Social perception and cognition: processing of gestures, postures and facial expressions in the human brain

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CONTENTS

Abstract

Humans are a social species with the internal capability to process social information from other humans. To understand others' behavior and to react accordingly, it is necessary to infer their internal states, emotions and aims, which are conveyed by subtle nonverbal bodily cues such as postures, gestures, and facial expressions. This thesis investigates the brain functions underlying the processing of such social information. Studies I and II of this thesis explore the neural basis of perceiving pain from another person's facial expressions by means of functional magnetic resonance imaging (fMRI) and magnetoencephalography (MEG). In Study I, observing another's facial expression of pain activated the affective pain system (previously associated with self-experienced pain) in accordance with the intensity of the observed expression. The strength of the response in anterior insula was also linked to the observer's empathic abilities. The cortical processing of facial pain expressions advanced from the visual to temporal-lobe areas at similar latencies (around 300–500 ms) to those previously shown for emotional expressions such as fear or disgust. Study III shows that perceiving a yawning face is associated with middle and posterior STS activity, and the contagiousness of a yawn correlates negatively with amygdalar activity.

Study IV explored the brain correlates of interpreting social interaction between two members of the same species, in this case human and canine. Observing interaction engaged brain activity in very similar manner for both species. Moreover, the body and object sensitive brain areas of dog experts differentiated interaction from non-interaction in both humans and dogs — whereas in the control subjects, similar differentiation occurred only for humans. Finally, Study V shows the engagement of the brain area associated with biological motion when exposed to the sounds produced by a single human being walking. However, more complex pattern of activation, with the walking sounds of several persons, suggests that as the social situation becomes more complex so does the brain response.

Taken together, these studies demonstrate the roles of distinct cortical and subcortical brain regions in the perception and sharing of others' internal states via facial and bodily gestures, and the connection of brain responses to behavioral attributes.

Tiivistelmä

Ihminen on sosiaalinen laji, ja meillä onkin erikoistuneita aivomekanismeja kanssaihmistemme välittämän sosiaalisen informaation käsittelyyn. Ymmärtääksemme muiden käyttäytymistä ja vastataksemme siihen tarkoituksenmukaisesti, meidän täytyy ymmärtää muiden ihmisten hienovaraisen kehonkielen — kuten eleiden tai kasvonilmeiden — välittämiä tunnetiloja ja päämääriä. Tässä väitöskirjatyössä tutkittiin tällaisen sosiaalisen informaation käsittelyä aivoissa. Väitöskirja tarkastelee aivotoimintaa toisten ihmisten tunnetilojen havainnoinnissa kasvojen ja kehon eleiden kautta sekä näiden aivovasteiden yhteyttä käyttäytymiseen.

Osatöissä I ja II tarkasteltiin toisen ihmisen kipukokemuksen havaitsemista kasvonilmeistä toiminnallisen magneettikuvauksen (fMRI) ja magnetoenkefalografian (MEG) avulla. Tutkimuksissa selvisi, että toisen ihmisen kivun kasvonilmettä katsottaessa ne aivoalueet, jotka osallistuvat myös itse koettuun kipuun, aktivoituivat sitä voimakkaammin, mitä voimakkaampaa kipua kasvonilmeen arveltiin välittävän. Aivoaktivaatio oli myös yhteydessä katselijan empatiakykyihin. Kipuilmeiden käsittely eteni näköaivokuorelta ohimolohkon alueille samassa ajassa kuin on aikaisemmin osoitettu pelon ja inhon ilmeille (noin 300–500 ms). Osatyössä III osoitettiin, että myös haukottelevien kasvojen havaitseminen aktivoi ohimolohkon alueita. Tulokset osoittivat myös, että mitä heikompaa mantelitumakkeen aktivaatio oli havainnon aikana, sitä enemmän koehenkilö tunsi tarvetta haukotella itse katsellessaan haukottelevia kasvoja.

Osatyössä IV tutkittiin vuorovaikutuksen havaitsemista kahden ihmisen tai kahden koiran sosiaalisista eleistä. Kummankin lajin vuorovaikutuseleiden katselu aktivoi aivoja samankaltaisesti, mutta koirien elekieleen perehtyneiden asiantuntijoiden aivovasteet kehon ja muiden havaintokohteiden käsittelyyn erikoistuneilla alueilla erottelivat koirien vuorovaikutustilanteet ei-vuorovaikutteisista tilanteista samaan tapaan kuin ihmisten väliset vastaavat tilanteet. Sen sijaan kontrollikoehenkilöiden aivovasteet erottelivat samalla tavalla vain ihmisten vuorovaikutuksen.

Osatyössä V osoitettiin, että biologisen liikkeen havaitsemiseen erikoistunut aivoalue (pSTS) aktivoituu yhden ihmisen kävelyääniä kuunnellessa, mutta aktivaatiokuvio leviää kuunneltaessa usean ihmisen kävelyääniä, mikä viittaa aivovasteiden monimutkaistumiseen riippuen sosiaalisesta ympäristöstä.

Acknowledgments

List of original publications

This thesis is based on the following publications, which are referred to by their roman numerals in the text.

I   **Saarela MV**, Hluschuk Y, C de C Williams A, Schürmann M, Kalso E, Hari R (2007). The compassionate brain: humans detect intensity of pain from another's face. *Cerebral Cortex* 17: 230–237.

II   **Kujala MV**, Tanskanen T, Parkkonen L, Hari R (2009). Facial expressions of pain modulate observer's long-latency responses in superior temporal sulcus. *Human Brain Mapping* 30: 3910–3923.

III   Schürmann M, Hesse MD, Stephan KE, **Saarela M**, Zilles K, Hari R, Fink GR (2005). Yearning to yawn: the neural basis of contagious yawning. *Neuroimage* 24: 1260–1264.

IV   **Kujala MV**, Carlson S, Hari R (submitted). Dog experts read body postures across species: Brain basis of interpreting human or canine social interaction.

V   **Saarela MV**, Hari R (2008). Listening humans walking together activates the social brain circuitry. *Social Neuroscience* 3: 401–409.

Abbreviations

ACC   anterior cingulate cortex

ANOVA   analysis of variance

AI   anterior insula

BEES   balanced emotional empathy scale

BOLD   blood oxygenation level dependent

dSPM   dynamical statistical parametric mapping

EBA   extrastriate body area

EEG   electroencephalography

EMG   electromyography

EOG   electro-oculogram

ERP   event-related potential

FBA   fusiform body area

FFA   fusiform face area

fMRI   functional magnetic resonance imaging

GLM   general linear model

IRI   interpersonal reactivity index

ISI   inter-stimulus-interval

LO   lateral occipital cortex

MEG   magnetoencephalography

MNE   minimum norm estimate

MRI   magnetic resonance imaging

NMR   nuclear magnetic resonance

pSTS   posterior superior temporal sulcus

SI   primary somatosensory cortex

SII   secondary somatosensory cortex

SEM   standard error of mean

SQUID   superconducting quantum interference device

ToM   theory of mind

1 Introduction

"Human is the measure of all things: of things which are, that they are, and of things which are not, that they are not."

<div align="right">Protagoras (~450 BC), referred to by Plato</div>

We humans reflect the outside world to ourselves: our perception is limited, we realize external measures with respect to our physical dimensions, and we even compare and understand other humans through our own experiences. It may be challenging to visualize the possible borders of the universe and the nothingness beyond; it is often much easier to see the happiness of our friend and share the joy. We are inherently social mammals, and in the past, have relied to the tight collaboration with the peers in order to survive (the term "*social*" here referring to the biological humane ability and interest for understanding the doings of others instead of a personality feature). The key features mediating effective social functioning are inter-individual similarity (Hodges et al., 2010) and synchrony (Hove & Risen, 2009): the more similar we are, the better we understand each other, and the more synchronized our time scales are, the more we can share. Thus, from the point of social sharing, being "in the right place at the right time" is of high importance. To comprehend others' behavior and to react accordingly, it is necessary to infer their internal states, emotions and aims, which are conveyed by subtle nonverbal bodily cues, such as postures, gestures, and facial expressions.

Understanding human social nonverbal communication goes through many levels: it arises from perceiving the body postures, smiles and frowns of the conspecifics, as well as interpreting the gazes of eyes, tones of voices and tensions of muscles. Some of these features are processed effortlessly and unconsciously in our brains — one's awareness of them may even hamper the interaction — but some social cues require both unconscious and conscious processing. A facial expression can be understood by a conspecific without requiring further analysis of the sight, but sometimes more elaborate conscious processing of the internal goals and purposes of another person is needed. These two, social perception and social cognition, go hand in hand in our everyday social interactions, and they are processed within a network of distributed brain areas working in parallel.

The most crucial mediator of human social functioning is perhaps the face, and the processing of faces is strongly associated with a network of specific regions within the human brain. Along with faces, whole bodies are important for gestural communication, providing the means of acquiring one's goals as well as a tool for interaction. People's emotional states are reflected in and recognized from their bodily postures and gestures, and their goals can be deduced from their movements and actions. This thesis explores human social cognition from the perspectives of sharing others' experiences via facial expressions (Studies I–III), body postures or movements (Studies IV–V), the role of expertise in interpreting communicational gestures across species (Study IV), and perceiving one or multiple persons concurrently (Study V).

Despite the experimental research on basic facial expressions of emotions that are recognized universally (Ekman et al., 1969), facial gestures outside this category have not attracted wide scientific attention. In Studies I–III, we explored the neural basis of such "non-emotional", yet meaningful, facial expressions associated with pain and contagious yawning. First, we asked how humans can "feel" someone else's pain merely by observing another's facial expression of pain; and how the strength of the observed pain or the empathic abilities of the observer affect the observer's brain responses (Study I). Second, we clarified the detailed temporal progression of the cortical responses to another's facial pain expressions with magnetoencephalography (Study II). Third, we explored the behavioral and neural mechanisms underlying the contagiousness of yawning (Study III).

Experience is known to enhance the brain responses in a variety of perceptual settings. However, it has not been previously assessed whether experience on social gestures of another species affects the respective brain function, or whether the neural correlates of perceiving social interaction of other species are similar than when perceiving conspecifics. This kind of expansion of social perception through expertise was explored in Study IV.

Finally, social gestures are most often studied with perception of one person at a time, whereas in real life, we often perceive multiple agents concurrently. We approached this topic by exploring how the human brain represents perceiving one person walking alone or multiple persons walking together (Study V).

This thesis begins with a presentation of the foundations of social cognition in the human brain. Different subareas of social perception and cognition are introduced in detail, followed by the specific aims of the studies and the experimental methods used in this thesis. Thereafter, each experiment is briefly introduced and discussed, and finally these results are set in a more general context of social brain research.

2 Background

Humans are born with sensitivity for social information: newborn infants attend to object combinations resembling faces more than other stimuli (Johnson et al., 1991), and copy the facial expressions of others (Meltzoff & Moore, 1977). Thus, some biological prerequisites for social perception are already present in infant brain, although social cognition is modified throughout life.

Social cues within the environment are first mediated through sensory areas of the brain, and further processed in brain regions that gather information at different perceptual and cognitive levels. Subprocesses of social cognition associate our own experiences with those of others (Rizzolatti & Craighero, 2004; Hein & Singer, 2008; Hari & Kujala, 2009), and evaluate social cues (Allison et al., 2000; Saxe & Kanwisher, 2003; Blakemore & Frith, 2004; Frith & Frith, 2006). Together, the brain areas associated with these functions form a network for processing social information (Figure 1; Beauchamp & Anderson, 2010).
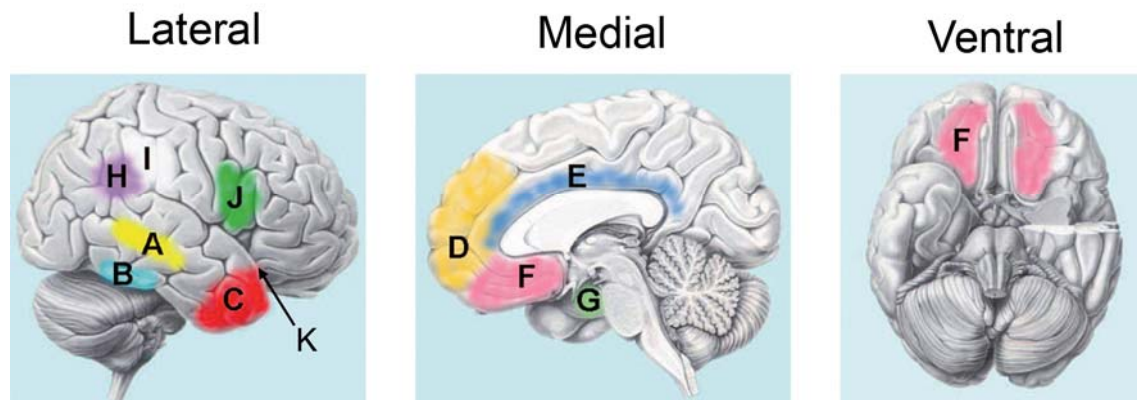
Figure 1. Key brain areas processing social information. Perception of facial and bodily gestures is associated with *superior temporal sulcus* (A), recognition of faces with *fusiform gyrus* (B), integration of emotion and perception with *temporal poles* (C), evaluation of social interaction with *medial prefrontal cortex and frontal pole* (D), shared sensory states with *cingulate cortex* (E) and *insula* (K; within the Sylvian fissure), emotional modulation with *orbitofrontal cortex* (F), emotions with *amygdala* (G), theory of mind with *temporo-parietal junction* (H), and motor mirroring with *inferior parietal cortex* (I), *inferior frontal cortex, and premotor areas* (J). Adapted from Beauchamp & Anderson (2010) with permission from American Psychological Association.

2.1 Processing of facial features

Face is perhaps the most important medium for social communication: face informs others of the person's identity and his or her emotions, feelings, intentions, impressions, motivations and even internal states such as excitement or anxiety. The movement and direction of a face and gaze provide information of a person's attention and interests, and following these social cues transmitted by another person enables us to momentarily share their perception of the world.

Studies I–III of this thesis concerned gestural cues transmitted by faces, and although the early visual perception or recognition of faces were not the specific targets of this thesis, perception of faces *per se* forms the basis for evaluation of the changing social cues of facial expressions. Thus, the early stages in cerebral processing of face perception are reviewed first, before introduction of facial expressions.

2.1.1 Perception of faces

Processing of faces, as well as any visual information of our surroundings, begins in the retina of the eyes, where the visual input is already spatially segregated and retinotopically organized. Subsequently, it advances along the visual pathway through the optic nerve and optic tract to lateral geniculate nucleus of the thalamus, and reaches the cerebral cortex in the most posterior part of the brain, the occipital lobe. The primary visual cortex in the occipital lobe is located around the calcarine sulcus, and processing of faces continues in the several adjacent, functionally segregated regions. Although the visually observed social information requires bottom-up processing from lower-level visual areas, our visual awareness of is also affected by expectations built on the basis of previous experience, guiding our attentional resources and motivations (e.g. Connor et al., 2004; Berman et al., 2008).

After the early visual processing, the visual analysis of faces is conducted within the occipito-temporal regions in the extrastriate visual cortices: inferior occipital gyrus (IOG), lateral fusiform gyrus, and the cortex around the superior temporal sulcus, STS (Figure 2; for reviews, see Allison et al., 2000; Haxby et al., 2000; Haxby et al., 2002).
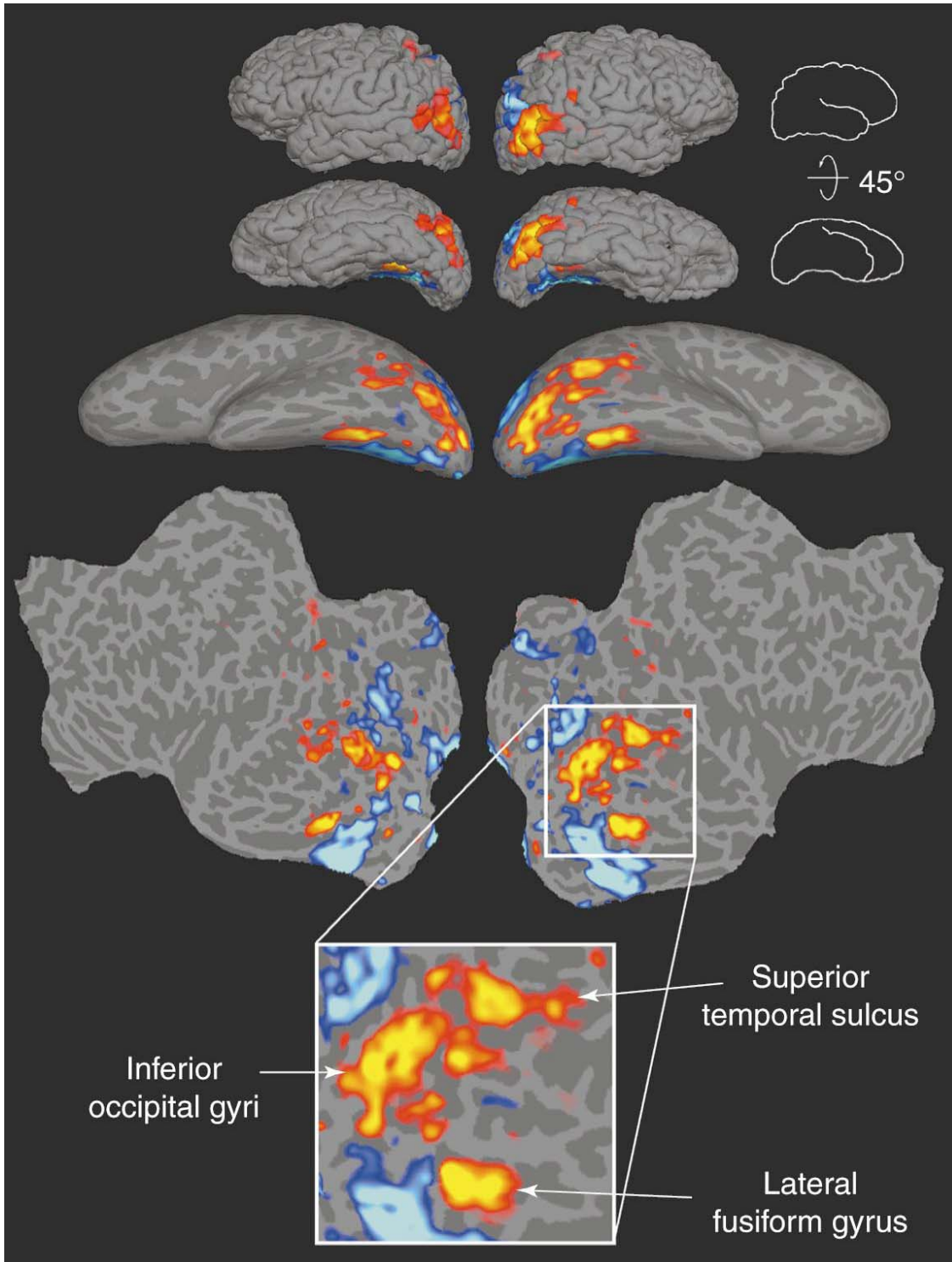
Figure 2. Cortical activation during fMRI measurement associated with the perception of faces. Brain areas shown in red to yellow responded more to faces than houses, and the blue regions responded more to houses than faces. Top: lateral views of the left and right cortical surfaces. The next row shows the cortical surfaces tilted back 45° to show both the lateral and ventral surfaces of the brain. The next rows show the cortical surfaces inflated to open the sulci and flattened into a two-dimensional sheet. Adapted from Haxby et al. (2000) with permission from Elsevier.

A region within the lateral fusiform gyrus shows stronger responses to faces than to any other visual stimuli, highly consistently across studies (e.g. Sergent et al., 1992; Allison et al., 1994; Haxby et al., 1994; Puce et al., 1995; Kanwisher et al., 1997; Halgren et al., 1999; Ishai et al., 1999; Hoffman & Haxby, 2000). Accordingly, it has been named "fusiform face area" (FFA, Kanwisher et al., 1997). The precise function of the FFA has been under an continuous debate for over a decade, including views of the region as either a specialized module for face perception (Kanwisher et al., 1997; McCarthy et al., 1997) or as a module specialized for visual expertise (Gauthier et al., 1999).

In single-cell recordings of the monkey brain, face-selective neurons have been found within the temporal cortex (Perrett et al., 1982). Many of these neurons respond primarily to either identity or expression: the identity-sensitive cells being present mainly in the inferior temporal cortex, and the expression-sensitive cells in the STS (Hasselmo et al., 1989a). According to human brain imaging, the putative human homologues for these regions are the lateral fusiform gyrus and STS (Puce et al., 1998; Hoffman & Haxby, 2000).

A cortical model for face perception, based on monkey experiments and the respective data on the human brain function (Hoffman & Haxby, 2000), divides face perception into processing of invariant and changeable aspects of faces. According to the model, the face-responsive area in the fusiform gyrus is responsive to the perception of identity through invariant facial features, STS for the analysis of changeable aspects within facial expressions and gaze direction that are important for social interaction, and IOG as an information transfer site between the two (Haxby et al., 2000; Haxby et al., 2002). The face-responsive area within IOG is a subsection of a more general object-processing area, lateral occipital complex (LOC, Malach et al., 1995), and in some studies, it is called occipital face area (OFA, Gauthier et al., 2000b). The OFA region has been suggested to participate in the recognition of faces (Steeves et al., 2006; Pitcher et al., 2007; Rhodes et al., 2009).

However, the cortical model for facial perception does not fully cover face processing. Even a newborn infant attends to facial configurations more than other similar stimuli (Johnson et al., 1991), although the adult-like pathways and the cortical representation of faces are not mature at birth. Attention to faces by infants is better

explained by a dual route of face processing: a quick subcortical representation for facial features with low spatial frequencies in the pulvinar – superior colliculus – amygdala route, and a slower cortical representation for facial features with high spatial frequencies culminating in the cortical face-responsive areas (Vuilleumier et al., 2003). The subcortical pathway for the low spatial frequency information is functional at birth whereas the cortical route is not, suggesting that the newborn looking preferences rely on the subcortical route (Johnson, 2005).

Adult-like cortical representations for faces start to mature at 3 months. At that time, stronger brain responses to faces than other objects are observed around 290 ms from the stimulus onset in EEG measurements (Halit et al., 2004) — resembling the adults' face-sensitive responses that peak around 170 ms (140–200 ms in different studies) in the temporo-occipital cortex (e.g. Allison et al., 1994; Sams et al., 1997; Puce et al., 1999; Halgren et al., 2000; Tanskanen et al., 2005). In adults, cortical face responses emerge with stimulus durations as short as 50–200 ms (Tanskanen et al., 2007), and the strength of the 170-ms temporo-occipital face responses correspond to the subjects' performance on face recognition (Tanskanen et al., 2005; Tanskanen et al., 2007).

2.1.2 Facial expressions: emotion, movement, and gestures

Besides more rigid information on identity, gender and even health, faces also provide a rich source of temporally varying information about the inner affective states and emotions of other people. Classically, six basic emotions are recognized from faces across cultures: happiness, sadness, surprise, fear, anger, and disgust (Ekman et al., 1969). Facial expressions of emotions are thought to be somewhat automatic displays, occurring as a direct function of the emotional experience of the individual (Darwin, 1872; Ekman, 1997). Emotional expressions have also been proposed to serve a social communicatory function in transmitting the valence of novel objects or situations between conspecifics (Blair, 2003). Supporting the second view of the social function, although not denying the first, our facial expressions (provoked by external social stimuli) are stronger when we are accompanied by other people (Malatesta & Haviland, 1982; Chovil, 1991; Fridlund, 1991).

The face perception model by Haxby and colleagues (2000) proposes that perceiving facial expressions (of emotions or other gestures) requires extraction of the facial features that can vary with movement (muscle contractions and flexions), and the involvement of the emotional-affective system. In agreement with the findings on the monkey brain (reviewed in Perrett et al., 1989), both extracellular intracranial recording (Ojemann et al., 1992) and human brain imaging studies have shown that the regions around STS are sensitive to many kinds of social information, including static emotional expressions of faces (Phillips et al., 1997; Vuilleumier et al., 2003; Winston et al., 2004; Engell & Haxby, 2007; Furl et al., 2007), gaze direction (Wicker et al., 1998; Hoffman & Haxby, 2000; Pageler et al., 2003; Pelphrey et al., 2004; Calder et al., 2007; Engell & Haxby, 2007; Sato et al., 2008; Nummenmaa et al., 2009) and perceived movement of either faces (Puce & Allison, 1999; Sato et al., 2004; Simon et al., 2006), eyes (Puce et al., 1998), mouth (Calvert et al., 1997; Puce et al., 1998; Nishitani & Hari, 2002), hands (Grezes et al., 1999; Nishitani & Hari, 2000) or the whole body (e.g. Bonda et al., 1996).

Although extensive literature exists on processing of emotional facial expressions, facial movement and eye gaze, studies of facial gestures other than the ones labeled as universal emotional expressions (Ekman et al., 1969; Ekman & Friesen, 1971) are still rare, although these gestures may also be socially meaningful. For example, a sight of a yawning face communicates decreased alertness of an individual and can cause other people to yawn, but the underlying mechanisms of the phenomenon have remained unclear. Studies of I–III of this thesis explore the neural correlates of such socially meaningful yet "non-emotional" gestures: the expression of pain and the gestural sequence of yawning.

Studies on facial expressions using time-sensitive electrophysiological methods have also focused on the classically defined basic emotional expressions or simpler facial motion. The perception of happy, disgusted, surprised and fearful faces provoke commonly stronger brain responses than control stimuli in the occipital and temporal regions 250–750 ms after stimulus onset (Carretie & Iglesias, 1995; Krolak-Salmon et al., 2001; Morel et al., 2009) — although some reports exist of earlier 110 ms separation of emotional (happy or sad) from neutral faces in the occipital area (Halgren et al., 2000). Eye or mouth movements irrespective of emotional content have been associated

with the temporo-occipital 170-ms responses (Watanabe et al., 2001; Miki et al., 2004). However, temporal correlates of brain responses are less well known for facial gestures that are not classified as basic emotional expressions. In Study II, we continued the exploration of such non-emotional gestures by characterizing the cortical activation sequence during observation of pain expressions.

In addition to brain structures specialized in face processing, facial expressions are also processed in the structures responsible for generating similar states in ourselves, such as and amygdala (regarding fear or threat) or anterior insula (regarding visceral sensations). Amygdala lesions are known to impair fear conditioning (Wilensky et al., 2006), and they are also consistently associated with impairment in recognizing fear in others (Adolphs et al., 1994; Calder et al., 1996; Adolphs et al., 1999; Schmolck & Squire, 2001), whereas these lesions rarely result in impairment of happy expressions (Adolphs et al., 1999). Furthermore, numerous brain imaging studies have shown enhanced responses of amygdala when observing facial expressions that require heightened caution from the perceiver, such as facial expressions of fear (Breiter et al., 1996; Morris et al., 1996; Phillips et al., 1998), sadness (Blair et al., 1999) or even suggested untrustworthiness of the other person (Winston et al., 2002).

Non-invasive brain imaging studies indicate the reactivity of the anterior insula to facial expressions of disgust (Phillips et al., 1997; Krolak-Salmon et al., 2003; Wicker et al., 2003), intracortical recordings show the peak of insular responses for faces with disgust at 300–500 ms (Krolak-Salmon et al., 2003), and patients with insular damage have impaired ability to recognize disgust (Sprengelmeyer et al., 1996; Calder et al., 2000). Knowledge of another's pain is also associated with insular responses (Singer et al., 2004), and Study I further explored the possible connection of insular responses also to perception of pain from facial expressions.

2.2 Body postures and gestures

The internal states of animals are linked with specific bodily expressions and behavior (Panksepp, 1998). A perception of the bodies of other intentional agents can provide information on their dispositions to the environment, and the possible causes of their actions. Social cues mediated by bodily gestures and movement were examined in the

Studies IV–V of this thesis, thus the brain correlates for perception of bodies are introduced first, followed by the concept of biologically produced motion.

2.2.1 Perception of bodies

The perception of human bodies shares many features with the perception of faces — for example, both faces and bodies have a clear spatial configuration. Some form of body recognition seems to occur developmentally rather early, since ERP recordings of 3-month-old infants show a decrease of P400 amplitude for configurationally distorted faces and bodies with respect to intact ones (Gliga & Dehaene-Lambertz, 2005). Also in the first stages of adult perception, the overall configuration of bodies is extracted rather than details (Reed et al., 2003; Stekelenburg & de Gelder, 2004), similarly as happens for faces (Valentine, 1988). Furthermore, observation of bodies consistently activates cortical regions of extrastriate body area (EBA) in the middle occipital gyrus (Downing et al., 2001) and fusiform body area (FBA) in the fusiform gyrus (Hadjikhani & de Gelder, 2003; Peelen & Downing, 2005b) more than other stimuli (Figure 3). The specific neural processing of body perception is suggested to be scattered in different brain areas depending on whether the processing of the posture, emotional expression, movement, or instrumental action is considered (de Gelder, 2006).

Emotions and sensations such as pain provoke distinctive facial expressions, but faces alone do not convey information about the cause of the emotion or sensation. In the natural social environment, facial expressions are accompanied by bodily gestures, which complement the information. A body can be detected from a distance, and it is sometimes enough to reveal the emotion of the actor. For example, fearful body expressions with faces blurred (compared with bodies gesturing a non-emotional action) activate areas processing emotional information (orbitofrontal cortex, anterior insula and nucleus accumbens), but also amygdala and right middle fusiform gyrus (Hadjikhani & de Gelder, 2003; de Gelder et al., 2004), which are also activated for facial expressions of fear alone (Morris et al., 1996). Observation of dynamical bodies expressing fear and anger, compared with neutral actions, activates the left amygdala and temporal cortices, as well as both ventrolateral and dorsomedial prefrontal cortices (Grezes et al., 2007; Pichon et al., 2009).
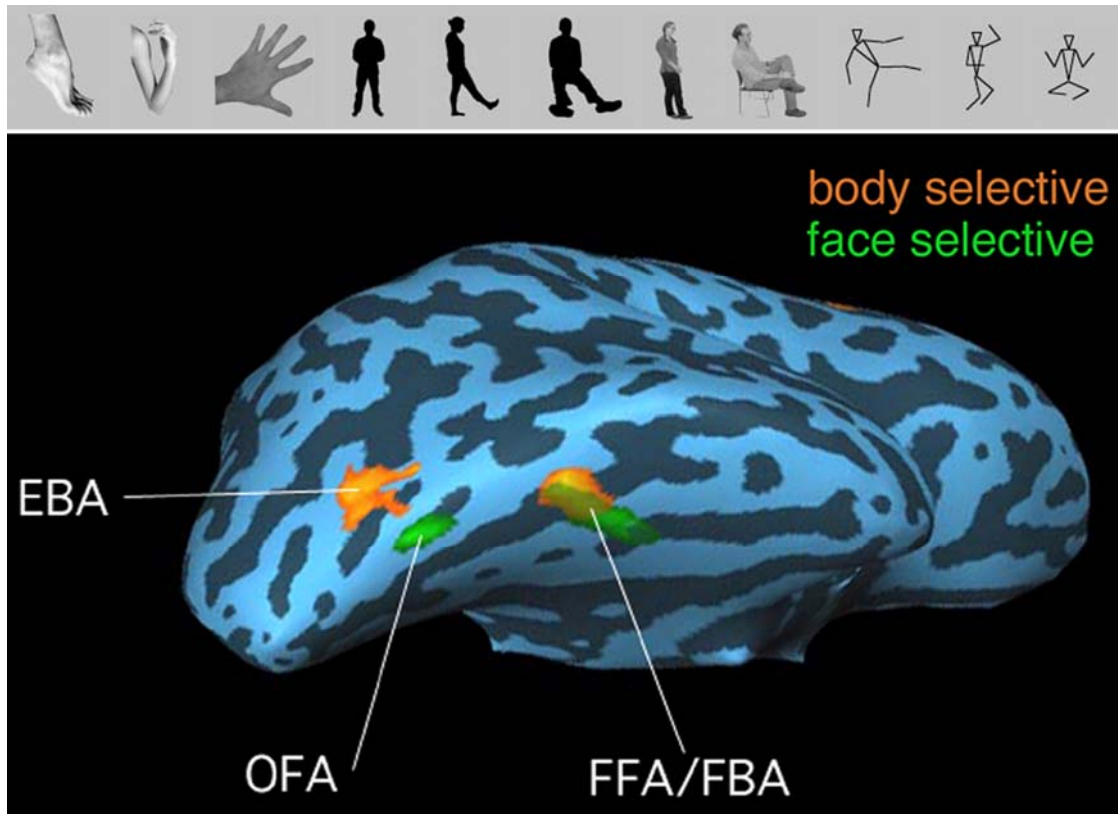
Figure 3. Top: Examples of stimuli used for localizing the body-sensitive brain areas. Bottom: Body-sensitive brain activation in the extrastriate body area (EBA) and fusiform body area (FBA) are shown in red-yellow, whereas the face-sensitive regions of occipital face area (OFA) and fusiform face area (FFA) shown in green. Adapted from Downing et al. (2001) and Taylor et al. (2007a) with permissions from The American Association for the Advancement of Science and The American Physiological Society.

Observation of bodies also produces an N170 response in the EEG (Stekelenburg & de Gelder, 2004), similarly as in face perception, although its amplitude seems somewhat smaller for bodies. Interestingly, perception of facial expressions of emotion is influenced by concurrently observed hand gestures (Hietanen & Leppänen, 2008), and incongruence between face and bodily expressions affects the brain responses within the first 100 ms of the perception (Meeren et al., 2005).

Thus, body-sensitive areas EBA and FBA respond consistently to the perception of bodies, but the analysis of specific bodily expressions seems to involve a wider neuronal network. The neural representation of emotional bodily expressions has been proposed to rely on two interconnected circuitries: a reflex-like system in the evolutionarily older subcortical structures and a cortical, more detailed recognition system, both of which

are modified through one's own body experience and awareness through somatosensory information and interoception (de Gelder, 2006).

To date, the studies on perception of bodies or body parts have concentrated in characterizing the response properties of the EBA and FBA areas, but less is known about the extent of processing within these areas: whether they only serve as recognition areas, or whether they process also meaning of social gestures or motor acts (Astafiev et al., 2004; Peelen & Downing, 2005a). Furthermore, the stimuli commonly used in the studies are figures of single humans or body parts, and it is not known whether these body-selective brain areas also process social cues transmitted by bodily gestures during perception of more than one person at a time. Study IV of this thesis contributed to the topic by exploring brain activation while the subjects observed photos of social interaction between two people.

2.2.2 Biological motion

The term "biological motion" refers to forms of naturally moving humans or animals, which contain ecologically valid information (reviewed in e.g. Blakemore & Decety, 2001; Puce & Perrett, 2003). The velocity profile of biological motion differs from the motion of non-biological origin (Kilner et al., 2007), making the movement of animals different from the environment. Biological motion can be perceived from a fully visible walking human, but also from mere "point-light" displays, where light sources have been attached to human walkers' joints in the otherwise dark environment, thus leaving only the moving lights visible (Johansson, 1973). The unified movement of the lights is enough to create a rough perception of a moving body, *e.g.* a walking or running human (Figure 4) or an animal, implying perceptual converge of motion and form.

Biological motion can be perceived even when it has been masked with dots (Thornton et al., 1998), but inverting the display of a point-light walker disturbs the perception (Dittrich, 1993; Pavlova & Sokolov, 2000). Although biological motion representing locomotion appears to be recognized most efficiently, also emotional facial expressions or social and instrumental actions can be recognized via point-light displays (Bassili, 1978; Dittrich, 1993).

The neural processing of biological motion shows similarities between monkeys and humans: in both species, the STS responds to a variety of natural social stimuli from faces to bodies. In macaque monkey, specific neurons in the anterior superior temporal polysensory area (STPa) respond to biological motion; the cells are selective for the sight of the same action either visible in full light or when inferred from the point-light displays (Perrett et al., 1990; Oram & Perrett, 1994; Oram & Perrett, 1996).

Figure 4. Examples of biological motion stimuli produced by attaching light sources to the actor's joints. Adapted from Johansson (1973) and Puce & Perrett (2003) with permissions from Psychonomic Society Publications and Royal Society Publishing.

In humans, the posterior STS responds most prominently to sights of biological motion, *e.g.* to body movement observed from either point-light displays (Bonda et al., 1996; Grossman et al., 2000), facial eye and mouth motion (Puce et al., 1998), walking mannequins (Thompson et al., 2005), or animated walking humans (Pelphrey et al., 2003). Observation of biological motion also engages the motion-sensitive area MT+/V5 in the occipito-temporal cortex similarly to non-biological motion stimuli such as moving circle gratings (Puce et al., 1998), arrays of dots (Grossman et al., 2000) or moving tools (Beauchamp et al., 2002). However, pSTS shows stronger responses for biological motion, whereas responses in MT+/V5 are more indifferent to the motion origins (Puce et al., 1998; Grossman et al., 2000; Beauchamp et al., 2002; Wheaton et al., 2004; Thompson et al., 2005).

The human perception of biological movement is also multimodal. Besides visually observed biological motion, the pSTS region is associated with listening to sounds of bodily movements and actions, such as footsteps (Bidet-Caulet et al., 2005), paper ripping, or gurgling (Gazzola et al., 2006). However these studies, as well as many other studies on biological motion, concentrate on the perception of single humans, whereas

the processing of concurrent perception of several moving agents is not well known. Study V of this thesis targeted this issue in the context of biological motion, by exploring the brain responses while the subjects were listening to sounds of humans walking either alone or together with another person. Furthermore, the stimuli of Study III contained dynamical biological motion of faces, and Studies II and IV included still snapshots of facial and bodily movements that can be interpreted as "implied motion".

2.3 Shared experiences and sensations

We humans communicate our views of the world often unconsciously by automated, bodily means: we share our attention with someone by joint eye gaze, we share a part of our mental contents with others by our actions, and we share our affective-emotional states through our expressions. According to neuroscientific studies, the mechanisms that generate emotional or certain sensory states in persons themselves seem to be utilized also in the recognition of similar states in other persons (e.g. Hari & Kujala, 2009). Such "mirroring", first introduced within the motor domain in monkeys (Rizzolatti et al., 1996), seems to exist also for sensory-affective systems, and to play a part in social cognition by providing a route for relating to others' experiences. Studies III and V of this thesis were discussed in relation to the motor mirror-neuron system and Study I concerned sensory mirroring of pain, thus the following chapters give some background on these subjects.

2.3.1 Motor mirror-neuron system

Although primarily associated with processing one's motor output, motor brain areas also participate in social processing. The original monkey neurophysiological measurements revealed the existence of "mirror neurons", which discharge both during execution and observation of a grasping action, located within the premotor F5 brain region (Rizzolatti et al., 1996), and in the parietal PF/7b region (Gallese et al., 2002). Direct intracranial data from the human homologues of these areas are not available, but in a recent single-neuron recording of human patients who were prepared for epilepsy surgery, neurons with mirroring properties — responding to both observation and

execution of the same actions — were found in supplementary motor area and hippocampus (Mukamel et al., 2010).

Action execution and perception have been shown to recruit similar motor brain areas, or modulate brain function similarly, also in studies of human brain imaging: in MEG (Hari et al., 1998; Nishitani & Hari, 2000; Nishitani & Hari, 2002), fMRI (Iacoboni et al., 1999; Buccino et al., 2001; Grezes et al., 2003; Leslie et al., 2004), EEG (Gastaut & Bert, 1954; Cochin et al., 1998), TMS (Fadiga et al., 1995; Strafella & Paus, 2000; Gangitano et al., 2001), and positron emission tomography (Grafton et al., 1996). In humans, the "mirror-neuron system" for other's actions contains inferior frontal gyrus (IFG), ventral premotor cortices and rostral inferior parietal lobule, which are associated with both action execution and observation, as well as STS, which is associated with action observation (reviewed in e.g. Hari & Nishitani, 2004; Iacoboni & Dapretto, 2006).

Since action sounds are processed in the premotor and motor cortices similarly to action vision, the motor mirror-neuron system is multimodal: this has been demonstrated in both monkey (Kohler et al., 2002; Keysers et al., 2003) and human studies (Gazzola et al., 2006; Caetano et al., 2007). The mirror responses also seem to contain somatotopical organization, since observing or listening to hand, mouth and foot actions activates the motor areas in a similar order than producing these actions oneself (Buccino et al., 2001; Gazzola et al., 2006).

2.3.2 Sharing pain and other sensations

Studying empathy for pain, Singer and colleagues (2004) measured fMRI brain responses during experimental pain caused either to the palm of the subjects themselves, or to the palm of their loved ones while the subjects observed the situation. The results showed activation of the ACC as well as the anterior insula (AI) during both felt and observed pain (Figure 5, Singer et al., 2004). Study I of this thesis explored the possible sensory mirroring of pain from facial expressions and the relation of brain responses to subjects' estimates of pain intensity and their empathic abilities. Since the first studies, the results on sensory mirroring of pain have been replicated for photos of body parts (hands or legs) observed in painful situations (Jackson et al., 2005; Cheng et al., 2007;

Gu & Han, 2007; Lamm et al., 2007b; Morrison & Downing, 2007; Ogino et al., 2007; Benuzzi et al., 2008) and unfamiliar faces expressing pain (Botvinick et al., 2005; Simon et al., 2006; Lamm et al., 2007a), suggesting the mechanism to be generally related to perceiving pain of others.

To date, sensory mirroring of pain has been shown to be affected by the features of the person being observed (Singer et al., 2006), the observer (Cheng et al., 2007; Moriguchi et al., 2007; Valeriani et al., 2008; Osborn & Derbyshire, 2010), attention to the pain (Gu & Han, 2007), and the situational context of pain (Lamm et al., 2007a; Akitsuki & Decety, 2009). Furthermore, also inter-individual differences in behavioral measures of empathy seem to modulate the brain responses for pain perceived in another: the higher the empathy scores, the higher the activation in AI and ACC (Singer et al., 2004; Singer et al., 2006). These results suggest that sensory mirroring of pain does not convey another's sensations with similar precision as in self-experienced pain — thus it should perhaps be considered more as a quick insight on another's internal state, filtered by our own individual differences.
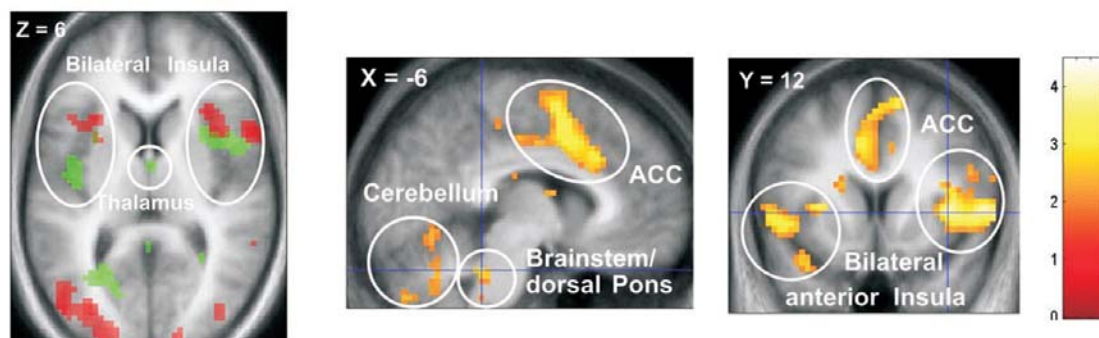
Figure 5. Left: Overlap of brain activation for experiencing painful stimuli oneself (*Self pain* vs. *Self no pain*), shown in green, and for receiving cues of another's similar experiences (*Other pain* vs. *Other no pain*) shown in red. Right: Conjunction analysis between the contrast pain vs. no pain of self and other (*Self pain* vs. *Self no pain* AND *Other pain* vs. *Other no pain*) at p < 0.001. Adapted from Singer et al. (2004) with permission from The American Association for the Advancement of Science.

The brain areas most consistently participating in the shared pain experience, ACC and AI, have some similar functions: they both are involved in integrating autonomic and visceral information (Pool & Ransohoff, 1949; Mesulam & Mufson, 1982), awareness of bodily feelings, *i.e.* interoception (Craig, 2004; Critchley et al., 2004), error and conflict processing (e.g. Taylor et al., 2007b), and attention to self-

experienced pain (Davis et al., 1997; Peyron et al., 1999; Longe et al., 2001; Bantick et al., 2002; Brooks et al., 2002).

In addition to the shared affect of pain, recent experiments using TMS suggest that the physical qualities of others' pain might be mapped in the sensorimotor cortex. Video clips showing body parts in painful situations increased the amplitudes of somatosensory evoked potentials (at the latency of 45 ms), which reflect the activity of the primary somatosensory cortex (Bufalari et al., 2007). Interestingly, the modulation correlated with the intensity but not with the unpleasantness of the observed pain. In similar TMS experiments, the motor evoked potentials have been found to increase in amplitude during pain observation (Avenanti et al., 2005; Avenanti et al., 2006).

Although nowadays perhaps the most studied phenomenon in the context of shared sensations and sensory mirroring, pain is not the only shared sensation. Also the neural mechanisms responsive for the sensations of disgust and touch seem to be involved in the perception of similar states in another. The responses of somatosensory cortices are modulated by either observing another person touch an object (Avikainen et al., 2002), or observing someone being touched (Keysers et al., 2004; Blakemore et al., 2005; Bufalari et al., 2007; Pihko et al., 2010), but the exact way of modulation seems complex and may vary greatly across individuals (Blakemore et al., 2005).

The experience of disgust seems to be partly mirrored through facial expressions (Phillips et al., 1997; Krolak-Salmon et al., 2003; Wicker et al., 2003; Keysers et al., 2004; Jabbi et al., 2008; Chen et al., 2009), but also through photos of disgust-provoking bugs or worms placed on someone's hand or feet (Benuzzi et al., 2008).

2.4 Affective states and interoception

The theories of emotion by William James (1884) and Carl Lange (1885/1922) proposed that afferent feedback from muscles and viscera provides the brain with a sensory 'image' or 'feeling' that characterizes the emotional state. Building on the same ground, Damasio (1994) advanced the somatic-marker hypothesis suggesting the representation of the homeostatic condition of the body to form a mechanism by which emotional processes guide behavior. Indeed, according to recent neuroanatomical and neurophysiological data, emotions and other affective states are connected to one's

internal feelings of the physical state of the body, *i.e.* interoception (Craig, 2002; Critchley, 2009), as well as to one's ability to acknowledge and empathize with similar states in others (for reviews, see Preston & de Waal, 2002; Decety & Jackson, 2004; Singer et al., 2009).

Afferent information of the physiological condition of the bodily organs is thought to give rise to a number of distinct bodily feelings, such as pain, itch, visceral sensations, hunger, thirst, taste, and touch. This interoceptive information is carried to cortical sites of ACC and insula along the tract of spinal dorsal column, medulla, brainstem, and hypothalamus (Craig, 2004). The insular cortices are activated under a variety of conditions involving bodily feelings, including the aforementioned pain and disgust, as well as thermal sensation (Craig et al., 2000), breathlessness (von Leupoldt et al., 2008; von Leupoldt et al., 2009), risk avoidance (Paulus et al., 2003), uncertainty (Huettel et al., 2006) and anticipation of both touch (Lovero et al., 2009) and unpleasant visual stimuli (Simmons et al., 2004).

Insular activity has also been connected to one's awareness of the bodily feelings. Subjective awareness of the timing of one's own heartbeat enhances insular and ACC activity, and furthermore, the accuracy of timing estimation, self-rated bodily awareness, and the individual anxiety level of subjects correlate with gray matter volume in right AI (Critchley et al., 2004). Additionally, individuals prone to anxiety show increased insula and amygdala activation while observing emotional faces (Stein et al., 2007), whereas anxiolytic drugs attenuate the responses (Paulus et al., 2005). These findings suggest that visceral responses are partly accessible to subjective awareness, and this connection is associated with the insular cortex.

2.5 Emotional empathy, cognitive perspective-taking and theory of mind

Empathy is often considered an inherently human ability to adopt someone else's point of view, to understand and share another's feelings and to appreciate their hardships — yet maintaining the dissociation between self and other (e.g. Batson et al., 1991; Hodges & Wegner, 1997; Eisenberg, 2000; Decety & Jackson, 2004; Hein & Singer, 2008). Empathy has been proposed, among others, to provide motivation for cooperative behavior and communication (de Vignemont & Singer, 2006) and to function primarily

through emotional contagion (Preston & de Waal, 2002). The definitions to date are somewhat murky and variable, but empathic abilities can be divided roughly into two different viewpoints: affective component, the ability to share the emotional experience of another in an embodied manner; and a cognitive component, the ability to represent situational perspective of another person (Decety & Jackson, 2004).

The affective component (also referred to as emotional empathy), develops earlier in life than cognitive component due its reliance on limbic structures (for review, see Singer, 2006). Emotional empathy also increases under certain circumstances in humans and other mammals: when the observer and the target of observation are more similar (e.g. of the same age or gender); when the observer has previous self-experience from the target's situation; when the situation of the target is more salient; when the situation is learned (either repeated or explicitly taught); or when the observer and the target are familiar with one another (for review, see Preston & de Waal, 2002). The affective component seems to function partly similarly in humans and other phylogenetically close animals (Plutchik, 1987; Brothers, 1989; Buck & Ginsburg, 1997), whereas the cognitive component of empathy seems closer to human capabilities of mentalizing or theory of mind (ToM, Vogeley et al., 2001; Siegal & Varley, 2002; Frith & Frith, 2003; Gallagher & Frith, 2003; Frith & Frith, 2006; Saxe & Powell, 2006).

A widely used assessment of human empathy by Davis (1980) is divided according to the two different viewpoints. It contains emotional categories of feeling distress of others' accidents (personal distress) and caring for others' misfortunes (emotional concern), as well as cognitive categories of using imagination as a tool for understanding others (fantasy scale) and understanding how arguments appear from another's perspective (perspective-taking).

Affective empathy seems to be partly connected to the responses in anterior insula. In human brain imaging, empathic abilities of subjects witnessing someone else's painful experience are associated with the activity of AI (Singer et al., 2004), but the AI responses, especially in males, diminish when the person receiving painful stimuli is considered unfair (Singer et al., 2006). Also, the lack of empathic abilities correlates with reduced grey matter volume of AI in adolescents with conduct disorder (Sterzer et al., 2007). Furthermore, the reduced AI and amygdala activity during emotion detection in psychopaths suggests connection of these structures to the lack of empathy and

emotional representation in the condition (Birbaumer et al., 2005). However, whether empathic abilities of healthy adults are associated with perception of affective facial expressions is not well known. Study I of this thesis sampled the connection of empathy to brain responses during observation of facial expressions of pain.

Cognitive perspective-taking has been found to modulate the brain responses during emotional empathy: responses to another's pain diminish when the subject knows the observed painful procedure has been an effective treatment rather than meaningless act (Lamm et al., 2007a). Furthermore, ToM tasks involving emotional rather than cognitive perspective-taking show stronger involvement of the orbitofrontal cortex (Hynes et al., 2006) — a structure associated with socio-cognitive evaluation of emotions — whereas tasks involving cognitive perspective-taking or mentalizing have been shown to activate *e.g.* the superior frontal gyrus, temporal poles, and the temporo-parietal junction (Ruby & Decety, 2001; Vogeley et al., 2001; Saxe & Kanwisher, 2003). The possible effect of perspective-taking abilities on expertise in social behavior of other species than human is not known, and it formed a part of Study IV.

2.6 Expansions of social perception and cognition

Social perception and cognition usually refer to the average human abilities of understanding the emotions, movements or intentions of our fellow conspecifics. However, some experimental work indicates that these abilities may be flexible and open for individual tuning rather than rigid and more or less identical across individuals. Thus, the neural mechanisms underpinning social understanding may expand through plastic changes. To clarify the possible association of this kind of changes in expertise in the social behavior of nonhuman species, Study IV of this thesis explored the brain responses of experts in dog behavior and control subjects while they observed and interpreted social interaction from photos of humans or dogs.

2.6.1 Effects of expertise

Experiences affect the respective neural function through cortical plasticity (Merzenich & Jenkins, 1993), and being an expert in some specific area represents an ultimate and accumulating experience on the area. Expertise has been shown to affect, for example,

the cortical representations of music perception (Pantev et al., 1998), motor performance (Schwenkreis et al., 2007), and object identification (Gauthier et al., 2000a; Op de Beeck et al., 2006).

Moreover, expertise may not be limited to our own performance, but it may affect the way we see, comprehend, and share the experiences of others. Professional dancers are experts of the movements they perform, and their expertise strengthens the neural responses also when merely observing similar movements performed by others (Calvo-Merino et al., 2005; Calvo-Merino et al., 2006). In some cases, being an expert on some area may require dampening the responses on another. For example, repeated exposure on the affective experiences of others may diminish the brain responses usually associated with such a situation. When asked to estimate the intensity of pain from facial expressions, health care professionals underestimate the observed pain (Prkachin et al., 2001), and a similar effect is found in non-professionals after repeated exposure to pain expressions (Prkachin et al., 2004). Along the same lines, the brain areas consistently activated in observing others' pain are suppressed in expert physicians, who instead show greater responses in areas associated with emotion regulation and mentalizing (Cheng et al., 2007).

2.6.2 Gestural communication across species

Social cognitive mechanisms enhance our understanding of our conspecifics, but some mechanisms seem to be shared also with other phylogenetically proximate species, providing a platform of behavior-reading or even communication across species through eye gaze, body movement, and vocalizations or other sounds. For example, the behavioral responses of cats (Blake, 1993) or chicks (Vallortigara & Regolin, 2006) to visual point-light walkers of their conspecifics suggest that the perception of biological motion also takes place in other animals: detection of biological motion might provide the basis of perceptual life-detection across species (Johnson, 2006). Furthermore, humans are able to detect the presence or absence of a living creature within a natural scene in half a second even with the peripheral vision (Thorpe et al., 2001), whereas recognition of digits or letters under similar circumstances is slower (Strasburger et al.,

1991; Juttner & Rentschler, 2000), pointing to the specificity of processing living animals for our perceptual mechanisms.

Some experimental results propose that mechanisms underlying human social perception are similarly utilized in the perception of non-conspecifics. Humans distinguish the movement direction from point-light walkers, whether the walkers are humans or other animals (Troje & Westhoff, 2006). Also, the face-sensitive brain responses are stronger to animal faces than to nonliving objects. In intracranial recordings from the human temporo-occipital area, cat and dog faces evoked 200-ms responses that were 73% of the responses to human faces (McCarthy et al., 1999). Similarly, the 170-ms responses around the temporo-occipital area were 50% weaker for animal than human faces, but 80% weaker for nonliving objects in an MEG study (Halgren et al., 2000). Furthermore, animal heads (Kanwisher et al., 1999) or dog faces (Blonder et al., 2004) elicit stronger BOLD responses in the FFA than do inanimate objects. Additionally, although the cortical area EBA responds strongest to human bodies or body parts, it also shows preference for animals over nonliving objects (Downing et al., 2001). Actions performed by nonhuman animals, but included in the human motor repertoire, also evoke similar activations in parietal and frontal areas belonging to the motor mirror-neuron system (Buccino et al., 2004). Study IV of this thesis continued to explore the brain correlates of perceiving nonhuman animals, and asked whether interactional gestures of dogs are processed similarly to respective human gestures.

In addition to similar neural responses for the perception of human and nonhuman animals, successful across-species communication is evidenced by a vast amount of behavioral data. Even humans who are not expert ethologists are able to categorize the emotional state of an animal either by auditory (Leinonen et al., 2003; Pongracz et al., 2005) or visual observation (Bekoff, 2007). Furthermore, not only humans comprehend animal behavior, but in some cases, the communication works bi-directionally. For example, non-human primates are able to use social cues, such as eye gaze, as a sign of someone's attention (Tomasello et al., 1998; Tomasello et al., 1999; Hare et al., 2000; Tomasello et al., 2003; Call et al., 2004), and domestic dogs understand human gestural cues (Soproni et al., 2002; Miklosi et al., 2003; Gacsi et al., 2004) similarly as young infants (Gacsi et al., 2005; Tomasello & Kaminski, 2009).

3 Aims of the study

This thesis investigates the correlates of social cognition and perception in the human brain using functional magnetic resonance imaging and magnetoencephalography along with behavioral methods. The specific aims of the studies were

1) to explore the brain function during perception of pain from the facial expressions of another person, and the connection of the responses to the empathic abilities of the subject (Study I)

2) to characterize the cortical activation sequence during observation of another's facial pain expressions (Study II)

3) to investigate how the contagiousness of yawning is represented and mediated in the human brain (Study III)

4) to study the brain correlates of interpreting natural interactional gestures between others, and to clarify how expertise on dog behavior influences the perception of the interaction between two humans or two dogs (Study IV)

6) to investigate the brain circuitry for processing walking sounds arising from either single human or multiple persons (Study V)

4 Materials and methods

4.1 Participants

The individual experiments in this thesis include data from 9–42 subjects. Altogether, data from 130 healthy adults are presented, analyzed and discussed; roughly half were male and half female, and the age range was 18–41 years. Most of the subjects had no prior experience in brain imaging or behavioral experiments, apart from Study III, where all subjects were laboratory personnel, and the behavioral parts of Studies I and III, where about half of the subjects were laboratory personnel. All subjects gave their written informed consent to the experiments, and all recordings had prior approval by the Ethics Committee of the Helsinki and Uusimaa district.

4.2 Stimuli

To effectively study the brain correlates of naturalistic facial expressions and bodily gestures, the stimuli in Studies I–IV were recorded with video and still cameras, processed digitally, and selected according to specific acceptance criteria. Stimuli used in Study V were obtained from the Sound Effects Library of the Finnish Broadcasting Company (Oy Yleisradio AB) specifically for this purpose.

For Study I, seven chronic pain patients were videotaped in the Pain Clinic of the Helsinki University Central Hospital, with the written permission of the patients themselves and a prior approval by the Ethics Committee. From the obtained material, the final brain imaging study included still photos from the videotapes of four patients. These stimuli were grayscaled, and phase-scrambled control images were generated from them for Study II. The yawning and control video stimuli for Study III were recorded originally from 20 volunteering actors of Helsinki University Medical Students' Theatre Company; 10–14 second video clips from 6 actors were used in the final experiment, and still photos obtained from the neutral expressions in these videotapes were re-used as control stimuli in Studies I and II.

For Study IV, five dancers from Theatre Academy of Finland, and nine dogs from the owners in local dog club (Espoon Koirakerho) were videotaped and photographed both alone and together with a conspecific. Still photos of 4 humans and 4 dogs, derived

from both still and video cameras, were processed digitally and used in the final experiment.

Stimulus presentation was controlled by Presentation® software (http://www.neurobs.com/). Visual stimuli of Studies I–IV were delivered on a projection screen with a micromirror data projector (Christie Vista 3X and VistaPro^{TM}, Christie Digital Systems, Cypress, CA), and in Studies I, III and IV, viewed by the subject via a mirror attached to the head coil. Auditory stimuli of Study V were delivered through an ADU2a auditory stimulation system (Unides Design, Helsinki, Finland), with plastic tubes attached to ER3A earphones (Etymotic Research Inc., USA).

4.3 Behavioral methods, questionnaires, and eye tracking

Behavioral or psychophysical testing separate from brain imaging measurements were conducted in Studies I, III and V. Post-scan questionnaires sampling subjects' perception or reasoning of, or attitudes towards the stimuli were collected in Studies I, III, IV and V, and eye tracking was conducted in Study IV simultaneously with functional magnetic resonance imaging (fMRI).

The behavioral measures in Studies I and III were applied to validate an effective subset of stimuli for the planned brain imaging experiments. In Study I, 30 subjects estimated "the intensity of pain experienced by the person in the photo" from altogether 125 still photos of the pain patients, resulting in a subset of 12 photos of provoked pain (rated highest) and 12 photos of chronic pain (rated lowest) for the usage in brain imaging study. In Study III, the "contagiousness" of yawns from videos of 6 actors was tested with 11 subjects, by quantifying the number of their overt and covert yawns from videotapes and electromyography (EMG) measurements of their facial muscles, while they observed the stimulus yawns.

Psychophysical testing was conducted in Study V to find a comfortable subjective listening level of the stimuli. The subject listened to the stimulus sounds from headphones and the volume was manually increased until the subject signaled detecting the sound; the same procedure was repeated for each stimulus type for 3–5 times, and the mean value of these was used as the hearing threshold.

In Studies I and IV, subjects' empathic abilities were quantified with Interpersonal Reactivity Index (IRI; Davis, 1980); in Study I, also Balanced Emotional Empathy Scale (BEES; Mehrabian & Epstein, 1972) was assessed. In Study IV, subjects' background expertise and exposure for dog behavior was quantified with a questionnaire.

During the fMRI recordings in Study IV, the subjects' eye movements were recorded with SMI MEye Track LR (long-range) eye tracking system (Sensomotoric Instruments GmbH, Berlin, Germany), based on video-oculography using the dark pupil – corneal reflection method. The infrared camera was set at the foot end of the bed to monitor subject's eye via mirror that was attached to the head coil. The camera was shielded properly (in house) and was checked not to affect the signal-to-noise ratio of the fMRI data. An infrared light source was placed on the mirror box to illuminate the eye, so that the eye was visible to the camera. The gaze data were recorded with iViewX software at sampling rate of 60 Hz. The software was controlled by the trigger signals from stimulus presentation program, and the eye tracker was calibrated prior to fMRI recording with 5 calibration points, which the subject first fixated on.

The eye movement data were analyzed with Begaze 2.0 software (Sensomotoric Instruments GmbH, Berlin, Germany). The fixations of the subjects were overlaid on top of the example photos, and gaze maps were calculated with a smoothing kernel of 70 pixels and a color coding for average fixation durations from 5 to 200 ms or over. Eye movements between experts and control subjects were compared further by selecting 6 sample stimuli from each dog or human category and calculating subjects' fixation durations within regions of interest that were drawn manually around human heads and bodies and dog heads, bodies and tails.

4.4 Structural and functional magnetic resonance imaging

4.4.1 Overview

Magnetic resonance imaging (MRI) is based on measuring a signal from atomic nuclei that contain quantum physical characteristics called nuclear magnetic resonance (NMR; magnetic moment caused by a moving electrical charge, and angular momentum resulting from an odd number of protons or neutrons). NMR is a quantum-mechanics

phenomenon, but can be partly visualized in the terms of classical mechanics. For example, the protons in hydrogen nuclei contain NMR qualities, and since hydrogen atoms are numerously present in water and therefore also throughout bodily tissues, they are commonly used as the basis for MR imaging of human tissue. The following brief overview is based on common textbooks (Frackowiak et al., 1997; Huettel et al., 2004), and it considers the MR measurement with respect to hydrogen nuclei.

When hydrogen nuclei are placed within a high magnetic field, their protons orient to precess along the field either parallel (low-energy state) or antiparallel to the field (high-energy state). In the MR measurement, energy in a form of a magnetic pulse of a certain radiofrequency (specific frequency depending on the imaged nucleus and the magnetic field strength) is applied to tilt the magnetization of a number of protons from their low-energy states to high-energy states; this occurs when protons absorb energy from the radiofrequency pulse (this stage is also referred to as spin excitation). When the pulse is turned off, some of the excited protons return to their original parallel orientation and concurrently emit the energy difference from high-energy to low-energy state as a measurable MR signal.

When the radiofrequency pulse is applied, two things, which are utilized with specific types of MR images, happen simultaneously. Firstly, the net magnetization of spins is tilted as described above, and secondly, the precession of spins becomes momentarily coherent, *i.e.* they precess at the same phase. Both of these effects return to their original states over time, during seconds. The return of spins to their parallel orientation is known as longitudinal relaxation; it is measured by T_1-weighted images and can be used for detecting different tissues and thus acquiring structurally accurate MR images of the brain. The return of the coherence of spin precession phases to incoherence is known as transverse relaxation and is affected by both the interaction of spins with one another and the local magnetic field inhomogenities. These two taken together are measured by T_2^*-weighted images, which are used in fMRI.

The most common form of fMRI is based on the different magnetic properties of oxygenated (diamagnetic) and deoxygenated (paramagnetic) hemoglobin in the blood, the latter cause local magnetic field inhomogenities that affect the transverse relaxation of spins. Thus, the local changes in the level of blood oxygenation can be measured, giving rise to the blood oxygenation level dependent (BOLD) signal (Ogawa et al.,

1990). The BOLD response depends on the oxygen consumption, cerebral blood flow, and the cerebral blood volume (reviewed in e.g. Logothetis, 2008).

Since neurons consume oxygen, their function can be inferred from the oxygen usage. Simultaneous recordings of fMRI and intracortical neural signals in monkeys (Logothetis et al., 2001; Wilke et al., 2006; Goense & Logothetis, 2008; Maier et al., 2008) suggest that the BOLD signal reflects the local neural processing (measured by local field potentials) more reliably than the spiking activity of individual nerve cells. According to different studies, the BOLD response may include excitatory, inhibitory and modulatory activity, depending on the specifics of the neural resources under study (Logothetis, 2008).

4.4.2 Measurement

All studies included in this thesis involved structural MRI, and Studies I, III, IV and V also fMRI. In Studies I, IV, and V, MRI was conducted with General Electric Signa® 3.0 T scanner at the Advanced Magnetic Imaging Centre, Aalto University School of Science and Technology, Finland (Figure 6), and in Study III with Siemens Sonata 1.5 T scanner at the Research Centre Jülich, Germany. In all fMRI studies (I, III, IV, and V), structural MRIs were taken for better spatial visualization and group alignment of fMRI results. In the MEG study (II), the structural images of 8/9 subjects aided in calculation and visualization of the generators of the measured MEG signals by constraining the possible source space. Structural T_1-weighted MR images were acquired in Studies I, II, IV, and V using a standard spoiled-gradient echo sequence, and in Study III using a standard MPRAGE sequence.

All functional MRIs were acquired using a standard head coil and gradient-echo planar imaging sequence with a field of view = 200×200 mm^2 (240×240 mm^2 in Study IV), time of repetition = 2000–3020 ms, time to echo = 32 ms (66 ms in Study III), flip angle of 75 (90 in Study III), and 31–42 axial slices with slice thickness of 3.0–4.0 mm in interleaved acquisition order (30 slices with slice thickness of 4.0 mm and interslice gap of 0.4 mm in Study III). Before the stimulations, 4–6 dummy volumes were acquired allowing the MR signal to stabilize.

4.4.3 Analysis

Functional MRI data of Studies I, IV and V were preprocessed and analyzed by BrainVoyager QX^{TM} software (Brain Innovation B.V., Maastricht, Netherlands), and in Study III with Statistical Parametric Mapping software (SPM99; Wellcome Department of Imaging Neuroscience, London). Preprocessing of the data included iso-voxelization, correction for motion and slice timing, high-pass filtering (at 0.008–0.01 Hz) and removing linear trends of the data.

For analysis of the data on a group level, the volumes of each subject were spatially normalized to a common atlas brain; to Talairach space with BrainVoyager QX^{TM} (Talairach & Tournoux, 1988), and to Montreal Neurological Institute (MNI) space in SPM99 (Evans et al., 1993). Subsequently, the data of Studies I and III were spatially smoothed with Gaussian kernels of 8 and 6 mm (full width at half maximum). The data of Studies IV and V only included slight smoothing (resulting from iso-voxelization and spatial normalization) to avoid illusory spatial overlap of activations between nonhomologous functional areas (see White et al., 2001; Goebel et al., 2006; Schürmann et al., 2006).

Further analysis was conducted at individual level with general linear model (GLM), where stimulus time course was convolved as explanatory variables or "predictors" with the hemodynamic response function (Friston et al., 1995). To extend the analysis to a group level, the statistical significance was assessed by inserting the estimated effects of each condition on individual data into a random-effects analysis. Thereafter, group-level statistical maps were obtained by contrasting the data from the stimulus conditions of interest with t-tests, and the resulting maps were examined with appropriate p-values and thresholds for the minimum size of conjoined clusters (Forman et al., 1995).

In addition, Studies I and IV included region-of-interest analyses of fMRI signal changes in task-relevant brain areas, defined on the basis of previous literature.

Figure 6. Left: The 3-tesla MRI scanner at the Advanced Magnetic Imaging Centre. Right: The whole-head MEG equipment at the Brain Research Unit, Low Temperature Laboratory. Both devices are located at the Aalto University of School of Science and Technology, Espoo, Finland.

4.5 Magnetoencephalography

4.5.1 Overview

Magnetoencephalography (MEG) is a non-invasive electrophysiological method for studying brain function with a millisecond-scale temporal resolution. The method is based on measuring net magnetic fields, generated by synchronous electrochemical activity of thousands of cortical nerve cells, from outside the head with sensitive superconducting quantum interference device (SQUID) sensors (see Hämäläinen et al., 1993; Hari, 2005). MEG is most sensitive to neural currents tangential to the surface of the head, *i.e.* to those in the cortical sulci, and least sensitive to sources deep in the brain (Hillebrand & Barnes, 2002). However, with a specific stimulation and recording setup tailored for the purpose, reliable responses can be obtained even from the auditory brainstem (Parkkonen et al., 2009). The majority of the magnetic fields measured during standard experiments likely arise from the apical dendrites of the cortical pyramidal neurons, which are aligned in parallel and provide the temporal summation of the signals necessary for detecting the net field outside the scalp (Hari, 1990; Okada et al., 1997).

MEG is complementary to an older electrophysiological method, electroencephalography (EEG). EEG measures the electric potentials produced by neuronal activity, whereas MEG measures the magnetic fields simultaneously emerging from the neuronal currents. An advantage of MEG is the more accurate identification of the cortical current sources, since the tissues and the skull between neurons and sensors distort the electrical signals more than their magnetic counterparts. However, this downside is avoided in intracranial EEG recordings of patients. Another advantage of MEG is the independency of the sensors from one another in comparison to EEG measurements, which reflect a voltage difference between a sensor (an electrode) and its reference (see e.g. Hari, 2005).

As a completely silent and non-invasive brain research method with a high temporal acuity, MEG has numerous applications. Some examples from our laboratory show its utilization in experimental setups ranging from sensory processing or social effects in auditory (reviewed in Hari, 1990), visual (Portin et al., 1999), somatosensory (reviewed in Hari & Forss, 1999), motor (Hari et al., 1998) and pain domains (Raij et al., 2004) and extending to the study of brain rhythms (Salmelin & Hari, 1994; Hari & Salmelin, 1997), language (reviewed in Salmelin et al., 2000), functional connections between brain areas (Kujala et al., 2008), developmental aspects in children (Parviainen et al., 2006) and the disorders of brain function in e.g. autism (Nishitani et al., 2004), schizophrenia (Schürmann et al., 2007), epilepsy (Hari et al., 1993; Forss et al., 1995), stroke (Mäkelä & Hari, 1992) and dyslexia (Salmelin et al., 1996; Renvall & Hari, 2003; Helenius et al., 2009).

4.5.2 Measurement

Study II of this thesis included neuromagnetic measurements, which were conducted in a magnetically shielded room with a whole-head Vectorview device (Figure 6; Neuromag, Helsinki, Finland; currently Elekta Neuromag Oy) comprising 306 sensors: a magnetometer and two orthogonal planar gradiometers within each of the 102 elements. MEG signals were band-pass filtered to 0.1–170 Hz, digitized at 600 Hz, and averaged from 200 ms before to 1000 ms after the stimulus onset. For data analysis and source modeling, the responses were low-pass filtered at 40 Hz, and a prestimulus

baseline window of 200 ms was applied. Trials contaminated by eye movements (detected with horizontal and vertical electro-oculograms) or excessive MEG signals were discarded prior to averaging.

4.5.3 Analysis

Event-related averages within the sensor-level data were inspected from gradiometers, which pick up the strongest signals directly above local current sources. First, vector sums of the two orthogonal planar gradients were calculated for each sensor element and condition. Second, areal averages were calculated for six channel pairs from five locations that showed prominent responses, and third, areal averages were tested statistically for the effects of stimulus category, hemisphere and measurement session with repeated-measures ANOVA and post hoc comparisons.

The neural generators of the evoked responses were estimated with noise-normalized minimum-norm estimate (MNE) for 8/9 subjects whose anatomical MRI data were available; all channels of the MEG system were used for the analysis. The signal-to-noise ratio was first improved with the Signal Space Separation method (Taulu et al., 2004), and the noise covariance estimate required by the MNE was obtained from the baseline periods (from –200 to 0 ms relative to stimulus onset) independently for all subjects. The anatomical MR images were processed with the FreeSurfer software package (Dale et al., 1999; Fischl et al., 1999) to obtain cortical surface reconstructions; the border of white and gray matter was tessellated and decimated to a 7-mm grid of MEG source points. Thereafter, cortically constrained and noise-normalized MNEs, also referred to as dynamic Statistical Parametric Maps (Dale et al., 2000) were computed using the 'MNE Software' package (developed by M. Hämäläinen, http://www.nmr.mgh.harvard.edu/martinos/userInfo/data/sofMNE.php; Lin et al., 2006). Finally, the individual cortical estimates were averaged at 400 ± 50 ms across subjects, and the results were visualized within an atlas brain.

5 Experiments

5.1 Observation of another's facial expression of pain recruits the affective pain system in a detailed manner (Study I)

Healthy adult humans are able to infer some features of the internal states of others from their gestures and behavior. For example, we immediately realize if someone in our vicinity is experiencing sudden acute pain, although we do not receive the noxious sensory input into our own pain processing system but merely the visuo-auditory input caused by the other human. Although the neural processing of perceiving classically defined emotional faces (Ekman et al., 1969) has been studied for some time, the neural underpinnings of other facial expressions signaling our internal states have remained less explored.

Similar to emotions, facial expression of pain contains communicative value: it may warn others of imminent danger and elicit helping behavior (Williams, 2002). Furthermore, previous fMRI studies have suggested a shared brain circuitry for experiencing pain and observing pain in others, similarly as has been found for facial expression of disgust (Wicker et al., 2003). The brain areas of anterior cingulate cortex (ACC) and anterior insula (AI) are among the most commonly activated regions found with fMRI studies of self-experienced pain (Peyron et al., 2000), and the same areas are also activated when the pain is merely observed or implied in others (Singer et al., 2004; Botvinick et al., 2005; Jackson et al., 2005).

In Study I, we aimed to investigate the brain responses involved in the perception of pain from the facial expressions of true pain patients. Furthermore, we explored the effect of the intensity of facial expression and the connection of brain responses to the empathic abilities of the subjects.

5.1.1 Methods

The stimuli included faces expressing chronic pain and provoked pain (Figure 7), and neutral faces as additional control stimuli (obtained from the original material for Study III). The pain expressions were recorded from the chronic pain patients in Helsinki

University Central Hospital: *Chronic* pain depicting pain patients during rest and *Provoked* pain presenting patients during a transient pain provocation (reproduction of the patients' own pain, *e.g.* cautiously stretching or pressing the painful leg; patients themselves signaled the end of the provocation period). During the recording, patients estimated the intensity of the pain in both conditions.

After the pain face stimuli were first rated for the intensity of pain in a behavioral study by 30 participants, the resulting stimulus set was presented to fMRI subjects in an event-related fMRI study. The faces were organized pair-wise, the faces of chronic and provoked states of the same patient following one another in a counterbalanced manner. Each stimulus was displayed for 2.5 s, with an intra-pair interval of 2.5–7.5 s and between-pair interval of 15 s; during intervals, the subjects viewed a white fixation cross on a black background. Subjects were instructed to view all stimuli attentively during the scan to be able to answer questions concerning the stimuli after the scan.

Subjects reviewed the pain faces after the scan to provide estimates of pain intensity and distress experienced by the patient, as well as their own self-distress when viewing the photo, on the scale from 0 to 10. The pain intensity estimates were also included in the fMRI analysis as an additional regressor. In addition, the subjects completed two questionnaires addressing empathy (Davis, 1980; Mehrabian, 2000).

5.1.2 Results

The fMRI subjects estimated all three post-scan measures higher for faces with *Provoked* than *Chronic* pain (mean ± SD for pain intensity 5.4 ± 1.9 vs. 2.3 ± 1.7, P < 0.01; for pain distress 5.5 ± 2.1 vs. 2.3 ± 1.8, P < 0.01; and for self-distress 2.8 ± 1.3 vs. 1.1 ± 1.0, P < 0.05, Wilcoxon). The patients' own pain ratings were consistently higher than the subjects' estimates of pain intensity, for both *Provoked* and *Chronic* pain faces (the difference mean ± SD for *Provoked* pain was 2.7 ± 1.7 and for *Chronic* pain 1.7 ± 2.0).

Provoked pain faces elicited consistently stronger brain activation than *Chronic* pain faces bilaterally in the inferior frontal gyrus (IFG), AI, and supplementary motor area (SMA), as well as in the ACC, premotor cortex, and inferior parietal lobe (IPL) of the left hemisphere. Furthermore, subjects' individual estimates of pain intensity covaried

with the BOLD activation strengths in the left ACC, left IPL, and bilateral AI, and the strength of activation in the left AI–IFG region during provoked pain faces correlated positively with the subjects' individual scores on the BEES scale (explained variance 37%, P = 0.035) and the personal distress subscale of the IRI (explained variance 49%, P = 0.012, Spearman; Figure 7).
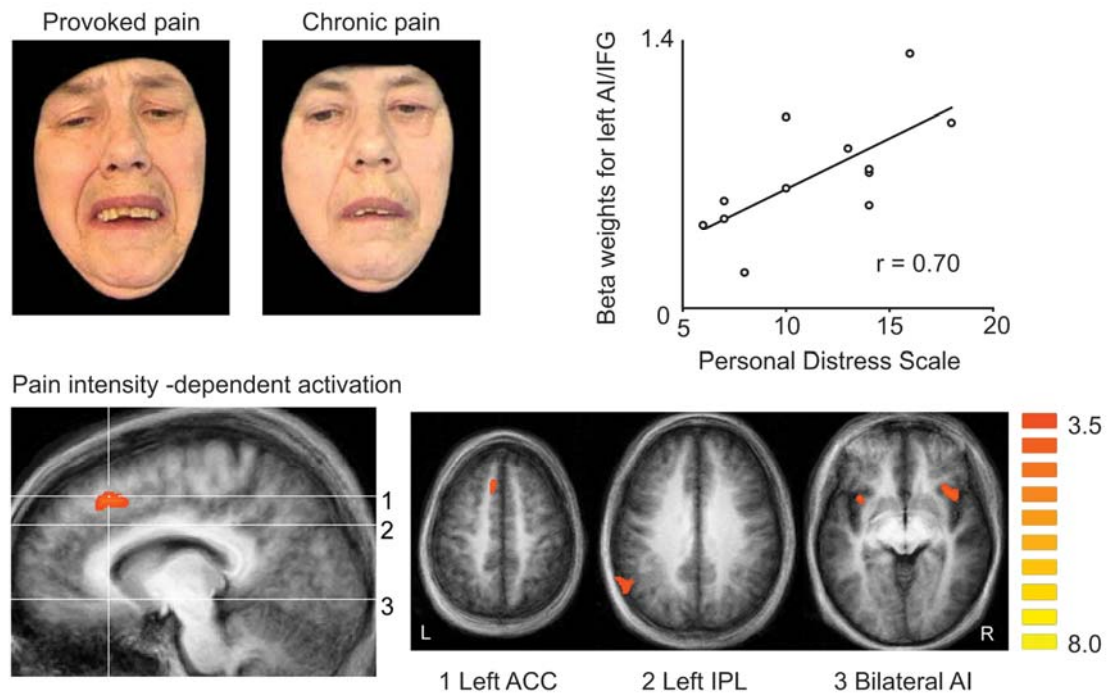
Figure 7. Top left: Examples of the stimuli. Top right: Beta weights of the left AI–IFG region during provoked pain faces as a function of the subjects' individual scores in personal distress scale; the line represents the linear best fit. Bottom: Brain areas where the BOLD response correlated with the subjects' individual estimates of observed pain intensity: 1) left ACC [peak coordinates –9, 23, 43], 2) left IPL [–58, –58, 28], and 3) bilateral AI [–37, 12, –7 and 37, 17, –4]. The color bar indicates the t-value.

5.1.3 Discussion

In brain imaging studies of direct pain, ACC and AI are the most prominently activated areas (Peyron et al., 2000). They contribute to the affective components of pain processing (Rainville et al., 1997; Price, 2000; Rainville, 2002) and they are also activated to pain perceived in others (Morrison et al., 2004; Singer et al., 2004; Jackson et al., 2005). Furthermore, their activations covary with both subjective pain intensity and applied physical strength of the nociceptive stimulus, and subjects' own percept of

pain intensity increases proportionally to the applied pain (Coghill et al., 1999). Our results indicate that the observers perceive the intensity of pain also from the faces of another person, and ACC and AI encode this intensity.

These results demonstrate that activation in the subjects' AI–IFG region during observation of provoked pain from the faces of true patients correlate positively with the empathy scales of BEES (Mehrabian & Epstein, 1972; Mehrabian, 2000) and personal distress of the IRI (Davis, 1980). Similar connections to subjects' empathic abilities have been found previously in situations where the subject has a close relationship with a person in pain (Singer et al., 2004). Here, the photos of true pain patients evoked strong distress in the observers (as suggested by the self-distress ratings of subjects as well as the correlation between AI–IFG and the IRI subscale of personal distress) although the patients were unknown to them, which strongly points to empathy involvement also in observing the pain of a complete stranger.

The AI was prominently activated by the facial expressions of pain in this study, but instead of being specific for pain perception or detection, it is possible that the region may represent a more general processing of unpleasant "gut" feelings due to its visceral input and connection to interoception.

5.2 Facial expressions of pain are differentiated at the latency of 300–500 ms in temporo-occipital cortex (Study II)

Although fMRI provides an excellent spatial resolution for studying the human brain, its temporal resolution is poorer than the one obtained with electrophysiological measurements. In Study II, we aimed to complement the fMRI results by inspecting the brain responses to facial expressions of pain from another perspective. More specifically, we aimed to characterize the temporally accurate cortical activation sequence of neuromagnetic brain responses during observing another's facial pain expressions.

5.2.1 Methods

The stimuli from Study I were re-used here with minor modifications: the photos depicting *Provoked* pain, *Chronic* pain and *Neutral* facial expressions were grayscaled

and also scrambled (phase-randomized) for creating a fourth category, *Scrambled* faces. Stimuli were presented in two subsequent recording sessions, and each stimulus was shown for 2 s, with and inter-stimulus-interval (ISI) of 2.0–2.5 s. Subjects were instructed to view all stimuli attentively.

Neuromagnetic signals were band-pass filtered to 0.1–170 Hz and digitized at 600 Hz. The responses were averaged from 200 ms before the stimulus to 1000 ms after the stimulus onset. For data analysis and source modeling, the responses were low-pass filtered at 40 Hz, and a pre-stimulus baseline window of 200 ms was applied. Before averaging, trials contaminated with eye movements (detected from horizontal and vertical electro-oculograms) or excessive MEG signals were discarded. In both recording sessions, ≥ 39 responses for each stimulus category were acquired.

For this study, the behavioral data of Study I were re-analyzed to examine whether the subjects' pain intensity ratings were affected by repeated exposure to the pain expressions of the same patient.

5.2.2 Results

Repeated-measures ANOVA of the pain ratings from the behavioral part of Study I revealed the main effects of both pain intensity and stimulus repetition on the pain ratings (repetition $\times$ intensity; $p < 0.001$ for intensity and $p < 0.05$ for repetition). The planned contrasts showed 9% decrease of the pain ratings for *Provoked* pain faces from the first to the last photo of a patient (from 7.14 ± 0.16 for the first photo to 6.48 ± 0.17 for the last photo; $p < 0.01$, paired-samples t-test), whereas the ratings of *Chronic* pain faces did not change (3.36 ± 0.15 for the first photo vs. 3.10 ± 0.15 for the last photo).

Characteristic visual responses peaked in occipital sensors around 100 ms to all stimuli, and face-sensitive responses peaked around 140 ms in bilateral temporo-occipital sensors for *Provoked*, *Chronic*, and *Neutral* faces (Figure 8). A much slower deflection for intact face stimuli peaked around 300–500 ms in the temporal-lobe sensors bilaterally, although with right-hemisphere dominance. For these responses, main effects were found for stimulus, session and hemisphere (repeated-measures ANOVA of stimulus $\times$ session $\times$ hemisphere; $p < 0.0001$, $p < 0.001$, and $p < 0.005$, respectively).

With minimum norm source modeling, the brain responses within 350–450 ms were localized around the middle STS (Figure 8). At sensor level, the responses were 30 ± 7% stronger for *Provoked* than *Chronic* pain faces in the right hemisphere, whereas the responses for *Chronic* pain vs. *Neutral* faces did not differ (p < 0.005 and p = 0.4, respectively; planned comparisons with paired-samples t-test). The responses to *Provoked* pain faces were about 40% stronger in the right than the left hemisphere in the first measurement session, and these responses decreased by 24 ± 4% in the second session compared with the first (p < 0.001; paired-samples t-test); no similar modulations were found for *Chronic* or *Neutral* faces.
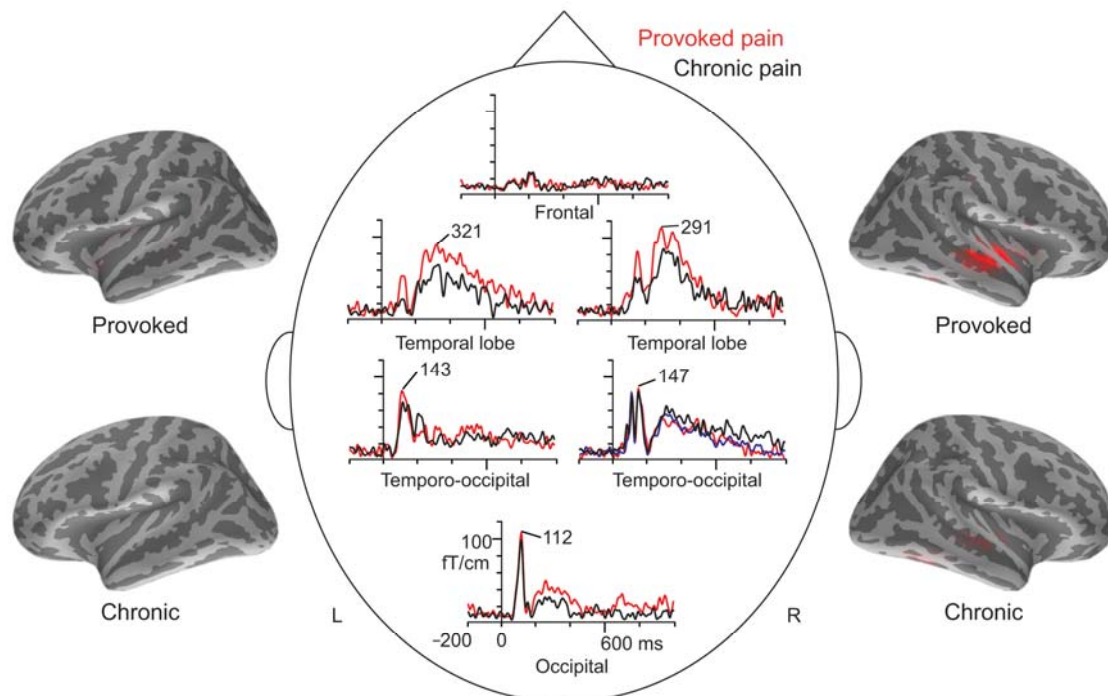
Figure 8. Middle: Magnified sample responses of a typical subject, shown as vector sums calculated from two orthogonal gradiometers, at six regions of the MEG channel layout as seen from above. The traces are from –200 ms to 1000 ms and the latencies of the peak amplitudes are marked; the amplitudes are given as fT/cm. Left and right: Across-subject average source models within the 350–450 ms time window, obtained by the cortically-constrained minimum norm estimates and shown on the atlas brain with opened sulci.

5.2.3 Discussion

The results demonstrated that the middle STS responds more strongly to facial expressions of *Provoked* than *Chronic* pain at 300–500 ms, with right-hemisphere dominance. The responses to *Provoked* pain expressions decreased from the first to the second session by a quarter, whereas no dampening was observed for *Chronic* pain faces; similarly, the behavioral ratings of the *Provoked* faces decreased after repeated exposure but ratings of *Chronic* faces remained the same.

Certain neuronal populations in STS respond specifically to faces and facial expressions both in monkeys (Perrett et al., 1982; Hasselmo et al., 1989a) and humans (Ojemann et al., 1992; Puce et al., 1999). Although the expressions of pain are not included amongst the universal facial expressions of emotions (Ekman et al., 1969), our results resemble previous findings on emotion expressions in latency (Krolak-Salmon et al., 2001; Ashley et al., 2004; Morel et al., 2009) and location (Winston et al., 2004; Engell & Haxby, 2007). Intensive facial expressions of fear, similarly to our *Provoked* pain, affect the brain responses over occipito-temporal EEG electrodes at 190–290 ms (Leppänen et al., 2007). Moreover, the middle STS responses for *Provoked* pain faces in our study were strongly right-hemisphere dominant, suggesting further similarities with emotion processing. Right hemisphere has been associated with negative emotional facial expressions, such as fear (Krolak-Salmon et al., 2001), and it has been suggested to have an important role in all urgent and threatening situations (Davidson, 1992; Van Strien & Morpurgo, 1992; Adolphs et al., 1996).

The decrease of the brain responses for *Provoked* pain expressions from the first to the second measurement session agrees with a similar decrease of the 300-ms MEG responses to fearful faces (Morel et al., 2009). Both this finding and our results show decreased responses to negative expressions, but no similar decrease to happy or neutral faces (Morel et al., 2009) or to chronic pain faces (this study). Together, these results may reflect an ecologically valid mechanism to save the observer's resources by diminishing the prolonged affective load — similarly as is proposed for health care professionals, who attribute less pain to facial expressions than nonprofessionals (Kappesser & Williams, 2002).

5.3 Contagiousness of yawning is mediated by brain areas associated with biological motion and emotion (Study III)

The contagiousness of yawning is a well known phenomenon: when we see another person yawn, we may be triggered to do the same. The underlying mechanism of the contagion, however, is not well understood. Low oxygen or high carbon dioxide levels in the shared physical environment of the yawners does not explain the contagiousness (Provine et al., 1987; Baenninger, 1997), whereas social functions of yawns as cues synchronizing group behavior seem more likely (Deputte, 1994; Daquin et al., 2001).

In Study III, we aimed to pinpoint how the perception of a yawning face is processed in the human brain, and furthermore, to investigate the neural correlates of yawn contagiousness when healthy adults observe other people yawn and feel the tendency to yawn themselves.

5.3.1 Methods

The stimuli were videos of 6 actors either yawning or producing a non-nameable tongue movement maneuver, which resembled the motor movement pattern during yawns without mimicking mild yawns (Figure 9). Prior to the fMRI experiments, the contagiousness of the yawns within the stimuli was confirmed in a psychophysical study on 11 subjects, none of whom participated in the fMRI part. In the pre-study, the subjects' facial movements during the *Yawn* and *Control* videos were videotaped and recorded with EMG electrodes attached to the facial muscles, to obtain an estimate of the subjects' overt or covert yawning frequency during both stimulus types.

In the fMRI experiment, blocks of *Yawn* and *Control* videos were presented in pseudo-randomized order, counterbalanced across subjects. The mean duration of blocks was 25 s in both conditions, and a blank screen was shown for 18–21 s between the blocks. The subjects were informed that the aim of the study was to investigate the perception of human faces, they were instructed to view the stimuli with full attention, and their overt yawning was prevented by constraining the subjects' head and chin using Stifneck collars (Laerdal Medical Corporation, Wappingers Falls, NY, USA).

In a post-scan questionnaire, the subjects estimated how strongly they were tempted to yawn during the *Yawn* and *Control* videos. For each subject, the difference between the mean estimate of *Yawn* videos and mean of *Control* videos served as a measure of yawn susceptibility rate during the scan session.
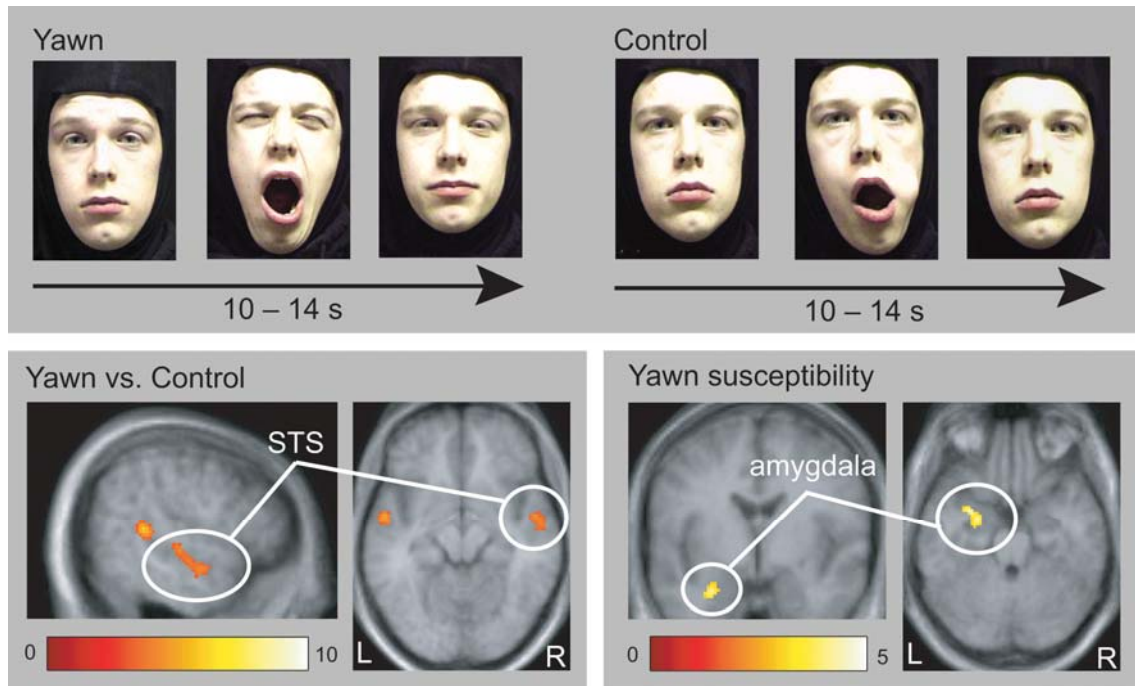
Figure 9. Top: Examples of the stimulus videos. Bottom left: *Yawn* stimuli contrasted with *Control* stimuli activated the right STS (56, –42, 6 and 54, –6, –20), and left STS (–56,–4, –16). Bottom right: Activation in the left periamygdalar region (–30, 0, –34) covaried negatively with the subjects' self-ratings of yawn susceptibility (p < 0.009, corrected). Color bars present the Z scores.

5.3.2 Results

Analysis of the pre-study video and EMG recordings of subjects' facial movements from the skin surface during the *Yawn* and *Control* videos showed more frequent overt or covert yawns during *Yawn* videos than during the *Control* videos (25 vs. 10 yawns; P = 0.016, Wilcoxon). Similarly in the fMRI study participants, *Yawn* videos evoked a stronger tendency to yawn than did *Control* videos (2.8 ± 0.2 vs. 1.4 ± 0.1 (mean ± SEM), respectively; P < 0.001, Wilcoxon).

Yawn videos provoked significantly stronger activation than *Control* videos in the posterior part of the right STS and in the anterior parts of STS bilaterally (Figure 9).

Furthermore, the subjects' yawn susceptibility showed a negative covariance with the signal from the left periamygdalar region during the contrast of *Yawn vs. Control*, whereas no regions with negative covariance were found in the corresponding analysis for *Control vs. Yawn* videos.

5.3.3 Discussion

The results quantify the tendency in two cultural samples — Finnish in the pre-test part and German in the fMRI part — to feel the urgency to yawn more frequently after seeing someone else yawn. The lack of motor mirroring in the inferior frontal cortex specific for the yawn observation suggested yawning to be a lower-level motor pattern, triggered rather automatically. Furthermore, the results show that the activation within the STS — particularly in the right hemisphere — differentiates perception of yawning from physically similar non-yawn gestures. The activation of the posterior part of STS agrees with the role of the STS in processing social cues of biological motion (Puce & Perrett, 2003) and orofacial gestures (Nishitani & Hari, 2002), as well as in the detection of the outcomes of an agent's behavior (Frith & Frith, 1999; Gallagher & Frith, 2003). In addition, the activation of the anterior part of STS was close to the site with specificity for facial movements over static faces (Puce & Allison, 1999).

Furthermore, the results demonstrate that the yawn susceptibility covaries negatively with amygdala activity (*i.e.* contagiousness increases as amygdalar activation decreases). Yawns are also more contagious for individuals with less schizotypal personality traits (have e.g. more trust towards others; Platek et al., 2003), and amygdala activation decreases when implicit trustworthiness of observed faces increases (Winston et al., 2002); these findings, together with our results, imply a possible relationship between yawn contagiousness and the trust/suspicion rising from the implicit analysis of human faces (Critchley et al., 2000; Phelps et al., 2000). This kind of interaction cannot be verified with the current data set but seems a relevant topic for future research on yawning.

5.4 Expertise on the behavior of another species is reflected in object- and body-sensitive visual areas (Study IV)

The ability of humans to infer nonverbal social cues from others depends on the perceptual systems, motor and affective mirroring mechanisms, and cognitive evaluation. However, we are not strictly limited to understanding our fellow humans, but we are also able to interpret the gestural communication of other species, especially social mammals such as domestic dogs. Even persons who have never owned a dog are able to recognize a dog's emotional state (Pongracz et al., 2005), and vice versa, domestic dogs are able to use the social gestures of humans as an aid for searching a target location (Gacsi et al., 2005), similarly to human infants (Tomasello & Kaminski, 2009).

To date, little is known about the underlying mechanisms of the ability to read social gestures of another species. In Study IV, we aimed to investigate the neural underpinnings of such across-species expertise, and clarify whether expertise in social interaction of another species affects the response profile of brain areas that usually process the interactive gestures of humans.

5.4.1 Methods

Two different subject groups participated in the study: dog experts with strong experience of dog behavior, and control subjects with no such experience. The stimuli included photos of two humans facing each other and greeting by *e.g.* shaking hands or hugging (*Human_inter*), two humans in the same photo but facing away and not interacting (*Human_away*), two dogs facing each other and greeting by sniffing and playing (*Dog_inter*), two dogs in the same photo but facing away, not interacting (*Dog_away*), and crystallized pixel figures used as control stimuli (*Pixel*; examples of the human and dog stimuli are shown in Figure 10).

Each stimulus was shown for 2.5 s in a continuous 25-s stimulus block, which alternated with 25-s rest blocks where the subject only saw the fixation cross on a moderately grey background. The subjects were informed that they would see images of people, dogs, and pixel compositions. They were instructed to explore the images freely

without moving their head, and inspect the attitude of the beings towards one another or towards their surroundings, whenever possible.

After the fMRI, the subjects filled in a background questionnaire concerning their expertise of dog behavior, and an empathy questionnaire (IRI by Davis, 1980).

5.4.2 Results

The numbers and durations of fixations within the areas of interests around human heads and bodies, and dog heads, bodies and tails did not differ between control subjects and experts, neither did the IRI scores. Instead, the background questionnaire quantified the group differences in expertise of dog behavior, attitudes towards dogs and the exposure for the presence of dogs: all measures showed less exposure for dog behavior in control than expert group.

The overall brain activations were very similar in both groups: the main effects of observing humans or dogs elicited bilateral activation within the brain circuitry associated with "visuomotor perception of emotional body language" (de Gelder, 2006), including *e.g.* the fusiform gyrus, amygdala, intraparietal sulcus (IPS), premotor cortex, and pSTS.

Both groups showed stronger brain activation in *Human_inter > Human_away* contrast in the amygdala and pSTS. Both groups had also stronger amygdala activation in *Human_inter > Dog_inter*, where non-experts had also stronger pSTS activation. Furthermore, *Dog_inter > Dog_away* contrast showed stronger activation of the left pSTS in dog experts only.

The ROI analyses of the pSTS–LO area, important for object (Grill-Spector, 2003) and body perception (Peelen & Downing, 2007), revealed stronger activations in both groups to *Human_inter* than *Human_away* in bilateral pSTS (Figure 10, top right). The pSTS–LO activations were stronger to *Dog_inter* than *Dog_away* in dog experts but not in non-experts (repeated-measures ANOVAs and planned contrasts). Furthermore, the experts' responses were stronger than those of controls for *Dog_inter* throughout pSTS–LO in the right hemisphere.

5.4.3 Discussion

The study explored how observing social interaction between others is reflected in the brain activity, and how expertise in the behavior of another species modulates this activity. Brain activations were remarkably similar when subjects observed people or dogs in corresponding interactional situations: brain regions involved in the processing of social perception were activated both in experts and control subjects. These results support the view that the same or overlapping brain regions process all interaction appearing intentional, as is previously shown for moving geometrical shapes (Castelli et al., 2000). Moreover, these findings suggest that the brain areas processing gestures of single humans also process the social interaction of two agents, whether human or dog.
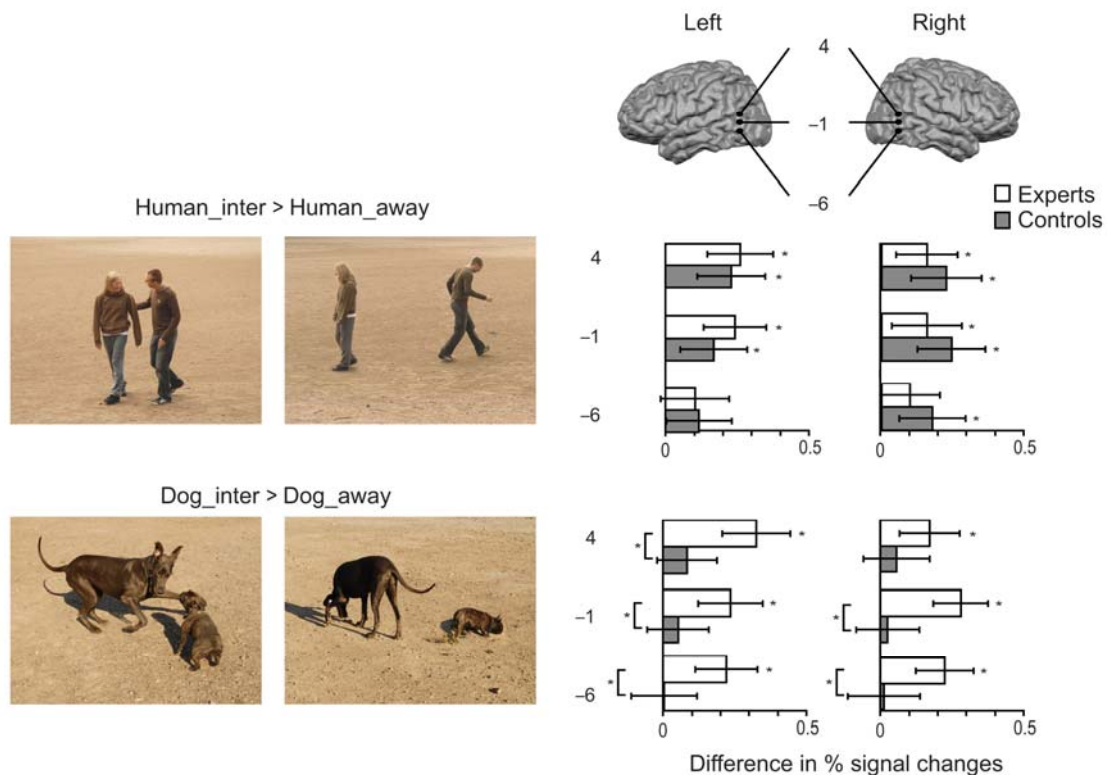
Figure 10. Left: Examples of the stimuli *Human_inter, Human_away* (top), *Dog_inter* and *Dog_away* (bottom). Top right: Three ROI locations along the z axis (4, –1 and –6) in the left and right hemispheres. Bottom right: Differences of the percentage signal changes between *Human_inter* and *Human_away* conditions in the three ROIs within left and right hemispheres, and the corresponding signals for *Dog_inter* and *Dog_away* conditions. White = experts, grey = controls.

The main goal of the study was to investigate how expertise in dog behavior influences the brain activity during interpretation of communicational bodily signals of dogs. The pSTS was activated more strongly for interacting than non-interacting humans in both experts and controls. Importantly, the dog experts' pSTS–LO activations were also stronger for interacting than non-interacting dogs, whereas control subjects showed no such difference. These results imply that expertise affects the brain responses for social gestures of other species. The findings also suggest that during the experience of the behavior of dogs, brain responses for dogs' social gestures are enhanced in the part of the temporo-occipital cortex that includes representations of objects, bodies, and motion (Peelen et al., 2006; Downing et al., 2007).

The cortical area that in dog experts showed sensitivity for the interactional gestures of dogs was in the midst of the temporo-occipital areas pSTS, EBA, MT+/V5, and LOC, thus supporting the finding that expertise in object identification alters the objects' representation in the right lateral occipital gyrus (Op de Beeck et al., 2006). Enhanced activation of experts to interacting dogs in this region might be interpreted as specialized processing of either the body form, implied biological motion, or "object" (dog) perception. First, since the EBA is partially activated for animal bodies, although less than for human bodies (Downing et al., 2001), the experts' enhanced responses to dogs' interaction gestures around this region may represent extension of the EBA for dog bodies in experts. Second, since implied body motion is processed also in the MT+/V5 complex (Kourtzi & Kanwisher, 2000; Senior et al., 2000), the observed activation may represent an engagement of this area in dog experts by the implied motion in dog photos. Third, since the object-sensitive cortex is thought to be associated with detecting shapes rather than contours of objects (Grill-Spector, 2003), the dog experts' enhanced activation may represent a part of the object-sensitive cortex specialized for dog body postures, if postures are considered as "shapes".

To summarize, our results show that similar basic processing of social interaction takes place across individuals in brain areas associated with the processing of gestures from single persons. Furthermore, the findings suggest that experts in the behavior of other species (here, dogs) develop sensitivity for interactional body gestures of the species in the temporo-occipital area related to perception of biological motion, bodies, and objects.

5.5 Sounds of humans walking alone or together activate the social brain areas with an increasing complexity (Study V)

Human footsteps carry a rich pattern of social information: it is often possible to infer the mood or gender of the walking person by only listening to the footsteps on a hallway. We may similarly be able to distinguish the number of walkers, whether people are walking together, and if one is escaping from or leading another. In Study V, we aimed to investigate the brain responses to sounds of either one person walking alone or two people (a small group) walking together.

5.5.1 Methods

The stimuli comprised sounds of human footsteps on asphalt and rhythmical bursts of white noise. The human walking sounds were either from one human male walking (*Step1*) or from two people walking (a female with high heels and a man; *Step2*), and the corresponding control stimuli were rhythmical bursts of white noise of constant amplitude (*Noise1*) or bursts of white noise with two different amplitudes (*Noise2*). Control sounds were matched to the walking sounds in duration, rhythm, and amplitude variation. The footstep sounds and the noise bursts were also matched in their intensity variation and in the total root mean square (RMS) power.

The sounds were presented binaurally in a pseudorandom order in blocks of 30 s for each (with the mean ± SD intensities across stimuli 54 ± 4 dB HL); every fifth block was rest without any stimuli. Subjects were asked to listen carefully to the sounds and to pay equal attention to all of them in order to be able to answer a questionnaire on the sounds after the scan. The presence of qualitative post-scan questionnaire, which concerned some stimulus qualities, was aimed to enhance the subjects' attention and cognitive evaluation of the stimulus sounds.

5.5.2 Results

The footstep sounds (*Step1* and *Step2* combined) and noise sounds (*Noise1* and *Noise2* combined) revealed activations bilaterally in cortical and thalamic auditory areas. Additionally, footstep sounds (*Step1* + *Step2*) activated bilateral pSTS region whereas noise sounds (*Noise1* + *Noise2*) did not.

59

In the comparison of *Step1 > Noise1*, main activations were in the left pSTS and left amygdala, whereas the comparison of *Step2 > Noise2* produced much more scattered activations *e.g.* in the right temporal pole, the bilateral subcallosal gyrus (Figure 11), and the right amygdala. In both contrasts, activation was stronger for noise than footstep sounds bilaterally in the auditory cortices.
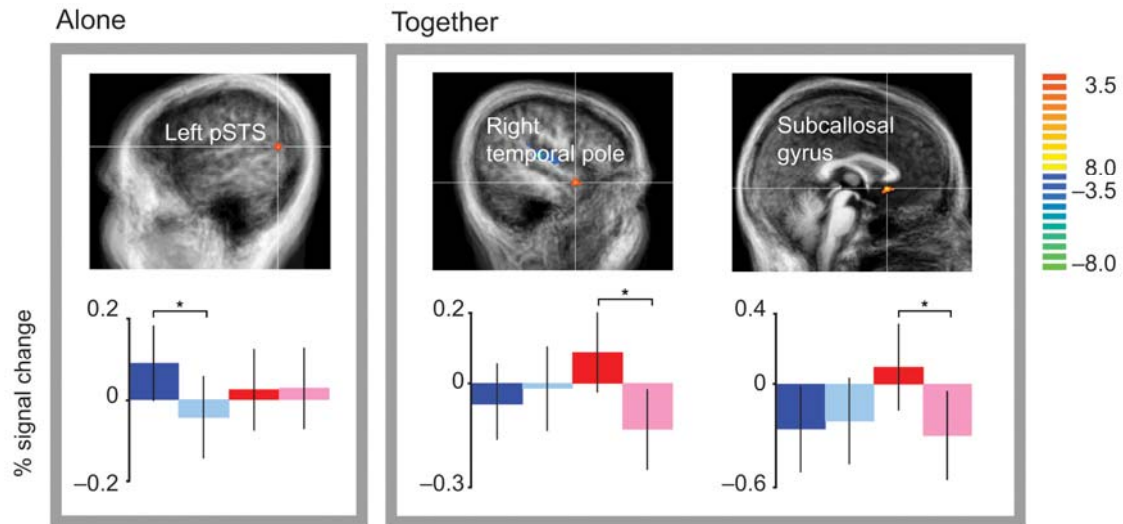
Figure 11. Clusters of activation depict the differences between stimulus conditions marked with asterisk (*) in the histograms below, where the percentage signal changes within the region are shown for all stimulus conditions. Left: Listening to the sounds of a person walking alone (*Step1*) contrasted with noise sounds (*Noise1*) activated left pSTS. Right: The sounds of two people walking together (*Step2*) contrasted with control noise sounds (*Noise2*) activated nodes within the right temporal pole and subcallosal gyrus. Blue = *Step1*, light blue = *Noise1*, red = *Step2*, pink = *Noise2*; the color bar presents the T values.

5.5.3 Discussion

The results show that listening to footstep sounds of another person activates the pSTS, and the activation is lateralized to left hemisphere during the listening of footstep sounds of a single person (*Step1 > Noise1*). The observed pSTS activation agrees with the prior data on association of the "biological motion area" (Puce & Perrett, 2003) with auditory walking (Bidet-Caulet et al., 2005).

Hearing other humans' mouth or hand actions may activate the motor mirror-neuron system (Gazzola et al., 2006), whereas the sounds of footsteps have failed to activate the premotor or IFG region (Bidet-Caulet et al., 2005), in line with our results. The lack of

IFG activation by footstep sounds could reflect the strong preference of the MNS to hand and mouth actions: in monkeys, the motor areas forming the core of the MNS (areas F5 and IPS) have representations mainly for hand and mouth (Luppino & Rizzolatti, 2000).

Although single footstep sounds activated mainly the pSTS area, the contrast *Step2 > Noise2* revealed activation of a more scattered network, comprising the right temporal pole, amygdala, and perigenual gyrus in the subcallosal cingulate area. Of these areas, temporal poles are considered to belong to the theory-of-mind circuitry (Siegal & Varley, 2002; Gallagher & Frith, 2003). Temporal poles are widely connected with other areas processing socio-emotional stimuli, such as amygdala, superior temporal gyrus, occipitobasal cortex, orbital gyrus and insula (Chabardes et al., 2002), and thus thought to integrate high-level perception with emotional responses (Olson et al., 2007). Additionally, amygdala is involved in recognition of emotion from body postures (de Gelder et al., 2004) and regulation of the personal space between individuals (Kennedy et al., 2009), and its activation here might reflect monitoring the emotional content of the auditory scene or the distance between two walkers. Also the perigenual gyrus is involved in emotional affect by taking part in self-generated sadness and happiness (Damasio et al., 2000), and its activity correlates with the increasing pleasantness of the listened music (Blood et al., 1999), suggesting connection between processing emotional auditory content and perigenual activity.

Social and emotional processing are intermingled in a complex manner during any normal social interaction, and the temporal poles are associated with both kind of processing (for a review, see Olson et al., 2007). According to our subjects' comments after the scan, the mere presence of two people in the same auditory scene provoked more mentalizing of their intentions (e.g. whether one is following another) than listening to the walking sounds of only one person. Thus, the activations of both temporal poles and emotion-related brain regions in the *Step2* condition might have been related to mentalizing of the intentions of the walkers.

Altogether, the present imaging results suggest that the analysis of auditory social scenes involving more than one agent recruits a right-hemisphere dominant social brain circuitry, with core nodes in the subcallosal area, the right temporal pole, and the left pSTS. The subcallosal area and the right temporal pole responded to the auditory scenes

involving two walkers instead of only one, whereas the left pSTS seemed to prefer simpler and more coherent single footsteps. Thus, this circuitry seems to treat differently single and double footsteps, implying separate processing for these two types of stimuli.

6 General discussion

This thesis explored spatial and temporal brain correlates of social perception and cognition in study setups involving perception of meaningful facial gestures and body postures (or movement) in social settings.

We discovered support to findings that pain perceived from another person engages the brain structures of ACC and AI that are also involved in the perception of self-experienced pain, and that the insular responses during pain observation correlate with the empathic abilities of the subject. In addition, we demonstrated that observation of pain expressions even from the faces of complete strangers recruits the affective pain system in a detailed manner: the activation of ACC and AI covaried with the pain intensity estimated from the facial expressions (Study I). We proceeded to address the temporal cortical activation sequence associated with facial pain expressions, and found that the responses for strong and mild pain expressions differ at 300–500 ms from the stimulus onset in the middle STS: the latencies and the cortical site are similar to those previously found for faces with classically defined basic emotional expressions (Study II). Furthermore, we established that dynamical yawning faces evoke middle and posterior STS activity, and that the social contagiousness of yawning correlates negatively with amygdalar activity (Study III).

Our results further showed that social interaction observed between two members of the same species, whether human or canine, both engage the brain areas commonly associated with social cognition. We continued further to address the effect of expertise on gestural communication of another species: dog experts showed differentiation of interaction from non-interaction for both human and dog stimuli in the body- and object-sensitive pSTS-LO area, whereas control subjects showed similar results for human stimuli only (Study IV). Finally, we demonstrated the engagement of pSTS during single human walking sounds, yet more scattered pattern of activation with walking sounds of multiple persons, suggesting increasing complexity in brain responses respective to more complicated social settings (Study V).

6.1 Perception of facial and bodily gestures

The perception of facial and bodily gestures was strongly associated with STS function in all studies of this thesis apart from Study I, in which we took extra care to obtain merely the brain activations related to pain expressions, not activations related to face perception as such or to variations in neutral expressions. Across studies, the STS region was consistently activated during perception of biological movement of faces (Study III; anterior and pSTS) and bodies (Study V; pSTS), as well as during perception of still images of faces (Study II; middle STS) or bodies (Study IV; pSTS) that contained merely implied movement with contracted muscles.

Indeed, brain regions around the superior temporal sulcus are associated with extraction of changeable features from faces relevant for social communication, such as gaze, movement, and facial expressions (Figure 12 and Allison et al., 2000; Haxby et al., 2000; Haxby et al., 2002). In monkeys, the STS region has been studied extensively for several decades, revealing neuronal populations specifically responsive for eye gaze (Perrett et al., 1985b), head orientation (Perrett et al., 1985b; Perrett et al., 1991), facial expression or identity (Hasselmo et al., 1989a; Perrett & Mistlin, 1990), head movement (Hasselmo et al., 1989b), body movement (Perrett et al., 1985a) or biological motion in general (Perrett et al., 1985a; Perrett et al., 1990; Oram & Perrett, 1994; Oram & Perrett, 1996). Furthermore, the neurons within STS have multisensory properties (Barraclough et al., 2005). In humans, the STS reacts similarly to many kind of social cues (reviewed in e.g. Allison et al., 2000; Haxby et al., 2000; Puce & Perrett, 2003).

The monkey single-cell recordings and human brain imaging studies suggest that the STS regions in humans and monkeys are similarly engaged during perception of facial features. If specific neural populations encode facial features also in the human brain, as suggested by intracranial studies (McCarthy et al., 1999; Puce et al., 1999), it is plausible that different combinations of static or dynamic facial and bodily gestures, transmitting one's emotional states and attitudes, activate the STS region with a specific pattern, as was found in our Studies II–V.
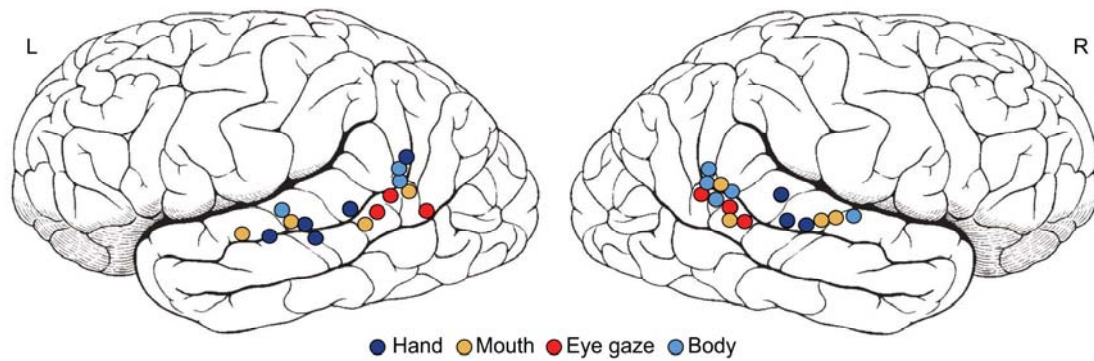
Figure 12. Meta-analysis of activation foci from a number of studies involving perception of dynamic or stationary hands, mouths, eye gaze, or bodies. Adapted from Allison et al. (2000) with permission from Elsevier.

Moreover, studies on the theory of mind have suggested that the part of pSTS in humans, closer to temporo-parietal junction, is involved in extracting intentions or intentional activity from the stimuli in a more general context — for example, from cartoons or geometrical shapes, not merely from other humans (Castelli et al., 2000; Blakemore et al., 2003; Gallagher & Frith, 2003). The results of our Study IV support this notion, showing similar activation of the STS close to temporo-parietal junction for stimuli with social interaction of two intentional creatures, whether they are humans or dogs. Interestingly, the cells in the monkey STS possess some plasticity, *e.g.* by changing their firing pattern after learning (Rolls et al., 1989). Similar capability for experience-derived plasticity of social perception in the human brain would partly explain our findings of expertise effects on the function of pSTS (Study IV), even though the cause and effect of becoming an expert in the behavior of another species remains to be studied.

6.2 Similarities of shared sensations

The neural mechanisms underlying sharing one's internal affective-emotional states with others was assessed in Studies I and III, although the concept can be broadly associated also with the other studies of this thesis. Transmission of another's strong internal state, pain, from a person's facial expressions was associated with activation of brain areas previously associated with self-experience of pain (Study I). On the other hand, a dynamical facial expression of a yawn was not associated with motor mirroring

of the movement, suggesting yawning to be a lower-level motor pattern triggered rather automatically (Study III). Additionally, the degree of subjects' urgency to yawn correlated negatively with amygdala activation, signaling the important role of trust and vigilance with a sensory state necessary for yawn contagiousness.

In general, shared sensations seem to include merely proximate, embodied senses: somatosensory (touch and pain), olfactory (disgust) or taste (disgust), whereas an idea of mirrored distal senses — vision or audition — seems absurd and unnecessary. We have no need for replaying another's experiences if we can gain the same information ourselves by just following another's attention; instead, we cannot get any information from the proximate senses of another person unless we are able to catch even a faint echo of what the other one is experiencing. The socially transmitted, immediate and internalized understanding of another's experience means an advantage for our own (as well as the peer's) survival, as it may bring us an effective warning (and helping) signal.

Of the mirrored sensations, pain and disgust are both results of something harmful and potentially dangerous happening within our body, likely containing relevant information also for our conspecifics: "Don't make the same mistake I'm making, this is no good". The social transmission of both pain and disgust seem to rely on ACC and AI that are associated with monitoring our own internal bodily states (Craig, 2002). Interestingly, the perception of another's pain seems to function similarly also in persons with congenital insensitivity for pain (Danziger et al., 2009), suggesting that it is not the nociceptive receptors as such, but the capability for representing the unpleasantness associated with pain that is necessary for pain mirroring.

The sensation of touch differs from mirroring pain and disgust: it presents a more intimate sense, revealing structures and textures of the environment or social relationships of others. Another's experience of touch may not convey the possibility of similar danger to observers like pain and disgust, but internalizing the nature of touch may be otherwise important within a human social community. Knowing whether a touch is violent or gentle helps to keep track of the relationships within the community and adjust one's behavior accordingly. In the persons with vision–touch synaesthesia, however, the matching mechanism may become overactive and limit the normal functioning of an individual (Blakemore et al., 2005).

6.3 Perceiving individuals or groups

Human groups are known to affect our behavior: acting within a group may aid in finding a creative solution to a problem (Hong & Page, 2004), but often one is also reminded of "ryhmässä tyhmyys tiivistyy" (a Finnish proverb, "Stupidity condenses within a group"), which points to the apparently diminished decision-making capabilities of an individual committed to a group: the effects of a mass panic or the functioning of *e.g.* football hooligans seem to rely strongly on such group cohesion. The effect of perceiving humans as individuals or as a small group of two was addressed in this thesis (Study V), in the simplified experimental setup where subjects listened to walking sounds of a man, or footstep sounds of a man and a woman walking together. Our results showed stronger activation of biological motion -sensitive pSTS during single human walking sounds respective to matched control (noise) sounds. Instead, more complex pattern of activation was associated with walking sounds of two people, including brain areas related to the theory of mind and emotional control. These results suggest that even in a very simple experimental setting, the number of humans perceived does not merely increase the responses engaged to perception of individual humans but increases the complexity in brain responses related to social environment.

Similar results were suggested by the unpublished data originally gathered for Study IV: observing two persons within the same stimuli, compared with stimuli including only one person, illustrated a widespread activation network that was even stronger when the two people were interacting than not interacting. Thus, the brain responses for one person are not merely multiplied when more people are observed at the same time, but the brain response patterns also get more complex. The study by Iacoboni and colleagues (2004) also reported enhanced brain activations while the subjects observed dynamic social interaction of two people compared with observing one person alone. From their choice of stimuli, they state:

"we opted not to show segments in which two actors are not interacting as a control condition ---. It seemed to us likely that viewers would anticipate or infer a relationship among people presented simultaneously on a split screen, even though these people were not directly interacting." (Iacoboni et al., 2004)

Despite the possibility of relationships inferred or imagined by the subjects as denoted previously, the results of Study IV established that a difference in brain activations for interacting and non-interacting conditions can be obtained, albeit the difference might be weaker than that obtained between perceiving single or multiple persons. However, the studies on perception of individuals or groups are still rare, and the topic is likely to become more extensively studied in the future.

6.4 Individual differences in behavior and brain responses

Humans share species-specific, general perceptual and cognitive mechanisms needed for social interaction, and the underlying processing can be partly localized in the human brain. However, everyone has a slightly different viewpoint on the world, thus one's individual social cognition likely contains unique features depending on the slight individual variation and "tuning" of the common mechanisms due to one's former interactions and life history.

In brain imaging, individual differences in responses often have to be ignored in the search for group-level effects, although the differences may contain important additional information. Understanding the connection of individual differences in brain responses with the behavior and experiences of the individuals would certainly shed light on the amount of plasticity within certain brain areas. In Studies I, III and IV of this thesis, subjects' differences in their self-reported percepts (Studies I and III) or past experiences (Study IV) were connected with the differences in brain activation. Similar behavioral information might have also benefited the analyses of Studies II and V.

Behavioral training is known to induce plastic changes in auditory, object-sensitive and motor cortices (e.g. Pantev et al., 1998; Gauthier et al., 2000a; Calvo-Merino et al., 2005; Calvo-Merino et al., 2006; Op de Beeck et al., 2006; Schwenkreis et al., 2007). In Study IV, we associated expertise in gestures of dogs to functional differences within body- and object-sensitive cortices. The results suggest that brain areas responsive to social information are modulated through experience, and understanding behavior of another species might rely on plastic changes in brain function.

Despite plasticity, part of the individual variation in social cognition and the associated brain processes may also depend on possible genetic differences across

individuals. As an example from a purely perceptual domain, a certain odor of androstenone (derived from testosterone) can be subjectively perceived as offensive, pleasant or neutral, depending on the genotypic variation in the odorant receptor (Keller et al., 2007). Similar links of subjective experiences to genetic differences might also explain part of the variation in brain responses underlying social perception and cognition. To which extent adult brains contain individual plasticity in processing social information remains to be explored, as do the genetic bases of social functions (Blakemore et al., 2004), and the effects of long-term training in *e.g.* professions strengthening or diminishing the reactivity for social information.

6.5 Methodological considerations

6.5.1 Complementary data on brain function with fMRI and MEG

The currently widely available brain imaging methods of fMRI (utilized in Studies I and III–V of this thesis) and MEG (in Study II) reveal slightly different properties of brain function: fMRI measures the hemodynamic changes reflecting the metabolic demand of neural activity, with high spatial sensitivity (Buxton et al., 1998; Logothetis, 2008), whereas MEG measures the magnetic fields generated directly by the neuronal activity, with high temporal acuity (Hari, 1990; Hämäläinen et al., 1993; Okada et al., 1997). Studies I and II of this thesis were designed as complementary views of perceiving facial expressions of pain utilizing the strengths of these methods: Study I assessing the pain-related activation deeper in the brain, and Study II characterizing the temporal processing chain in the cortex. Indeed, the studies did reflect some fundamental differences of the methods.

With the hemodynamic measures, ACC and AI were found to be more strongly activated during observation of intense than mild pain faces (Study I), whereas the MEG measures did not show activation of ACC or AI (Study II). The differences may be explained by several factors. First, ACC and AI are difficult to detect in MEG recordings since both sources are deep in the brain, leading to weaker MEG signals with respect to more superficial source of equal strength; according to our simulation, the source current in AI has to be 3–4 times stronger than that in more superficial STS to produce an MEG response of the same magnitude. Second, the ACC is a symmetric

brain structure, which leads to signal cancellation from synchronous but opposite currents in nearby cortical walls. Third, some currents in the insula are radial with respect to the skull surface, which hinders their visibility in MEG (Hämäläinen et al., 1993). The poor detectability of insular responses in MEG has been also demonstrated by studies of acute pain, where the same painful stimulus evoked AI activation in fMRI measurements (Raij et al., 2005), whereas the MEG responses were adequately explained by activation of the SII cortex (Forss et al., 2005).

With the neuromagnetic measures of Study II, the temporal progression of cortical visual processing of facial expressions of pain was obtained, and additionally, a quick repetition suppression of the STS responses was detected, whereas no similar effect were obtained in the fMRI measurements of Study I. Of course, Study I was designed to exclude the basic face processing responses including STS activity, but since the fMRI data analysis involved averaging the stimulus-locked data over several repetitions, it is likely that the sort of adaptation observed in the MEG data would have gone unnoticed and merely reduced the signal.

Thus, the results obtained in this thesis suggest that fMRI and MEG provide complementary information under certain circumstances. If a neural event is highly synchronous but short-lived causing no extensive demand for the metabolism, or if it involves fast changes in the response pattern, it may be visible with MEG but not fMRI. Additionally, if a neural source is deep in the brain, has highly symmetrical anatomy or is radial with respect to the skull surface, it may be detected with fMRI but not with MEG.

6.5.2 Effects of data presented with statistical maps

Due to the arbitrary units obtained by the technique, the results of fMRI studies are commonly given in the form of contrast voxel maps thresholded at a certain statistical level, as was done in Studies I and III–V of this thesis. Although these maps illustrate statistical differences between experimental situations and do not directly reveal the amount of firing or synaptic activity of neurons, the map form affects its interpretation. Since the maps always involve an amount of uncertainty, also the data presented in this thesis only represent one interpretation of the results.

FMRI studies with contrast maps (experimental condition 1 *vs.* experimental condition 2) often include lists of peak coordinates of activation, as in Studies I and III–V of this thesis, within the standardized coordinate systems such as Talairach or MNI space. While the coordinates are important for forming a basis for across-studies comparison, the clusters of activations that survive corrections can be quite large, extend over several gyri in the brain and include more than one submaximal focus area, which renders peak coordinates a rough simplification of the data.

In some brain areas — especially primary sensory cortices — it is justified to assume the neuronal activity to be local and very specialized for a certain function, but the level of specialization may decrease within the brain regions with higher-order evaluative functions, such as those related to social cognition. However, the presentation of the results in the form of statistical maps leads thinking into all-or-none patches regardless of the brain area, such as "that region is" and "the next region isn't" involved in processing a certain feature, although the extent of a significantly activated region may depend on the cut-off value of the statistical threshold, the number of subjects, as well as the possible smoothing. Some of the pitfalls of the statistical contrast maps are avoided in resolving voxel-based activation patterns including submaximal responses: the approach provide small-scale patternal information of brain activation, which is more detailed than the large-scale regional data obtained by the traditional contrast maps (e.g. Haxby et al., 2001; Staeren et al., 2009; Op de Beeck, 2010).

6.5.3 Comparison of the social neuroscience data from different species

The studies on sensory mirroring (such as in Study I) commonly scrutinize brain responses while subjects experience something themselves and when they perceive the same experiences of another person. This kind of experimental setup enables resolving whether the same brain regions are activated in both situations, similarly to the original motor mirror-neuron experiments with single-cell recordings on monkeys (Gallese et al., 1996; Rizzolatti et al., 1996). However, the monkey studies address the function of individual neurons, showing that the same cells respond both to action execution and perception, whereas the human noninvasive brain imaging reaches the level of larger brain areas. Currently, only one experiment exists showing that a subset of neurons

within SMA and hippocampus respond to both observation and execution of grasping actions and facial expressions (Mukamel et al., 2010). A part of these neurons showed excitation during action execution and inhibition during action observation, suggesting a mechanism for distinction between self and others during motor mirroring. However, no single-cell data are available from human inferior frontal or parietal mirror-neuron areas, thus it is unresolved whether exactly the same neurons respond both to observation and execution of an action in these areas, or whether the neurons are separate but located in the same area and adjacent to one another.

Additionally, there are no current data of sensory mirroring in monkeys similar to the results obtained with neuroimaging studies of humans (as in Study I), thus it is not known whether such sensory mirroring mechanisms exists in other animals. However, behavioral data suggests that prosocial behavior through emotion transfer and emotional empathy mechanisms, reminding those of humans (Zahn-Waxler et al., 1983; Eisenberg et al., 1994; Farver & Branstetter, 1994; Eisenberg et al., 1996), also exist in other mammals, such as monkeys (Masserman et al., 1964), chimpanzees (O'Connell, 1995), and rats (Church, 1959; Rice & Gainer, 1962).

6.6 Conclusions

The studies comprising this thesis focused on the perception of facial and bodily gestures and movements, which are not classically defined within the range of pancultural emotional expressions and thus have previously remained under marginal scientific focus. Taken together, these studies clarified the roles of distinct cortical and subcortical brain regions in perceiving and sharing others' internal states, as well as the connection of brain responses to behavioral attributes.

More precisely, the studies demonstrated 1) the modulation of the cortex around superior temporal sulcus in response to both static and dynamic gestural stimuli (Studies II–V), 2) the recruitment of the brain areas, which in previous literature have been associated with painful experiences, also by observation of the same experiences from another's facial expressions (Study I), and 3) the association of behavioral attributes with certain features of the brain responses (Studies I–IV). Study I used behavioral attributes to scrutinize the connection of the estimated intensity of observed pain, as

well as the connection of the subjective empathy measures, with brain hemodynamic responses during pain observation (in AI/ACC regions). Behavioral attributes were also utilized in obtaining a similar decrease of both the estimates of pain intensity and the neuromagnetic brain responses to pain expressions (in STS regions, Study II); in obtaining a negative correlation of the yawning contagiousness, measured by subjects' tendency to yawn, and brain hemodynamic activation (in amygdala, Study III); and in obtaining the effects of expertise in the behavior of another species to the hemodynamic brain responses (in pSTS–LO, Study IV).

These studies associate large-scale brain responses with perceptual observations of social stimuli as well as subjects' behavioral characteristics. In the future, the plasticity and individual tuning of social responses require more detailed examination. Furthermore, the knowledge of the interplay between brain areas under social settings becomes of even more importance, along with simultaneous measurements of autonomic nervous system and brain function. Finally, the challenging future topic for study is to examine brain activation in more natural and salient settings involving real-time interaction of two individuals.

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