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fMRI Studies of Humor

Interest in brain imaging research has increased rapidly over several decades. In that time, there have been numerous studies revealing details of how the brain functions. The majority of these studies have been conducted using functional magnetic resonance imaging (fMRI; Gorgolewski & Poldrack, 2016). fMRI was invented in 1991 and built on the existing technology of magnetic resonance imaging (MRI; Logothetis, 2008), which provides detailed images of anatomical structures of the body, including the brain. As the name suggests, the technology involves exposing the body to a strong magnetic field. MRI is routinely used in hospital settings, to identify problems, such as tumors, broken bones, or torn ligaments. MRI provides excellent information about anatomy, but no information about temporal changes occurring in the body during the scanning. fMRI was invented to do just that. Images generated with fMRI provide information about activity in the body occurring over a time interval (e.g., 6 seconds or more). This chapter begins with an overview of the methodology, followed by a review of early fMRI studies of humor comprehension. The chapter will also review recent fMRI evidence that supports the three-stage model of humor comprehension is also reviewed. Finally, several studies that have used fMRI to investigate the comprehension of humorous forms of irony are also discussed.

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The Cognitive Neuroscience of Humor, by S. M. Kennison

OVERVIEW OF THE fMRI METHODOLOGY

fMRI and MRI involve recording the body when it is exposed to a strong magnetic field. Changes in the cells of the body when the magnet is turned on, then off are recorded. During scanning, participants must lie horizontally within a small cylinder for the duration of the study (i.e., 60–120 minutes) as motionless as possible. Movements during scanning can lead to brain response, which may make it harder to detect the relatively small changes in blood flow that are related to cognitive processing during the task of interest (Haller & Bartsch, 2009). The most common form of fMRI uses blood-oxygen-level dependent (BOLD) imaging, which involves sophisticated computer programs to transform the recorded data into images that show the amount of blood in different brain regions (Logothetis, 2008; Mettler & Guiberteau, 2012). Since the work of Angelo Mosso (1846–1910), researchers have recognized that blood flow changes in the brain occur and can be measured (Raichle, 2009). Regions with more blood flow are viewed as more active during processing and viewed as playing a larger role in the processing than in the regions with less blood flow.

Since the introduction of fMRI, researchers have developed multiple procedures for presenting task stimuli to participants during scanning and for creating composite images of the activity occurring during specific periods of time during processing. In early fMRI studies, researchers tested different conditions with participants using a block design (Tie et al., 2009). Participants would experience all instances of one type or condition of stimuli (e.g., nonhumorous cartoons), then rest, and then they would see all instances of a second type or condition of stimuli (e.g., humorous cartoons). With advances in computer software, researchers now have the option to intermix instances of all conditions in the testing session. This type of design is referred to as the event-related design and has been used in most of the studies on humor processing. Some have criticized the event-related design in fMRI studies on statistical grounds, as the measurement of blood flow captured during a single instance of a condition may be unreliable (Buckner, 1998; Rosen et al., 1998). Tie et al. (2009) compared results for the same stimuli using block and event-related designs, finding that the event-related design yielded similar results compared with the block design. It is important to note that neither design provides information about changes in the brain that occur millisecond-by-millisecond (Logothetis, 2008), which would be useful in understanding simple cognitive processes (i.e., recognizing a picture or word). Eye movement research has shown that the recognition of a single word may occur as rapidly as 50 ms (Rayner et al., 2012). For this reason, it is important to remember that fMRI studies provide good information about the brain regions for a complete cognitive process, but they may not provide insight into the activity of brain regions involved in stages of processing that occur along the way. As with EEG/ERP, one would expect that to observe differences in brain responses to stimuli that involve different sensory systems. Processing of visual stimuli would be expected to involve more activity in the occipital lobes (vs. other sensory regions) to a greater extent than processing of auditory stimuli, which would be expected to activity in the temporal lobes (vs. other sensory regions).

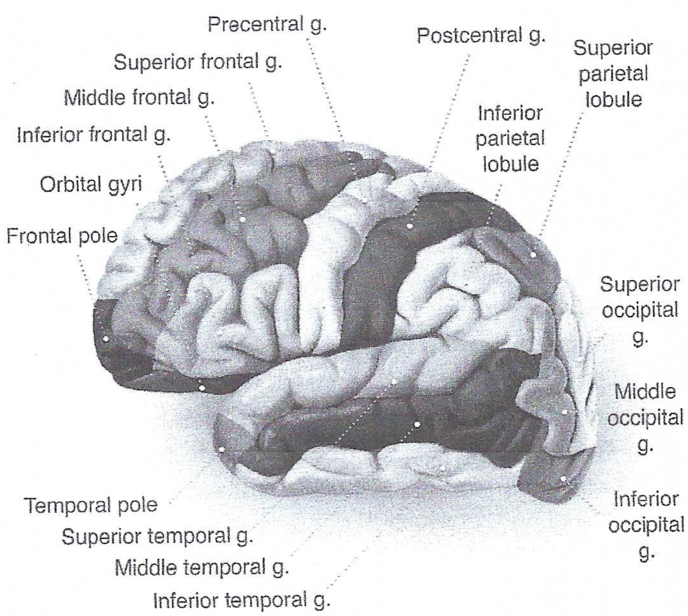
Most fMRI studies commonly use comparisons of brain activity when participants carry out tasks involving different cognitive processes. There continues to be debates among fMRI researchers about how the vast amounts of data generated should be analyzed (Ashby, 2011). One such technique is referred to as the subtraction paradigm in which brain activity recorded during a baseline (control) condition is subtracted from brain activity recorded as an experimental condition (Kemmerer, 2015). An alternative approach involves correlating the activity recorded in different brain regions during conditions that vary in complexity (e.g., baseline control condition that does not include the target cognitive process and an experimental condition that does include the target cognitive processing). In the studies that I review later in this chapter, researchers typically have compared processing in a humorous condition (e.g., reading or listening to a joke) with processing in a nonhumorous condition (e.g., reading or listening nonhumorous statements). In some studies, researchers have included multiple types of humorous stimuli (e.g., puns vs. other types of humor). Because puns (e.g., "Reading while sunbathing makes you well red") are likely to involve processing related to the sounds of words in the joke in addition to the meanings, researchers have hypothesized that brain activity occurring during the processing of puns may differ from brain activity occurring during the processing of other types of jokes (Y.-T. Chang et al., 2019; Coulson & Severens, 2007).

In recent years, researchers have attempted to carry out studies in which the excellent temporal information using electroencephalography/event-related brain potential (EEG/ERP) methodology can be recorded along with the excellent location information using fMRI methodology (Huster et al., 2012; Lei et al., 2012). Combining the two methodologies is sometimes not possible, because most researchers use metal electrodes (e.g., stainless steel, silver, tin) that are incompatible with a strong magnetic field. One solution is to have participants perform the cognitive task twice in quick succession, once while fMRI scanning is carried out and once while EEG/ERP recording is carried out. The advantage of this approach is that researchers obtain good temporal and location information about the brain's activity during the cognitive task. The disadvantage is that the repeated testing may lead to participants to carry out the task somewhat differently the second time. Another solution is to use carbon wire electrodes, which enable data collection during fMRI scanning (M. C. Meyer et al., 2020; Negishi et al., 2008). This strategy is used less frequently, perhaps because of the higher cost of carbon wire electrodes. Although none of the studies on humor processing reviewed in this chapter used fMRI with EEG/ERP, this innovation would be the next logical step in understanding more completely how humor is processed.

EARLY fMRI STUDIES OF HUMOR COMPREHENSION

fMRI researchers began reporting studies on humor processing in the 2000s (Bartolo et al., 2006; Goel & Dolan, 2001; Mobbs et al., 2003, 2005; Moran et al., 2004; A. C. Samson et al., 2008; Watson et al., 2007; Wild et al., 2006). In the earliest study, Goel and Dolan (2001) scanned 14 right-handed participants (gender not specified) as they listened to jokes, which were either semantic jokes (e.g., "What do engineers use for birth control? Their personalities") or phonological jokes or puns (e.g., "Why did the golfer wear two sets of pants? He got a hole in one"). They used an event-related design, which allowed them to present the jokes in random order to participants intermixed with nonjoke control items. For each joke, participants heard the setup of the joke, followed by a pause of 1,580 ms, then the punchline. Following each joke or nonjoke control, participants were asked to provide a rating of the item's humorousness using a keypad. The BOLD response was recorded from the midpoint of the presentation of the punchline to the keypress. The results show that during joke comprehension, there was increased blood flow in multiple brain regions: an area in the prefrontal cortex that was ventral and medial (i.e., ventromedial prefrontal cortex) and an area in the posterior region of the middle temporal

FIGURE 4.1. Location of the Prefrontal Cortex and the Middle Temporal Gyrus



Note. The surface of the brain contains multiple gyri. The major gyri of the left hemisphere are illustrated here. Each of the gyri also occur in the right hemisphere. g. = gyrus. From *Neuroanatomy: Lateral Cortex (Diagrams)*, by F. Gaillard, n.d., Radiopaedia.org (https://radiopaedia.org/cases/neuroanatomy-lateral-cortex-diagrams?lang=us). CC BY 4.0.

gyrus (i.e., posterior medial temporal gyrus). Figure 4.1 displays the location of the prefrontal cortex and the middle temporal gyrus. The results also show that semantic jokes produced more bilateral activity than puns, which produced more left hemisphere than right hemisphere activity. For both types of jokes, increases in blood flow were larger for jokes that participants rated as more humorous. Goel and Dolan suggested that some of the regions are involved in the comprehension aspects of humor processing while others are involved in the emotional aspects of humor processing (i.e., experiencing amusement).

Mobbs et al. (2003) scanned 16 right-handed participants (seven men, nine women) as they viewed cartoons, which were humorous or nonhumorous, using an event-related design. Nonhumorous cartoons were created by removing text from the cartoon, which was the source of the humor. They recorded BOLD signals for 6 seconds following the presentation of each cartoon. Their results indicated that there was increased blood flow in four regions in the left hemisphere during comprehension of the cartoon: (a) a region where the occipital lobe borders the temporal lobe (i.e., temporal-occipital junction; see Figure 1.5, Chapter 1, this volume); (b) a region including the inferior frontal gyrus (see Figure 4.1) as well as the most anterior region of the temporal lobe; (c) a region including the supplementary motor area (see Figure 2.2, Chapter 2, this volume) and encompassing the presupplementary motor area and the dorsal anterior cingulate cortex (see Figure 1.7, Chapter 1, this volume); and (d) ventral subregions of the basal ganglia (see Figure 2.1, Chapter 2, this volume), the amygdala, and the hypothalamus (see Figure 1.7, Chapter 1, this volume). Activity in the right hemisphere was observed for the latter group of regions. Mobbs et al. suggested that the observed activity was consistent with Suls's (1972) two-stage model involving incongruity detection followed by resolution. They suggested that increased blood flow in the temporoparietal junction coincided with incongruity detection. Increased blood flow in the inferior temporal gyrus (roughly Broca's area) may have reflected participants' semantic integration during the resolution of the incongruity. Increased blood flow in the regions controlling movement may have coincided with participants' smiling, laughing, and/or feeling of amusement.

Moran et al. (2004) recorded blood flow in the brain as participants watched complete episodes of television comedies, displayed visually while audio was played over headphones. The participants were instructed only to watch and were not required to respond in anyway. In Experiment 1, 12 right-handed participants (five men, seven women) viewed an episode of *Seinfeld*. In Experiment 2, 13 right-handed participants (six men, seven women) viewed an episode of *The Simpsons*. Participants heard the original laugh track of *Seinfeld*, but the researchers created a laugh track for *The Simpsons* by recording the natural laughter of a group of college students who watched the episode. Both experiments used an event-related design. Moran et al. were interested in understanding the brain regions involved in the distinct stages of getting the joke and appreciating the joke. They identified humorous moments (confirmed by independent coders) where laughter occurred in the laugh tracks. BOLD signals were recorded for 2 seconds before the laughter of the humorous moment and also for varying durations following the humorous moment. The results suggested that the cognitive processing involved in the humor processing was related to increased blood flow in the left posterior temporal lobe and the left inferior frontal lobe areas. Moran et al. further linked emotional processes involved in the humor appreciation with increased activity in the amygdala (see Figure 1.7, Chapter 1, this volume) and the insula, which is located in the sulcus of the sylvan fissure (see Figure 4.1). Activity was observed bilaterally in these areas (i.e., in the left and right hemispheres).

Bartolo et al. (2006) compared brain activity as 21 right-handed participants (eight men, 13 women) comprehended pairs of cartoons, which contained no text, but told a single story with the second cartoon containing the elements in which the humor was discovered. Funny cartoon pairs were compared with cartoons pairs that were not funny (as determined by independent raters). The researchers used an event-related design in which humorous and non-humorous cartoon pairs were randomly presented, and BOLD signals were recorded. Each trial involved each cartoon in the pair presented for 3 seconds with a 500 ms blank between them. Brain activity was recorded for 10 seconds following the presentation of the second cartoon. Their results showed that during the processing of humorous cartoons, brain activity was higher in four regions: left cerebellum (see Figure 2.1, Chapter 2, this volume), the left middle temporal gyrus, the left superior temporal gyrus, and the right inferior frontal gyrus (see Figure 4.1). Bartolo et al. also found that there was increased blood flow in the left amygdala when participants comprehended the funniest cartoons, suggesting that these areas are involved in processing the positive emotion that occurs during humorous experiences. The authors suggested that the participants' perception of the humor in the nonverbal cartoon pairs occurred when they considered the intention of a character in the cartoons.

Wild et al. (2006) scanned 13 right-handed men while they comprehended nonverbal cartoons, which were either humorous or nonhumorous. The authors used an event-related design in which the order of cartoons were randomized, and BOLD signals were recorded. Participants were also video-taped to determine on whether smiling occurred. On some trials in which a nonhumorous cartoon was displayed, participants were instructed to smile, a condition that Wild et al. referred to as nonhumorous smiling. The results showed that when participants comprehended the funny cartoons, there was increased blood flow in the left temporal-occipital-parietal junction and the left anterior prefrontal cortex. When cartoons evoked smiling by participants, there was increased blood flow observed in the bottom area of the left and right temporal lobes. When participants smiled as instructed while viewing nonhumorous cartoons, there was increased blood flow in the areas of the motor cortex (see Figure 2.2, Chapter 2, this volume), which controls movement of the face and other body parts. Wild et al. concluded that there are distinct brain regions associated with voluntary, unemotional smiling and the smiling that accompanies the emotional experience of humor. The next chapter will show that this conclusion is supported in studies in which specific brain regions are stimulated directly with electricity.

Only a few fMRI studies have compared brain responses for different types of humorous stimuli within the same experiment (Chan & Lavallee, 2015; A. C. Samson et al., 2008; Watson et al., 2007). For example, Watson et al. (2007) compared changes in blood flow during the comprehension of cartoons that were either language-based cartoons (i.e., the caption was required for the humor) and visual-based cartoons (i.e., the humor stemmed from the drawing itself). They scanned 20 right-handed participants (12 men, eight women) using an event-related design in which the different types of cartoons and nonhumorous control cartoons were presented in random order. At the end of each trial, participants were asked to rate the humorousness of the cartoon. The results showed that different patterns of responses were observed for the two types of stimuli with visual areas in the occipital lobe showing increased blood flow during the comprehension of visual humor and language processing areas (e.g., the inferior temporal gyrus, the superior temporal sulcus, the middle temporal gyrus) showing increased blood flow during the comprehension of language-based jokes. For both types of jokes, there was increased blood flow in the amygdala and regions located in the midbrain, which was viewed as likely related to the experience of amusement, as well as increased blood flow in the anterior cingulate gyrus (see Figure 1.7, Chapter 1, this volume) and the anterior region of the insula, within the sylvan fissure (see Figure 4.1).

A. C. Samson et al. (2008) compared blood flow as participants viewed four types of nonverbal cartoons: semantic cartoons; visual puns, which included ambiguity among visual elements in the cartoon; theory of mind cartoons, which required the perceiver to consider the intention of a character in the cartoon; and cartoons that contained irresolvable incongruity (i.e., there was no clear way to interpret the meaning of the image). A. C. Samson et al. scanned 17 participants (eight men, nine women) using an event-related design as they comprehended each stimulus. After each trial, participants provided a rating of the cartoon's comprehensibility. After the entire session, participants rated the humorousness of the cartoons. The results showed that for all types of humorous stimuli, when participants resolved incongruity, there were increases in blood flow in left hemisphere regions, specifically the ventromedial prefrontal cortex, inferior frontal gyrus, and the border between the temporal and parietal lobes (i.e., the temporoparietal junction). Comprehending visual puns led to increased blood flow in the visual processing area of the occipital lobe (see Figure 1.5, Chapter 1, this volume). When participants comprehended cartoons involving theory of mind processing, there was increased blood flow in three regions in the left and right hemispheres: the temporoparietal junction; the precuneus (see Figure 4.2); and the fusiform gyrus, which is located below the inferior temporal gyrus (see Figure 4.1). When participants viewed cartoons with unresolvable incongruity, there was increased blood flow in a region of the anterior region of the cingulate (see Figure 1.7, Chapter 1, this volume).

FIGURE 4.2. Location of the Precuneus

Note. The precuneus (outlined region) is located in the posterior parietal lobe and borders the occipital lobe. Each hemisphere contains a precuneus region. Adapted from *Precuneus*, by G. B. Hall, 2011, Wikimedia Commons (https://commons.wikimedia.org/wiki/File:Precuneus.png). CC0 1.0.

Among the early fMRI studies of humor comprehension, several investigated individual differences, most comparing humor processing in men and women (Azim et al., 2005; Kohn et al., 2011) and one exploring individual differences in personality (Mobbs et al., 2005). Azim et al. (2005) had 20 right-handed participants (10 men, 10 women) view 70 cartoons, which they then rated in terms of funniness. The authors used an event-related design in which humorous and nonhumorous cartoons were presented in random order, and BOLD signals were recorded for 6 seconds as participants viewed the cartoon. The results indicated that for men and women, there was increased blood flow in three brain regions: the inferior frontal gyrus; the temporal pole, which is located at the most anterior location of the temporal lobe; and the temporal-occipital junction. For women, there was greater blood flow than there was for men in regions in the left prefrontal cortex (see Figure 4.1) and the mesolimbic regions, which are located in the ventral region of the basal ganglia. The mesolimbic regions are known to be involved in experiencing pleasure and reward processing from a variety of activities including eating, having sex, and using opioids (Berridge & Kringelbach, 2015).

In a similar study, Kohn et al. (2011) recorded brain activity in 29 right-handed participants (15 men, 14 women) as they comprehended nonverbal cartoons using an event-related design in which humorous and nonhumorous cartoons were presented in random order. Participants were scanned for 7 seconds while viewing each cartoon. Their results observed differences in men and women's brain activity, but in regions different from those studied by Azim et al. (2005). Kohn et al. found that when comprehending humorous cartoons, women had more blood flow than men in three brain regions: the amygdala (see Figure 1.7, Chapter 1, this volume); the insula, which is located in the sulcus of the sylvan fissure; and the anterior region of cingulate cortex, which is located just above the corpus callosum (see Figure 1.7, Chapter 1, this volume).

Mobbs et al. (2005) investigated brain activations with fMRI during humor processing for individuals varying in personality. Individuals reporting higher levels of extraversion produced greater activation during humor processing, specifically in the temporal lobe of the left hemisphere and several right hemisphere regions, including the orbital frontal cortex, the ventrolateral prefrontal cortex, and the temporal lobe. Individuals reporting higher levels of introversion produced greater activation during humor processing in the left and right amygdalae.

In summary, the early fMRI studies of humor comprehension used multiple types of stimuli (e.g., jokes, cartoons, television shows) and identified a variety of brain areas that became more active during humor comprehension. Two studies observed differences in brain responses during humor processing for men and women with women exhibiting larger responses in the prefrontal cortex and mesolimbic regions than men. Individual differences in extraversion/introversion were also found to be related to differences in the amount of activation in brain areas during humor processing. A summary of the early fMRI studies of humor processing is provided in Table 4.1.

fMRI EVIDENCE FOR A THREE-STAGE MODEL OF HUMOR COMPREHENSION

A series of fMRI studies by Chan and colleagues (Chan et al., 2012, 2018; Chan, Chou, et al., 2013; Dai et al., 2017) has extended the work of earlier studies, not only confirming the involvement of specific brain areas in humor processing, but also supporting a three-stage model of humor processing. In one of the earliest studies, Chan, Chou, et al. (2013) recorded BOLD signals as 22 right-handed participants (nine men, 13 women) listened to humorous, nonhumorous, and nonsensical stories. They used an event-related design in which the 16 stimuli for each of the three conditions and 16 additional filler nonhumorous stimuli were intermixed. Each story was presented in two parts: the setup for 20 seconds and the ending for 9 seconds, which was a punchline in humorous conditions. Participants provided a rating of the stories' comprehensibility. By comparing brain responses during the processing of different pairs of conditions, they were able to identify brain regions involved incongruity detection, which involves semantic processing by comparing brain

TABLE 4.1. Summary of Early fMRI Studies of Humor Comprehension

Study	Type of stimuli	Brain regions
Goel & Dolan (2001)	Jokes	ventral medial prefrontal cortex posterior middle temporal gyrus
Mobbs et al. (2003)	Cartoons	left temporal-occipital junction Broca's area and other left frontal areas
Moran et al. (2004)	Television comedies	the left inferior frontal lobe left posterior temporal lobe amygdala and insula
Mobbs et al. (2005)	Cartoons	left and right temporal lobe right orbital frontal cortex right ventrolateral prefrontal cortex
Azim et al. (2005)	Cartoons	the inferior frontal gyrus the temporal pole the temporal-occipital junction left prefrontal cortex mesolimbic region
Wild et al. (2006)	Cartoons	left temporal-occipital junction
Bartolo et al. (2006)	Cartoons	the left middle temporal gyrus the left superior temporal gyrus the right inferior frontal gyrus left cerebellum amygdala
Watson et al. (2007)	Jokes and cartoons	anterior insula the anterior cingulate cortex amygdala and midbrain regions
A. C. Samson et al. (2008)	Cartoons	left ventromedial prefrontal cortex left inferior frontal gyrus left temporoparietal junction anterior cingulate cortex
Kohn et al. (2011)	Cartoons	amygdala insula anterior cingulate cortex

activity in nonhumorous conditions versus nonsensical conditions. These regions were the right medial temporal gyrus and right medial frontal gyrus (see Figure 4.1, which displays the corresponding regions in the left hemisphere). Chan, Chou, et al. were able to identify brain regions involved in incongruity resolution by comparing brain activity in humorous and nonsensical conditions. These regions were the left inferior frontal gyrus, the left superior frontal gyrus, and the left inferior parietal lobe (see Figure 4.1). On the basis of their results and results of prior research, Chan, Chou, et al. speculated that the brain regions involved in humor elaboration, which ultimately brings about the feeling of mirth, included the left ventromedial prefrontal cortex, the right anterior cingulate, the left and right amygdalae, and the left and right parahippocampus gyrus. Table 4.2 displays the brain regions associated with the three stages of humor processing.

More recently, Dai et al. (2017) provided a revision to the three-stage model of humor processing. They hypothesized that the processing of incongruity–resolution and nonsense humor may involve different neural regions because nonsense humor involves incongruity that may be unresolvable yet results in humor and amusement. They recorded BOLD signals from 27 right-handed participants (15 men, 12 women) who comprehended short stories that ended a punchline that involved incongruity–resolution humor, nonsense humor, or neutral meaning, which served as the nonhumorous control. For each humorous story, the nonhumorous control was created by changing the punchline to remove the humor. Participants were scanned for 14 seconds as they read the setup of the story and 9 seconds as they read the punchline. After each story, participants provided a humorousness rating. The results showed that for both types of humorous condition, humor comprehension was associated with activity in the middle temporal gyrus and the middle frontal gyrus. However, Dai et al. observed differences in activity for brain regions for the two types of humor. They concluded that incongruity resolution for humor involving an incongruity–resolution structure led to increased blood flow in the temporoparietal junction in the precuneus, which is located in the posterior parietal lobe, including the portion that borders the occipital lobe (see Figure 4.2). Humor elaboration for incongruity–resolution humor led to increased blood flow in the posterior region of the cingulate cortex, which lies just above the corpus callosum (see Figure 1.7, Chapter 1, this volume), the amygdala, and the parahippocampal gyrus, which is a layer of tissue surrounding the hippocampus. In contrast, when participants comprehended nonsense humor, humor comprehension was associated with greater blood

TABLE 4.2. Brain Regions Involved in the Three Stages of Incongruity–Resolution Humor Processing

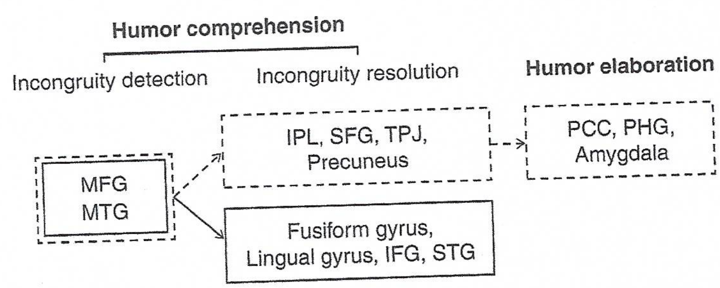
Stage of humor processing	Type of processing	Brain regions
Incongruity detection	Semantic processing	medial frontal gyrus middle temporal gyrus
Incongruity resolution	Semantic selection and integration	inferior frontal gyrus superior frontal gyrus inferior parietal lobe
Humor elaboration	Emotional response (amusement)	ventromedial prefrontal cortex anterior cingulate cortex amygdala parahippocampal gyrus

Note. From "Towards a Neural Circuit Model of Verbal Humor Processing: An fMRI Study of the Neural Substrates of Incongruity Detection and Resolution," by Y.-C. Chan, T.-L. Chou, H.-C. Chen, Y.-C. Yeh, J.P. Lavallee, K.-C. Liang, and K.-E. Chang, 2013, *NeuroImage, 66*, p. 175 (https://doi.org/10.1016/j.neuroimage.2012.10.019). Copyright 2013 by Elsevier. Adapted with permission.

flow in the inferior frontal gyrus, the superior temporal gyrus, the fusiform gyrus located below the inferior temporal gyrus (see Figure 4.1), and the lingual gyrus (located above the fusiform gyrus extending from the medial temporal lobe into the medial occipital lobe). Figure 4.3 displays Dai et al.'s (2017) three stages of processing for incongruity–resolution and nonsense humor.

Other fMRI studies have observed results that have proven to be largely consistent with a three-stage model of humor processing (Amir et al., 2015; Campbell et al., 2015; S. Feng, Ye, et al., 2014; Franklin & Adams, 2011; Nakamura et al., 2018; Osaka et al., 2015; Shibata et al., 2014; Tian et al., 2017; see also Bekinschtein et al., 2011). Shibata et al. (2014) recorded BOLD signals from 20 participants (five men, 15 women) in an event-related design as they comprehended short discourses composed of three sentences. They were innovative in their construction of materials, as they created humorous and nonhumorous stimuli that had the same first and last sentences. This enabled them to compare processing on the punchline in humorous conditions, which had the same words as the nonhumorous conditions. Their results indicated that in humorous conditions, there was increased blood flow in the right middle temporal gyrus (see Figure 4.1), which was described as incongruity detection, and also in the left inferior frontal gyrus, the left inferior parietal lobe and the left superior frontal gyrus, which corresponded to incongruity resolution. Shibata et al. also noted that participants' brain responses revealed connections between the midbrain, which may be involved in the emotional response to humor (i.e., humor elaboration), and three regions in the cortex:

FIGURE 4.3. The Three-Stage Model of Processing Incongruity-Resolution and Nonsense Humor



Note. Dai et al. (2017) proposed that there are different brain regions involved in three stages of humor processing for incongruity-resolution humor (boxes with dotted lines) and nonsense humor (boxes with solid lines). MFG = medial frontal gyrus; MTG = medial temporal gyrus; IPL = inferior parietal lobe; SFG= superior frontal gyrus; TPJ = temporo-parietal junction; IFG = inferior frontal gyrus; STG = superior temporal gyrus; PCC = posterior cingulate cortex; PHG = parahippocampal gyrus. From "To Resolve or Not To Resolve, That Is the Question: The Dual-Path Model of Incongruity Resolution and Absurd Verbal Humor by fMRI," by R. H. Dai, H.-C. Chen, Y. C. Chan, C.-L. Wu, P. Li, S. L. Cho, and J.-F. Hu, 2017, *Frontiers in Psychology, 8*(498), p. 11 (https://doi.org/10.3389/fpsyg.2017.00498). CC BY.

the right middle temporal gyrus, the left inferior parietal lobe, and the inferior frontal gyrus.

Osaka et al. (2015) scanned participants as they comprehended a series of four cartoon panels (i.e., Manga style cartoons). They used an event-related design in which each panel was presented for 3 sec with a blank panel in between, which was presented for either 6 seconds or 7.5 seconds. In Experiment 1, 16 participants (nine men, seven women) viewed 24 cartoons that were either presented in the appropriate order (humorous conditions) and 24 cartoons that were presented in a random order (nonhumorous condition). In Experiment 2, 18 participants (14 men, four women) viewed 24 funny Manga cartoons and 24 nonhumorous cartoons. In both experiments, the punchline in humorous conditions occurred in the fourth panel in the sequence. Following the presentation of the fourth panel, participants were asked to rate the humorousness of the four-frame sequence. The results showed that when participants comprehended the second cartoon in the sequence, which provided the setup for the humor, there was increased blood flow in the temporoparietal junction, which Dai et al. (2017) claimed to be involved in incongruity resolution. Further, the results showed that as participants viewed the third cartoon, which provided more information about the setup, there was increased blood flow in the frontal and temporal lobes, which may have reflected additional processing related to incongruity resolution. As participants viewed the final cartoon in the sequence and comprehended the humor, there was increased blood flow in the medial prefrontal cortex (see Figure 4.1) and the cerebellum (see Figure 2.1, Chapter 2, this volume) as compared with conditions in which there was no humor. These results may be consistent with the third stage of humor processing, which involves humor elaboration leading to the feeling of amusement.

Campbell et al. (2015) investigated differences in brain activity that were related to humor comprehension, which occurs early in processing, and humor appreciation, which occurs later in processing and includes the positive emotional response to the humor. They used an event-related design in which 24 right-handed participants (10 men, 14 women) viewed 120 cartoons with captions. Three conditions were compared: cartoons with a high level of humor, cartoons with a low level of humor, and nonhumorous cartoons. Nonhumorous cartoons were created by changing the caption in humorous cartoons to remove the source of the humor. In the fMRI experiment, BOLD signals were recorded for 10.5 seconds as each cartoon was comprehended. At the end of each trial, participants rated the humorousness of the cartoon. Campbell et al. aimed to isolate the brain activity involved in humor appreciation by comparing brain activity occurring during the processing of humorous cartoons with activity occurring during the processing of nonhumorous cartoons. The results showed that humor comprehension was associated with increased activity in the left temporoparietal junction, and humor appreciation was associated with increased activity in the superior frontal gyrus (see Figure 4.1).

Several recent studies have explored individual differences in brain responses during humor processing, each focusing on a different variable, including gender (Chan, 2016), personality (P. Berger et al., 2018a), differences in self-control when comprehending aggressive humor (X. Liu et al., 2019), and differences in humor ability (Amir & Biederman, 2016). In a study of gender differences in humor processing, Chan (2016) scanned 26 right-handed participants (13 men, 13 women) as they read jokes presented in two parts (setup for 12 seconds then punchline for 9 seconds) using an event-related design. Different types of verbal humor were tested: ambiguity jokes, which involve multiple meanings; exaggeration jokes, which involve a meaning that has been exaggerated; and bridging-inference jokes, which require participants to draw an inference between the punchline and the joke setup. For each trial, participants were scanned for 12 seconds as they read the setup and 9 seconds as they read the punchline. They were then asked to provide a humorousness rating. The results showed that overall, there was higher activity in the anterior prefrontal cortex for women than for men, and higher activity in the dorsolateral prefrontal cortex for men than for women. Sex differences were observed in brain activity during the processing of each type of joke. During the processing of ambiguity jokes, there was greater activity in prefrontal cortex and parahippocampal gyrus for men than for women. During the processing of bridging-inference jokes, there was greater activity in orbitofrontal cortex, anterior prefrontal cortex, temporoparietal junction, parahippocampal gyrus, insula, and supplementary motor areas for women than for men.

P. Berger et al. (2018a) investigated individual differences in brain responses during humor comprehension in a study with 19 right-handed participants (nine men, 10 women) who provided self-reports of personality (i.e., Extraversion, Openness to Experience, Agreeableness, Conscientiousness, and Neuroticism; see Widiger, 2017, for a review). They used an event-related design in which humorous and nonhumorous cartoons were presented and participants were scanned for 7 seconds during comprehension. Participants provided a humorous rating for each trial. The results showed that blood flow in the right amygdala and the left insula were related to individual differences in personality, specifically extraversion and neuroticism. However, participants' ratings for the humorousness of the cartoons were not significantly related to personality.

In the only fMRI study that has investigated brain responses during the production of humor, Amir and Biederman (2016) recorded the brain activity of novice and professional improvisational comedians as they generated either humorous or nonhumorous captions for *New Yorker* cartoons. Novice comedians showed increased activation in the medial prefrontal cortex when producing humorous captions. In contrast, professional comedians had increased activation in areas in the temporal lobes but decreased activation in the medial prefrontal cortex and the striatum, a region in the midbrain's basal ganglia.

SUMMARY

Studies using fMRI have revealed numerous brain regions involved in the comprehension of humor. Recent studies have proposed that the pattern of activity across these regions reflect three distinct stages of humor processing: incongruity detection, incongruity resolution, and humor elaboration, which includes the positive emotion associated with mirth. Different brain regions were found to be involved in the resolution of nonsense humor, which presents incongruity that may be more difficult or impossible to resolve than in the resolution of incongruity–resolution humor. Across the studies, these three stages of processing have been captured as participants comprehend humorous cartoons or punchlines preceded by verbal content for a period of time not longer than 11 seconds. When the brain regions identified in fMRI studies are compared, there is some consistency with the brain regions suggested in Du et al.'s (2013) EEG/ERP study. Du et al. identified the anterior cingulate cortex as involved in the second stage of humor processing (i.e., incongruity resolution). This region was also identified in many of the fMRI studies but was associated with humor elaboration in the study by Chan, Chou, et al. (2013). Du et al. identified the medial frontal lobe and the fusiform gyrus as involved in the third stage of humor processing (i.e., humor elaboration), which includes the experience of mirth. These regions were also associated with humor elaboration in the fMRI study by Chan, Chou, et al. (2013). A few regions were linked with humor in only a few studies, suggesting that more research is needed to determine the extent to which those regions are related to humor processing (e.g., cerebellum in Bartolo et al., 2006; insula in Kohn et al., 2011; Moran et al., 2004; Watson et al., 2007). Nevertheless, a limitation of the fMRI studies is the lack of diversity, with studies including a small number of right-handed individuals. It remains unclear whether the observed results will be observed in future studies with larger number of participants and, more important, with different types of participants (i.e., different age groups, education levels, cultural backgrounds, etc.). A few studies have observed individual differences in brain responses to humor for several types of differences (e.g., gender, personality, self-control, humor ability).