Abstract. Humor is a very interesting phenomenon in human cognitive and emotional processing, and it is unique for human beings. Humor is based on a large number of complex biological processes taking place in the brain and peripheral nervous system. This paper describes the main theoretical frameworks of humor research and reviews the recent findings in neural mechanisms of humor processing involved in the cognitive and emotional processing of humor, including studies of humor with patients with localized brain damage as well as studies of normal subjects using neuroimaging techniques and electrophysiological studies.

1. Introduction

Humor is one of the most interesting and puzzling aspects of human behavior. It is a universal aspect of human experience, occurring in all human cultures and virtually all human individuals throughout the world (Lefcour and Thomas 1998). Like all psychological phenomena, humor is based on a large number of complex biological processes taking place in the brain and nervous system (Martin 2006). In the present paper, I will describe neural mechanisms and brain areas involved in the cognitive and emotional processing of humor, including studies of humor with patients with localized brain damage as well as studies of normal subjects using Electroencephalography (EEG), Event-Related Potentials (ERP), as well as Functional Magnetic Resonance Imaging (fMRI).

Before reaching that stage, I will describe shortly the main theories of humor perception, because many brain studies refer to, contradict with or reinforce these theories. Three branches of humor theory are commonly known as superiority theories, relief/release theories and incongruity theories. It is worth noting that these theories can coexist because they do not contradict each other, emphasizing different aspects of humor processing.

Relief Theories

Theories of relief came from psycho-dynamical approaches. Sigmund Freud (1928) suggested that laughter can release tension and “psychic energy”. This energy is continuously built up in one’s nervous system, as an aid for suppressing feelings in taboo areas, like sex or death. When these taboo thoughts are entertained, the psychic energy can be released as laughter. Humor is referred to as a substitution mechanism which enables us to convert aggressive impulses to acceptable ones rather than wasting mental energy on suppressing them (Freud 1928).

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Superiority Theories

Superiority theories argue that humor is a form of expressing our own superiority over other people (Portmann 2000). According to superiority theories, humor is always targeted against one person or group on different grounds (gender, political, ethnic and etc (Martin 2006). As opposed to relief theories, superiority theories are socially oriented as they are concerned with the function humor plays in social relationships (Attardo 1994, pp. 47–50).

Incongruity Theories

Regardless of the theoretical framework concerning the purpose of humor, most researchers agree that humor is related to either comprehending or producing an incongruity: the simultaneous occurrence of incompatible elements or sudden contradiction of expectations (Martin 2006). Incongruity theories, therefore, focus on the cognitive phenomenon of humor. One of the earliest references to an incongruity theory of humor is found in Aristotle, who claimed that the contrast between expectation and actual outcome is often a source of humor. He also drew a distinction between surprise and incongruity, whereas the latter is presumed to have a resolution that was initially hidden from the audience (Attardo 1994, pp. 47–50)

The two-stage incongruity-resolution model is the most widely accepted theory of humor perception (Suls 1972). According to this model, humorous stimuli are processed in two stages: first, the incongruity has to be detected and then, it has to be resolved. Suls contends that the process of detection and reconciliation of the incongruity makes humor comprehension a problem-solving task (Suls 1972).

2. Humor and the Brain

Early evidence regarding brain mechanisms of humor processing was derived from lesion studies. Alterations of the sense of humor among brain-injured patients were found in early studies (Luria 1970), but no experiments had been conducted specifically to test effects of specific brain damage on the patient's sense of humor. In the first of such studies, Gardner and colleagues (1975) found out that patients with brain injuries performed more poorly than did normal controls in distinguishing the funny from the non-funny cartoons. There wasn’t, however, any difference between patients with lesions in the left and right hemisphere. Further, several studies showed that patients with right hemisphere damage performed worse compared to patients with left hemisphere lesions on humor tasks (see, e.g., Shammi and Stuss 1999; Wapner, Hamby and Gardner 1981). Brownell and colleagues found that patients with defects in the right hemisphere were able to detect the surprise element of a joke, but were unable to discern which of several surprising endings is funny (Brownell et al. 1983). The findings indicate that patients with right hemisphere damage are sensitive to the incongruity element of humor, but not to its resolution (Brownell et al. 1983)

Extending these initial findings, Shammi and Stuss (1999) indicated that right frontal lobe is necessary for integrating cognitive and affective information, and that humor appreciation involves the interpretation of current information based on past experience. These researchers studied patients with single, focal brain lesions
restricted to the frontal or non-frontal regions. Results showed that damage of the right frontal lobe had the greatest disruptive effect on the ability to distinguish humorous cartoons from non-humor humorous. Moreover, patients with right frontal lobe damage were impaired in displaying emotional responsiveness to humorous stimuli. While studies with patients showed clear right lateralization of humor processing, recent neuroimaging studies with intact subjects showed that both hemispheres are involved in humor processing. Thus, Ozawa et al. (2000) used fMRI to measure Blood-Oxygen-Level Dependence (BOLD) signal in subjects while listening to either jokes or non-joke sentences. Sentences that the subjects rated as funny induced activation in Broca’s area (left hemisphere) and the middle frontal gyrus. In another study (Goel and Dolan 2001), subjects were presented with two types of jokes: phonological jokes (puns) and semantic jokes (humor related on context rather than simple language play). Researchers found that different types of humor are processed by separate networks. While semantic jokes activated a bilateral temporal lobe (left posterior middle temporal gyrus, left posterior inferior temporal gyrus, right posterior middle temporal gyrus and the cerebellum), phonological jokes activated the left hemisphere network involving posterior middle temporal and left inferior frontal gyrus. Using Positron Emission Tomography (PET), Iwase and colleagues studied subjects’ facial reactions to funny movies (Iwase et al. 2002). Humor-associated laughter/smiling was followed with increased activity in the visual association areas, left anterior temporal cortex, bilateral supplementary motor areas, left putamen and orbitofrontal and medial prefrontal cortices. Mobbs et al. (2003) demonstrated that humor modulates activity in several subcortical regions including the nucleus accumbens — a key component of the reward system. Such finding may explain the pleasurable effect created by humor (Mobbs et al. 2003). These limbic structures have reciprocal connections with frontal lobes, specifically with ventromedial prefrontal cortex (VMPFC) (Rolls 1990). In view of the importance of VMPFC in the integration of cognitive and affective information, this region may be quite critical for humor appreciation (Baldwin 2007). Humor-related VMPFC activation was found in several studies with fMRI. In the already mentioned study of Goel and Dolan (2001), cerebral activity in the medial ventral prefrontal cortex positively correlated with the subject's post-scan ratings of joke funniness and, indicating affective component of humor. Moran, Wig and Adams (2004) also found distinct neural networks for humor comprehension and humor appreciation and specified that humor appreciation is supported by bidirectional connections of the VMPFC and amygdala.

Another niche of humor research is electrophysiological studies. To date there are only a few electrophysiological investigations of humor. The so-called Event-Related Potential (ERP) technique may shed light on temporal processing of humor and validate theoretical models like incongruity-resolution.

New infrequent stimuli raised a positive peak around 300 ms after onset (P300). Incongruent, context-different stimuli caused a long negative peak around 400 ms (N400) and a long positive peak after around 600 ms (P600) (Hillyard and Kutas 1984). Thus, these ERP components may serve as the window to humor processing. In the first ERP study of humor, Derks and his colleagues reported a peak of activity ~300 ms (P300) after hearing the punch-line of a joke followed by a general depolarization ~100 ms later (N400) (Derks, Gillikin, Batolome-Rull and Bogart 1997). These two waves were suggested by authors to parallel the two-stage model of humor processing. In addition, results showed that mood could influence humor
processing: positive mood, compared with negative one, was accompanied by greater differences in ERPs between funny and not funny jokes.

More recently, Coulson and his colleagues performed several studies using ERP. (Coulson and Kutas 2001; Coulson and Lovett 2004; Coulson and Williams 2005; Coulson and Wu 2005; Coulson and Severens 2007). Coulson (2001) proposed an alternative model of incongruity humor, the frame-shifting model. Coulson and Kutas (2001) assumed that to really ‘get’ the joke, the listener must go beyond surprise and formulate a new, coherent interpretation (Coulson and Kutas 2001). Frame-shifting is a process of activating a new frame from long-term memory in order to reinterpret information already in working memory (Coulson 2001). Coulson and Kutas (2001) tested the frame-shifting model of humor by comparing the processing of one-line jokes with non-joke sentences, with final words matched on close probability.

Unexpected straight endings elicited smaller N400 responses than joke endings (Coulson and Kutas, 2001). In addition, good joke comprehenders responded to jokes with higher amplitudes of P600, and sustained N400 over left frontal sites. By contrast, with poorer joke comprehenders, the punch-words elicited right frontal N400.

Authors argued that P600 reflects a surprise component of a joke, and the N400 indicates frame-shifting. Both components were elicited within the same time window in different brain regions. Temporal overlap of the joke-related ERP effects contradicts the classic two-stage model that assume some hierarchical time-course of activation.

Coulson and Lovett (2004) investigated laterality of joke comprehension influenced by handedness. Similarly to the previous study, they found out larger N400 and P600 in response to jokes compared to cloze-equated straight endings. N400 of right-handers was larger over anterior left lateral sites and P600 was the largest over right hemisphere centro-parietal electrodes. But frontal asymmetry in N400 was seen only in right-handers and was absent in left-handers. In addition, P600 in left-handers was larger and more broadly distributed than in the right-handers’ ERPs. The authors proposed that inter-hemispheric interaction is more efficient in the left-handers, as they are reputed to have relatively larger corpus-callosum.

Two studies (Coulson and Williams 2005; Coulson and Wu 2005), tested the so-called Coarse Coding theory. Coarse Coding (Jung-Beeman, 2005) assumes some difference in the breadth of semantic activation. According to the coarse coding hypothesis, the Left Hemisphere (LH) strongly activates a restricted set of related concepts, whereas the Right Hemisphere (RH) weakly activates broader set of concepts. Such broad activations of RH may be very useful for recalling additional schemes and resolving the incongruity of the joke (Jung-Beeman 2005)

Coulson and Williams (2005) examined ERPs to jokes and matched non-joke sentence which were presented to different hemifields. Jokes elicited larger N400s than straight endings only when the punch-line word appeared at the right visual field (RVF, left hemisphere). With left visual field (LVF, right hemisphere) presentation, jokes and non-jokes endings elicited similar N400s. A sustained frontal negativity and late fronto-central positivity to jokes did not differ with visual field of presentation. This finding suggests that RH semantic activation facilitates joke comprehension. At the follow-up study by Coulson and Wu (2005) the same kind of stimuli was used, but they measured the response to the probes that were preceded by either a joke or a non-joke. Jokes were related to the probe while non jokes were not-related. The results showed more N400 for probes after joke endings, but only when
those appeared in the LVF, consistent with the idea that the RH contains more joke-related information than the LH.

In an additional study Coulson and Severns (2007) investigated each hemisphere’s ability to appreciate puns. Whereas appreciating a joke requires a switch from one interpretation of the situation to another, appreciating a pun requires the active maintenance of multiple meanings of an ambiguous word or phrase. Coulson and Severens (2007) recorded ERPs to laterally-presented probe words following an auditory presented pun. When the probes immediately followed the pun, facilitation was seen in the rVF/LH for words associated with both of the word’s meanings in the pun, but facilitation in the lVF/RH was limited to the most expected meaning. After a delay of 500 ms, activation of both meanings was similar in both hemispheres. Thus, there was no advantage for a RH in multiple meaning processing during pun comprehension.

The work of Coulson and her colleagues suggests that both hemispheres are involved in processing of higher-order language structures with activations of multiple meanings associated with a particular word, like in jokes and puns. ERP studies show difference in the contributions of the two hemispheres to joke and non-joke processing.

3. Concluding Remarks

There are three main frameworks of humor: relief, superiority and incongruity theories. Instead of being contradictory, these theories represent different aspects of humor processing. Whereas incongruity theories deal with cognitive and linguistic aspects of humor, the superiority and relief theories emphasize the social and psychophysiological aspects, respectively. Perhaps an “ideal joke” would integrate the elements of these three main views, but would cramming all those different aspects would necessarily make a joke better?

The aforementioned theories, however, do not differentiate between humor comprehension and humor appreciation. These two sub-processes appear to be operated by anatomically distinct brain pathways. Specifically, humor comprehension might depend critically on frontal brain areas involved in understanding and resolving incongruities, whereas humor appreciation might rely primarily upon engagement of limbic pathways involved in the processing and expression of affect (Goel and Dolan 2001; Moran, Wig and Adams 2004). Studies of individuals’ brain lesions provide evidence that the right hemisphere is necessary for the perception of humor and that its frontal areas are particularly critical. Neuroimaging studies support the importance of frontal lobes for integrating information during humor comprehension. Nevertheless, several studies showed strong left activation in response to verbal jokes. Neuroimaging studies showed highly distributed networks involved in humor processing, including medial temporal lobes, frontal lobes, language-related regions, anterior cingulated gyrus and other. Some researchers especially emphasized VMPFC contribution to humor comprehension and appreciation. VMPFC is also connected to limbic systems which are activated in response to jokes. These activations follow to sympathetic activity and may explain the euphoric effect and related physiologic changes during humor perception. Electrophysiological studies using ERP techniques also provide a support to the incongruity-resolution model and extend it. Thus, Coulson and colleagues propose and support the frame-shifting model and show that
different joke-related ERP effects overlap in time. In addition, they suggest that both hemispheres are involved in processing of humor, but the hemispheres differ in their contribution to different aspects of humor processing. The nature of lateralization is still unclear and additional research is needed.

To summarize, we can conclude from this overview that humor is a highly multidisciplinary field of research. In spite of its importance in our life many humor components remain unclear. For broad understanding of nature of humor, its role, and mechanisms, research should integrate diverse scientific disciplines. From the other side research on humor, because of its multidisciplinary facets, can serve as a bridge between different fields of study and consequently contribute to scientific interdisciplinarity, shed light on basic scientific questions and will have implication in psychotherapy, medicine, entertainment and other spheres of life.

Bibliography


