et al., 2006; Chan, 2023; Chan et al., 2023b) and one-liner jokes (Chan et al., 2018b) (Table 1). Some humor studies have used verbal jokes with auditory stimuli (e.g., Goel & Dolan, 2001). Few humor studies have used video to present the stimuli (e.g., Moran et al., 2004; Neely et al., 2013).
### Table 1

Examples of one-stage and two-stage humor structure (setup and punch line) in the cartoons and verbal jokes

<table>
<thead>
<tr>
<th>Humor structure</th>
<th>Cartoon humor</th>
<th>Verbal joke</th>
</tr>
</thead>
</table>
| **A. Single-panel humor**  
Chan et al. (2018a, 2022) | | |
| **B. One-liner jokes**  
Chan et al. (2018b) | | I admire myself so much, sometimes I want to kowtow when I look in the mirror! |
| Setup | + | |
| Punch line | | |

| **C. Two-stage humor**  
Chan (2023)  
Chan et al. (2023b) | **D. Two-stage jokes**  
Chan et al. (2012, 2013, 2016, 2023a)  
Chan and Lavallee (2015)  
Chan (2016a, 2016b) | |
| Setup | | One day, Kevin and Bob went mountain climbing together, but Kevin unexpectedly fell in the valley. Bob contacted Kevin with walkie-talkie, “How are your arms?” Kevin replied, “OK.” Then Bob asked, “How are your legs and feet?” Kevin said, “OK.” And Bob asked, “Can you climb back by yourself?” |
| Punch line | | Keven replied, ”I don’t know, I’m still falling.” |

Note: The humor cartoons were created within the Cognition, Humor and Affect Neuroscience Laboratory (CHAN Lab) by colleagues of the corresponding author.
Humor can be further divided into two categories: incongruity-resolution humor and nonsense humor (Chan et al., 2023b). Incongruity-resolution humor, discussed at length above, represents the ‘typical’ form of humor. Nonsense humor (also known as absurd humor) refers to obviously impossible, unreal, abnormal or exaggerated situations to generate incongruity but the incongruity is either only partly resolved or not resolved at all. Nonsense humor thus represents an ‘atypical’ form of humor in which no real resolution may be possible following the surprise generated by the punch line (Chan et al., 2023b; Samson et al., 2008, 2009, Ruch, 1992) (Table 2).

**Table 2**

*Humor structure and types: incongruity-resolution humor versus nonsense humor*

<table>
<thead>
<tr>
<th>Humor structure</th>
<th>Incongruity-resolution humor (Incongruity and resolution components)</th>
<th>Nonsense humor (Incongruity-only component)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Setup</td>
<td><img src="image1.png" alt="Setup Image" /></td>
<td><img src="image2.png" alt="Setup Image" /></td>
</tr>
<tr>
<td>Punch line</td>
<td><img src="image3.png" alt="Punch line Image" /></td>
<td><img src="image4.png" alt="Punch line Image" /></td>
</tr>
</tbody>
</table>

Note: The humor cartoons were created within the Cognition, Humor and Affect Neuroscience Laboratory (CHAN Lab) by colleagues of the corresponding author.

The processing of incongruity-resolution humor compared to that of nonsense humor shows greater activation in the left anterior medial prefrontal cortex (aMFG), bilateral superior frontal cortex (SFG), bilateral temporo-parietal junction (TPJ), left angular gyrus, and right posterior middle temporal gyrus (pMTG), suggesting that incongruity-resolution humor involves more theory of mind (ToM), understanding others’ intention, and filling the gap. The processing of nonsense humor, compared to that of incongruity-resolution humor, shows increased activation in the left anterior inferior frontal gyrus (aIFG, BA 46), left inferior frontal junction, right IFG, and left extrastriate cortex (BA 39/19), suggesting that nonsense humor involves less self-reference (Samson et al., 2009).

Our lab conducted an fMRI study using
dynamic causal modeling (DCM) with a parametrical empirical Bayes (PEB) approach (Frison et al., 2016; Zeidman et al., 2019a, 2019b, 2023) to investigate incongruity-resolution humor and nonsense humor (Chan et al., 2023b). The processing of incongruity-resolution humor showed effective connectivity from the ventral tegmental area (VTA) of the midbrain to the amygdala (VTA → amygdala) and from the amygdala to the precuneus (amygdala → precuneus), while the processing of nonsense humor involved effective connectivity from the VTA to the amygdala (VTA → amygdala) and from the amygdala to the IFG (amygdala → IFG) (Fig. 1).

Our lab also compared incongruity-resolution humor, nonsense humor, and non-humor using event-related potentials (ERPs) and electromyography (EMG). The incongruity-resolution humor elicited larger N400 responses than did the nonsense humor, while nonsense humor evoked larger P600 than the incongruity-resolution humor, suggesting that nonsense humor is easier to understand. Both types of humor elicited larger “late positive potential” (LPP) than the non-humor condition. The LPP was followed by an EMG to measure the motor response required to generate laughter, whose modal start time was 1200-1400 milliseconds (Hsieh, 2020).

Fig. 1

**Effective connectivity in processing typical and atypical forms of humor**

The processing of incongruity-resolution humor showed effective connectivity from the amygdala to the precuneus (amygdala → precuneus) during humor comprehension and from the VTA to the amygdala (VTA → amygdala) during humor appreciation, while the processing of nonsense humor involved effective connectivity from the amygdala to the IFG (amygdala → IFG) during either only partly resolved or not resolved at all and from the VTA to the amygdala (VTA → amygdala) during humor appreciation. IFG = inferior frontal gyrus, PCu = precuneus, IPL = inferior parietal lobule, VTA = ventral tegmental area, AMG = amygdala.
1.2 Humor content

The content of humor can vary widely and can include aggression, sex, political, horror, or disgust. Table 3 shows the examples of aggressive, sexual, and disgust humor.

Aggressive humor refers to jokes with hostile content (Chan et al., 2016). The superiority theory of humor suggests that the pleasant feeling of amusement from humor arises from the “sudden glory” we feel when the joke suggests our superiority over others (Hobbes, 1651/1982). The better-known relief theory of humor, from Freud’s Jokes and Their Relation to the Unconscious, suggests that laughter releases nervous and repressed energy (Freud, 1905/1974).

Based on the superiority theory and relief theory of humor, a previous study employed 2 (type: aggression and non-aggression) × 2 (joke or not: joke and non-joke) two-way repeated-measures factorial design, including aggressive jokes (aggressive and funny), aggressive non-joke (aggression only), non-aggressive jokes (non-aggressive and funny), and non-aggressive non-jokes (non-aggressive and not funny) (Chan et al., 2016). Aggressive humor compared to aggressive non-humor (baseline) showed greater activation in the dorsomedial prefrontal cortex (dmPFC) and midbrain. Conversely, non-aggressive humor, compared to non-aggressive non-humor (baseline) demonstrated greater activation in the ventromedial prefrontal cortex (vmPFC), amygdala, midbrain, ventral anterior cingulate cortex (vACC), and nucleus accumbens (NAc). Interestingly, aggressive humor compared to non-aggressive humor exhibited increased activation in the mesocortical pathway of the dmPFC and midbrain, while non-aggressive humor compared to aggressive humor showed increased activation in the mesolimbic pathway of the amygdala and midbrain.

Chan et al.’s (2016) study further employed psychophysiological interaction (PPI) analysis of functional connectivity (Friston et al., 1997). The PPI analysis further displayed dmPFC-dlPFC and midbrain-dmPFC functional connectivity for aggressive humor, while non-aggressive humor showed functional coupling in the vmPFC-midbrain, midbrain-amygdala, amygdala-midbrain, and amygdala-NAc functional couplings. Combining the brain and behavioral results showed aggressive humor was not perceived as funnier than non-aggressive humor (Chan et al., 2016). However, previous behavioral studies have shown aggressive humor was perceived as funnier than non-aggressive humor (e.g., Weinstein et al., 2011). Future studies could further investigate the sex/gender differences in appreciation of aggressive humor, perhaps with a focus on the target of the humor (men or women).
### Table 3

*Examples of humor content: aggressive jokes, sexual jokes, and disgust jokes*

<table>
<thead>
<tr>
<th>Humor techniques</th>
<th>Humor structure</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Setup</td>
</tr>
<tr>
<td>Aggressive jokes</td>
<td>Female: Do you see the man sitting over there? He has been drinking every day since I rejected his marriage proposal five years ago.</td>
</tr>
<tr>
<td>Sexual jokes</td>
<td>Wife: If there were only 5 minutes left until the end of the world, what would we do? Husband: Have sex, of course!</td>
</tr>
<tr>
<td>Disgust jokes</td>
<td>There was a competition to see who would dare to eat the most disgusting food. One man ate feces, but only got second place. What did the first-place winner eat?</td>
</tr>
</tbody>
</table>

### 2. Humor techniques

Successful humor makes use of distinct humor techniques in the presentation of the key features of the humorous situation and the key relationships between them via humor structure or humor content. Such techniques include bridging-inference (as in incongruity-resolution humor), logical impossibility (as in nonsense humor), ambiguity, exaggeration, pun, irrelevance, inappropriateness, reasoning, imitation, pretense, or contradiction. Bridging-inference requires the use of logical inferences to “fill the gap” left by the detection of an incongruity, in order to restore coherence to the situation. The ambiguity technique makes use of semantic, phonological, and syntax ambiguity to generate humor. The exaggeration technique requires violation of “common sense” limits to do the same thing (Chan & Lavallee, 2015) (Table 4)
To laugh or not to laugh: That is the question of humor techniques and sex differences

Table 4
Examples of humor techniques

<table>
<thead>
<tr>
<th>Humor techniques</th>
<th>Humor structure</th>
<th>Setup</th>
<th>Punch line</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bridging-inference jokes</td>
<td>Jack had dreamed of being a writer since he was little. His dream came true at 30 when his book was finally published. One month later, Jack asked his friend: “Have you seen my book yet?” his friend says: “Yes, I bought a copy.”</td>
<td>Jack happily responses: “Ah! That was you.”</td>
<td></td>
</tr>
<tr>
<td>Ambiguity jokes</td>
<td>It was Christmas and the judge was in a benevolent mood as he questioned the prisoner. &quot;What are you charged with?&quot; he asked.&quot; Doing my Christmas shopping early,&quot; replied the defendant.&quot; That's no offense,&quot; replied the judge. &quot;How early were you doing this shopping?&quot;</td>
<td>“Before the store opened”, replied the prisoner.</td>
<td></td>
</tr>
<tr>
<td>Exaggeration jokes</td>
<td>One day, Kevin went to a dentist. When he opened his mouth, the dentist said “Oh, your cavity is so deep. Oh, your cavity is so deep.” Kevin got upset and said “I know I have bad teeth, but I don't think you need to repeat it three times!”</td>
<td>The dentist replied, “I didn't! That’s an echo.”</td>
<td></td>
</tr>
</tbody>
</table>

The existence of different techniques raises further questions. Are different brain areas involved in processing humor constructed in different ways? One study seeking to answer this question used a 3 (type: bridging-inference, exaggeration, and ambiguity) × 2 (joke or not: joke and non-joke) two-way repeated-measures factorial design, including six conditions (Chan & Lavallee, 2015). For all joke types, humor comprehension showed increased activation in the left dorsolateral prefrontal cortex (dPFC), while humor appreciation showed greater activation in the left ventral anterior cingulate cortex (vACC). Bridging-inference jokes compared to baseline non-jokes showed increased activation in the bilateral temporoparietal junction (TPJ), right middle temporal gyrus (MTG), and left orbitofrontal cortex (OFC), suggesting the use of theory of mind (ToM) processing and understanding others’ intentions to fill the gap. The processing of exaggeration jokes compared to the baseline non-jokes showed increased activation in the bilateral inferior parietal lobule (IPL), right inferior frontal gyrus (IFG) and right amygdala. Finally, the processing of ambiguity jokes compared to the baseline non-jokes showed increased activation in the left vACC and right parahippocampus. The findings suggest that the cognitive operations required for filling the gap, dis-exaggeration, and disambiguation do indeed differ (Chan & Lavallee, 2015).

3. Sex differences in humor

Sex/gender differences in humor have been a topic of interest for years (Azim et al., 2005; Chan, 2016b; Kohn et al., 2011). The sexual selection theory (Darwin, 1872), evolutionary theory of humor (Miller, 1908, 2011), and
evolutionary neuroandrogenic theory (ENA) (Ellis, 2011) have all been drawn on to suggest a key role in the evolution of humor by sexual selection and evolutionarily-shaped genetic factors. These theories involve sex differences in humor processing.

Previous studies have shown that the neural correlates of humor comprehension and humor appreciation are different for men and women. Women demonstrate greater activation in the prefrontal cortex (e.g., IFG, dPFC, MFG) and mesolimbic regions (e.g., nucleus accumbens, NAc) than men, areas associated with executive function and the reward system, respectively (Azim et al., 2005). Women have also been found to display greater activation in the limbic system (amygdala, insula and ACC), while men have been shown to display increased activation in the dorsal stream (e.g., dIPFC) (Kohn et al., 2011).

Based on earlier findings related to joke types (Chan & Lavallee, 2015), Chan attempted to analyze the neural correlates of sex differences underlying humor processing (Chan, 2016b). Based on Chan’s (2016b) tri-component theory of humor framework, Chan used a 2 (sex: men and women) × 3 (type: bridging-inference jokes, exaggeration jokes, and ambiguity jokes) two-way mixed factorial design (Chan, 2016b).

Results revealed that, for bridging-inference jokes, women showed greater activation than men in the anterior prefrontal cortex (aPFC), TPJ, parahippocampus gyrus, insula, OFC, and supplementary motor area (SMA). The TPJ plays a key role in understanding others’ intentions. The OFG is involved in evaluating value and in emotion regulation. The SMA plays a role in laughter response. For exaggeration jokes, women demonstrated greater activation than men in the aPFC, amygdala, midbrain, parahippocampus gyrus, and insula. For ambiguity jokes, women showed greater activation than men in the aPFC. Conversely, men showed greater activation than women in the dIPFC for bridging-inference jokes, and dorsal prefrontal cortex (dPFC) for exaggeration jokes. Also, for ambiguity jokes, men showed greater activation than women in the dPFC and parahippocampal gyrus. In sum, women demonstrate greater activation in the subcortical areas (e.g., midbrain, amygdala, and insula) during humor appreciation, while men demonstrate greater activation in the cortical areas (e.g., dPFC) (Chan, 2016b).

A further study on sex differences conducted by our lab, this time in response to monetary versus humor rewards, was conducted effective connectivity using a DCM-PEB approach (Chen, 2019). Men showed greater effective connectivity than women from the vmPFC to the NAc following the receipt of monetary rewards, while women displayed greater effective connectivity from the amygdala to the midbrain than did men upon receipt of humor rewards. The findings provide a better understanding of where and how underlying neural correlates interact with sex and reward types.

4. Implications of the neuroscience of humor for education

Humor is an adaptive coping mechanism (Chan et al., 2023a). Although some people possess an innate sense of humor, it is a skill that can be learned. Employing humor techniques can lead to an enhanced sense of humor. People are, therefore, skilled at using humor in conversation, novels, and social settings. Humor training can improve one’s ability to be creative and generate humor (Chan et al., 2018b). The efficacy of the training can be assessed by comparing the neural plasticity that happens prior to and following humor
training. For instance, the term “gelotophobia” refers to the fear of receiving ridicule from others (Ruch & Proyer, 2009). Gelotophobes (i.e., individuals with gelotophobia) may improve their sense of humor and decrease their social anxiety by acquiring humor techniques, which is advantageous for humor training (Chan, 2016a).

Regarding “humor techniques,” men preferred ambiguous jokes, while women found bridge-inference and exaggeration jokes more amusing than men. Humor enhances students’ focus on the instructor and the material being taught. Does humor enhance the learning process for students in the classroom? Does the utilization of humor in the classroom enhance students’ attention? Previous studies on using humor to enhance learning in educational settings indicated that male teachers were more inclined than female teachers to incorporate humor into their instruction. However, sex differences have lately diminished (e.g., Bryant et al., 1980). Future research may look into using humor in instruction in an educational setting by male and female teachers utilizing the fMRI approach. Furthermore, forthcoming research investigates the impact of sex differences in aggressive and sexual humor, explicitly focusing on the differences in “humor content” between the sexes (Chan et al., 2022).

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Declaration Statement

Data Availability Statement
The data the support the findings of this study are available from the corresponding author upon request.

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Conflict of Interest Disclosure
The author declares no conflict of interest.

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Participant Consent Statement
All participants signed written informed consent forms prior to the experiment.

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