Valuation of socially relevant facial expressions and gestures:

fMRI and behavioral investigations

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What you do speaks so loud that I cannot hear what you say.

(Ralph Waldo Emerson)

Hiermit versichere ich, dass ich die vorliegende Synopse selbstständig sowie die für den Kumulus vorliegenden Schriften als Erstautorin verfasst habe. Damit trage ich die inhaltliche und methodische Verantwortung für die aufgeführten Schriften. Die Arbeit hat in der gegenwärtigen oder in einer anderen Fassung keiner anderen Fakultät oder Universität vorgelegen.

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(Denise Prochnow)

Düsseldorf, 13.10.13

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ABBREVIATIONS

ACC	anterior cingulate cortex
ALE	activation likelihood estimation
aPFC	anterior prefrontal cortex
BA	Brodmann area
BOLD	blood oxygenation level dependent
DLFC	dorsolateral frontal cortex
DMFC	dorsomedial frontal cortex
e.g.	exempli gratia (“for example”)
et al.	et alii (“and others”)
FFA	fusiform face area
fMRI	functional magnetic resonance imaging
hMNS	human mirror neuron system
HRF	hemodynamic response function
IFG	inferior frontal gyrus
IPL	inferior parietal lobule
MACM	meta-analytic connectivity modeling
MPFC	medial prefrontal cortex
ms	millisecond/s
OFA	occipital face area
pre-SMA	pre-supplementary motor area
s	second/s
STS	superior temporal sulcus
ToM	theory of mind
TPJ	temporo-parietal junction

1. INTRODUCTION

The body is an important communicator of people’s feelings, thoughts, and intentions. Facial expressions and gestures constitute the two most important means of nonverbal body language [1] and have fascinated researchers all over the world [2-8].

In face-to-face situations, body language has an important social function both for the person generating the action (sender), and the person observing it (observer). Body language can be employed voluntarily in order to reinforce a verbal message or to make a specific statement, e.g. eye rolling to signal contempt or thumbs up to show approval. Conversely, unintentionally produced body language allows the observer to look behind the façade of social desirability and detect deception [9, 10]. Some facial expressions and gestures can be reliably recognized by most people since they possess cultural or even universal validity [11, 12]. In the context of facial expressions these are happiness, sadness, disgust, surprise, fear, and anger, typically referred to as basic emotions [2]. Ekman (1992), however, does not consider each of the basic emotions as one single affective state but as a family of emotional states sharing important characteristics [11].

Body language is characterized by a high degree of variability and dynamics [11, 13, 14]. This requires quick adaptability of the observer in order to ensure appropriate social functioning. Being able to quickly evaluate the communicative signals of other people also has a self-protecting function. Here are three examples: Recognizing the angry facial expression of someone approaching us on the street makes us change sides in order to avoid physical harm. Becoming aware that the woman we are trying to impress is sitting there with legs crossed and an averted gaze while her foot is slightly kicking might prompt us to change our strategy in order to prevent disgrace. Detecting incongruence between a friendly verbal message and a malicious facial expression allows us to identify hypocrisy. According to Ekman (1969, 1988), people tend to focus their attention more on facial cues than on cues from other parts of the body because the face has the highest sending capacity of the body. It is not only its most visible part, it has also the shortest transmission time of only seconds or fractures of seconds, and can realize a very high variability of stimulus patterns [9, 10].

Appraisal theories postulate that novelty, valence, and relevance are other important criteria during the evaluation of different kinds of stimuli. Identifying whether a facial expression or gesture is relevant does not only bear a self-protecting function as mentioned earlier but also helps the individual to save cognitive resources necessary for processing stimuli of high self-profitability which require more profound processing [15]. Based on these theoretical assumptions, Rohr et al. (2012) propose that happy and angry expressions are more relevant than fearful and sad expressions because they have behavioral implications for the observer. On the contrary, sadness and fear have a self-disclosing function for the sender but the corresponding behavioral consequences are more diffuse [16]. In other words, the emotion expressions differ in their degree of social impact.

The functional magnetic resonance imaging (fMRI) studies of this dissertation focus on different aspects of emotional facial expression and gesture evaluation as it might appear in social face-to-face situations. These comprise general aspects concerning the effect of communicative signals when certain features are varied like their duration and accessibility to consciousness, and their social impact. In addition, the evaluative process was subdivided into several components in order to disentangle the associated brain areas. Thus, the superordinate goal of this dissertation was to contribute to a better understanding of how the brain processes emotional body language and which brain circuits become involved in different aspects of affect evaluation.

2. THEORETICAL BACKGROUND

“When I wish to find out how wise, or how stupid, or how good, or how wicked is any one, or what are his thoughts at the moment, I fashion the expression of my face, as accurately as possible, in accordance with the expression of his, and then wait to see what thoughts or sentiments arise in my mind or heart, as if to match or correspond with the expression.”

Edgar Allan Poe, The Purloined Letter, In: The Gift 1845, p. 52 [17]

2.1 The concepts of empathy and theory of mind

Emotion research has shown that people tend to match their facial expression to an expression they are confronted with, even under conditions of limited awareness [18, 19]. There is evidence that these rapid facial reactions should not be interpreted as simple physical reactions, but instead appear to reflect some degree of emotional contagion [20, 21]. A typical example would be the spilling over of a smiling expression to a by-standing observer who is unaware of the origin of the happy state of mind in the smiling person.

Emotional contagion is closely linked to the concept of empathy and can be interpreted as one of its components. Empathy describes the capacity of understanding and sharing the affective states of others. In other words, empathizing with someone means “putting oneself in the shoes of others” in the awareness that the other’s feelings might differ from one’s own feelings [22]. According to Preston & De Waal (2002), this is mediated by the automatic and unconscious representation of an observed emotional state and the corresponding autonomic and somatic reactions in the observing person [23]. Neuroscientific research points to two different forms of empathy: *Emotional empathy* as the basal and automatic empathic response, and *cognitive empathy* as the active process of inferring other people's emotional states [24-26].

Higher-order empathy conceptually overlaps with *theory of mind* (ToM). Being able to form a ToM allows the individual to attribute mental states like beliefs, intentions or emotions to others while simultaneously being aware that these mental states might differ from one's own mental state. The term "theory" arises from the fact that the mental states of others are not directly accessible and thus usually cannot be checked for validity [27]. In analogy to the concept of empathy, an attempt has been made to differentiate between reasoning about an emotional state (*affective ToM),* and reasoning about other mental states that require more cognitive effort like beliefs (*cognitive ToM)* [28, 29].

The cognitive prerequisites to build metarepresentations necessary for ToM are acquired in an accumulating manner beginning in early childhood [30]. By the age of 3-5 years, toddlers are usually able to understand that other people may have beliefs that can differ from their own beliefs and that these may sometimes be wrong. At about this age, children also begin to discriminate appearance from reality [31]. This insight is followed by the understanding that people can also have beliefs about beliefs (second-order beliefs) [32-35].

In autistic children, the development of these capacities is impaired which leads to severe deficits in forming a ToM and predisposes them for social isolation [36-40]. However, despite their deficits in higher order ToM and cognitive perspective-taking, autistics have been shown to have preserved basal empathic abilities. The reverse pattern was found in individuals with psychopathic tendencies [41]. These findings support Blair's theory of ToM and empathy as at least partly independent capacities [42]. Recent evidence, however, suggests that affective ToM highly draws on empathic skills [43], suggesting that there might be common and distinct aspects. The following chapters give an overview about the neural bases of ToM and empathy, thereby shedding some light on whether both rely on similar or different brain circuits.

2.2 Mirror neuron system

Being originally discovered by single cell recordings from area F 5 of the macaque monkey's brain, mirror neurons are a group of neurons that become engaged both during the active performance of a motor act and its passive observation in others [44, 45]. Following this important discovery in primates, accumulating evidence from functional neuroimaging studies has suggested the existence of mirror neurons in the human brain as well [46-48]. Especially, the posterior portion of the inferior frontal gyrus (IFG) located in Brodmann area 44 (BA 44), the adjacent premotor cortex (BA 6), and the inferior parietal lobule (IPL) are considered to accommodate mirror neurons in the human brain [45]. Activity of the putative human mirror neuron system (hMNS) is associated with imitation and imitation learning [49, 50], thereby providing a direct link to the involvement of the hMNS in automatic rapid facial expressions and emotional contagion [51-54]. In line with these findings, the IFG and adjacent anterior insula have been suggested to be the key neural substrate of basal forms of emotional empathy [25, 26]. Likewise, these regions have been shown to correlate with self-reported emotional contagion and empathy [55-57].

Mirror neuron activity is commonly observed in tasks involving all kinds of empathy or shared representations [25, 56-58], and facial expressions and gestures appear to act as important elicitors of a mirror neuron mediated empathic response [4, 7, 8, 59-62].

2.3 Other neural correlates of empathy and theory of mind

De Waal (2008) understands empathy as a capacity composed of different layers, with higher order empathic processes building upon low-level empathy and mirroring mechanisms [24]. In line with De Waal's idea, mirror neuron mediated basal empathic reactions are considered to rely on bottom-up processing, whereas cognitive empathy and ToM require top-down processing [63].

In the context of top-down processing, the medial prefrontal cortex (MPFC) has been ascribed a key role in ToM, as its activation is commonly accompanied by activity in the superior temporal sulcus (STS) or the temporo-parietal junction (TPJ), as well as in the temporal poles [25, 55, 64-73]. For empathy and ToM, it is of particular importance that the brain distinguishes between the self and the other perspective in order to disentangle which mental states are intrinsic and extrinsic. If there was no decoupling of self- from other-related representations, empathizing would result in confusion in the case of contradictory affective states between addresser and addressee [74]. In this context, the right hemisphere is considered to be highly relevant for processing self-related information [73-76]. Differences between the representations of self- and other-perspectives appear to be mediated by parts of the MPFC, STS, TPJ and IPL, while the lateral inferior aPFC was reported to be involved in monitoring perspective selection [57, 67, 71, 72, 77, 78].

The anterior cingulate cortex (ACC) and paracingulate cortex are other regions commonly activated during the inference of mental states [55, 57, 65, 68, 69]. ACC generally refers to BA 24/32, while the paracingulate cortex is located at the border of BA 32 and BAs 8/9/10 [79-81]. According to a meta-analysis of various tasks, the pre- and subgenual portion of the ACC responds primarily to affective tasks, while its dorsal part is recruited when the task is predominantly cognitive [82]. Within the ACC, the anterior mid-cingulate cortex was identified as an important neural correlate of cognitive-evaluative forms of empathy [25], a finding corroborating Seitz and colleagues' (2006) interpretation that this area is crucially involved in the valuation of thought [83]. Cognitive ToM, also referred to as mentalizing, usually engages pregenual parts of the paracingulate cortex [68, 81, 84-86] as well as the lateral aPFC [87-89].

In line with De Waal's (2008) Russion Doll Model of layered components of empathy, *affective* more than *cognitive ToM* is often accompanied by low-level empathic activation, suggesting that in dependence on the task, they share important nodes of an underlying brain network [24, 25, 55, 81, 85]. However, this is not mutually exclusive to evidence that the brain regions involved in basal empathy, *cognitive empathy / affective ToM*, and *cognitive ToM* are at least partly dissociable [25, 26, 29, 88, 89].

2.4 Brain regions supporting empathy and theory of mind

Empathy and ToM are complex brain functions involving a number of subprocesses which are not empathy-inherent but have a supporting effect on it [78]. At first, it is of fundamental importance that the cues coming from body language are properly identified concerning their formal features. Therefore, it is essential that facial expressions and gestures are quickly and accurately visually processed. Among other visual areas, the fusiform face area (FFA) and occipital face area (OFA) have been ascribed a crucial role in processing facial cues [90, 91]. Hand gestures have been found to be particularly related to activation increases in the IPL, intraparietal sulcus, and pre-supplementary motor area (pre-SMA) [7, 92-95], while processing their motion has been associated with an involvement of the STS [78].

In addition to appropriate stimulus processing, selective attention, working-memory, and executive functions come into play as well as they are necessary for successful inference of the mental states of others. For example, monitoring one's attentional focus during mental state attribution while simultaneously inhibiting the processing of irrelevant information facilitates focusing on the other instead of the self [78]. These higher-order functions have been considered to be mediated by the aPFC, especially by its lateral anterior parts located in BA 10, with attention being processed slightly more anterior than working-memory, and multitasking being associated with most anterior activations [87].

The dorsolateral frontal cortex (DLFC), in the context of this dissertation referred to as the lateral portions of BAs 8, 9, and 46 [96], has traditionally been linked to the maintenance of cognitive control [97-99], the resolution of cognitive conflict [100, 101], and working-memory [102, 103]. DLFC activation is frequently observed in empathic and ToM tasks [4, 8, 55, 56, 81]. This has raised the question whether the DLFC plays a supportive role in ToM or whether it is crucially involved in it due to the close relationship between ToM and executive functions [33]. Evidence from functional imaging and lesion studies argues for the former explanation, showing that ToM and executive functions are mediated by adjacent but clearly distinct brain regions [104]. Moreover, performance on ToM and on executive tasks was independent from each other in patients with prefrontal lesions [105, 106].

Recently, the DLFC has come into focus in decision-making research, implicating this portion of the prefrontal cortex in normative decisions [107], social decisions [108], uncertain or ambiguous decisions [109, 110], economic decisions [111], moral decisions [112], and stimulus discrimination or categorization [113-115]. Many tasks that are used to study ToM or empathy involved aspects of decision-making, e.g. when the logical ending of a story has to be selected [81] or an emotional state has to be chosen from a forced alternative choice menu [55].

Taken together, it becomes evident that a number of different brain functions contribute to ToM and empathy. They are highly intermingled with both capacities, but are likely separable into different neural substrates.

3. PRESENT RESEARCH

This dissertation is based on five manuscripts studying different aspects of affective body language in healthy subjects from a behavioral and neuroimaging perspective, thereby contributing to a refined understanding of the processing of these highly socially relevant bodily acts.

In manuscript # 1 [116], the cerebral processing of evolving facial expressions and gestures with social impact was examined using fMRI. Being embedded in a valence discrimination paradigm, the study focused on two temporally separated points in time within the discrimination process. It aimed at disentangling the brain regions activated during incomplete and still ambiguous, as well as clearly recognizable and discriminable facial expressions and gestures. Manuscript # 2 [117] addressed the question whether facial expressions of emotion that occur below the threshold of subjective awareness (subliminally) serve as important social cues triggering an automatic empathic response. In addition, manuscript # 3 which is based on the same fMRI study as manuscript # 2 [117] sheds light on the role of the dorsolateral frontal cortex in affective decisions based on subliminal emotional facial cues. In manuscripts # 4 & 5, the cerebral circuits involved in empathic reasoning were investigated. While manuscript # 4 focused on the differences in processing related to reasoning about emotional states of high and low social impact, manuscript # 5 compared the brain activation patterns related to emotional state reasoning in young and old adults.

3.1 Methodological considerations

All five manuscripts were based on fMRI studies. FMRI as a common non-invasive neuroimaging research method permits mapping of brain activation patterns associated with specific tasks by measuring the related changes in blood oxygen level dependent (BOLD) signal changes [118]. It is based on the assumption that a task-induced increase in cerebral activity leads to a hemodynamic response (HRF) which is reflected by a decrease of deoxygenated haemoglobin whose paramagnetic properties can be captured by fMRI [119]. The course of the BOLD signal is mediated by the local concentration of oxygenated and deoxygenated haemoglobin. Typically, the BOLD signal in response to a single stimulus event can be characterized by a slow increase in cerebral blood flow reaching a peak after approximately 5-6 s, and a subsequent decrease resulting in an undershoot before its return to baseline [120].

The common designs used in fMRI research are blocked and event-related designs [121, 122]. All manuscripts presented here used event-related designs. While in blocked designs same-type stimuli are arranged in short blocks, generally in alternation with resting state blocks, these can be presented randomly in event-related designs, allowing for better control of habituation and predictability effects [120]. Event-related designs, and especially rapid designs, also permit the study of natural-like scenarios with varying types and durations of stimuli and varying inter-stimulus-intervals. In an event-related design, the event of interest can be the neural responses evoked by an externally presented stimulus and / or the subject’s response to them (e.g. button press indicating a choice).

Due to the delay of the BOLD response, it is possible that HRFs substantially overlap and BOLD signals accumulate when stimuli are too closely spaced in fMRI designs. In blocked designs where same-type stimuli are presented in a row, one aims at capturing the accumulated BOLD signal which typically reflects sustained cerebral activity. In event-related designs, however, transient activity in response to consecutive events can be measured [123]. Typically, in modern designs, the events are presented in randomized order and in rapid succession which does not allow the HRF to return to baseline after every event. In later data-analysis the problem of overlapping HRFs is resolved by deconvolving the HRF in order to assign each HRF to its corresponding event [120]. For this reason, rapid event-related designs require exact data logging and more fine-grained data analysis compared to blocked designs.

3.2 Summary of manuscript # 1

As stated in the introductory chapter, studying the effects of emotional body language has fascinated researchers all over the world. Interestingly, despite some exceptions [60, 124, 125], most studies examining the brain areas activated during confrontation with facial expressions used static expressions as stimuli [8, 59, 126-129], while the neural correlates of gestures or body movements conveying an emotional message are mainly studied using video-clips [4, 7, 94]. In real life social interactions, both gestures and facial expressions are highly dynamic. Accordingly, dynamic expressions were shown to provoke stronger and differing neural responses than static pictures [124, 130]. For these reasons, manuscript # 1 aimed at mapping and comparing the brain activation patterns related to facial expressions and gestures which dynamically evolved from (emotionally) neutral to meaningful. Viewing the evolving stimuli was embedded in a valence discrimination paradigm in which the subjects were instructed to watch the video-clips carefully and to indicate by a button press whether the facial expression seen showed anger or whether the seen gesture seen conveyed a negative meaning. By capturing brain activity at a time where the expressions were still incomplete and thus ambiguous and a subsequent point in time when the subjects were able to discriminate them by their button press, manuscript # 1 [116] also allowed for a more fine-grained look at the corresponding cerebral processes likely to occur in social encounters.

Previous research has shown that a broad cerebral network including occipito-temporal, parietal and frontal areas becomes active when people recognize facial expressions gestures with social impact [5, 7, 131]. Specifically, it has been shown that nonverbal body language activates brain areas that have been associated with the putative hMNS [7, 56, 57, 59]. The IFG as a core structure of the hMNS has been suggested to be crucial for basal emotional empathy [25, 26, 60]. Higher order empathy or ToM, respectively, has been found to elicit activation of the medial frontal cortex [8, 25, 63, 66, 73, 83, 132, 133]. Therefore, in manuscript # 1 [116] it was hypothesized that viewing incompletely evolved facial expressions and gestures of high social impact elicited activity in the IFG and medial frontal cortex due to their key roles in mirror neuron mediated basal empathy, and affective ToM. In addition, DLFC activation was expected to occur at the subsequent point in time related to the discrimination between angry and other facial expressions, and gestures of negative and positive valence, respectively. The second hypothesis was based on past findings implicating the DLFC in ambiguous decision-making [110], stimulus discrimination [115], and information manipulation [134].

Manuscript # 1 [116] presents fMRI data from a sample of sixteen healthy right handers with normal emotional competence as obtained by the Toronto Alexithymia Scale (TAS-20) [135, 136]. As expected, early stages of viewing the incompletely evolved facial expressions and gestures not only lead to activation of temporal areas associated with a formal visual analysis, but also activated the IFG and parts of the dorsomedial frontal cortex (DMFC) in both hemispheres. This suggested both, an automatic empathic response, and the subjective valuation of their social meaning. Right-left comparisons of the extracted parameter estimates revealed stronger activations in the right inferior temporal gyrus and right DMFC supporting the notion of right hemisphere dominance in processing emotion. In line with previous research, discriminating the facial expressions at a later stage of their evolution went along with an activation increase in the DLFC. Taken together, manuscript # 1 [116] sheds further light on the neural circuits involved in the intuitive understanding of nonverbal body language and affective decision-making.

3.3 Summary of manuscript # 2

Building on manuscript # 1 [116], manuscript # 2 [117] concentrated on another important characteristic of facial expressions as one of the most important means of emotional body language. In everyday social encounters, people are confronted with a large number of social stimuli conveying messages about the emotional state of the counterpart. Typically, and among others, verbal information is accompanied by affective prosody, gestures, and facial expressions of emotion. Due to the short appearance and strong dynamics of these communication signals, as well as limited attention capacity, people might not be aware of all these stimuli at every moment during a conversation. They might, however, nevertheless experience a ‘gut feeling’ giving them information about the emotional state of their counterpart. This is of particular importance when the nonverbal message contradicts the verbal message. One crucial factor contributing to peoples ‘gut feeling' in situations as just described might be affective priming. According to the affective primacy hypothesis [137], affective reactions can be elicited in a person even when the affect generating stimulus is very short and not consciously accessible. In other words, the affective response occurs in the virtual absence of additional cognitive processing.

In fact, it has been repeatedly shown that emotional facial expressions that are presented below the level of subjective awareness affect peoples' behavior, judgments, and brain activation patterns [138-141]. From manuscript # 1 [116] and past research carried out by others, we knew that an empathic response as shown by activation of bottom-up modulated mirror neuron associated brain areas and top-down modulated higher order prefrontal areas can be evoked by consciously accessible facial expressions of emotion [8, 57, 59, 116]. Beyond that, there is increasing evidence that similar empathy-associated regions become active when the expressions are presented outside of subjective awareness [142-144].

Thus, one aim of manuscript # 2 [117] was to replicate and extend these findings by comparing conditions of supra- (400 ms, consciously accessible) and subliminal (40 ms, consciously not accessible) face presentation in the framework of an emotional adjective forced choice paradigm using event-related fMRI. Importantly, unlike some other studies [145], we applied a masking procedure in which a subliminal emotional expression (40 ms) was masked by a neutral expression (360 ms) of the same actor, thereby creating a more natural setting. We hypothesized that regardless of their conscious accessibility, supra- and subliminal emotional facial expressions elicit activation in the empathy and face processing network as evident from event-related fMRI.

In addition to the fMRI study, a behavioral study was performed in order to control different aspects of the subliminal presentation. For example, according to the affective primacy hypothesis [137], affective reactions evoked by subliminal information are diffuse and general. However, recent evidence suggests that processing of not consciously accessible facial expressions was not reduced to a global valence-based level but that there was a certain degree of specificity in relation to the subjective relevance of an emotional state to the observer [16]. Manuscript # 2 [117] therefore used emotional facial expressions which in line with theoretical assumptions [15, 16] were considered to have high behavioral relevance for the observer (happy, angry) or were less self-profitable (sad). Moreover, the behavioral study contained control conditions in which either only the neutral face mask was shown or in which the subliminal emotional expression was replaced by a non-emotional nonsense screen. The behavioral study aimed at showing that subliminal emotional information was able to influence people's judgments in a relevance-dependent and specific manner.

Manuscript # 2 [117] presents behavioral data from a sample of twenty-three healthy volunteers and fMRI data from a sample of twelve healthy right handers. All subjects were pre-selected based on pre-defined inclusion criteria including unimpaired general emotional competence (Toronto Alexithymia Scale, TAS-20) [135, 136], mood (Beck's Depression Inventory) [146], and empathy (Saarbrücker Persönlichkeitsfragebogen, German adaptation of the Interpersonal Reactivity Index, available online). Testing and scanning was followed by a debriefing interview with increasingly specific question about the stimuli and the rationale of the study to assure unawareness of the subliminal stimuli. As hypothesized, the behavioral study confirmed that the emotional information of facial expressions presented outside of conscious awareness spilled over onto the neutral expression mask and influenced the subjects' judgments in the emotional adjective forced choice paradigm. Our data revealed a strong global valence positive-negative discrimination effect but for a discrimination between highly relevant and less relevant emotional expressions as shown by Rohr and colleagues (2012) only a trend was observed [16]. On the neural level, consciously accessible and subliminal emotional facial expressions shared a widespread network of brain areas including the FFA [90], the TPJ, as well as inferior, dorsolateral, and medial frontal regions. Taken together, manuscript # 2 [117] shows that emotional facial expressions that occur outside of subjective awareness can function as important triggers of empathic reactions and are able to alter people's judgments.

3.4 Summary of manuscript # 3

Being based on the same fMRI study as manuscript # 2 [117], manuscript # 3 focuses on the role of the DLFC in affective decisions based on subliminal emotional information. The DLFC known as a higher order control region [101, 147] which has come into focus in decision-making research [110, 111, 148, 149], and which we also identified as crucial for affective decisions in manuscripts # 1 & 2 [116].

The manuscript's rationale was based on the theoretical assumption that a decision cannot be seen as one single process but instead consists of several partly interacting sub-processes. The decision itself is preceded by a pre-decision phase during which decision values are calculated and compared, and is followed by a post-decision consolidation phase [150]. The emotional adjective forced choice paradigm already mentioned in the description of manuscript # 2 [117] permitted us to capture brain activation changes during presentation of the masked subliminal facial expressions prior to the actual decision taking place when the subjects made their emotional adjective choice. We hypothesized that the DLFC is involved in both, the pre-decision phase when most likely decision values were calculated and the decision itself [107, 108, 151]. In more detail, we expected a topographic diversity reflecting a certain degree of functional specialization within the DLFC [96, 97]. Specifically, it was hypothesized that functional specialization would be reflected by different patterns of interareal connectivity. To corroborate this hypothesis, fMRI data analysis was complemented by meta-analytic connectivity modeling (MACM) based on the clusters of activation found in the DLFC.

It was shown that the preparatory phase of the decision during which the subject evaluated the masked subliminal facial expressions went along with an activation increase in a right posterior portion of the DLFC. The MACM analysis revealed co-activations in the left IFG. In contrast, the decision itself was associated with activity in a more anterior portion within the right DLFC which featured co-activations in its left homotope, the adjacent premotor cortices, the DMFC, the left pre-SMA, and the left intraparietal sulcus. The results argue for partially independent sub-regions within the large DLFC which are suitable to support the notion of dual associative processes in intuitive judgment [152]. While the posterior DLFC sub-region became engaged early during the decision process, the anterior sub-region appeared to be crucial for the actual decision based on ambiguous information [107-111].

3.5 Summary of manuscript # 4

The ability to infer the emotions, intentions, and beliefs of others from their body language is fundamental in social interactions. On the one hand it can help consolidate interpersonal relationships, and on the other hand it bears a self-protecting function.

In social encounters, facial expressions as one central means of body language are an important source of information about a particular emotional state of another person. Manuscripts # 1-3 [116, 117], as well as a broad body of literature, have shown that facial cues also act as key players in eliciting an empathic response in the observer [8, 59, 60, 66, 116, 153]. As already taken into account in manuscript # 2 [117], facial expressions of emotion differ in their degree of behavioral relevance for the observer [15, 16], and thus can be considered to have either high or low social impact.

Manuscript # 4 aimed at mapping the brain areas related to emotional state reasoning using a paradigm in which the subjects were asked to attribute an emotional state seen in a depersonalized emotional facial expression [154] to one of four short descriptions of affect-laden situations. Importantly, the paradigm did not require explicit facial affect recognition since the emotional facial expressions were expected to evoke an automatic empathic response (see manuscript # 1, [116]). However, inferring the cause of a particular emotional state required the ability to form a ToM. In our paradigm reasoning about the emotional state itself would theoretically refer to the concept of affective ToM while conclusions of its origin would extend affective ToM abilities and require a cognitive ToM [29, 88]. Furthermore, based on theoretical assumptions explained earlier [15, 16], some emotional states represented by the facial expressions had high social impact because they were highly self-profitable, while others were considered to have low social impact. Thus, one additional goal of manuscript # 4 was to explore whether there was a difference in how the brain processes emotional facial expressions and reasoning associated with either high or low social impact.

We hypothesized that high social impact expressions were preferentially processed due to a salience effect, thereby initially binding more cognitive resources, but finally leading to a more accurate reasoning performance than low social impact expressions. On the neural level, we expected this to be reflected by more pronounced recruitment of mirror neuron related brain regions mediating a basal empathic response such as the IFG and the IPL [25, 54, 56, 57, 59, 69, 116]. As a consequence of more efficient processing of high social impact expressions, we expected reasoning about emotional states of high social impact to elicit stronger activations in higher order top-down modulated prefrontal areas such as the ACC or paracingulate cortex [25, 68, 86], the pre-SMA ([8, 83, 116], see also manuscript # 1), the STS [64, 155], the aPFC [87], and the DLFC ([109, 116], see also manuscripts # 1-3) as compared to reasoning about low social impact expressions.

Manuscript # 4 presents fMRI and behavioral data from a sample of twenty-six healthy right handers with normal neutral face recognition, mood, general emotional competence, self-reported empathy, and facial affect recognition ability ([135, 136, 146, 156]; Saarbrücker Persönlichkeitsfragebogen available online). Our behavioral data revealed that accuracy of reasoning about high impact facial expressions was significantly higher, and was characterized by a prolonged response latency as compared to reasoning about low impact expressions. However, according to correlation analyses, the accuracy related to high social impact emotional states was higher, the less time the subjects took for the reasoning process, while the contrary pattern was found for low impact emotional states. On the neural level, we expected mirror neuron activity during viewing of facial expressions as an expression of basal empathy. Indeed, high social impact facial expressions activated the IPL, while low social impact expressions led to an activation increase in the right premotor cortex [58]. However, contrary to our hypothesis, directly comparing expressions of high and low social impact did not yield any differences in mirror neuron related areas. Reasoning about high and low social impact emotional states activated brain regions located in the inferior frontal cortex, anterior insula, the paracingulate cortex and superior DMFC, among others. While contrasting reasoning related to high with reasoning about low social impact states did not yield any differences in brain activation, more pronounced activity in the parahippocampal gyrus, the lateral superior dorsomedial frontal, dorsolateral and inferiolateral anterior prefrontal cortex was found in favor of reasoning about low impact expressions.

Taken together, our data suggest that facial expressions as the basis of emotional state reasoning elicit mirror neuron activity in the brain, regardless whether they are of high or low social impact for the observer [58]. However, we found differences in the way the brain processed reasoning about emotional states of high social impact as compared to low social impact. Although higher order empathy and decision-making associated regions ([72, 88, 89, 116], see also manuscript # 1) were more strongly recruited during reasoning about low social impact expressions, this did not lead to a higher rate of accuracy as compared to reasoning about high social impact emotional states. Instead, our data suggest that when an emotional state is not directly linked to self-profitability, the brain on the one hand requires more cognitive resources to respond to it which on the other hand does not necessarily result in better outcomes.

3.6 Summary of manuscript # 5:

Manuscript # 5 is based on the same data and study design as manuscript # 4, but has a different focus. While manuscript # 4 addressed the question of whether there are differences in the way the brain processes reasoning about emotional states of high and low social impact, manuscript # 5 compared young (22-39 years) and old adults' (42-61 years) performance on the empathic reasoning paradigm, and aimed at detecting differences in the brain activation patterns of young and old adults and the way the brain handles the task.

The rationale of manuscript # 5 was derived from observations that the ability to build a ToM declines with age [157-159], and that the observed impairment appears to be global in nature [160]. However, recent evidence suggested a motivational component in ToM tasks, showing that the deficit in old adults was restricted to topics which were of low relevance to them [161].

One goal of manuscript # 5 was to replicate the findings of a ToM deficit in old adults found in past research. Therefore, old and young adults completed several standardized questionnaires assessing their mood, general emotional competence, and self-reported empathy ([135, 136, 146, 156]; Saarbrücker Persönlichkeitsfragebogen available online). Following the actual empathic reasoning task, they were furthermore required to complete an explicit facial affect recognition task in order to exclude impaired facial affect recognition abilities as a confounding factor as found by others [162]. By comparing reasoning accuracy associated with high and low social impact emotional states (for theoretical assumptions see descriptions of manuscripts # 2 & 4) between old and young adults, manuscript # 5 also aimed at shedding light on the relevance effect observed by Richter & Kunzmann [161].

While there is a broad body of literature examining the brain regions involved in empathy and ToM in young adults [8, 55-57, 69, 71, 86, 116, 117]; see also manuscripts # 1, 2 & 4), neuroimaging data in old adults is virtually lacking. In the context of empathy, some evidence suggests that viewing stigmatized people resulted in stronger activation in a lateral medial prefrontal area in old adults as compared to young adults. Also, in high functioning old adults stronger activation in the inferior frontal cortex associated with the regulation of emotional responses was observed [163]. In addition, Charlton and colleagues (2009) found a correlation between ToM performance and white matter integrity in young and old adults and presumed that as a consequence in old age white matter connections relevant for ToM could be altered [164]. To the best of our knowledge, there are no neuroimaging studies investigating the brain activation patterns underlying the differences between young and old adults in emotional state reasoning. Manuscript # 5 attempted to fill this gap by contrasting young and old adults' brain regions during viewing facial expressions as the basis for evaluation, and subsequent reasoning about their emotional state as reflected by the attribution of one of four descriptions of affect-laden situations.

We hypothesized that older adults require more cognitive resources to manage the task when compared to young adults. Although we expected young and old adults to share important primarily bottom-up modulated empathy-related areas, we hypothesized that due to the stronger reliance on cognitive resources, old adults exhibit stronger activation increases in top-down modulated lateral and medial prefrontal areas associated with higher order control functions, empathy and affective ToM [8, 57, 58, 63, 87]. Moreover, we predicted basal empathy-associated areas like the IFG and the IPL to correlate with self-reported empathy and explicit facial affect recognition abilities [55, 56], whereas we expected higher order empathy or ToM areas such as the aPFC, the ACC or paracingulate cortex or the superior DMFC to be associated with reasoning accuracy [8, 79, 83, 87, 116].

Manuscript # 5 presented behavioral and fMRI data from twelve old adults and fourteen young adults showing that both recruited similar bottom-up and top-down modulated brain areas reflecting empathy, ToM, and cognitive control related activity [25, 82, 83, 87, 116]. Instead of being reflected by the recruitment of other brain circuits, the difference between both groups became apparent in the time course the regions became activated during the empathic reasoning paradigm. While the time course of old adults was characterized by an early engagement of higher order control regions during viewing the facial expressions, in young adults these became first activated when all necessary information for a goal-directed response was available. Taken together, manuscript # 5 suggests that the impairment in emotional state reasoning which is found consistently in old adults most likely resulted from an inefficient mechanism leading to a recruitment of higher order prefrontal areas at a too early stage during the reasoning process, thereby binding necessary cognitive resources to successfully accomplish the task [165].

4. DISCUSSION AND OUTLOOK

This dissertation aimed at mapping the brain activation patterns associated with different aspects of emotional body language from an observer’s perspective. These were common attributes of facial expressions and gestures which characterize them in everyday social situations: dynamics, ambiguity, accessibility to consciousness, and social impact. In addition, we were interested in the neural correlates of decisions in an affective context. This was based on the rationale that decision-making is an integral part of everyday life, thereby giving the individual the opportunity to ensure its well-being and to consolidate relationships. Finally, with respect to findings of a decline in ToM with increasing age, the brain activation patterns related to emotional state reasoning were compared in young and old adults.

This discussion is structured as follows: first, the impact of the different facial expression and gesture inherent attributes and their most important neural correlates are discussed. Thereafter, the discussion focuses on the decision aspect of the paradigms used. In a final step, the differences in the neural circuits of young and old adults are discussed with emphasis on possible explanations of the obtained results.

Manuscript # 1 [116] focused on the first two aspects, dynamics and ambiguity, by capturing the BOLD signal increases during evolving but not yet clearly recognizable emotional facial expressions and gestures. We found activation in the putative hMNS, as well as in the superior portion of the DMFC extending to the pre-SMA. Manuscript # 2 [117] showed that facial expressions which were presented outside of conscious awareness affected the evaluation of subsequent neutral expressions by adding an emotional flavor that altered the subjects' judgments. The fMRI data analysis yielded a similar pattern of activations as manuscript # 1 [116] when mapping the brain regions associated with consciously accessible and not consciously accessible facial expressions of emotion. However, while both elicited strong activation in the hMNS, supraliminal expressions additionally recruited the pre-SMA. In manuscript # 4, the neural correlates of viewing and subsequently reasoning about facial expressions of high and low social impact were compared. Both, viewing high impact and low impact expressions, yielded activations in mirror neuron related brain areas. Beyond the hMNS, reasoning about the corresponding emotional states of either high or low social impact also engaged parts of the DMFC, primarily located in BA 8, and the aPFC. Reasoning about low impact expressions as compared to reasoning about emotional states of high impact yielded stronger activations in the DMFC and inferolateral aPFC.

Taken together, our studies consistently activated parts of the putative hMNS, and are thus in line with previous research on empathy and ToM [8, 55-57, 60, 69]. In more detail, mirror neurons were recruited when the subjects were confronted with dynamically evolving but still ambiguous emotional body language (manuscript # 1 [116]), as well as static supraliminal and masked subliminal facial expressions of emotion (manuscript # 2 [117]), and during viewing facial expressions of high and low social impact (manuscript # 4). They were also involved in judgments about masked subliminal expressions (manuscript # 3) and reasoning about emotional states of high and low social impact (manuscript # 4). Especially, the IFG and adjacent anterior insula which have been suggested to represent a key neural substrate of an automatic bottom-up modulated empathic response [25, 26] and have been shown to correlate with self-reported empathy [55] were involved in these tasks. Importantly, while in manuscripts # 4 & 5 the subjects were instructed to empathize with the presented facial expressions, no such instruction was given in manuscripts # 1-3 [116, 117], corroborating the assumption that mirroring takes place automatically [45, 58, 63]. Here we additionally show that the putative hMNS appears to become activated regardless of whether an emotional expression was still ambiguous or clearly recognizable, consciously accessible or not, or related to an emotional state of high or low social impact.

Manuscripts # 1-4 [116, 117] consistently found DMFC activation, although the tasks were slightly different (see Figure 1 for an overview). In manuscripts # 1 & 2 [116, 117], a cluster of activation was located in the pre-SMA. Activity in anatomically overlapping areas was found in tasks requiring the formation of a ToM, predominantly an affective ToM with a self-referential component [4, 56, 57, 59, 86]. Seitz and colleagues therefore proposed that the pre-SMA might represent an important relay between an observed external mental state and the internal frame of reference [8, 83]. Notably, according to a recent activation likelihood estimation (ALE) based meta-analysis, its activity was primarily related to external, not self agency [166].

In manuscripts # 3 & 4, the DMFC activations were located more anterior in the medial and superior frontal gyrus of BA 8, extending to the dorsal portion of the paracingulate cortex and ACC (BA 32). Corresponding to the so-called cognitive subdivision of the ACC [82], activity increases in similar brain regions have been found in predominantly cognitive ToM tasks [64, 68, 72, 86]. However, there is also evidence for an involvement of these areas in affective ToM [25, 57, 89, 167]. Activation of the DMFC (BA 8) overlapped with an activation increase that was observed during viewing of evolving but not yet recognizable

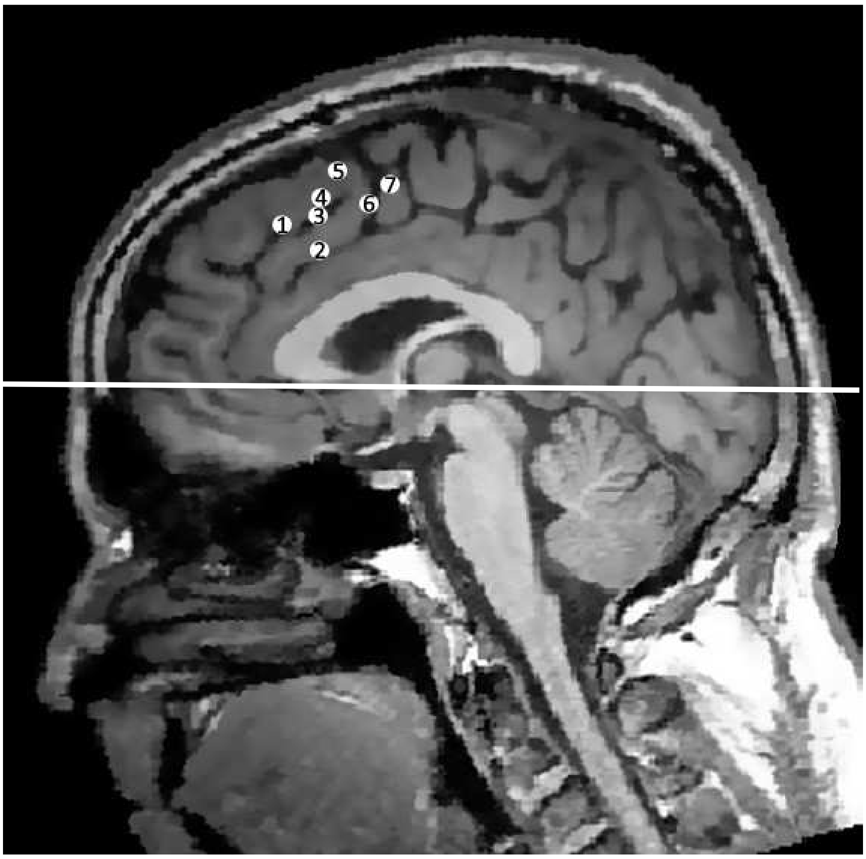

Figure 1 Location of activation peaks related to the different studies within in the DMFC.
All peaks of activation are superimposed on x = -1 in Talairach space. The white line marks the AC-PC plane.
1 = manuscript # 4: reasoning about low impact emotional states,
2 = manuscript # 3: decisions based on subliminal information,
3 = manuscript # 4: reasoning about high impact emotional states,
4 = manuscript # 1: viewing evolving emotional facial expressions,
5 = manuscript # 4: reasoning about high impact emotional states,
6 = manuscript # 1: viewing evolving gestures,
7 = manuscript # 2: viewing supraliminal emotional facial expressions

facial expressions, and their subsequent discrimination (cf. manuscript # 1 [116]). The latter study did not involve an explicit instruction to empathize with the expression, but instead required the subjects to detect whether a seen evolving expression represented anger or not. However, the engagement of the DMFC (BA 8) suggested that at least some degree of cognitive empathy / affective ToM was involved. Interestingly, a more laterally located cluster of activation in dorsomedial BA 8 was observed in manuscript # 4 when comparing reasoning about emotional states of low impact with reasoning about those of high social impact. The lateral DMFC activation corresponded to activations reported by others during confrontation with social eye gaze [86], reading ToM stories [65], and inference of the mental state of dissimilar others [72]. In addition, activation of the lateral portion of dorsomedial BA 8 has been shown to be strongly associated with the processing of uncertainty [168] which might have been a contributing factor in the above-mentioned studies as well. It also fits our observations of stronger engagement of this area during inference of emotional states of low social impact because these were considered to be associated with only diffuse behavioral consequences for the observer [16].

As explained in the introductory chapter, inferring other's mental states cannot be considered a purely curiosity-driven process since it fulfills an important social function. The close relationship of ToM and decision-making becomes evident when imagining the consequences if someone correctly identified his / her counterpart's aggressive state of mind but did not decide to leave the situation. In other words, forming a ToM is dysfunctional when it does not lead to the appropriate context-dependent conclusions. For this reason, a decision aspect can be found in all studies conducted in the context of this dissertation. In manuscript # 1 [116], the subjects had to decide whether an evolving facial expression was angry or not, and whether a dynamic gesture was friendly or threatening. In manuscripts # 2 [117] & 3, the adjective had to be chosen that best reflected the emotional state seen in a previous supraliminal or masked subliminal face. And finally, in manuscripts # 4 & 5, the subjects were required to choose one out of four possible situations which most likely was the origin of a previously seen facial expression. In all studies, affect-related decisions went along with activation in the DLFC (see Figure 2 for an overview). This

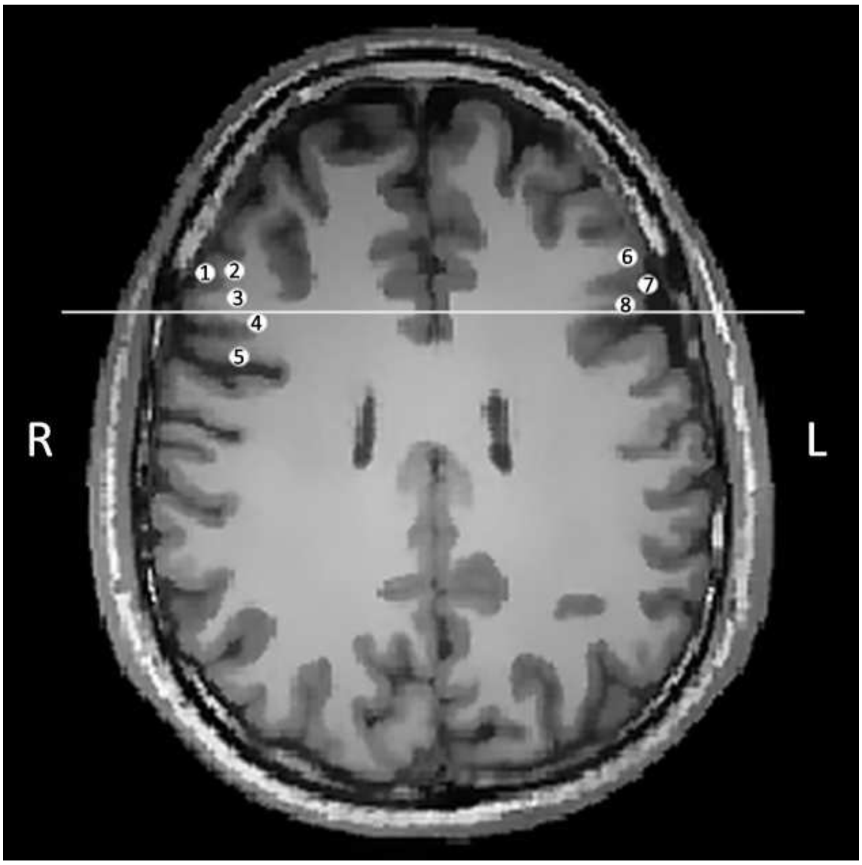

Figure 1 Location of activation peaks related to the different studies within in the DLFC.

All peaks of activation are superimposed on z = 30 (transversal view) in Talairach space in order to show their location in anterior-posterior direction. They grey line marks the borderline between the posterior section related to the preparatory stage of decision, and the anterior section related to the decision itself.

1 = manuscript # 4: reasoning about high impact emotional states,
2 = manuscript # 3: decisions based on subliminal information,
3 = manuscript # 1: discrimination of emotional facial expressions,
4 = manuscript # 2: viewing subliminal emotional facial expressions,
5 = manuscript # 2: viewing supraliminal emotional facial expressions,
6 = manuscript # 4: reasoning about low impact emotional states,
7 = manuscript # 4: reasoning about low impact emotional states,
8 = manuscript # 4: reasoning about high impact emotional states

result concurred with findings from the literature, implicating the DLFC in various kinds of decisions [107-111, 113, 114], as well as guessing [169] and decision conflict [170]. Many of these studies involved social or moral aspects [107, 108, 112], uncertainty or ambiguity [109, 110], or emotional aspects [111, 113, 149, 171], aspects which might be related to our tasks.

In manuscript # 3, we sought to disentangle the role of the DLFC in different phases within the decision process, based on Svenson's (1996) Differentiation and Consolidation Theory [150]. According to the theory, decisions have a preparation phase during which a comparison of choice alternatives and the attribution of decision values takes place, the moment of the decision itself, and a post-decision consolidation phase. In our study (cf. manuscript # 3), the preparatory stage of the decision represented by facial stimuli as the basis on which subsequently an adjective could had to be chosen, was associated with activity in the posterior portion of the DLFC. The actual decision yielded an activation increase in a more anterior part of the DLFC. A similar pattern of DLFC activations was observed in manuscript # 1 [116]. While the main effect of early stage facial expression and gesture observation led to an activation of the posterior DLFC, its activity was located more anterior but not as anterior as in manuscript # 3 during their discrimination. Manuscript # 4 failed to show DLFC activity during the preparatory decision phase but choosing a situation that might have happened to the previously seen person yielded several activation clusters in the anterior portion of the DLFC. The anterior DLFC was also found to be more strongly engaged during reasoning about low social impact emotional states compared to high impact emotional states, probably because the decision was perceived as more difficult and required more cognitive resources due to the diffuse behavioral implications.

Beyond mapping the DLFC activation associated with the pre-decision phase and the decision itself, manuscript # 4 also aimed at identifying the co-activation patterns of the anterior and posterior DLFC. While the latter featured co-activations in the left IFG, anterior DLFC was accompanied by premotor, DMFC, pre-SMA, and parietal activations. Although the left IFG has traditionally been associated with Broca's speech area [172] and might therefore reflect covert speech, it has also been identified as a key player in mediating a basal empathic reaction [25, 26]. In our studies (cf. manuscripts # 1-3, [116, 117]) posterior DLFC activity was consistently accompanied by activation in the inferior frontal cortex, and at the time when posterior DLFC activity occurred, no speech component was present in the paradigms. Contrary to the co-activation patterns observed in the meta-analysis (cf. manuscript # 3), in our studies pre-SMA activation was primarily found prior to the actual decision. As discussed earlier, pre-SMA activity might reflect the embedding of an externally perceived mental state into one's own frame of reference [83], and thus it is not contradicting that it was observed already during the preparatory stage of affect-based decisions. Broader DMFC activation most likely reflecting cognitive empathy / affective ToM occurred during both, the pre-decision phase (cf. manuscript # 1, [116]), and the actual decision (cf. manuscripts # 3 & 4), and was thus in line with the results obtained by the meta-analysis (cf. manuscript # 3).

As described in chapter 2.3, DLFC activity has not only been found in decision-making paradigms but also in various other tasks involving executive functioning [99-101, 173]. It is impossible to completely disentangle whether an activation increase observed in the DLFC reflected one or the other since many executive tasks appear to implicitly study decision-making [98-100, 173, 174] and vice versa [109, 175]. In our studies, we carefully chose our control conditions in order to subtract signal changes related to processes we did not wish to study. For example, in manuscript # 1 [116], deciding whether an evolving facial expression reflected anger or not was contrasted with alternating button presses in response to the same evolving stimuli. This permitted us not only to subtract motor-related activity but also some degree of executive function-related activity because the subjects also had to monitor the screen and their motor response carefully. However, as stated earlier, there is no perfect control condition, and thus it is still possible that executive function has contributed to DLFC activation in our task.

In summary, it was shown that brain areas considered accommodating mirror neurons like the IFG and the IPL, as well as parts of the DMFC are recruited during the processing of emotional body language. Our data further supports the notion that an empathic response is generated automatically, as well as intentionally initiated when people are confronted with emotional facial expressions or gestures, regardless of whether they are dynamic or static, still ambiguous or clearly recognizable, consciously accessible or not, or have high or low social impact. Moreover, we show that the DLFC is involved in affect-based decisions, and provide first evidence that there might be at least some degree of functional specialization in the representation of pre-decision processing and the decision itself.

A vast body of behavioral evidence shows that the ability to form a ToM declines with age [158-160, 176-179]. Based on these observations, we compared empathic reasoning abilities of young and old adults while simultaneously mapping their brain activation patterns (cf. manuscript # 5). Both groups did not differ in educational level, general face recognition, mood, self-reported emotional competence and empathy, as well as explicit facial affect recognition. Assessment of affective ToM abilities revealed that old adults performed as well as young adults when they had to select one out of four emotional attributes that best described the emotional state of a pair of eyes (Eyes Test) [180]. However, they performed worse when they were required to attribute one out of four affect-laden situations to a previously seen depersonalized face, independent of whether the facial expression reflected an emotional state of high or low impact. This result stands in contrast to findings of Richter & Kunzmann (2011) who showed that the differences between old and young adults vanished when the self-relevance for old adults was increased [161]. Following theoretical assumptions based on appraisal theories [15, 16], we considered angry and happy expressions to be of high social impact because of their high degree of self-profitability and their clear behavioral implications. Thus, these expressions must have signaled high relevance to both, young and old adults, which should have led to an adjustment of performance levels. Since that was not the case, we assume that motivation was not the major factor explaining the age-related differences in affective ToM. Compared to young adults, old adults exhibited similar response latencies during inference of high impact emotional states, but responded significantly faster when reasoning about low social impact emotional states was required.

On the neural level, we observed striking differences between both age groups. During the viewing of the facial expressions to which subsequently an affect-laden situation had to be attributed, old adults showed stronger activations in mirror neuron related brain areas, as well as dorsomedial and dorsolateral frontal, and anterior prefrontal regions. In contrast, during actual emotional state reasoning, the young adults exhibited stronger activity in a similar but aPFC and ACC / paracingulate cortex dominated network. In combination with the behavioral results, these findings argue for an inefficient mechanism in performing and processing the task in old adults. Even though both groups recruited similar brain areas which are known to be involved in basal empathy, affective ToM, and cognitive control [25, 57, 87, 89], there were important differences in the neural time course of when they were recruited. Higher-order aPFC areas might have been activated at a too early stage of reasoning, thereby upregulating other top-down modulated ToM areas at a point in time when a goal-directed response was not yet possible [165]. In addition, the early engagement of higher-order areas most likely bound cognitive resources in old adults that might have additionally hampered subsequent reasoning. In young adults, on the contrary, ToM and higher-order control associated areas in the ACC / paracingulate cortex and aPFC were first recruited during actual reasoning which might represent better cognitive resource management and more goal-directed processing [25, 55, 69, 165, 181].

Possible limitations of the current studies should not go unmentioned. First, manuscripts # 1 & 2 [116, 117] aimed at capturing brain activation related to an automatic empathic response and thus did not instruct the subjects to empathize with the seen body language. This means that we had to conclude from the brain activation patterns we observed whether an empathic reaction had been generated or not. This approach, known as reverse inference is common practice in social neuroscience but also bears a certain risk when brain regions respond to multiple tasks. For example, this was the case for the DLFC which has been implicated in different aspects of executive control and decision-making (see above). However, we did not interpret activation of a brain region in isolation, but instead always focused on all activated brain areas which orchestrated a certain task. In addition, we carefully chose our control conditions that permitted us to subtract confounding brain activation. In manuscripts # 2 [117] & 3, the impact and neural correlates of subliminal facial expressions were studied. Despite the well-proven masking technique being applied, some participants had suspicions about the presence of hidden emotional expressions and speculated about the nature of the study. These subjects were excluded from data analysis because the stimuli were no longer subliminal in nature to them due to their lower threshold of conscious awareness. This has led to a relatively small sample size. However, due to the high number of repetitions per condition, we believe that this limitation is negligible.

Taken together, the current dissertation sheds new light on how the brain processes various important aspects of emotional body language, as well as on the role of the DLFC in affect-related decisions. In addition, it provides new evidence which might explain the often observed decline in ToM abilities in higher adulthood.

In future studies it would be interesting to apply the used paradigms to different patient groups which have been shown to be impaired in different aspects of emotion processing, e.g. patients with multiple sclerosis [182, 183], Parkinson's disease [184, 185], or epilepsy [186, 187]. This could lead to a better understanding of the nature and extent of their impairment. In addition, comparing the performance and brain activation patterns of patients with those of old and young adults could give important insights into the mechanisms and origins of the observed deficits.

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6. OVERVIEW OF PUBLISHED AND SUBMITTED ARTICLES

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Prochnow D, Brunheim S, Steinhäuser L, Seitz RJ. Reasoning about the implications of facial expressions: a behavioral and fMRI study on low and high social impact (submitted to Brain and Cognition).

Prochnow D, Steinhäuser L, Brunheim S, Seitz RJ. Different mechanisms underlying emotional state reasoning in young and old adults: evidence from behavioral and neuroimaging data (submitted to Behavioural Brain Research).