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Neural mechanisms of understanding of truth, lie and irony

Neurální mechanismy vnímání pravdy, lži a ironie

Diploma thesis

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Prague, 2022

Declaration:

I hereby declare that this diploma thesis is the result of my own work and to the best of my knowledge, it contains no materials previously written by another person. All used resources are listed in the References.

Prague, 4 January 2022 Signature: .....

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Abstract

Ironic statements are commonly used in our everyday communication. They are characterised by a meaning opposite to the literal one. They rely on mutual understanding of the contrast in the expressed ironic statement, which is based on common experience, knowledge, or understanding of the situational context. In this experiment, we aimed to find the neural correlates involved in the understanding of irony, as well as differences between brain regions involved in the understanding of deceits and the truth.

The theoretical part of this thesis places irony into the broader context of higher cognitive functions and provides a solid theoretical background for its understanding from different points of view, such as neurobiological and psychological. Moreover, it describes a method called functional magnetic resonance imaging (fMRI) as a non-invasive imaging technique allowing researchers to have deeper understanding and locate activations in various conditions.

Practical part provides a detailed description of the experiment, including description of participants, methods, and analysis methods. Specifically, 17 healthy volunteers – 10 females and 7 males took part in this fMRI project. They were to evaluate 20 statements in 3 different contexts – ironic, deceitful, and truthful.

Measured data in form of brain activations are discussed in the respective chapter of this thesis.

Keywords: irony, truth, lie, Theory of Mind, fMRI

Abstrakt

Ironická vyjádření jsou běžnou součástí naší každodenní komunikace. Charakteristickým prvkem je jejich obsah, opačný k tomu doslovnému. Oboustranné vnímání tohoto kontrastu založené na společných zkušenostech, znalostech a pochopení situačního kontextu jsou důležité pro pochopení těchto ironických vyjádření.

Cílem tohoto experimentu bylo nalézt neurální koreláty pochopení ironie, a také nalézt rozdíly mezi mozkovými oblastmi, které jsou zapojené v chápání lží a pravdy.

Teoretická část této práce je tvořena teoretickými základy nevyhnutnými pro chápání a porozumění ironie, a to z různých úhlů pohledu, jako jsou například neurobiologický či fyziologický. Navíc je zde popsána neinvazivní zobrazovací metoda nazývána funkční magnetická rezonance (fMRI), díky které jsou vědci schopni lépe pochopit dané téma, a také lokalizovat aktivace na rozličné podněty.

Praktická část této práce obsahuje detailní popis experimentu, včetně popisu účastníků, metod a způsobu analytického zpracování. Konkrétně šlo o 17 zdravých dobrovolníků – 10 žen, 7 mužů, kteří se účastnili tohoto experimentu s využitím funkční magnetické rezonance. Jejich úkolem bylo zhodnotit 20 tvrzení ve 3 různých kontextech – ironickém, lživém a pravdivém. Naměřená data – aktivace mozku jsou diskutovány v příslušné kapitole této práce.

Klíčová slova: ironie, pravda, lež, teorie mysli, fMRI

List of abbreviations

ACC	anterior cingulate cortex
ASD	autistic spectre disorder
BA	Broca´s area
Bl	baseline
BOLD	blood-oxygen-level-dependant
CC	cingulate cortex
d(U)	degree of ironicalness
d_a	degree of allusion
d_e	degree of indirect expression of negative attitude
d_i	degree of pragmatic insincerity
DLPFC	dorsolateral prefrontal cortex
FG	fusiform gyrus
fMRI	functional magnetic resonance imaging
IFG	inferior frontal gyrus
IPG	inferior parietal gyrus
IPL	inferior parietal lobule
iTG	inferior temporal gyrus
MFC	medial frontal cortex
MFG	middle frontal gyrus
MNS	mirror neuron system
mOFC	medial orbitofrontal cortex
mOG	middle occipital gyrus
MPFC	medial prefrontal cortex
MRI	magnetic resonance imaging
mTG	middle temporal gyrus
OFC	orbitofrontal cortex
PreCG	precuneus
PCC	posterior cingulate cortex
PFC	prefrontal cortex
PFG	prefrontal gyrus
PG	precentral gyrus
RO	Rolandic operculum
sFG	superior frontal gyrus
SFMiG	superior frontal middle gyrus
SMA	supplementary motor area
SMG	supramarginal gyrus
STG	superior temporal gyrus
STS	superior temporal sulci
ToM	Theory of Mind
TP	temporal poles
TPJ	temporoparietal junction
U	utterance
vmPFC	ventromedial prefrontal cortex

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1 Introduction

Social interactions play an irreplaceable part in human life. Apart from the basic exchange of important information between one another, people also share their opinions and feelings. In order to mentalize - understand each other, people need to use a neural network behind the Theory of mind (ToM), which enables one to differentiate between his own feelings and those of the other person (Gallagher & Frith 2003). Due to this, one can feel a certain emotion without getting it mixed with possibly different emotions of the second person.

A parallel line can be drawn between sharing feelings and information. They both tend to be literal – we believe what we feel, and we suppose that our perception of other person´s feelings is truthful as well. The same applies to statements – they are meant to carry their original meaning, and both speaker and listener believe what is being said. However, things are not like that all the time. From time to time, there are situations when people choose to say a statement, which contradicts either the commonly accepted reality or the speaker´s own beliefs. From this point, there are two options – if the speaker intends to place this false belief into the listener´s mind, the statement is called a lie or deceit (Shany-Ur et al. 2012). On the other hand, when both the speaker and the listener are aware of the inconsistency between the statement and the reality, the statement is considered to be ironic or sarcastic, the latter is based on additional negative emotion accompanying the statement (Rankin et al. 2009).

The difference between various statements may be very subtle, and therefore cause difficulties in distinguishing between one another to everybody. However, certain neurological conditions affect specific brain areas, which might worsen one´s ability to tell the statements apart and react appropriately. Neuroimaging techniques and specifically the functional magnetic resonance imaging made it possible to come closer to the understanding of neural correlates of the social interactions and explain the neurobiology of the specific complex cognitive processes such as irony, truth, and deceit.

2 Theoretical background

Interactions with other people are an inevitable part of human life. People interact with each other on a daily basis. However, the purpose differs from a basic smile as a greeting to having a chat with a stranger at a bus stop, to more important motivations as sharing information and feelings with those, who are closer to us. All these would not be possible without the so-called social brain (Brothers 1990; Dunbar 1998; Frith 2007) – brain regions that enable us to perceive others emotions, non-verbal communication including feelings behind it and set them apart from our own feelings, as well as predict future development of events based on the context of social interaction, knowledge, and experience. Among these regions are the amygdala, posterior part of the superior temporal sulcus (STS), medial prefrontal cortex (MPFC), and temporal poles (TP), including temporoparietal junction (TPJ) (Frith 2007). Based on the previous experimental evidence, it seems there is a connection between the size of the neocortex, and the size of a social group – the bigger the neocortex, the bigger is the social group of the individual (Dunbar & Shultz 2007). Mentioned brain areas are used as a ground for ToM, and are frequently mentioned in connection with the mirror neuron system (MNS) as well (Gallese & Goldman 1998).

Using these neural substrates, people manage their everyday life in social groups, as well as create greater bonds or more complicated social networks in their respective environments. When many people share a common space, many opinions tend to clash with each other as well. Perception of reality differs between people - based on their knowledge, experience, and expectation from reality. There is a common ground, on which true perception is built, and therefore, it can be perceived as truthful. When a speaker consciously shares an idea, which is not based on the common reality, it is false. There are many purposes when false statements are used and, in those cases, they take the form of a joke, irony, sarcasm, or a lie – albeit an intentional or an unintentional one (Harada et al. 2009). There are two common types of false statements noncomplying with reality – lies and irony or sarcasm (Shany-Ur et al. 2012). Though quite basic by the first glance, lying is a complex mental process, which requires several social cognitive skills to be involved both on the side of the lying speaker and the listener, as he either understands the deceit or believes the speaker, and acts accordingly. By Chisholm & Freeman (1977), a lie is defined as a statement used to instil a false belief into the mind of the listener, all in order to deceive him. However, when the statement is perceived as clearly false not only by the speaker, but also by the listener, a term irony or sarcasm is used, though

contextual, facial or intonational ques are usually present to aid the listener to distinguish between those two, and the reality as well (Rankin et al. 2009; Shany-Ur et al. 2012), especially when the contextual information or shared beliefs are missing. In some experiments, there have been cases when these two terms have been used interchangeably as in some contexts, their distinctions are becoming rather uneven and blurry (Attardo et al. 2003). In the case of this thesis, the term "irony" will be used, carrying its original meaning.

In next chapters, the involvement of ToM in the idea of truth, lie, and irony will be explained, giving common ground of knowledge for further understanding of the concept of the irony from the neurobiological view, which is central for this thesis, and for the experiment applied.

2.1 Irony

Humour has an important role in the everyday life of people as many of them use it regularly, and randomly in their conversations – jokes, funny statements, or word swaps. By engaging in humorous dialogues, people brighten up their days, otherwise full of obstacles, and worries (Samson et al. 2009). Humour is thought to be an integral part of any social group, as people use it to share their thoughts, emotions, and feelings with each other. However, in order to understand the basis of humour in the ongoing conversation, shared knowledge end memories are necessary (Norrick 2006).

Among other forms of humour, there is a particular place for irony and sarcasm. They both do not comply with the reality – the same as deceit. However, the difference between them and lies is the perception of the listener – in the case of lies, the speaker wants the deceit to remain hidden; for uncovering the lie, the listener has to understand the difference between the actual situation and the speaker´s statement (Bosco & Bucciarelli 2008). On the other hand – in the case of irony and sarcasm, the speaker expects the listener to understand the untruthfulness of the specific statement (Shany-Ur et al. 2012). In other words – irony and sarcasm highlight the specific attributes of the reality by a lie and relies on being uncovered, and the second one – deceit – tends to hide the reality from the other person and hopes to keep the reality hidden (Bosco & Bucciarelli 2008; Monetta et al. 2009).

The distinction between irony and sarcasm is less obvious – based on its dictionary meaning, the word "irony" is used either when one wants to point out that the ongoing situation is substantially different from the expected course of events, or when one expresses verbally in

the opposite way to his own opinion (Merriam Webster dictionary). “Sarcasm” is partially the same, as it also describes an ongoing situation in the opposite way, though the added value is represented by an intention of an insult or an irritation (Merriam Webster dictionary), or criticise the listener in a less hurtful way then would a truthful expression would do (Shany-Ur et al. 2012). Sarcasm is a less thoughtful way of sharing a negative opinion about the reality, and can be perceived as a stronger form of verbal irony (McDonald & Pearce 1996; McDonald 1999). In other experiments, it has been suggested the sarcasm is a subtype of irony (Rankin et al. 2009; Matsui et al. 2016).

Perception and understanding of metaphorical expressions have been studied for a substantial period – how one perceives spoken words when they do not carry respective literal meaning remains questionable. The same applies to irony. For its understanding, one must go beyond syntactical and lexical language processing (Eviatar & Just 2006). Before making an ironical statement, one needs to compare the reality with his expectations. Based on this comparison and given an unanticipated conflict with the reality is present, the ironical statement can be made. By using it, the speaker points out the reality does not comply with the presumed reality. To understand the irony within the statement, the listener must also understand beliefs and intentions of the speaker (Bosco & Bucciarelli 2008). As a result, irony has two basic characteristics: firstly, the speaker expresses his opinion about something, and secondly, the opinion is clearly insincere.

There are two dominant types of cues used to understand that an ironic utterance is being used – it is either prosody or contextual disparity between the utterance and the reality (Matsui et al. 2016). In some situations, it is enough to have only of them to be sure that an ironic remark is said by the speaker. or one cue can be more apprehensible than the other. A functional magnetic resonance (fMRI) study with 5-year olds showed that children manage to understand the irony in the utterance based on the typical prosody, without having any deeper understanding of the contextual cues (Laval & Bert-Erboul 2005). A different study on adults showed, that when ironical or sarcastic prosody is combined with neutral context, people tend to perceive it as irony, though when there is only contextual cue without the specific prosody, it is frequently considered rather neutral than ironical (Woodland & Voyer 2011).

It is obvious that lies, truth, and irony have different levels of complexity – the truth being the simplest and irony being the most complicated one, with lies standing somewhere in the middle

of these two terms. This different complexity indicates that there might be certain differences in neural substrates, which are responsible for the comprehension of respective types of statements.

2.1.1 Linguistic models of Irony

The use of irony would not be possible if there were no language and speech development in the course of human development. In order to grasp the topic entirely, it is necessary to use partly linguistic and philosophical approaches to irony. Language, and speech, is by classical philosophy divided into two categories – direct and indirect. As defined by Searle (1975), these two units differ from one another by their complexity, which can be explained in the following sentences:

a. What is the outside temperature today?
b. Would you mind telling me what is the outside temperature today?
c. I was wondering if you could tell me what the outside temperature is today.
d. I am leaving my house and I am not sure whether to put on a coat or not.

Direct speech (sentence a.) conveys only one intention directly from the speaker to the listener, with no additional phrasing. Meanwhile, indirect speech (sentences b., c., d.) requires some mentalizing and shared knowledge about the situation, which also differs by the complexity of the statement – though longer than the direct statement, statements b. and c. convey the intention with a certain level of clarity. However, the sentence d. requires the listener to grasp the ongoing situation and mental state of the speaker, including his hesitance or lack of knowledge about the outer conditions. It means that for the understanding of indirect speech, the listener needs to use mentalizing as a method of grasping the full idea of the compact statement (Searle 1975).

Bosco and Bucciarelli (2008) propose, that the same division applies to the utterances themselves - there are two types of ironical statements – simple and complex. Simple ironical statements can be characterised as statements with a meaning opposite to their literal content, e.g. a child faking a cry in his chair when he seeks the attention of a parent, who reacts to something that he thought was a cry, though, in reality, it is just an ironical attempt of his non-crying child to attract his attention, which was, in the end, successful (Reddy 1991). Oppositely, the complex ironies do not only require certain abilities on the side of the speaker, but also on the listener´s side, as he must connect the told statement with the reality and comprehend the

irony of the statement (Bosco & Bucciarelli 2008). A problem with irony lies in the fact, that one statement can be all – truthful, deceitful, and ironic. What adds meaning to the statement is the context when the statement is said (Bosco et al. 2017). By saying "What a beautiful day", the speaker may imply 3 different things:

- The weather is beautiful, and the speaker points it out.
- The weather is horrible, but the speaker consciously chooses to tell the listener the opposite to confuse him.
- The weather is horrible but making fun of it makes it less unpleasant.

Context and prosody of the statements are what help the listener understand the irony of the situation. The same applies to humour in general. Widely accepted model of humour incongruity-resolution theory (Suls 1972; Wyer & Collins 1992; Samson et al. 2009; Nakamura et al. 2018)postulates, that a situation is funny when a certain order of events is followed: the listener enters any situation with certain assumption, e.g., the state of events or context of the conversation. If there is an incongruity between the assumption and the reality and the listener notices it, the first step of the theory is completed. The second step consists of the mental work of the listener, who needs to either find some fault in the original assumption or discover a new connection between the incoherent elements and thereby replace the original assumption. Understanding of either one of them elicits humour (Nakamura et al. 2018). The same theory can be applied to ironic statements, though after having a closer look, the explanation of irony and its difference from non-irony is not that simple.

There are several theories, which aim to explain irony from a psycholinguistic point of view, and each has both stronger and weaker points, which are mostly represented by problematic distinguishing between irony and non-irony. However, it is still important to mention them, in order to get a complete picture. The most relevant are the pragmatic theory, the echoic interpretation theory, the pretense theory, and the implicit display theory.

Pragmatic theory (Searle 1979; Haverkate 1990), as the name already gives away, proposes a straightforward explanation of ironical utterance – when there is an incongruity between the reality and the statement, the statement is considered as ironic. However, it does not take into account, when there is necessarily no pronounced conflict (Utsumi 2000) – either when participants of the same discussion do not share the same experience, on which was the ironical

statement based or when there is no incongruity between the statement and the reality, but other cues like prosody and facial expression give away the irony.

Another theory called the echoic interpretation theory (Sperber & Wilson 1986) derives from the mentioned theory (Sperber & Wilson 1981) and proposes that irony is present only when there is some conflict between what the speaker says and either his expectations, experience, or an utterance he reacts to in terms of the conversation. The problem of this theory is evident at the first glance – not every irony can be fitted into the given explanation and therefore is considered incomplete (Utsumi 2000).

Another point of view – the pretense theory is based on pretense as the key element of irony (Clark & Gerrig 1984) – only when the speaker takes the role of somebody else and comments on the current situation is the statement perceived to be ironic. Though the same problem comes up – in reality, it is not necessary to pretend to be somebody else as one can comment on the situation from his point of view (Utsumi 2000). Each of the previous theories tries to complete the overall picture of irony by placing other details, which were missed before. Unfortunately, by placing something new, another previously accepted thought or idea goes missing.

As a result of continuous struggle to find a comprehensive theoretical model of irony, another one has been proposed - Implicit display theory (Utsumi 2000), which says that an ironic utterance can be characterised both by the environment, as well as its implicit expression in the utterance accompanied by certain cues. There are two groups of cues, which speakers use to express their negative opinion on the subject: non-verbal cues like facial expression or behavioural cues (laughter, gestures) and verbal cues – metaphors, adjectives (amazing), adverbs (really), injections (Oh!), paralinguistic cues, expressions of counterfactual emotions (Kreuz & Roberts 1995; Utsumi 2000). This theory postulates that irony can be distinguished from non-irony using a formula calculating the degree of ironicalness, d(U), (Utsumi 2000) expressed by the utterance (U) when compared to a prototype of irony. The result can be calculated using the following factors:

d_a - the degree of allusion – how much is the U consistent with the speaker´s expectations.
d_i - the degree of pragmatic insincerity – how much does the U contradict pragmatic principles.
d_e - degree of indirect expression of negative attitude – number of ques accompanying the U.

Taken together, their interrelationship goes as follows:

$$d(U) = d_a + d_i + d_e$$

The formula can be further modified according to the expectations of the speaker and polarity of the U (Utsumi 2000). The theory proposes that the more ironical the environment is or the more ironical is the utterance itself, the faster goes processing of the utterance. Since the publication of this study, it has gained validation and has been used widely used to explain the psychology behind the understanding, both in theoretical an experimental settings.

2.1.2 Theory of Mind

The social brain, including ToM, is one of the essential constructs of cognitive neurobiology. This theory postulates that a person is able to perceive his own thoughts, desires, and opinions, and tell them apart from ideas, thoughts, and opinions of the other person (Gallagher & Frith 2003). On account of the ToM, one can understand that his beliefs are different from the beliefs of the second person and this allows one person to understand what can be the possible content of a lie and when it might be beneficial to use it (Lee 2013). Lying can be defined as conscious sharing of false beliefs for one´s own benefit while maintaining own beliefs about the respective topic, and staying within some boundaries of reality so the lie remains believable (Oey et al. 2019). In order to achieve success with this deceit, it is necessary to create a false belief in the mind of the partner in the dialogue and maintain one´s own belief at the same time (Talwar & Lee 2008). The better the grasp of the ToM the better and more profound the lie can be (Ding et al. 2015). As for the brain regions, the ToM commonly recruits the following brain structures: anterior paracingulate cortex, STS, TP, additionally amygdala, ventromedial prefrontal cortex (vmPFC), and orbitofrontal cortex (OFC) (Gallagher & Frith 2003; Carrington & Bailey 2009; Bodden et al. 2013). Further evidence implies, that basal ganglia are involved in the neural processing of the ToM, as well (Bodden et al. 2010)

In connection to ToM, MNS is frequently mentioned (Gallese & Goldman 1998), as MNS is the background of action understanding, sharing emotional states of other people, and consequently, understanding what they are feeling, or if there are some common experience or knowledge, what they are going through as well. However, there remains the distinction between “self” – own feelings and “other” – feeling of the other person, which is crucial for

any social interaction (Gallese & Goldman 1998; Schulte-Ruether et al. 2007). Mirror neurons constitute a group of neurons with sensorimotor and visual/auditory properties, which means they are activated both in the perception of a movement being performed, as well as performing the movement personally (Gallese & Goldman 1998; Rizzolatti & Craighero 2004). Neural structures that are usually activated during these processes, and attributed to the MNS are the premotor cortex, inferior parietal cortex, supplementary motor cortex (SMA), and primary somatosensory cortex (Gallese & Goldman 1998; Molenberghs et al. 2009; Kilner & Lemon 2013). MNS is also involved in language processing – thanks to its spatial proximity to language centres called Broca´s area (Gallese 2008; Corballis 2010).

ToM network plays an important role in accessing and responding to the social environment, as it helps people to understand, interpret, and react to intentions, behaviour, emotions, and actions of other people (Gallagher & Frith 2003; Talwar & Lee 2008). However, it is not only ToM network activated in understanding and production of both deceitful and ironic statements. Other brain areas from the social brain and the limbic system are activated as well. More on involved brain areas in the next chapter.

2.1.3 Neural correlates of Irony

Although a task to name neural correlates of irony sounds trivial, there has been an ongoing discussion about this topic. As understanding of irony is not a basic nor straightforward task for the human brain, presumably more than just one neural network implies this process. In the past 20 years, there have been several studies, which aimed at understanding of the irony and its neural correlates. Altogether, three methods were used – magnetoencephalography (Akimoto et al. 2017), cognitive tests in lesion study (Shamay-Tsoory et al. 2005) but the vast majority of them used fMRI as the main method. The summary of the existing research studies with typically developing and healthy participants, including their description, can be found in Attachment I – List of fMRI studies on irony.

In the only magnetoencephalography study, event-related desynchronisation of alfa waves was measured to evaluate temporal-spatial neural signatures in situations with ironic context (Akimoto et al. 2017). Results showed a desynchronisation in the anterior TP, indicating an ongoing activation in ironic situations. These findings were consistent with other studies, which also implied activation in the temporal region – TPJ, TP, and STS (Wakusawa et al. 2007; Shibata et al. 2010; Varga et al. 2013; Obert et al. 2016; Bosco et al. 2017). Activation of the temporal regions suggests language processing, understanding of shared intentions in

communication, and attribution of mental states, which is a part of the ToM network (Saxe & Wexler 2005; Herold et al. 2009). Other regions, which participate in the ToM network are the precuneus (PC) and MPFC (Saxe et al. 2004). Their activation was also observed in a number of fMRI irony tasks. PC plays an important role in self-centred processes in the brain, as well as well-functioning working memory, especially its autobiographical component (Cavanna & Trimble 2006). Ironic statements resulted in its stronger activation than the literal ones (Shibata et al. 2010; Varga et al. 2013), which implies that the mentioned components are important for both acknowledgement and comprehension of irony. In some cases, activation of PC extends to MPFC, another part of the ToM network. Several studies reported changes in signal during an irony task (Wang et al. 2006a, 2006b, 2007; Shibata et al. 2010; Spotorno et al. 2012; Filik et al. 2019). MPFC is one of the higher cognitive centres and has a number of roles in the overall mental processes. Some of those are learning or error processing, as well as making own prediction about outcomes of future events (Alexander & Brown 2011), especially when speaking about its part called the anterior cingulate cortex (ACC). Moreover, mPFC is also important in the establishment of associations between events, memories, contexts, and emotional responses of those individual situations, as well as being an important crossroad for interaction between different types of memories (Euston et al. 2012).

Apart from those already mentioned areas as MPFC, ACC, and STS, areas like the amygdala and the anterior insula are also important components of emotional processing (Frith & Frith 2007). Insula´s functions span widely. As it is frequently co-activated in decision-making processes, as well as general social cognitive tasks (Rapp et al. 2013) and irony comprehension in terms of language processing (Spotorno et al. 2012). Amygdala is believed to play a role in the perception of and rewards, as well as emotional processing (e.g., fear) connected to memory formation (LeDoux 2007). Its activation was found to be connected to the decoding of ironic messages, with changes in activity level based on the degree of irony (Akimoto et al. 2014). However, it is hypothesized whether the activation happens based on the ironic statement, or effective communication as the speaker managed to pass his feelings with the listener (Stephens et al. 2010; Akimoto et al. 2014). Finally, the amygdala, together with the orbitofrontal cortex (OFC), hippocampus, and the cingulate cortex (CC) are a part of limbic system, which is the main structure involved in emotion processing and has a key role in any cognitive processing, as well as memory and behaviour (Mega et al. 1997).

Some disorders are characterised by deficits in social cognitive processing or understanding of these ironic situations. It is very common to see these deficits in schizophrenia patients, both in acute phase and during remission period (Sugranyes et al. 2011; Varga et al. 2013). Studies have shown, that these deficits are present when it comes to the understanding of irony as well and result in worse performance in irony comprehension tasks (Rapp et al. 2013; Varga et al. 2013; Herold et al. 2018). This inability to grasp irony is frequently explained by deficits in the ToM network (Rapp et al. 2013) or deficits in the right hemisphere (Winner et al. 1998; Langdon & Coltheart 2004). However, providing schizophrenic patients with linguistic help tends to minimize these differences in performance in irony comprehension tasks (Varga et al. 2013).

Deficits in irony comprehension have also been investigated in patients with dementia and Alzheimer´s disease (Rankin et al. 2009; Shany-Ur et al. 2012). These experiments implied impairment of ToM network, represented by an inability to take a perspective and perceive other´s emotions an ongoing social situation, especially in patients with dementia, who were also unable to tell apart sincere statements from lies and irony (Shany-Ur et al. 2012). Further analysis showed, that these changes might have been caused by worse connectivity in the respective regions (Shany-Ur et al. 2012) or their smaller volume (Rankin et al. 2009). However, some further investigation is necessary to determine more precise causes of these impairments in irony comprehension in patients with dementia and Alzheimer´s disease.

Another such example of deficits in irony comprehension tasks can be autistic spectre disorders (ASD), which are also frequently characterised by deficits in ToM and language processing abilities (Sugranyes et al. 2011). Several fMRI studies have confirmed these findings using irony comprehension tasks (Wang et al. 2006a, 2007; Williams et al. 2013). These studies point out several things: the importance of prosody and facial cues to the ASD listener/observer, as well as rather problematic use of contextual cues in the process of understanding of ironical statements. One additional study has shown, that ASD children have evolved compensatory mechanism, which balances the deficit of language processing areas in typically developing children (Colich et al. 2012), as their brains manage to redistribute the workload to different nodes (Williams et al. 2013).

As for differences between age groups, Wang (2006b) investigated a possible shift in the framework used to process irony or communicative intention in general. Results from the

respective fMRI study showed, that children used their frontal regions (e.g., MPFC, which is an integration centre of numerous signals coming into the frontal areas) more than adults, who, on the other hand, showed greater activation in the fusiform gyrus (the area responsible for emotion detection and perception of faces) (Haxby et al. 2002; Wang et al. 2006b).

No studies have so far identified any intersexual differences in neural correlates for irony comprehension, though according to some (Colston & Lee 2004), irony fits better into the male verbal repertoire and they use it more frequently than females. Further research is still necessary to determine any possible neural correlates, which might be connected to this statement.

2.2 fMRI

Imaging techniques have undergone substantial development in recent decades. Not only advances in technology but also continuous progress in physiology have contributed to the development of magnetic resonance imaging (MRI). Since the first MRI scanner, all has improved immensely, and nowadays, MRI can be used for subtle signals as those, which are of interest in neuroscientific brain research. Standard MRI is being used in clinics and provides detailed structural images of the brain, with its focus being a high spatial resolution. In functional magnetic resonance imaging (fMRI), it is possible to measure Blood-oxygen-level-dependant (BOLD) changes, or in other words changes in haemodynamics (Logothetis et al. 2001). As the name implies, this type benefits from different magnetic properties of oxygenated and deoxygenated blood. Deoxyhaemoglobin does not exhibit a strong signal as it is paramagnetic, unlike haemoglobin with oxygen bound to it.

If the area requires more oxygen, it implies that there is an ongoing activation of that area. Activated brain regions require more intensive supply of oxygenated blood to satisfy the high metabolic need for biochemical substrates. The previously strong signal of oxygenated blood decreases swiftly and implies deoxygenation of the haemoglobin carrier and utilisation of the substrates. As the regulatory systems cannot leave any part of the brain without any oxygen available, physiological responses like changes in blood flow or arterioles diameter follow to speed up the blood flow. Consequently, as the blood moves faster, the oxygen supply is increased and followed by a return to the baseline after the oxygenation is restored to normal. Given the properties of fMRI, it is possible to measure these changes in oxygenation in individual brain areas in time.

When these changes are measured one after another, a certain haemodynamic trend can be established. The ongoing signal can usually be measured as the first peak, followed by the decrease in the signal´s strength and the last increase, which is usually present after 4-6 seconds and finalised with the return to the baseline.

3 Specific Aims

The aim of this experiment was to determine neural correlates involved in the comprehension of three different types of statements - irony, truth and lies in healthy subjects. The next goal was to compare brain activations in the stated conditions and determine both shared and different substrates involved in their processing, focusing on the condition of irony.

Assuming different complexity of truthful, deceitful, and ironic statements - the truth being the least complex and irony being the most complex one, we hypothesize that their neural substrates differ from each other as well. To confirm or deny the hypothesis, fMRI was chosen as the method of definition of the brain activity in the stated conditions, as it is a non-invasive imaging method widely used in the neuroscientific and physiological research.

4 Method

Following subchapters aim to elaborate on participants, who took part in this experiment, as well as used methods.

4.1 Participants

Altogether, 20 healthy, German speaking participants volunteered to take part in the experiment, 10 females and 10 males. Due to technical problems during fMRI scanning of two male participants, which resulted in incomplete data, we could not proceed in analysis of these data and therefore decided to omit them completely. Mean age was 32 years (28 - 43 years). All the participants signed an informed consent form before participation in the experimental part.

4.1.1 Exclusion and Inclusion criteria

Among exclusion criteria, there were disorders of psychiatric or neurological character, substance abuse. Furthermore, the usual contraindications for an fMRI measurement applied, such as epilepsy diagnosis, metal implants or pacemakers. On the other hand, experiment inclusion criteria were IQ above 85, an age between 20 and 45 years and right handedness.

4.1.2 Ethics

The present study has been approved by the ethics commission of the Ludwig-Maximilians-University Munich, Germany.

4.2 Irony task method

Experiment was carried out on Großharden Clinic of the Ludwig Maximilian University of Munich, Germany. fMRI scan was 1.5 T, Magneton AVANTO, Siemens, Germany. Functional T2 – VI received with the experiment parameters: TR = 2 sec, Flip angle was at 90°, Field of view (FoV) 64 mm x 64 mm x 64 mm, number of volumes varied on the speed of task completion of each of the participants (event-related design). During the fMRI scan, participants were lying in their backs, watching a screen through a system of mirrors and holding a controller with two buttons in either of their hands.

The irony task included 3 various conditions. 20 statements (originally 25, but 5 were later omitted) were projected on the screen, one after another, in 3 different contexts. Whether the

statements were the truth, a lie or an irony depended on these contexts. For the complete list of stimuli, see Attachment II: List of Stimuli.
Example: At the hairdresser´s, the woman´s hair was dyed using the wrong shade of the dye. One of 3 statements followed:

1. The woman loves experimenting and says: “What a lovely colour!” (Truth)
2. The woman is not satisfied with the result, but she says: “What a lovely colour!” (Lie)
3. The woman is angry and says: “What a lovely colour!” (Irony)

This way, the participants had to read the statements and determine, whether the statement was ironical based on its context. Their answer was submitted using a controller: button 1 – irony, button 2 – not irony. Stimuli of each condition were projected in quasi-randomized order.
Stimuli projection started simultaneously with the scanning. Followed by one another, on the screen appeared following slides: an instruction slide (5000 msec), a blank slide (1000 msec), a slide with a description of the situation – context until direct speech (4500 msec), and a slide with the statement indirect speech, which had to be categorised as “irony” or “not irony” (given time was 6000 msec, but the screen changed after submitting an answer). After the respective answer, a blank slide appeared (1500 msec) and the whole cycle began again. The first cycle, consisting of context – statement – answer – blank slide was not analysed, as it was only a training one. After the training cycle, 60 cycles followed, 20 cycles for each condition. Based on these cycles, data from the experiment were received for further data analysis.

5 Data Acquisition and Analysis

Next part of the thesis will describe data acquisition and analysis procedures, including used software and conditions of analysis.

5.1 Data acquisition

In the process of behavioural data acquisition, received answers from the fMRI experiment were analysed. Microsoft Office Excel was used for the determination of the time used to evaluate the statements, as well as to check the correctness of the chosen answer. The data showed that some of the participants corrected their answers – participant number 4 did so 19 times, number 5 once, and number 13 twice. In some cases, the statements were evaluated before being shown on the screen – in case of the participant number 4 – 51 times, and number 13 only once; or even unanswered at all – participants 5 and 17, both once. In the stated cases, it was decided to measure the time in the following ways:

- If there was no answer at all, the respective cell for answer duration remained blank.
- If there was an answer before the appearance of the statement – the cell remained blank.
- If there was a correction – time was measured from the appearance of the statement until the second (corrected) answer.
- If the answer was the same before and after the statement appeared – time was measured from the appearance of the statement until the second answer.
- If one answer was given before the blank slide appeared and the second one after its appearance - time was measured from the appearance of the statement until the second answer.

As mentioned before, participant number 4 answered before seeing the statement (85 %) and kept correcting himself (31,7 %), which meant he did not follow the rules of the task completion. Due to these fails, as well as the discovery of a cellular malformation in his brain, it was decided to exclude him from further analysis. As a result, our final sample size consisted of 17 participants (10 females and 7 males).

5.2 Data processing

As a result of behavioural data analyses from fMRI, we received a count of correctly chosen answers (*Table 1*), as well as time spent for the respective choice for each of the participants (*Table 2*).

Table 1: Number of correctly chosen answers

Participant´s number	Truth	Irony	Lies
2	0,79	0,70	0,65
3	0,89	1,00	0,05
5	0,20	0,85	0,30
7	0,90	0,95	0,68
8	0,21	0,75	0,39
9	0,67	0,70	0,16
10	0,84	0,95	0,61
11	0,85	0,95	0,58
12	0,89	0,35	0,63
13	0,45	0,61	0,26
14	0,95	0,89	0,83
15	0,78	0,89	0,70
17	0,21	0,89	0,15
18	0,74	0,67	0,70
19	0,68	0,70	0,55
20	0,95	1,00	0,53
21	0,83	0,95	0,75
Mean rate	**0,69**	**0,82**	**0,49**

In order to receive a statistical significance of the difference between correctness and time spent on choosing the answer in conditions of the truth, irony and lie, we compared the coupled data using a T-test in a statistical software SPSS. Using the data from the *Table 1*, we managed to define a statistically significant difference between the correctness of identification of the irony and lie conditions ($t(16) = 4.34$, $p<0.001$) and lie and truth conditions ($t(16) = -3.41$, $p< 0.004$). In those conditions, which included the truth and irony conditions, the was no statistical significance found ($t(16) = 1.66$, $p> 0.10$).

Data from the *Table 2* were processed identically. As a result, statistically significant was the difference in reaction times for the answers in lie and truth conditions ($t(16) = 6.23$, $p< 0.001$), irony and lie conditions ($t(16) = -3.05$, $p<0.01$), and irony and truth conditions ($t(16) = 2.41$, $p<0.05$).

Table 2: Participants' reaction time (in ms) in correctly chosen answers

Participants Number	Truth	Irony	Lie
2	11659,13	12403,64	13841,77
3	6838,5	7536,211	11351
5	22619	22699,53	25917
7	14702	17499,39	15553,92
8	23589,75	24014,69	27796,67
9	14728,5	14718,64	14889,67
10	14899,25	16398,95	15257,36
11	23142,53	25113,74	24971,73
12	19828,81	20048,29	23369,5
13	13390	12644,64	15081,2
14	15284,5	17973,47	18227,13
15	13292,29	15459,53	17066,71
17	12986,75	12460,06	14187
18	18690,5	21610,17	21946,21
19	11986,23	16312,71	15623,82
20	7802,611	6341,85	7701,3
21	13067,07	11666,16	14156,07
Mean time	**15206,32**	**16170,69**	**17466,94**

5.3 fMRI data analysis

Preprocessing

As a first step of the analysis of the fMRI data, the images were preprocessed in order to make them comparable and correct for temporal and spatial differences. The first step, realignment, was done in order to correct spatial differences caused by head movement during the scanning process in X, Y and Z axis direction. Secondly, the scans were corrected for temporal differences. The functional images underwent a slice-timing step.

Subsequently, the functional images are compared to T1 weighted anatomical images of the participants. This step, called coregistration, was done in order to later be able to decide which anatomical areas are the ones showing a haemodynamic response.

The shapes and sizes of brains differ significantly between different people. In order to still make them comparable, they needed to be standardized. During the step of normalization, they were conformed to fit the size and shape of a standard brain provided by the Montreal

Neurological Institute. This step allows comparison within the study, but also across different studies using the same system. Smoothing at 8 mm was the last step used during preprocessing and it is used to improve small remaining differences between the brains being compared. It was done by comparing every voxel to its' neighbours in order to reduce noise and artifacts.

5.3.1 Definition of contrast

During the definition of contrasts, conditions were compared to each other or to a resting baseline. Here, each voxel was examined and compared in between the three conditions (Truth, Lie, Irony). Differences in voxel activations are seen as activated clusters. Firstly, all conditions were compared to a baseline (e.g., Irony vs. baseline, Truth vs baseline). Secondly, the conditions of irony, truth and lie were compared with each other. Statistical analysis was carried out using the general linear model. Statistical significance was set at p = 0,01 and considered significant at p FEW 0.05. We also reported the results on the p uncorr. 0.05 since they presumably could provide additional cues of the neural structures involved in the processing of irony, truthful and deceitful statements.

6 Results

This chapter shows results of the experiment. Beginning with main effect and proceeding to comparison of various conditions. Only significant results are showed. All results, including their MNI coordinates are stated in the *Table 3.* Description of each comparison can be found below.

Table 3 – Significant activations with MNI coordinates

Main Effect		Cluster values				MNI coordinates		
	H	pFWE-corr	kE	p uncorr.	Peak Level ZE	X	Y	Z
frontal mid g.	L	1.000	53	0.049	4.61	-32	12	56
frontal inferior orb g.	R	0.374	145	0.003	4.44	48	30	-12
frontal inferior orb g.	L	**0.000**	535	0.000	4.22	-40	28	-12
frontal superior med g.	R	**0.000**	488	0.000	3.87	10	42	38
supplementary motor area	L	0.270	160	0.002	3.58	8	32	54
cingulum posterior	R	0.407	141	0.003	3.49	-48	-62	22
Truth vs. Baseline								
postcentral g., parietal inferior g., rolandic operculum	L	**0.000**	2784	0.000	4.41	36	-64	40
frontal superior med g., cingulum anterior, supplementary motor area	L	**0.000**	1785	0.000	3.95	8	34	30
supramarginal g.	R	**0.000**	948	0.000	3.88	60	-14	30
frontal inferior operculum	R	0.518	200	0.008	3.43	46	0	6
insula	L	0.663	176	0.011	3.40	-30	30	-16

Lie vs. Baseline								
cingulum mid frontal, superior med g., supplementary motor area	Bilat.	**0.000**	3654	0.000	4.77	8	38	32
precentral g., postcentral g.	L	**0.000**	1895	0.000	4.45	-30	-18	56
supramarginal g.	L	**0.020**	663	0.000	3.82	58	-48	46
frontal inferior orbital g., insula	L	**0.000**	849	0.000	3.80	-34	20	-16
Irony vs. Baseline								
precentral g., parietal inferior g., supramarginal g.	L	**0.000**	4680	0.000	4.76	-36	-24	56
frontal inferior orbital g., insula	L	**0.000**	1278	0.000	4.23	-34	18	-20
cingulate mid g.		**0.000**	3421	0.000	4.02	4	34	30
frontal mid g.	L	**0.006**	564	0.000	4.00	-38	40	30
postcentral, supramarginal g.	R	**0.001**	705	0.000	3.84	56	-46	48
cerebellum	R	0.119	317	0.001	3.76	18	-48	-16
Irony vs. Lie								
frontal mid g., frontal superior medial g.	R	0.999	76	0.077	2.80	20	64	26
Irony vs. Truth								
frontal superior medial g.	L	1.000	72	0.084	2.96	4	50	26
Lie vs. Irony								
nucleus caudatus	R	0.657	177	0.011	3.51	20	18	12

Lie vs. Truth								
frontal inferior orbital g.	L	0.507	202	0.007	3.56	-38	44	-12
frontal mid g.	L	0.785	156	0.016	3.33	-36	60	10
nucleus caudatus	R	0.995	91	0.056	3.31	18	16	16
Truth vs. Lie								
insula	R	0.999	80	0.071	2.94	38	0	4

H - hemisphere, L - left, R – right, g. – gyrus

pFWE-corr - family wise error correction, kE – cluster size, peak level – maximum peak of the activation, MNI coordinates – coordinates for Montreal Neurological Institute.

Frontal gyrus activation was very common in all conditions, especially evident in their comparisons, apart from truth vs. lie and lie vs. irony. Inferior (IFG) and medial (MFG) parts were both coactivated and activated individually, as discussed in the next parts.

Main effect

As for the main effect, activation in MFG was present, especially in the left middle and right superior parts. Another significant activation was in orbital regions of IFG, both left and right. Activated cortex areas include left insula, SMA and cerebellum.

6.1 Comparison of the conditions vs baseline

Irony vs. Baseline

The wide range of activations found by comparing irony condition with baseline. Both middle and frontal gyri were activated, in particular left pars orbitalis and insula in IFG. However, the biggest area was found in the parietal lobe, dividing into two clusters by different lateralisation: one being left precentral gyrus (PreCG), left supramarginal and left inferior gyri and the second being lateralised to the right – right supramarginal and postcentral gyri. Twice as big activation as in MFG was found in middle cingulate cortex. The smallest but also significant activation was found in the right cerebellum (Fig.1).

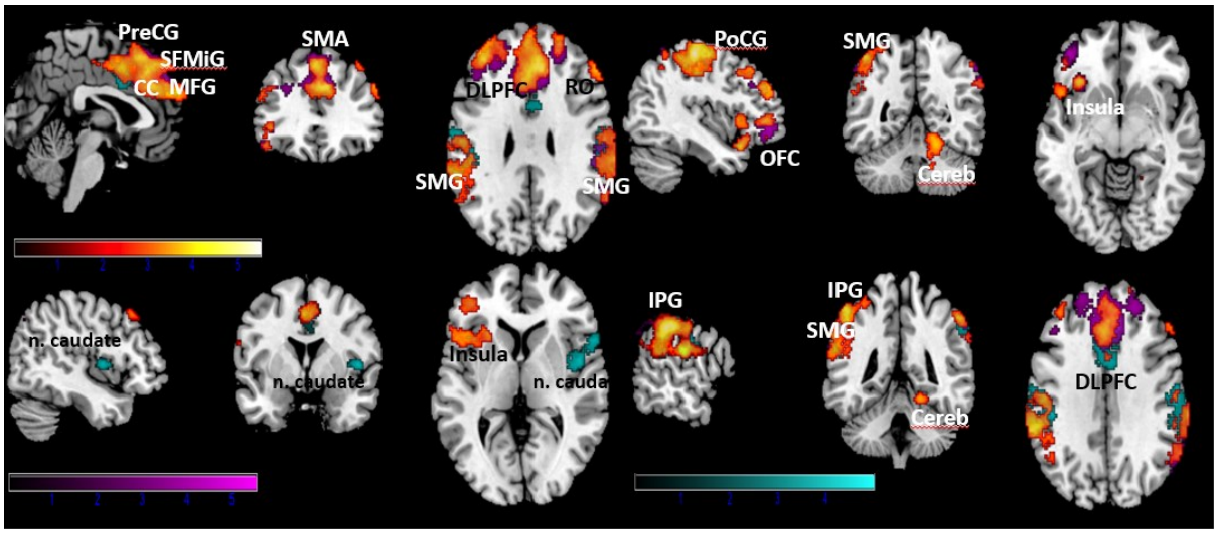
Truth vs. Baseline

By comparing truth and baseline conditions, the activation was found in both right (supramarginal gyrus) and left parts of (rolandic operculum, postcentral and inferior areas) of parietal cortex, the former being smaller and latter bigger. Other significant activations included left superior part of MFG, ACC, and SMA, followed by pars opercularis of right IFG and left insula (Fig.1).

Lie vs. Baseline

As for comparison of lie and baseline conditions, four clusters with the significant activations were found: middle cingulum, left and right parts of superior frontal gyrus and left and right SMA. Another significant cluster was found in precentral and postcentral parts of parietal lobes. Following activations were smaller but significant – left supramarginal area (SMG) of parietal lobe and left insula (Fig.1).

Figure 1: Comparison of the truth (purple), lie (cyan) and irony yellow) conditions to baseline.



PreCG – precentral gyrus, SFMiG – superior frontal middle gyrus, CC – caudate cortex, MFG – medial frontal gyrus, SMA – supplementary motor area, SMG – supramarginal gyrus, DLPFC – dorsolateral prefrontal cortex, RO – Rolandic operculum, PoCG – posterior cingulate gyrus, OFC – orbitofrontal cortex, Cereb - cerebellum, n.caudate - nucleus caudate , IPG - inferior parietal gyrus.

6.2 Between-conditions comparison

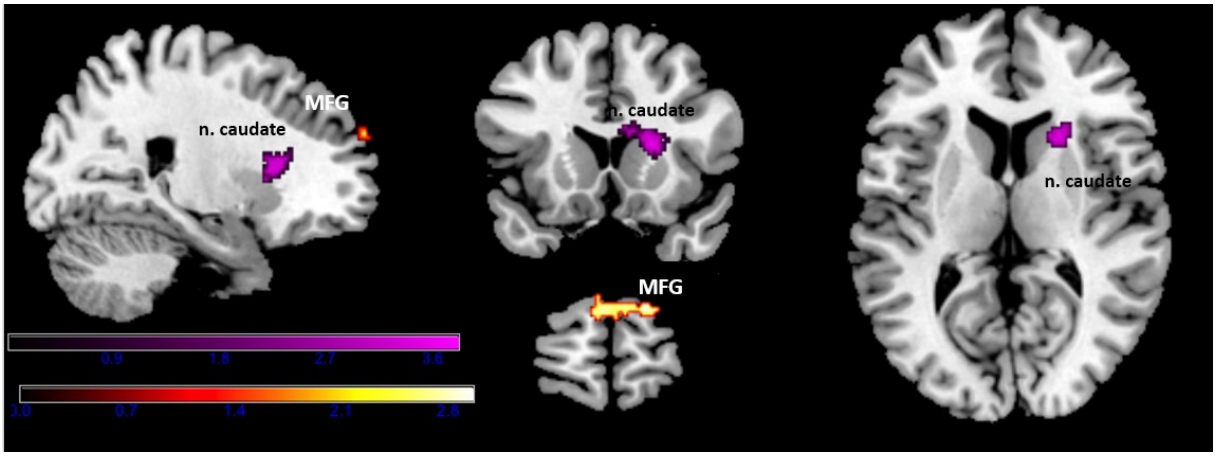
Irony vs. Lie

By comparing conditions of irony and lie, only one area was activated significantly – medial frontal gyrus, with highest peaks in middle and superior medial parts (trend p uncorr 0.07) (Fig. 2, Fig. 3).

Lie vs. Irony

By comparing activations in lie and irony conditions, only one was significant, and that is in right nucleus caudate (p uncorr <0.05) (Fig. 3).

Figure 3. Activations in irony vs. lie (yellow) and lie vs. irony (purple)

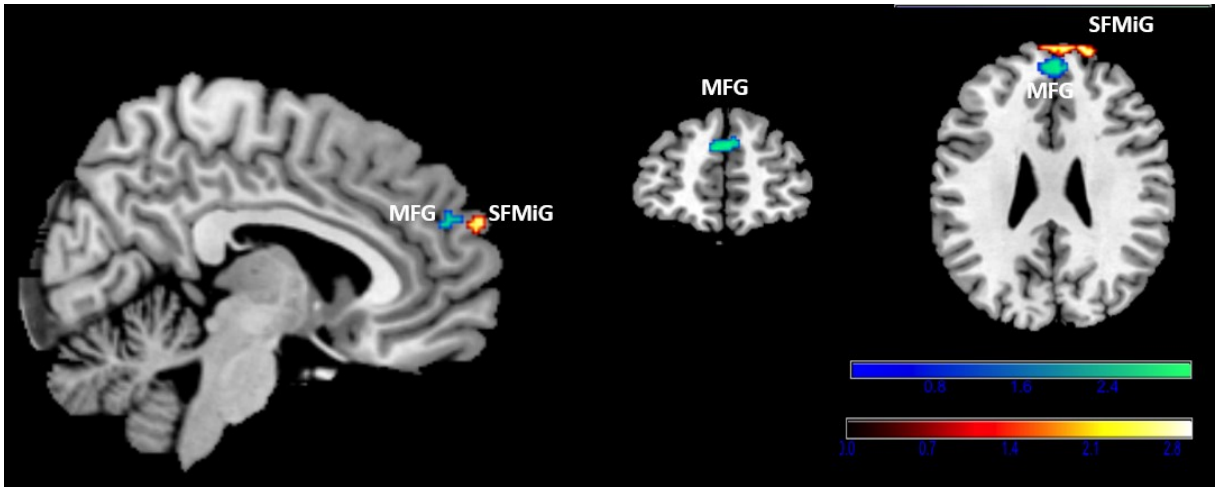


n.caudate – nucleus caudate , MFG – middle frontal gyrus

Irony vs. Truth

Similar situation was present by comparing irony and truth conditions. Left superior medial part of frontal gyrus was significantly activated (trend p =0.084) (Fig. 2).

Figure 2. Activations in irony vs lie (green) and irony vs. truth (yellow)



MFG – middle frontal gyrus, SFMiG – superior middle frontal gyrus.

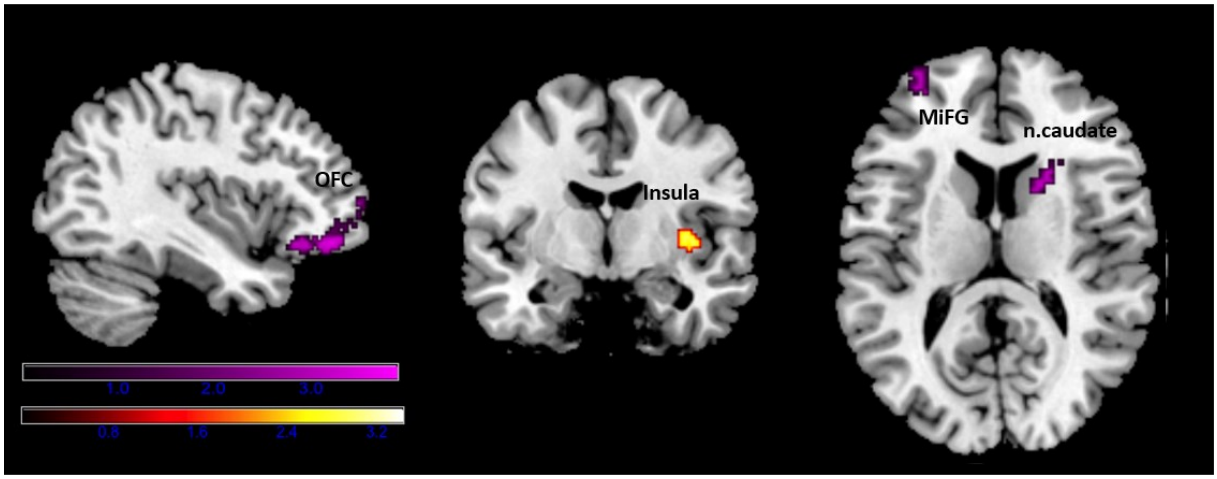
Truth vs. Lie

In comparison of truth and lie conditions, there was only one significant activation – right insula (trend p =0.071)(Fig. 4).

Lie vs. Truth

Activations in IFG and MFG were similar in size and lateralisation to the left. Additional activation was found right nucleus caudate (p uncorr <0.05) (Fig.4).

Figure 4. Activations in truth vs. lie (yellow) and lie vs. truth (purple)



OFC – orbitofrontal cortex, MiFG – middle frontal gyrus, n.caudate – nucleus caudate

7 Discussion

This study investigates neural correlates of irony processing when compared to truth, lies. It explores differences in activated brain areas between individual conditions and points out shared neural structures as well.

Based on the behavioural results from the fMRI, it is evident that the participants were the most successful in identification of irony condition, slightly less successful in differentiating the truth from the irony and least successful in the remaining conditions – lies from the irony, as the success rate was on a level of a random guess.

Meanwhile the success rate was not connected to the reaction time. The shortest time was spent for identification of the truth, a little bit longer for the irony and the longest time for distinguishing the lie from the irony condition. On one hand, these results reflect the complexity of the individual conditions and demands posed on the participants while identifying these language structures: the least demanding was the truth, the most demanding the irony with lies lying somewhere in between.

However, this hierarchy seems to be changed. Based on the given task to the participants in the fMRI, they were to respond whether the statement was ironic or not. It indicates that their task was not to identify the truth, the irony nor the lies, but to identify the irony in the list of truthful and deceitful statements. Consequently, distinguishing irony from the truth is the simplest task as in case of the truth, the participants answered swiftly and correctly that the statement is not ironic. Complications occurred when deceitful statements were projected. As structurally speaking, they are similar to ironic ones, but they are not irony. This might also be the reason for the highest number of false identifications and why it took the longest time for participants to decide whether the statements were ironic or not. In this case, the identification of irony was intermediately difficult, as understanding of ironic statements takes longer time that of the truthful ones. At the same time, they required less time for answering that the statements were ironic then for answering about non-ironicalness of the deceitful statements, as they first had to understand that the statements were lies, and then press the button indicating they were non-ironical statements. As a result, the hierarchy changed from “truth – lie – irony” ito “truth – irony – lie”.

The fMRI data provided us with some interesting results as well. Major part of the measured activations was found in the MPFC. This part of the brain is directly involved in the ToM network, as basis for any social interaction, with wide scope of functions, as making predictions about future outcomes, mentalizing, correct interpretation of social situations (Shamaytsoory et al. 2007; Alexander & Brown 2011; Euston et al. 2012). Our results comply with results from other studies (Spotorno et al. 2012), which indicate that the Tom network becomes active when processing ironic statements. Other experimental evidence shows, that MPFC´s role in irony comprehension may be in understanding of the situational context (Akimoto et al. 2014). These seems to be a strong link between MPFC and IFG, as it is suggested that IFG acts like a language integration centre, especially when Sportorno (2012) compared results of processing of literal and ironic statements.

Additionally, superior medial frontal gyrus is also believed to be connected to already mentioned motor areas is MNS, which consist of neurons with sensorimotor properties. They are believed to be located in primary motor areas and inferior parietal lobule (IPL) (Kilner & Lemon 2013). These regions might be activated due to sensory information about motoric actions (Gallese 2008), which were projected on the screen in fMRI. One part of IPL is supramarginal gyrus (SMG), which was originally creating visuomotor maps of movement and mediating skilled movements. It has also been shown that SMG is activated in comprehension of written words (Stoeckel et al. 2009). From a behavioural point of view, its activity may indicate change in perception of time and duration of visual stimuli (Wiener et al. 2010). There have been studies with this area being activated in social judgment tasks, especially when egocentric perception of the social situation was not beneficial to the viewer (Silani et al. 2013). Thereafter, we propose that activation of this area happened due to impersonal tasks, where egocentric approach would not help the person decide about the irony in the provided statements.

By comparing our results from all conditions, several shared points of activation were observed, and that was in PreCG. It is located in the posterior part of frontal lobe, being the location of primary motor area. As the name indicates, this area is primarily activated in action execution, especially hand and finger movements (Ghez & Krakauer 2000), or during a process of motor learning (Dupont-Hadwen et al. 2019). As our subjects' task was to press a button when choosing whether the statement was irony or non-irony, we think this might be the reason of this area´s activation in all the conditions.

Anatomically and functionally connected to the primary motor area is SMA. It is also activated during execution of finger movements (Shibasaki et al. 1993), and we think the previously mentioned finger movement might be one of the reasons for its activation. Another one can be involvement of SMA in motor memory system (Tanji & Mushiake 1996) and therefore can its activation be explained by active work with a memory of motoric behaviour - pushing the respective button. SMA is also one of the regions frequently activated in the ToM network (Bodden et al. 2013). Its precise role still remains unclear, it is thought SMA participates in intentional processes behind action plans, including gathering of contextual information (Wiesendanger 1985). Close to SMA, there is another region called superior medial frontal gyrus (or superior frontal middle gyrus, SFMiG) or sometimes preSMA. It plays an important role in cognitive inhibitory control, which allows a person to modify his behaviour by inhibiting the undesired one (Floden & Stuss 2006). Moreover, its stronger activation is not caused by any inputs from the outer world, but only coming from the inside, as a result of some prior inner decision (Hsu et al. 2011). This area is frequently activated in conflict monitoring and potentially resolution as well (Garavan et al. 2003). We propose that activation of this region might have been caused by the necessity to concentrate on the assigned in the fMRI not given by an fMRI operator but coming from the inside of the person.

Next common area of significant activation is cingulate cortex. It has two subdivision – affective and cognitive, the former being connected to amygdala, periaqueductal grey and motor nuclei of the brainstem, the latter to spinal cord and red nucleus (Devinsky et al. 1995). The affective division is responsible for evaluation of motivation and allocation of emotional value to internal and external stimuli, meanwhile the cognitive one has premotor function and processes demanding cognitive tasks (Devinsky et al. 1995), like reading a statement, selecting an answer and consequently pressing a button (Bush et al. 2000). It seems that language processing as such is also an important role of CC, especially of its anterior part (aCC), as well as response selection and selectively directed attention, which is key in distinguishing between two stimuli presented at the same time (Devinsky et al. 1995). Another study shows, that aCC plays a role of decision making centre and facilitates doing so in novel environments (Kennerley et al. 2006). This indicates that activation of aCC was due to the subjects´ will to concentrate on the task and statements, and additional processes, which forewent decision about the correct answer. Moreover, CC also works as an error detection network of our brain, modifying cognitive and behavioural outputs and facilitating the choice of the correct one, based on the

statement´s emotional and motivational contents (Bush et al. 2000; Kennerley et al. 2006). Greater activation is frequently measured in those with higher social insight and a high level of self-control (Allman et al. 1987).

Last common activation was found in left insula. It is activated in situations when one subjectively perceives emotions and interprets them, as well as in self-awareness in terms of own body (Pavuluri et al. 2015). It is known to be activates in feelings like fear and disgust, as well as roles in language processing, which have not been precisely assigned yet (Gasquoine 2014).

Besides the common activations above, we have also observed some differences between individual conditions. Activation of inferior parietal gyrus (IPG) and Rolandic operculum (RO) was observed only in the truth condition. As RO takes part in processes of working memory, action inhibition and attention interface (Zhang et al. 2016), we think that its activation may be the strongest in the truth condition as the subject has no doubt about condition of the statement and does not even evaluate the option of lie nor irony condition, as the statement seems truthful. Therefore, the participant can pay his whole attention to pushing the respective button, with no necessity to activate side regions used for non-literal meaning of statements. Its activation may be strengthened by inner rehearsal of the statement as a control mechanism of the answer´s correctness, as it has been shown that RO is also activation in speech processing, and especially its prosody part (Wang et al. 2007). Moreover, if we perceive the IPG in the Broca´s functional division, we get into the Broca´s area (BA) 40, which is majorly responsible for acoustic working memory loop, which may be connected to the previously mention inner rehearsal of the statement (Paulesu et al. 1993).

On the other hand, we found no activation of BA 6 – PreCG in the truth condition (Zhang et al. 2012). The reason for this may have been its involvement in attribution of negative judgment on ongoing situation (Blackwood et al. 2000), which is logically not present in the truth condition, unlike the irony and lie ones.

Another area, which was dominantly activated in both irony and lie conditions, is the orbitofrontal gyrus (OFG). OFG is activated by higher cognitive functions as information processing and emotion assessment (Burks et al. 2018; Geng et al. 2021) as one needs for abstract meanings of lies and irony. This activation is in agreement with another experimental

evidence showing , that this region, together with the rest of medial orbitofrontal cortex, is predominantly activated in metaphor and irony comprehension, especially in task-dependant irony (Wakusawa et al. 2007), as well as emotional clues detection (Blackwood et al. 2000). This region is also included in the ToM network (Frith & Frith 2007).

We have observed lateralisation of SMG in the irony and lie conditions, right SMG being activated in irony and left one in lie conditions. As it has been already mentioned, SMG is activated in understanding of written words, as well as events, when self-centred approach is not beneficial for the individual. There may have been an explanation of such lateralisation, which lies in their complexity, as described in chapter 2.2. Irony. The truth represents the least complex and irony the most complex statements, with lies placed in the middle of this complexity line. The explanation of the left part involved in lies comprehension may therefore in a necessity to use working memory and process the written statements correctly (Guidali et al. 2019), without additional emotion comprehension of the context or the statement. On the other hand, when processing ironic statement, one needs to evaluate emotional valence of the statement (Wada et al. 2021) and as the participant was not a direct participant of the situation, he needed to do it with a not egocentric approach, which was ensured by activation of right SMG (Silani et al. 2013).

Surprisingly, we also observed an activation of cerebellum, solemnly in irony condition. At a first glance, cerebellum is not regarded as a classical neural correlate for social cognition tasks. After conducting a meta-analysis of more than 350 fMRI studies (Van Overwalle et al. 2015) showed, that there is a pattern in cerebellum´s activation in social cognitive tasks, and that is an element of probability or uncertainty. When it is necessary to anticipate or predict future events, or hypothesise about the past one´s, activation of cerebellum can be observed (Sokolov 2018), which is substantial in assessment of irony. There has also been some experimental evidence that cerebellum connects a certain input with some inner representation of this input in the brain and speeds up the processing of environmental inputs with social importance (Clausi et al. 2019). Consequently, seems that the cerebellum does not play one specific main role, but instead performs in supporting roles in social tasks, which include mentalizing, language procession and the activation grows with rising complexity of cognitive tasks (Van Overwalle et al. 2015). Which, as mentioned before, may also be the point for its activation in irony comprehension, but not in truth and lies.

Activations in nucleus caudate were also observed. It is believed to be one of the correlates involved in decision making about dishonesty, and its use in communication (Yin & Weber 2018). Moreover, its activations were also observed in situations where some kind of award was offered (Diekhof et al. 2012). On the other hand, punishment - both and effective, seems to activate this area, especially when some the punisher can benefit from the given punishment (De Quervain et al. 2004). Evaluating all these options as a consequence of a used deceit (Yin & Weber 2018) might pose an important role on nucleus caudate.

As a general conclusion, our experiment demonstrated substantial involvement of the prefrontal cortex and its medial part into the processing of ironic, truthful and deceitful statements. Irony differed from truth and lie by additional activation of superior and medial frontal gyri, parts of the TOM network that put into play the mentalizing process and a necessity to understand beliefs and intentions of the speaker. Insula cortex activation in the truth statements processing, might indicate increased self-consciousness and situational public self-awareness facilitating truth/lie detectability, while the lie, becomes more demanding perhaps requiring a consideration of reward and punishment issues (stands for the activation of nucleus caudate) and as a result an excessive decision-making process.

7.1 Limitations of the study

Along with the FEW corrected results, we report the findings with the uncorrected values. Lowering down the threshold helped us to unveil broader scope of structures activated in the irony, truth and lies comprehension. Indeed, we observed some structural differences in direct contrasts. These activations corresponded with the previous findings, where activations of IFG and MFG (Bosco et al. 2017), or nucleus caudate and insula (Rapp et al. 2013; Obert et al. 2016) were observed.

The sample size is another limitation. Initial subject sample comprised of 20 subjects, with the drop-out rate of 15 %, which is a common rate for fMRI experiments. In the future, we will try to overcome these limitations. Despite the limited sample size, we observed the different neural correlates activated in the truth, irony and lie comprehension and confirmed our hypothesis.

8 Conclusion

Writing of this master thesis included preparation of the experimental part, as well as fMRI data analyses and interpretation. Work with fMRI data has some specifics, mainly due to high level of their complexity and different approaches of results´ interpretations. Work with human participants has taught me a lot about ethics, specifics of this model, and differences from other models, which are more frequently used in the neuroscientific research.

Our assumption about the different brain structures involved in comprehension of the irony, truth and lies was confirmed, with further evidence of activated brain areas.

In the course of writing this thesis, I came across many topics, which haven´t received much of explanation nor validation in the modern scientific research. In order to move forward with our current knowledge on social cognition, ToM, statement comprehension and irony in particular, it might be beneficial to seek answers in experimental settings. Deepening of knowledge on the topic of irony comprehension and connected topic of metaphorical and literal language processing may serve as a valuable substrate for understanding of psychopathological changes in the brain, which occur in e.g., ASD, schizophrenia or dementia.

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Attachment I – List of fMRI studies on irony

	Author	Title	Year	Study Design*	Hypothesis	Activated Brain regions
1	Akimoto et al.	Irony comprehension: social conceptual knowledge and emotional response.	2014	17F, 18M, 20.2, (18-23)	Conceptual knowledge of irony is represented by the anterior superior temporal gyrus representing social concepts	aSTG, situational context: MFC, aIFG; degree of irony: amygdala, hippocampus, parahipp.gyrus
2	Bosco et al.	Neural correlates underlying the comprehension of deceitful and ironic communicative intentions.	2017	9F, 14M, 22.7, (19-27)	Is TP, IFG, MFG, MTG or STG strongly activated in the comprehension of irony when compared to deceit?	left TPJ, left IFG, lMFG, left MTG, left DLPFC
3	Eviatara et al.	Brain correlates of discourse processing: An fMRI investigation of irony and conventional metaphor comprehension	2006	7F, 9M,	Does the processing of literal and nonliteral statements result in activation of the same brain areas? Will the distribution of activation be the same for two types of figurative language, irony and metaphor?	right STG, MTG
4	Filik et al.	What is the difference between irony and sarcasm? An fMRI study	2019	10F, 7F, 24, (19-29)	Are IFG and MFG activated more for sarcasm/irony, than literal statements?	IFG, mPFC
5	Herold et al.	Altered Neural Activity during Irony Comprehension in Unaffected First-Degree Relatives of Schizophrenia Patients-An fMRI Study	2018	7F, 5M, 37.00 ± 9.08, (26-55)	Altered comprehension of irony is a trait-like marker of liability to schizophrenia.	left DLPC, right IFG
6	Obert et al.	Neural Correlates of Contrast and Humor: Processing Common Features of Verbal Irony	2016	10F, 11M, 22,1, (20-27)	In connection to verbal irony comprehension, brains regions recruited by contrast would respond quadratically to humor	bilateral IFG, left caudate, left STG, STS, left lingual gyrus.

7	Rapp et al.	Neural correlates of irony comprehension: the role of schizotypal personality traits.	2010	15 F, 28, (21-52)	Is there a difference in brain regions involved in irony comprehension caused by schizotypal personality traits?	left MFG, left IPL
8	Rapp et al.	Isn't it ironic? Neural Correlates of Irony Comprehension in Schizophrenia	2013	15F, 28.1	Impairment in irony comprehension in both schizophrenia and autism may be caused by right hemisphere dysfunction. Dysfunction of the brain's frontotemporal language system may be crucial in the pathophysiology of the difficulties experienced by patients with schizophrenia in interpreting ironic remark	mTG, rolandic operculum, postcentral gyrus. LH insula
9	Shibata et al.	Neural substrates of irony comprehension: A functional MRI study.	2010	3F, 10M, 23.8, (20-29)	Are neural substrates activated in ironical sentences comprehension different from those activated in comprehension of literal sentences?	right mPFC, left precuneus, left STS, STG, PG
10	Spotorno et al.	Neural evidence that utterance-processing entails mentalizing: the case of irony.	2012	12F, 8M, 22	Is the ToM network involved in the on-line processing of ironic utterances?	mPFC, bilateral IFG - triangular and orbitalis parts, left insula, bilateral TPJ
11	Varga et al.	Irony comprehension and context processing in schizophrenia during remission – A functional MRI study	2013	14F, 10M, 33.96 ± 8.51, (23–55)	Patients with schizophrenia perform worse and exhibit an abnormal brain activation pattern during irony comprehension.	left TPJ, posterior division of left MTG, right PCC/precuneus, left sFG, pars triangularis of left IFG
12	Wakusawa et al.	Comprehension of implicit meanings in social situations involving irony: a functional MRI study	2007	17 F, 21 M, 22,3 (18-38)	Intentional processing of implicit social meanings as irony and metaphor is reflected in task-dependent activation	right TP, mOFC
13	Wang et al.	Developmental changes in the neural basis of interpreting communicative intent	2006	Children: 6F, 6M, (9-14); Adults: 6F, 6M, 26.9 ± 3.5 years (23-33)	Scenarios involving irony comprehension elicit greater activity in right hemisphere and prefrontal regions than scenarios containing only literal speech.	mPFC, left IFG, bilateral FG, mOG, iTG, STG,

14	Wang et al.	Neural basis of irony comprehension in children with autism: the role of prosody and context.	2006	18M, 11.9 ± 2.3, (8.1–15.7)	Children with ASD use prosodic and contextual cues to interpret irony differently from typically developing children	mPFC, left IFG
15	Wang et al.	Reading affect in the face and voice: neural correlates of interpreting communicative intent in children and adolescents with autism spectrum disorders	2007	18M, 11.8 ± 1.9, (9-15)	Scenarios involving irony detection elicit greater activity in the medial prefrontal cortex and superior temporal gyrus than scenarios containing only literal utterances in typically developing children.	dorsal and ventral mPFC, bilateral STG
16	Williams et al.	Brain function differences in language processing in children and adults with autism	2013	Children: 2F, 12M, 12,5 ± 1.5; Adults: 1F, 11M, 21 ± 3.7	Subjects with autism differ from typically developing subjects in functional connectivity in language comprehension and irony	left MFG, left pars triangularis, left and right MTG, left pars opercularis (IFG)
17	Yang et al.	Figurative language processing after traumatic brain injury in adults: a preliminary study	2010	27.6 ± 7.05, (25-48)	Traumatic brain injury patients display decreased activation of the left inferior frontal gyrus in comparison with healthy controls	left IFG

*Subjects (females, males, mean age ± standard deviation, age range)

Attachment II – List of stimuli

Number	Condition	Statement	% - of correct identification
1	L	A woman gets the wrong dye at the hairdresser's. But she wants to be nice and says: What a great color.	88
2	T	An athlete injured his leg. He wins the gold medal with the run and says: That was a great race.	94
3	I	A housewife's cake is burned. The man wants to tease her with it and says: It's just as good as always.	88
4	T	A gardener is lying in a hammock. He worked hard all day long and says: Man, that is exhausting work.	75
5	L	A goalkeeper goes wrong - 0: 1. His coach wants to comfort him despite the mistake and says: That was simply untenable.	94
6	I	A little girl is disguised as a ghost. Her sister wants to tease her and says: Huuuuh, I'm so scared.	81
7	T	A girl throws the ball at a boy. He's having fun with the game and says: It's very funny.	94
8	L	A woman travels to the mountains. She only does this because she loves her husband so much. She says: Oh, I love skiing.	100
9	L	A student misses the lecture. In order not to turn the lecturer against himself, he says: What a shame, such an exciting topic.	88
10	I	The party is very boring. A woman is disappointed with lost time and says: What a great party.	81
11	I	A man has a bad hangover. He looks into his pathetic reflection and says: I really do lead a healthy life.	100
12	I	The juice was really sour. A man grimaces in disgust and says: Tastes pretty sweet.	75
13	L	An old woman wants to cross the street. Nobody helps. Nevertheless, she later says to her grandson: The youth of today are really nice.	75
14	T	A singer fails several times in concert. A listener does not hear the mistakes and says: What a talented artist.	88
15	L	A woman's red nail polish is way too bright. Her friend wants to comfort her and says: You should always use this color.	100
16	I	A painter gets mixed up in color. The customer complains about the work and says: That looks wonderful.	94
17	I	A man is honored. But his boss insulted him several times in the speech. The man says:	88

		Thank you for the wonderful words.	
18	L	An apprentice brings the wrong snack. The boss does not want to burden the boy and says: Hmm, that's delicious.	88
19	T	The weather is too bad for a barbecue. Still, the party will be great. The host says: What a wonderful day!	100
20	L	The new car is often broken. The owner tries to sell it again and says: This is really the greatest car I've ever had.	94
21	I	A woman travels to the mountains. It rains there for days and she breaks her leg. She says: Oh, I love skiing.	100
22	L	An athlete injured his leg. He wants to hide this from his mother and says: That was a great race.	100
23	T	A man is honored. His boss gives a funny and deeply grateful speech. The man says: Thank you for the wonderful words.	100
24	I	An old woman wants to cross the street. A man sees her but leaves her there. She says: The youth of today are really nice.	100
25	I	A goalkeeper goes wrong - 0: 1. A fan is mad about the stupid mistake and says: That was simply untenable.	63
26	T	A little girl is disguised as a ghost. Her little brother is really scared and says: Huuuuh, I'm so scared.	94
27	I	The new car is often broken. The owner complains to the manufacturer and says: This is really the greatest car I've ever had.	100
28	L	A singer fails several times in concert. But a listener wants to be nice and says: What a talented artist.	88
29	T	The juice was really sour. A man is used to extreme tastes and says: Tastes pretty sweet.	75
30	I	A student misses the lecture. The subject doesn't interest him at all. He yawns and says: What a shame, such an exciting topic.	75
31	T	A housewife's cake is burned. The man doesn't even notice it and says: It's just as good as always.	81
32	I	A woman's red nail polish is way too bright. Her boyfriend wants to tease her and says: You should always use this color.	100
33	T	The party is very boring. But a woman talks to an old school friend and says: What a great party.	63
34	L	A gardener is lying in a hammock. He calls his wife at home, whines and says: Man, that is exhausting work.	94
35	L	A girl throws the ball at a boy. He doesn't like that, but wants to please her and says: It's very funny.	100

36	T	A man has a bad hangover. He usually does not drink and does a lot of sport. He says: I really do lead a healthy life.	88
37	I	An apprentice brings the wrong snack. The boss looks disgusted and says: Hmm, that's delicious.	81
38	T	A painter gets mixed up in color. The customer is surprised, loves the color and says: That looks wonderful.	94
39	L	The weather is too bad for a barbecue. But the host really wants to celebrate and says: What a wonderful day!	63
40	I	A woman gets the wrong dye at the hairdresser's. She gets very angry and says: What a great color.	100
41	L	The party is very boring. But a woman doesn't want to be rude and says: What a great party.	100
42	T	A goalkeeper goes wrong - 0: 1. A reporter sees action replay in slow motion and says: That was simply untenable.	81
43	I	An athlete injured his leg. He is annoyed by the severe pain and says: That was a great race.	88
44	T	A woman's red nail polish is way too bright. Her boyfriend thinks it's sexy and says: You should always use this color.	94
45	L	A man is honored. His boss gives an excruciatingly boring speech. The man says: Thank you for the wonderful words.	88
46	I	A gardener is lying in a hammock. Once again, he has nothing to do and says: Man, that is exhausting work.	100
47	T	An old woman wants to cross the street. A man takes her hand to help. She says: The youth of today are really nice.	100
48	T	A student misses the lecture. Because it was his favourite subject, of all things, he says: What a shame, such an exciting topic.	100
49	I	A singer fails several times in concert. A listener is disappointed and angry and says: What a talented artist.	93
50	I	A girl throws the ball at a boy. The hit hurts him, and he says: It's very funny.	81
51	T	A woman travels to the mountains. There is fresh snow there and the sun is shining. She says: Oh, I love skiing.	100
52	L	The juice was really sour. A man wants his friend to try it and says: Tastes pretty sweet.	94
53	T	A woman gets the wrong dye at the hairdresser's. She likes experiments and says: What a great color.	81
54	L	A little girl is disguised as a ghost. Her father wants to make her happy and says:	80

		Huuuuh, I'm so scared.	
55	L	A housewife's cake is burned. The man doesn't want to offend her and says: It's just as good as always.	94
56	I	The weather is too bad for a barbecue. It is pouring rain and the host says: What a wonderful day!	100
57	T	An apprentice brings the wrong snack. The boss is happy about the surprise and says: Hmm, that's delicious	81
58	L	A painter gets mixed up in color. But the customer doesn't want to have an argument and says: That looks wonderful.	100
59	T	The new car is often broken. But it's very nice and very fast. The owner says: This is really the greatest car I've ever had.	75
60	L	A man has a bad hangover. He pretends to be okay with his boss. He says: I really do lead a healthy life.	100