Frei, Luisa Sophie (2012) *Interpreting EEG and MEG signal modulation in response to facial features: the influence of top-down task demands on visual processing strategies.*
PhD thesis.

Interpreting EEG and MEG signal modulation in response to facial features: the influence of top-down task demands on visual processing strategies

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SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

SCHOOL OF PSYCHOLOGY
COLLEGE OF SCIENCE AND ENGINEERING
UNIVERSITY OF GLASGOW
JULY 2011

This thesis presents research conducted at the
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For Przemek, Mama, Papa and Janna

Abstract

The visual processing of faces is a fast and efficient feat that our visual system usually accomplishes many times a day. The N170 (an Event-Related Potential) and the M170 (an Event-Related Magnetic Field) are thought to be prominent markers of the face perception process in the ventral stream of visual processing that occur ~ 170 ms after stimulus onset. The question of whether face processing at the time window of the N170 and M170 is automatically driven by bottom-up visual processing only, or whether it is also modulated by top-down control, is still debated in the literature. However, it is known from research on general visual processing, that top-down control can be exerted much earlier along the visual processing stream than the N170 and M170 take place. I conducted two studies, each consisting of two face categorization tasks. In order to examine the influence of top-down control on the processing of faces, I changed the task demands from one task to the next, while presenting the same set of face stimuli. In the first study, I recorded participants' EEG signal in response to faces while they performed both a Gender task and an Expression task on a set of expressive face stimuli. Analyses using *Bubbles* (Gosselin & Schyns, 2001) and Classification Image techniques revealed significant task modulations of the N170 ERPs (peaks and amplitudes) and the peak latency of maximum information sensitivity to key facial features. However, task demands did not change the information processing during the N170 with respect to behaviourally diagnostic information. Rather, the N170 seemed to integrate gender and expression diagnostic information equally in both tasks. In the second study, participants completed the same behavioural tasks as in the first study (Gender and Expression), but this time their MEG signal was recorded in order to allow for precise source localisation. After determining the active sources during the M170 time window, a Mutual Information analysis in connection with *Bubbles* was used to examine voxel sensitivity to both the task-relevant and the task-irrelevant face category. When a face category was relevant for the task, sensitivity to it was usually higher and peaked in different voxels than sensitivity to the task-irrelevant face category. In addition, voxels predictive of categorization accuracy were shown to be sensitive to task-relevant, behaviourally diagnostic facial features only. I conclude that facial feature integration during both N170 and M170 is subject to top-down control. The results are discussed against the background of known face processing models and current research findings on visual processing.

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Acknowledgements

Philippe: Thank you for giving me this opportunity to work with you at the forefront of our field. I greatly admire your multidisciplinary scientific knowledge and creativity. You enabled me to grow as a scientist and as a person.

Joachim: Thank you for providing invaluable input on my research and for supporting and guiding me tactfully and purposefully at the toughest of times.

Nicola: Without your day-to-day guidance, practical help and advice, motivating words of comfort and enjoyable company I wouldn’t be, where I am now. I will be forever grateful and indebted to you.

Marie: I greatly valued your practical help in the beginning of my Ph.D. and subsequent (mostly) email and telephone advice and input. You provided me with some much-needed objectivity whenever I lost track of the bigger picture.

Guillaume: Your input on robust statistics and analysis was invaluable. Thank you for showing me that it is necessary and worth to go beyond the conventional.

Michael: I admire your knowledge of pretty much everything, your endurance during your Ph.D. despite the worst possible circumstances and I am so glad we got to be office mates. Your friendship gave me the best insight into Scottish culture and mentality (good and bad) and I thank you for rescuing me from its pitfalls more than once.

All my office mates over the course of those 3.5 years: Despite the frequent changes, I was always lucky to have office mates, who were both quiet, helpful and up for a friendly chat, whichever was necessary. Thank you for that!

Balazs, Anja, Flor, Jude, Thaissa and all my other friends: Thanks for helping me maintain a healthy work-life balance and for being patient with me during the final months. I am lucky to have such friends.

My parents, sister and the extended family: Thank you for always believing in me and supporting me with whatever means necessary to get me to where I am now.

Przemek: Words cannot express my gratitude and joy in having you. Thanks for listening, kicking my ass and putting me back on my feet more than once. This is it. Off to new horizons!

Author's Declaration

I certify that this doctoral dissertation is my original work and that all references to the work of others contained in it have been clearly identified and fully attributed.

Key to abbreviations

AP	Action Potential
BGS	Backus-Gilbert-Spread
BOLD	Blood Oxygen Level Dependent
CI	Classification Image
CSD	Current Source Density
EEG	Electroencephalography
ERF	Event-Related Field
ERP	Event-Related Potential
FFA	Fusiform Face Area
fMRI	functional Magentic Resonance Imaging
ICA	Independent Component Analysis
LCMV	Linearly Constrained Minimum Variance
LGN	Lateral Geniculate Nucleus
MAD	Median Absolute Deviation
MEG	Magnetoencephalography
MI	Mutual Information
MT/MST	medial temporal/medial superior temporal area
NAI	Neural Activity Index
OFA	Occipital Face Area
PCA	Principal Component Analysis
PET	Positron Emission Tomography
PG	Planar Gradient
SD	Standard Deviation
SF	Spatial Frequency
SQUID	Superconducting Quantum Interference Device
STS	Superior Temporal Sulcus
V1, V2 etc.	Primary, secondary, etc. visual cortex
VC	Visual Cortex

I. Introduction

The perception of our visual environment is a complex, yet efficient feat, which a healthy brain performs almost continually during our waking hours. At first glance, a natural visual scene is simply a collage of colours, patterns and shapes, which might change, move or stay static over time. Extracting meaningful and relevant information from this abundance of stimulation in the fastest possible way is the key target of our visual system. Which information is meaningful and relevant, or – in other words – *diagnostic* in any given situation, depends on a large variety of factors. When looking for a friend in a room full of people, we will probably look for his face, hair colour, height or type of clothing, whereas when we are asked to judge a dance performance, we will pay attention to the movements rather than person specific attributes. When perception becomes purposeful in this way, our brain exerts top-down control on our bottom-up visual information processinging by making certain information more salient.

For an average person, faces will be among the most frequent and most consistent visual stimuli they encounter during their lifetime. In addition, faces are highly relevant for social interaction as they communicate important and potentially life-saving signals, such as looming danger (e.g. angry or fearful faces), the mood of our partner in a conversation or sometimes even whether the other person is lying to us (e.g. during professional poker, players tend to shield their eyes in an effort to hide any potential clues as to whether they are bluffing or not). It is therefore hardly surprising that our visual system has adapted to processing these signals quickly and efficiently. Like any visual perception, face perception can be facilitated or directed by top-down control. In a counselling session, for example, the therapist can gauge his reactions to the patient's facial emotional expression. Therefore, the main aim of this thesis is to examine how top-down control impacts on and changes the way meaningful, diagnostic information is extracted from a face during early face processing. The following subchapters will give a brief introduction on the visual system, top-down control and face perception in particular.

1. Anatomy of the Visual System

In order to understand face perception, it is essential to understand the basics of visual anatomy. From the retina, visual information is projected through the optic nerve, via the optic chiasm, the pulvinar and the lateral geniculate nucleus (LGN) of the thalamus to the primary visual cortex (V1) in the occipital lobe (Figure 1.1). Another visual pathway, often referred to as a secondary and subcortical visual pathway, goes through the superior colliculus and reaches visual areas in the parietal and temporal lobes. The main pathway from the LGN to V1 consists of two main anatomically separate streams, the magnocellular (M) and parvocellular (P) pathway, each of which are associated with another aspect of visual processing. Whereas the faster M pathway is thought to process the movement and location of objects, the P pathway is often associated with the processing of object-based features (Brown & Narayanan, 2009).

After V1, cortical processing is again divided into two streams, the dorsal “where” stream and the ventral “what” stream (Figure 1.2). Originally, the subcortical P pathway was thought to mainly input directly into the cortical ventral visual processing stream to the temporal lobe, which plays an important role in object processing. Similarly, the M pathway was thought to mainly input into the dorsal stream to the parietal lobe, where objects are processed spatially (see Figure 1.2; Brown & Narayanan, 2009; Haxby et al., 1991). However, this notion has been questioned (Merigan & Maunsell, 1993). Specifically, it seems the input to the ventral stream is derived from both M and P pathways. Unlike the M and P pathways, the dorsal and ventral streams are not entirely segregated. There are a large number of connections between temporal and parietal areas, which allow cross-talk and the integration of the visual percept (Merigan & Maunsell, 1993).

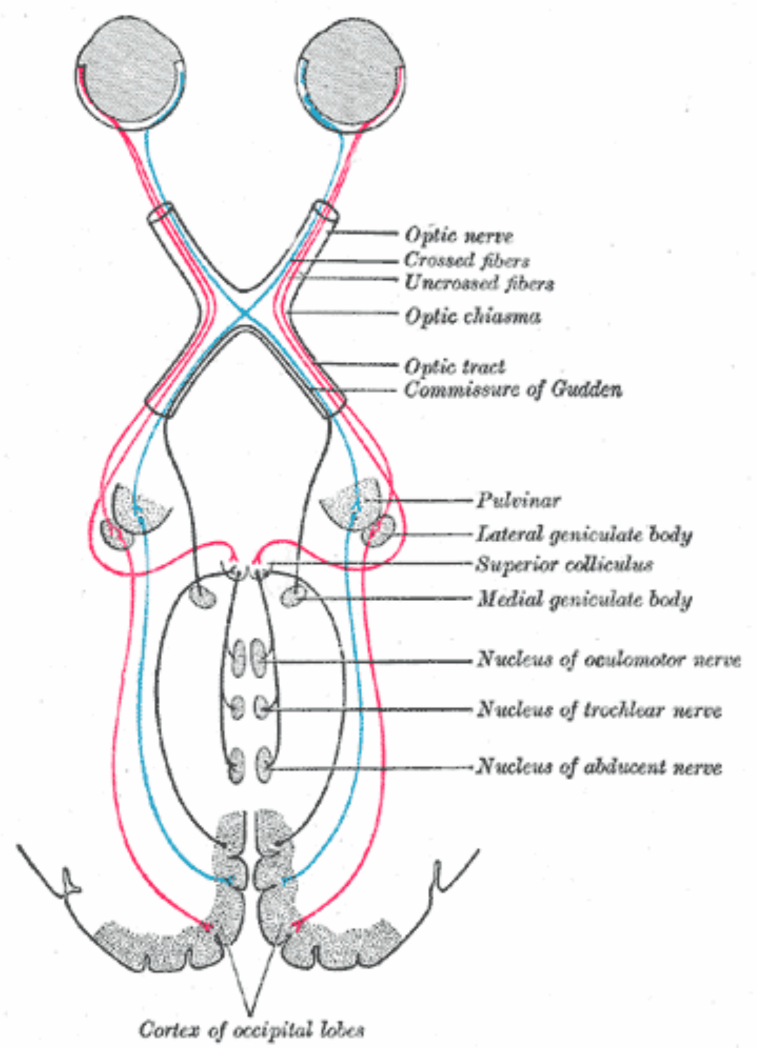

Figure 1.1: The low-level visual pathways from the retina to the primary visual cortex, via optic chiasm, pulvinar and LGN (from: Gray's Anatomy of the Human Body, 20th Edition, 1918)

2. The ventral stream: object and scene processing

Even though faces are of great importance for social interaction, they are simply put nothing but a highly similar category of objects. So a first step towards understanding face perception may be to understand object perception. Hence, in the following subchapters, the ventral ('what') stream and how it achieves its feat of object processing will be examined in more detail.

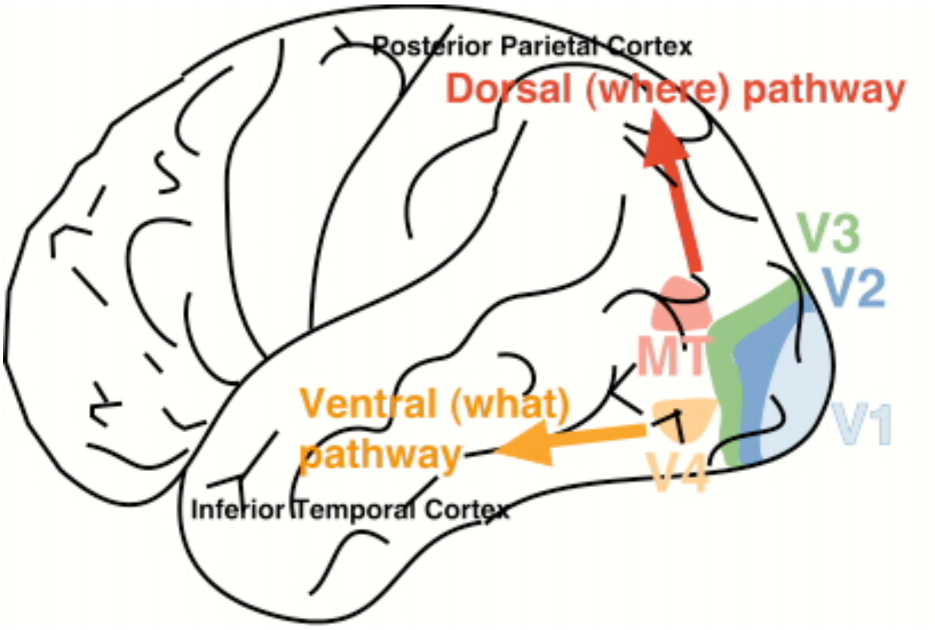

Figure 1.2: The two main cortical visual pathways. The ventral stream is involved in object processing while the dorsal stream is mainly involved in the processing of spatial location.
(from: http://www.mindcorner.org/2009/12/16/visual-system-how-do-we-see/, correct on 23.9.10)

2.1 Hierarchical coarse-to-fine organization

The canonical picture from the literature on object recognition is that ventral bottom-up processing might be organized in a coarse-to-fine or global-to-local manner (Menz & Freeman, 2004). Early psychophysical studies were able to show that longer stimulus exposure times enabled a more detailed stimulus perception and that global features take temporal precedence over local features (Navon, 1977; Reynolds, 1981). However, even though visual processing is more complex with longer exposure times, even with exposure times as short as 20 ms the visual system is able to perceive the general gist of a scene (Thorpe, Fize, & Marlot, 1996). In addition, Thorpe and colleagues (1996) posit that complex natural scenes can be classified in less than 150 ms.

This rapid visual processing of an abundance of input information, may suggest that there is a bottleneck in visual perception (and in information processing in general, see for example Marois & Ivanoff, 2005). Before the bottleneck, processing is parallel and allows for a great intake of information without loss when more information is taken in. The bottleneck is generally thought to be the attentional focus that is eventually employed by the visual system to enable more detailed processing of part of the visual field, and this attentional processing stage is capacity-limited (Broadbent & Broadbent, 1987). Any process after the bottleneck is considered high-level processing, and this includes recognition and categorization (Li, VanRullen, Koch, & Perona, 2002).

2.2 Coarse-to-fine processing has been challenged

Even though the coarse-to-fine principle is widely accepted and seems to be correct for early stages of the visual processing pipeline, there have also been numerous studies, which challenge this simple processing strategy. For example, Smallman (1995) suggested, that coarse-to-fine processing is complemented by a separate fine-to-coarse process, starting with sensitivity to edges, simple shapes and orientations and progressing to more complex and specific shapes and finally objects. The primary visual cortex V1 has been shown to contain cells with surrounding receptive fields that are selective to different stimulus orientations, movement and movement direction, (simple) shapes and edges (light-dark boundaries), and locations (Hubel & Wiesel, 1959). Furthermore they show that neighbouring cells, organized in columns, are sensitive to the same or similar stimulus orientations.

Going up the hierarchy of the ventral stream, this information is subsequently used to create more complex stimulus representations, which are then either compared with stored information from memory and recognized or stored as new memories. In the inferotemporal and parietal cortices, many neurons are selective to certain shapes or sizes (Murata, Gallese, Luppino, Kaseda, & Sakata, 2000), colours or more complex patterns, like faces, other body parts or common objects (Desimone, 1991). The use of microstimulation has established a causal relationship between these neurons and the perception of their associated object (Afraz, Kiani, & Esteky, 2006). Which features the neurons in these higher areas are sensitive to is largely if not entirely dependent on experience and visual learning (Freedman, Riesenhuber, Poggio, & Miller, 2006). It is therefore unsurprising that a large number of interconnections exist between bottom-up and top-down streams in the brain (Gilbert & Sigman, 2007).

In addition, there are several studies by Schyns and colleagues, who demonstrate that the order of this process can be changed depending on top-down influences rather than following a fixed protocol (Oliva & Schyns, 1997; Schyns & Oliva, 1994; Schyns & Oliva, 1997). To summarize these studies, they contend that spatial frequency (SF) channels, i.e. spatial filters in the visual system, which are tuned to different levels of detail in a scene, are flexibly used depending on task demands. In particular, the authors conclude that the nature of a categorization task will prompt an observer to process a specific set of information within a stimulus, the diagnostic information, which leads to a correct categorization (Schyns, Goldstone, & Thibaut, 1998; Schyns & Rodet, 1997). The concept of spatial frequencies is widely known to be an important factor in visual perception, and the visual system seems to apply filters of several different SF bands to visual input (Campbell & Robson, 1968). SFs, like temporal frequencies, measure two-dimensional periodic signals that can be obtained by a Fourier transformation of any two-dimensional visual scene. High SFs encode fine-grained information, like sharp edges, fine contours, and little details, whereas low SFs encode coarse information, like general lighting, shadows, and rough contours.

Based on the conclusion that categorization tasks lead to differential processing of diagnostic information, Gosselin and Schyns developed their reverse correlation technique *Bubbles* (Gosselin & Schyns, 2001). *Bubbles* works by randomly sampling the stimulus input space with Gaussian apertures. After the experiment, the location of each bubble can be reverse-correlated to behavioural response accuracy, yielding the information, which was required and crucial for the task, i.e. that enabled correct categorizations. However, response accuracy is only one of the possible response functions that the bubble-masked stimulus information can be regressed against. Bubbles in conjunction with classification image techniques (Schyns, Petro, & Smith, 2007) or a mutual information approach (Schyns, Thut, & Gross, 2011) can reveal sensitivity of brain activity to features of a visual scene or face. *Bubbles* is a central method used to study face perception in this thesis and will be explained in detail in the Methods section (Chapter II).

2.3 Summary

Faces are a category of visual objects. The ventral stream is concerned with object, scene and face processing. Numerous studies suggest that feature encoding progresses from very basic shapes, orientations and edges in V1 to very specialized neurons in the inferior temporal cortex, which are sensitive to specific objects like faces and other common objects. However, this simple hierarchical structure has been disputed, with other studies suggesting that the visual system applies spatial frequency filters flexibly and in response to top-down control. Faces are broadband stimuli; it is therefore possible that top-down control influences the processing of diagnostic features. This leads to the question of how top-down control is exerted on the visual system and what mechanisms it applies.

3. How Cognition and Perception Interact: Top-down Influences on the Visual System

Visual information processing takes place as soon as our eyes are open. Sometimes, certain objects are more salient for our visual system than others, depending on their stimulus properties, such as size, colour, motion or shape (Koch & Ullman, 1985). For example, one red flower in the middle of an otherwise green meadow will pop out visually (Nothdurft, 1993; Posner, 1980). Automatic visual processing that proceeds in one direction from the sensory input to higher level processing is called bottom-up processing. Whenever this bottom-up processing is altered or influenced by experience, expectation or attention from higher-level brain areas, our brain exerts what is called top-down control (Corbetta & Shulman, 2002). To use the same example, if someone asks us to find a red flower, then we will specifically look for the colour red and the shape and size of a flower and these features will become more salient, allowing a faster detection (Treisman & Gelade, 1980). Typically, bottom-up and top-down processing strategies interact to optimise our perception. We may be consciously looking for a red flower, but at the same time, the bright colour red amidst a green background will facilitate our search (Dehaene, 1989; Saenz, Buracas, & Boynton, 2003).

There are several kinds of top-down influences, such as priming or task (Wiese, Schweinberger, & Neumann, 2008), context (Bar, 2003), attention, expectation, or hypothesis testing (Gilbert & Sigman, 2007), but it is difficult to sort them into distinct categories, as they are overlapping to various degrees. For example, it is almost impossible to say whether the expectation for an object to be present in a visual scene is different from object-based attention. Hence the following subchapters will focus on two well-studied kinds of top-down control: attention and context.

3.1 Attention modulates early visual processing

3.1.1 'Units' of attention and their interactions

Visual attention can be divided into different 'units': location-based or spatial attention, object-based attention and feature-based attention (Kanwisher & Wojciulik, 2000). Evidence for all three kinds of attention has been provided by numerous studies. For example, in a spatial cueing paradigm, Downing (1988) discovered, that perceptual sensitivity (as measured by signal to noise ratio d') to luminance or differences in either orientation, form or brightness of a target was enhanced at the target location, but dropped quickly with increasing distance from the target location. These results indicate that spatial attention lead to an increase of perceptual sensitivity at the attended location. Corbetta et al. (1990) found, that, with the same display of stimulus features, selective feature-based attention to either one of the features of the same visual display (shape, colour, velocity) improved discriminative sensitivity. Furthermore, using PET (positron emission tomography), they found that different regions in the extrastriate cortex were activated depending on the attended attribute of the visual display. Feature-based attention therefore seems to influence both behavioural and physiological measures. Another study by O'Craven, Downing and Kanwisher (1999) investigated the interaction of feature-based and object-based attention. Their stimuli consisted of an overlay of faces and houses, one of them was stationary and the other one moved, while maintaining a certain degree of overlap to keep the location constant. Subjects attended to either the face, the house or the motion while their fMRI BOLD activity was recorded. When subjects attended to faces or houses, the specific object-sensitive areas became activated (the fusiform face area, FFA, or the parahippocampal place area, respectively). However, when they attended to the motion, both the motion sensitive MT/MST area and the object-sensitive areas were activated, suggesting that object-based attention is imperative for feature-based attention mechanisms to take place.

3.1.2 A neural network for spatial attention

Given the different units of attention and their influence on bottom-up processing, it stands to reason to look for evidence of their existence and interaction in the structure and functional activity of the brain. Most of the research on attention and top-down and bottom-up networks in the brain has been done using spatial manipulations of attention. Corbetta and Shulman (2002) conducted a meta-analysis on fMRI studies of attention networks and were able to differentiate two partially segregated networks that seem to be related to bottom-up and top-down attention processing. One network involving the dorsal posterior parietal and frontal cortex seems to be related to top-down mechanisms like the attentional selection of spatial stimuli and responses. The other network is lateralized mainly to the right hemisphere and includes the temporal parietal and ventral frontal cortex. This system was mostly active in response to behaviourally relevant, but unattended and unexpected stimuli, therefore indicating bottom-up processing. These results have since been backed up by more recent studies (Berman & Colby, 2009; Bisley, 2011). It is worth mentioning another recent line of research, which proposes that top-down facilitation in inferotemporal cortex originates from a fast connection through the magnocellular pathway and dorsal stream, which activate parietal and frontal regions of the attention network (Laycock, Crewther, & Crewther, 2008; Laycock & Crewther, 2008; Laycock, Crewther, & Crewther, 2007). This would imply that the magnocellular pathway and subsequent dorsal stream could be the primary driver of visual attention and processing facilitation.

3.1.3 Feature-based attention as a separate functional unit in the brain

In terms of relevance for this thesis, feature-based attention (especially facial features) is the primary focus of interest; hence the following paragraph will discuss recent evidence for feature-based attention mechanisms in the brain. As mentioned before, O’Craven et al. (1999) detected different brain responses involved in either feature- or object-based attention (also see Polk, Drake, Jonides, Smith, & Smith, 2008). However, in their study they did not differentiate attention related areas from feature or object related areas. Most studies on feature-based attention are relatively recent and quite often it has been studied in contrast to spatial attention. The reason for this is that the location of a stimulus could be considered to be just another feature, rather than a completely different mechanism (Treue & Martinez-Trujillo, 2007), implying that these two kinds of attention might rely on very similar mechanisms. Yet, there is evidence that they are two functionally independent systems. For example, several studies found that attention to different stimulus features (motion and colour) at an attended location enhanced the activity of cortical visual areas to the same feature at another unattended location (Bichot, Rossi, & Desimone, 2005; Saenz, Buracas, & Boynton, 2002; Saenz et al., 2003), whereas Stoppel et al. (2007) found the same effect for motion only, suggesting that motion might be biologically more relevant in contrast to colour. In addition, Serences and Boynton (2007) were able to show that attention to different directions of motion spread across the entire visual field, even to locations that did not contain any stimulus. Similarly, feature-based attention enhances the response of neuronal subpopulations in V1 to a certain feature, even when the unattended feature occupies the same location in the visual field as the attended feature (using orientation as feature, T. Liu, Larsson, & Carrasco, 2007).

If spatial attention and feature-based attention are functionally independent, we could expect them to be anatomically independent as well. As discussed above, the spatial attention system seems to be localized in parietal and pre-frontal areas (Hopfinger, Buonocore, & Mangun, 2000; Vandenberghe, Gitelman, Parrish, & Mesulam, 2001). Several studies suggest that feature-based attention is located in the same anatomical structures as spatial attention (Shulman et al., 1999; Weissman, Mangun, & Woldorff, 2002; Wojciulik & Kanwisher, 1999). However, despite the fact that they seem to be located in the same brain regions, these regions respond differentially depending on which function is exerted. For example, Giesbrecht et al. (2003) found, that feature-based attention is controlled by the same fronto-parietal network as spatial attention, but with different subregions being more active for spatial than non-spatial attention (when comparing location to colour cues). Egner et al. (2008) found different peaks of activation for either spatial or feature-based attention, but these effects were not significant. Instead, examining additive integration of search information, they found independent representations of spatial and feature-based search information in the intraparietal sulcus (IPS), the frontal eye fields (FEF), the inferior frontal cortex/anterior insula (IFC/AI), and the presupplementary motor area/anterior cingulate cortex (preSMA/ACC), all part of the frontoparietal network of attention. Finally, they discovered lateralized and localized effects for spatial cue information and spatially global effects for feature-based cue information in the IPS. These results provide evidence that even though spatial and feature-based attention are represented in the same anatomical regions, these representations are functionally independent mechanisms. A more recent study emphasizes the importance of the posterior parietal cortex as common hub for attention shifts, with different subpopulations of neurons being responsible for attention shifts to either features or location (Greenberg, Esterman, Wilson, Serences, & Yantis, 2010).

3.1.4 The timing of attentional top-down control

The next question one needs to ask is, at which temporal and spatial point during visual processing attentional mechanisms start modulating the bottom-up visual processing stream. There are two hypotheses concerning the timing of top-down control: the early selection view and the late selection view. As the name suggests, the early selection view (Broadbent, 1982) postulates that the bottom-up stream only provides a very basic perceptual input and that attention is imperative early along the processing timeline to allow for more detailed perceptual processing. In contrast, the late selection view (Deutsch & Deutsch, 1963) assumes that all visual information is processed to a very high level and only then a subset of the scene is selectively attended. What both views have in common is that visual processing consists of two main stages: a low-level pre-attentive stage and a high-level attentive stage. According to Stigchel et al. (2009), the pre-attentive stage allows for processing of the entire visual scene, whereas attentive processing has limited capacity and therefore can only focus on part of the visual field. Treisman and Gelade (1980) proposed in their Feature Integration Theory (FIT), that bottom-up processing results in a local salience map of the visual field, which guides attentional feature selection. However, later studies proved that this is not entirely true and that attention can enhance the salience of certain features in advance (Wolfe, Cave, & Franzel, 1989). In addition, Wolfe shows that a visual stimulus, which shares a salient feature with a visual search target, will attract more attention than other irrelevant stimuli. Reflecting on the earlier example, when someone is looking for a red flower in the grass, then the colour red will become salient and this will indeed influence how quickly we find the flower. At the same time, any other red object will also capture our attention more easily, for example, instead of to the red flower our attention might first be drawn to a red mushroom or a red butterfly (Wolfe et al., 1989). So it seems that the term ‘pre-attentive’ for this early visual processing stage might be inappropriate after all.

The timing of the influence of attention can be investigated using electrophysiological techniques, which benefit form a high temporal resolution, or single-cell recording. A recent study recording single cell activity in the monkey thalamus, was able to show a clear modulation in the LGN and the thalamic reticular nucleus (TRN) less than 50 ms after stimulus onset, caused by shifts of spatial attention (McAlonan, Cavanaugh, & Wurtz, 2008; Rees, 2009), suggesting that even the low-level visual pathway is influenced by attention. ERP components sensitive to spatial attention have first been identified by Eason et al. (1969), Groves and Eason (1969) and Van Voorhis and Hillyard (1977). Specifically they identified two early ERP components, the

P1 (70-130 ms) and the N1 (150-200 ms), which had greater amplitudes when the location of a stimulus was attended than when it was not. Even though studies recording single-cell responses in monkeys found clear evidence of early top-down modulation of firing rates in V1 (Gilbert & Sigman, 2007; Roelfsema, 2005), studies in humans suggest that the P1 and N1 components originate from higher visual areas (Heinze et al., 1994; Rossion, de Gelder, Pourtois, Guèrit, & Weiskrantz, 2000; Woldorff et al., 2002). This view is supported by Hopf and Mangun (2000), who found the same occipito-parietal P1 and parietal N1 to attended vs. unattended stimuli, suggesting they originate in extrastriate regions (also see J.-M. Hopf et al., 2000, and Schoenfeld et al., 2007). At the same time, however, while examining the effects of attention-directing cues separately, they discovered top-down spatial attention modulations from 200 - 400 ms over occipito-parietal cortex. A slightly later (300 - 500 ms) frontal attention-related ERP component was observed as well. These latter two components correspond closely to the attention network identified by fMRI studies (see above, i.e. Egner et al., 2008; Giesbrecht et al., 2003). In order to investigate the interaction and timing of attention networks further, a recent study by Zanto et al. (2010) used both fMRI, EEG source analysis and phase coherence to perform a functional connectivity analysis while manipulating feature-based attention (colour vs. motion). They discovered that attention to colour was highly dependent on prefrontal areas, while attention to motion was connected to both prefrontal and parietal areas. The only area sensitive to both colour and motion processes was the right inferior frontal junction (IFJ). This was supported by the EEG source analysis. The source analysis also suggested that attention-related modulations took place before 200 ms after stimulus onset. They also proposed that top-down modulation, especially of colour processing, between IFJ and visual cortices were induced by long-distance alpha phase coherence (also compare Grent-'t-Jong & Woldorff, 2007, for another suggestion of the mechanism and timing of top-down modulation).

Despite these findings, the question of when and how attention can modulate the bottom-up visual processing stream, how salience is determined and how bottom-up and top-down influences interact is still thoroughly debated. Comprehensive reviews about theories of attention, early and late selection, the limits of top-down attentional control and models of top-down and bottom-up interactions can be found in Stigchel et al. (2009) and Walther and Koch (2007). In fact, it has also been suggested, that when reevaluating older studies with a single parametric model, their results can be reconciled by an interaction and combination of attentional mechanisms (Boynton, 2009).

3.1.5 Summary

Attention can be divided into three functional units: spatial, object-based and feature-based attention. There is empirical evidence for all three units. Of these three, feature-based attention is of the highest relevance for this thesis, as it links directly to the processing of facial features. Using fMRI, evidence suggests that feature-based and spatial attention, even though localized in the same fronto-parietal network in the brain, are functionally separate units, operating independently from each other. The issue of the timing of top-down control has been addressed with various experimental manipulations and electrophysiological evidence suggests that top-down ERP modulations can start in extrastriate visual regions as early as 70 ms after stimulus onset, while single-cell recordings revealed top-down modulations in the LGN and V1 in monkeys before 50 ms. However, these very early attention modulations were elicited by shifts in spatial attention only, so it still stands to debate whether shifts of feature-based attention within a face would elicit the same response.

3.2 Context-based top-down modulations on visual bottom-up processing

In a natural visual scene, objects rarely occur on their own; they are usually surrounded by an environment that creates a certain context. Imagine for example an office scene. You would expect to see – among other things – a computer, a desk, a chair, pens, and papers. The knowledge of what to expect in an office scene will enable the visual system to detect and process these objects faster and more reliably than when they appear out of context and this processing advantage is due to contextual expectations (e.g. Bar & Aminoff, 2003). These expectations do not only involve semantic context (the probability of an object to be in a certain scene), but also physical relations between objects such as relative size, position in the scene, support (e.g. a table supports a computer screen) or interposition (e.g. a solid object in front of another one will cover the other object and not let it shine through). Biederman et al. (1982) examined these five classes of relations in both a target detection task and a relation violation detection task. They found that targets undergoing one or more violations had higher miss rates and longer reaction times, and this effect was at least as strong for the semantic violations as for the physical violations, suggesting that semantic expectations operated as quickly as physical ones. Similar results were obtained for the violation detection task. Numerous studies have confirmed and corroborated context effects (Auckland, Cave, & Donnelly, 2007; Brockmole, Castelhano, & Henderson, 2006; Davenport & Potter, 2004; Gordon, 2004; Palmer, 1975; Torralba, 2003; however see Hollingworth & Henderson (1998) for a discussion on response bias). It is interesting to note that missing context can be inferred by the visual system in V1 as measured with fMRI (F. W. Smith & Muckli, 2010). However, due to the low temporal resolution of fMRI, it is unclear how early these effects occur.

Another form of context-based top-down processing advantage was identified by Bar (2003). He postulates that one single object can already initiate top-down facilitation of its own recognition, by activating certain context frames. Specifically, this mechanism is initiated during bottom-up processing, when a partially processed version of the input (‘context frame’) is sent to the prefrontal cortex (PFC), where certain expectations as to the object’s identity are activated (‘initial guess’) and immediately sent back to the temporal cortex, where they are integrated with the bottom-up analysis of the ventral stream to facilitate object recognition. Bar predicts, that early activity in the prefrontal cortex will be determined by the low spatial frequency (LF) content of the image, because LF are processed faster via the magnocellular pathway and are therefore a likely candidate for the activation of ‘initial guesses’ (Gronau, Neta, & Bar, 2007; Luu et al., 2010). An even more detailed model, taking into account both local and global features of a scene, is provided by Torralba et al. (2006). In fact, their *contextual guidance model* brings context and attention together by showing that context directly influences the allocation of attention. Their model postulates two parallel processing pathways, one for global and one for local feature processing. The local feature pathway is part of bottom-up processing (saliency), while the global feature pathway is driven by context, which in turn activates top-down processes, that guide where and what the observer fixates and attends. According to Oliva and Torralba (2007), the context of a scene can efficiently be processed by the statistical summary of its elements, using either texture-based models or spatial layout models (Fei-Fei & Perona, 2005; Lazebnik, Schmid, & Ponce, 2006; Torralba, 2003; Torralba & Oliva, 2003).

3.2.1 Summary

Objects usually occur within a context and it has been found that this context can facilitate visual perception. Several models have attempted to explain this mechanism and how it interacts with attention. The research on top-down control in the visual system generally suggests that the recognition of objects and scenes is dealt with by a highly complicated system, that is not only driven by the bottom-up visual input, but also by different mechanisms of executive control, that facilitate and speed up the process. The following subchapter will close the circle and discuss face perception networks and possible bottom-up and top-down interactions.

4. Face processing: the Ins and Outs

As stated before, faces are a highly homogenous and frequent category of objects, and all healthy humans are highly skilled in perceiving subtle differences in a face's appearance. These two attributes of faces make them ideal candidates to study object perception, as they keep stimulus variance low, but subject performance high. Due to their significance in social interactions, it has been suggested that faces have a special processing status in the brain (Ellis, 1975). From infancy onwards, faces are probably among the most useful and most preferred pieces of information in our environment (Johnson, Dziurawiec, Ellis, & Morton, 1991). Evidence suggests that a cortical specialization for faces gradually emerges over childhood and is only fully developed in adults (Cohen Kadosh & Johnson, 2007). This specialization leads to a fast-acting attention bias of face processing, that can be overcome to a certain extent by top-down control, but remnants of it remain nonetheless (Bindemann, Burton, Langton, Schweinberger, & Doherty, 2007; Langton, Law, Burton, & Schweinberger, 2008). Due to this specialization, face perception has often been thought to be different from normal object perception, but this notion is highly debated (Diamond & Carey, 1986; Ellis, 1975; Farah, Wilson, Drain, & Tanaka, 1998; McKone, Kanwisher, & Duchaine, 2007; Parr, Dove, & Hopkins, 1998; Tovee, 1998). The following subchapters will summarize the most important theories and findings about face perception and how these findings relate to the subject of this thesis: to explore the impact of top-down control on early facial feature processing.

4.1 Models of Face Perception

Bruce and Young (1986) captured the then existing, but fairly random and scattered scientific knowledge about face perception in a theoretical framework. First they identified seven kinds of information 'codes' that are derived from faces: pictorial, structural, visually derived semantic, identity-specific semantic, name, expression and facial speech codes. Then they described how these different codes are generated and processed by functional units. All codes are important for face processing, but essential for every-day recognition of faces and their identity are the structural code, the visually derived semantic code and the identity-specific semantic code. Structural codes make sure that we recognise familiar faces from different visual angles and under various lighting conditions or partial occlusion. Visually derived semantic codes are attributes of a person that can be more or less easily obtained from almost any face, whether familiar or unfamiliar, such as gender, ethnic group or approximate age. In contrast, identity-specific semantic codes encode only information specific to one person and can often not be derived easily just by looking at a face, such as occupation, social circle, marital status or hobbies. Other codes, which are not essential for person recognition, are expression and facial speech codes. These codes are important for social interaction regardless of whether we know the person we interact with or not. The first stage in Bruce and Young's functional model is structural encoding (Figure 1.3). Any view-centred descriptions are encoded and passed on to expression and facial speech analysis units, as well as being input to a directed visual processing unit. View-independent descriptions (i.e. structural codes) are passed on to face recognition units (and again the directed visual processing unit), which in turn interact with person identity nodes (one for each person) and name generation. All functional units input into and interact with the cognitive system, which acts as the final hub to integrate the results of the face perception and recognition system. This cognitive-perceptual framework (Figure 1.3) has become a widely accepted norm and is supported by most studies on face recognition and perception (Calder & Young, 2005).

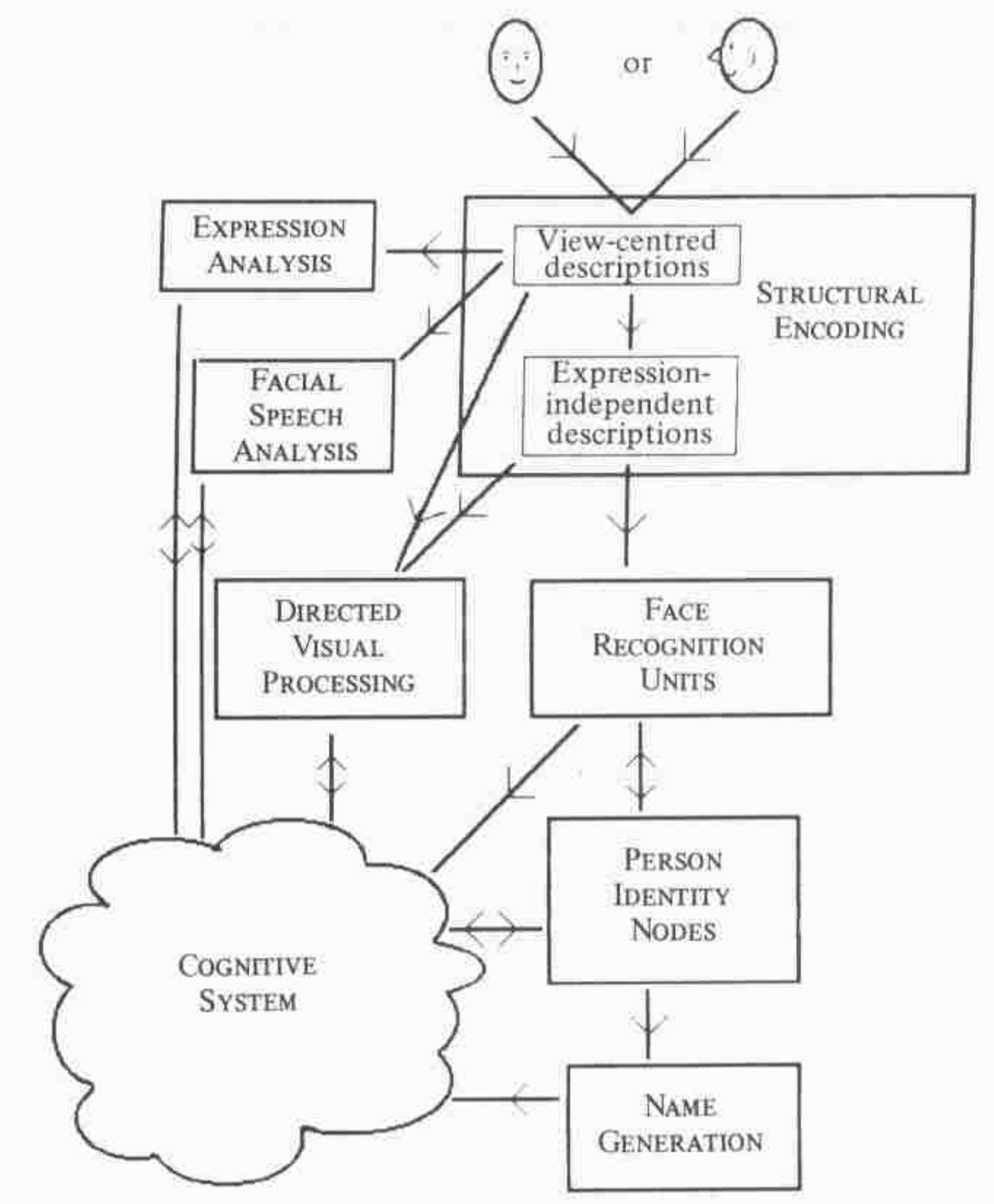

Figure 1.3: Bruce and Young's functional model of face perception (1986). The first stage is the structural encoding stage. View-centred descriptions are fed into different pathways than expression-independent descriptions. Finally, all processes feed their results into the cognitive system (figure from Bruce and Young, 1986).

A more recent model of face perception was suggested by Haxby, Hoffman and Gobbini (2000). Their model incorporates findings from functional neuroimaging and postulates a neural network for face processing, which consists of two parts, the core system and the extended system (Figure 1.4). The core system contains three bilateral brain structures, the inferior occipital gyrus/occipital face area (OFA), the fusiform gyrus/fusiform face are (FFA) and the superior temporal sulcus (STS). The authors contend, that each of these structures has a different function: the inferior occipital gyrus is responsible for the early processing of facial features, the fusiform gyrus processes invariant aspects of faces, such as identity or gender, and the superior temporal sulcus processes the changeable aspects of faces, such as facial expressions (Arsalidou, Morris, & Taylor, 2011; Haxby et al., 2000; Kanwisher, McDermott, & Chun, 1997; Sergent, Ohta, & Macdonald, 1992). All three regions interact with one other and the latter two also send and receive input to the extended system. Recent research has partly corroborated, but also questioned these claims. Pitcher et al. (2011) and Kadosh et al. (2011) gathered evidence for the OFA as an initial feature processor: it is sensitive to the mouth, the eyes and the nose and it is essential for accurate face perception (Dricot, Sorger, Schiltz, Goebel, & Rossion, 2008). Equally in congruence with the model is the finding that the OFA and FFA were sensitive to spatial relations in faces, whereas the STS was not (Rhodes, Michie, Hughes, & Byatt, 2009), implying that these stable spatial relations contribute to identity recognition. In contrast to Haxby et al.'s predictions, some studies found the FFA to be sensitive to expressions as well (Halgren, Raij, Marinkovic, Jousmaki, & Hari, 2000; Lewis et al., 2003). The STS has consistently been shown to respond to and differentiate between facial expressions (Furl, van Rijsbergen, Treves, Friston, & Dolan, 2007; Said, Moore, Engell, Todorov, & Haxby, 2010; Said, Moore, Norman, Haxby, & Todorov, 2010; Simon, Craig, Miltner, & Rainville, 2006). However, researchers from other areas have claimed the STS to be essential for their studied behaviour as well, and ample evidence confirms the notion that the STS is not only facial expression specific, but also supports different cognitive functions depending on the task-dependent network connections involved (Allison, Puce, & McCarthy, 2000; Hein & Knight, 2008).

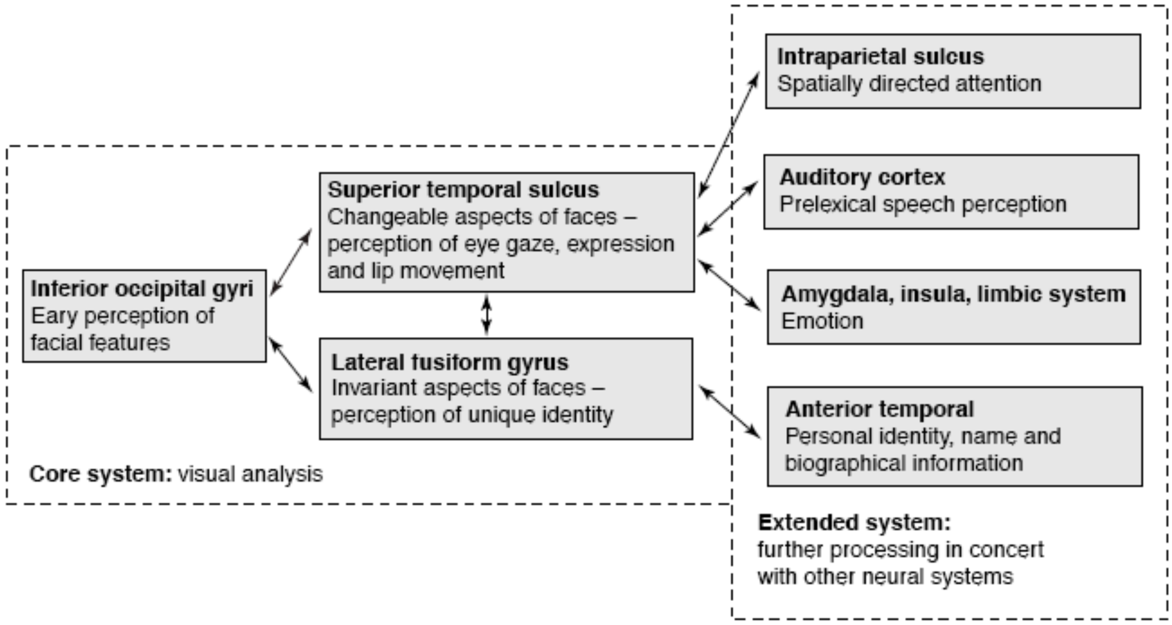

Figure 1.4: Haxby et al.'s anatomical and functional model of face perception (2000). The model assumes a core system and an extended system. The core system consists of areas in the visual ventral stream, whereas the extended system contains brain structures located in several different regions of the brain, that also belong to different functional systems (figure from Haxby et al., 2000).

The extended system of Haxby et al.'s model (2000) consists of the intraparietal sulcus (Cowan, 2011), the auditory cortex (Price, 2010), the amygdala, insula and the limbic system (Adolphs, 1999, 2002a, 2002b; Dolan & Vuilleumier, 2003), and the anterior temporal cortex (Gainotti, 2007). The amygdala in particular is thought to be involved in the emotional evaluation of faces and its numerous connections to both the core system of face processing, the primary visual cortex and prefrontal cortex areas make it a likely candidate for top-down influence on early visual processing (Palermo & Rhodes, 2007; Yamasaki, LaBar, & McCarthy, 2002).

Just like Bruce and Young's model, Haxby et al.'s model assumes a divergent processing of changeable (STS, view-centred descriptions) and invariant (FFA, structural code) aspects of faces. Specifically, this would suggest that expression and identity of a face are processed "by functionally and neurologically independent systems" (Calder & Young, 2005). However, Calder and Young (2005) review the evidence for and against independence of expression and identity processing and conclude that there is no study giving conclusive evidence for complete separation of these changeable and invariant aspects of faces. Instead, the evidence seems to support a relative segregation, with faces being processed by the same neural structures, but on different stimulus dimensions. As mechanism of encoding they suggest a PCA framework, which can extract both identity and expression as factors from a set of faces. Along the same lines, Vuilleumier and Pourtois (2007) review the evidence from EEG and fMRI studies and conclude, that emotional facial expression processing is too widely distributed in the brain to be only processed by the STS. They suggest, that the FFA is sensitive to both emotional expression and identity, refuting the notion that these two processes are entirely independent. Further details about the dynamics of face processing can be found in several comprehensive reviews (Dekowska, Kuniecki, & Jaśkowski, 2008; Gobbini & Haxby, 2007; Palermo & Rhodes, 2007; Posamentier & Abdi, 2003; Vuilleumier & Pourtois, 2007).

This thesis compares gender categorization (an invariant face dimension) with expression categorization. Although a solution to the question of differential processing streams for invariant and changeable aspects is not the primary aim of this thesis, the results will later be discussed in this theoretical context.

4.2 EEG and MEG research reveals face-preferential brain responses

In the field of face perception, one of the major research areas has focussed on studies with EEG and event-related potentials (ERPs) and MEG and event-related fields (ERFs). In contrast to fMRI, these two methods allow an analysis of brain activity on a very high temporal resolution and complement findings from fMRI studies about a face network in the temporal domain.

One particular EEG brain event is a negative ERP component which occurs ~170 ms after stimulus onset over occipito-parietal areas, the N170. The N170 is one of the earliest and probably the most prominent face preferential potential (Rousselet & Pernet, 2011) and is therefore of special interest for the study of the visual system (Bötzel, Schulze, & Stodieck, 1995). Bentin and colleagues (1996) found that the N170 amplitude for face stimuli is significantly larger compared to non-face stimuli like cars or butterflies. This finding has been reproduced in numerous studies (Eimer, 2000; Rossion, Gauthier, et al., 2000). Research on face processing with MEG has yielded similar results to EEG. Analogous to the N170, a face-preferential M170 has been identified (Kloth et al., 2006; J. Liu, Harris, & Kanwisher, 2002; J. Liu, Higuchi, Marantz, & Kanwisher, 2000; Lueschow et al., 2004; Tanskanen, Nasanen, Montez, Paallysaho, & Hari, 2005).

It should be noted, that while probably being the most researched ERP and ERF components, the N170 and M170 are neither the only nor the earliest face-sensitive modulations of surface brain activity. In fact, some studies indicate a face-specific activation difference over extrastriate visual areas as early as 100 ms after stimulus onset (J. Liu et al., 2002; Pegna, Khateb, Michel, & Landis, 2004). Other studies identified early (100 – 150 ms) activity modulations in frontal areas in response to different facial expressions, which could be connected to top-down control (Eimer & Holmes, 2002; Holmes, Winston, & Eimer, 2005; Streit et al., 2003). Bentin and Deouell (2000) identified a later fronto-central negativity, the N400, which was sensitive to familiarity of the faces. They suggested that this component was connected to the retrieval of semantic/identity information.

Measuring brain surface activity with EEG and MEG reveals a multitude of modulations in response to faces, however, in order to make inferences about involved brain regions and a face perception network, it is necessary to estimate activity sources from surface data. Evidence from MEG source localization data suggests that the M170 picks up activity in and around the FFA and/or the middle occipital gyrus (Herrmann, Ehlis, Muehlberger, & Fallgatter, 2005; Japee, Crocker, Carver, Pessoa, & Ungerleider, 2009; Schweinberger, Kaufmann, Moratti, Keil, & Burton, 2007; Taylor, Bayless, Mills,

& Pang, 2011; Taylor, Mills, Smith, & Pang, 2008). This is confirmed by some EEG source localization studies (Deffke et al., 2007; Itier, Herdman, George, Cheyne, & Taylor, 2006; Jemel, Coutya, Langer, & Roy, 2009; Pizzagalli et al., 2002; Rossion, Joyce, Cottrell, & Tarr, 2003) and one fMRI/EEG study (Corrigan et al., 2009). However, with EEG data the results are more varied. Some studies also find the STS as an activity generator of the N170 (Eryilmaz, Duru, Parlak, Ademoglu, & Demiralp, 2007; Itier & Taylor, 2004). Due to this variation in results and the different methods and tasks applied to obtain them, the question arises whether the elements of the core system might be task-dependent. A recent fMRI study confirmed this idea (Cohen Kadosh, Henson, Cohen Kadosh, Johnson, & Dick, 2010).

4.3 Top-down influences on the N170 and M170 and the core system

Cohen Kadosh et al.'s results (2010) suggest task-dependent activity in the different components of the core system. By manipulating explicit task demands, attention is directed to different aspects of visual processing, and it therefore constitutes a kind of top-down control (Gilbert & Sigman, 2007).

N170 and M170 research on task-dependent processing paints an inconsistent picture. Several studies found no top-down effects on latencies or amplitudes of the N170 or M170 peak (Carmel & Bentin, 2002; Cauquil, Edmonds, & Taylor, 2000; Furey et al., 2006; Guillaume & Tiberghien, 2001; Lueschow et al., 2004; Philiastides & Sajda, 2006; Rousselet, Gaspar, Wieczorek, & Pernet, in press; Rousselet, Husk, Bennett, & Sekuler, 2007), suggesting that there is no top-down modulation at this stage of face processing. Specifically, they argue and present supporting evidence, that the early face selective event-related potential – the N170 – which is said to be a function of structural encoding (Bentin et al., 1996), is purely a basic visual encoding process and cognitively impenetrable (Pylyshyn, 1999).

In contrast however, several other studies have found attention/task effects on the N170 or M170, by using various manipulations like stimulus discriminability (Sreenivasan, Goldstein, Lustig, Rivas, & Jha, 2009), perceptual load (Mohamed, Neumann, & Schweinberger, 2009), task demands (Okazaki, Abrahamyan, Stevens, & Ioannides, 2008; Wronka & Walentowska, 2011) and spatial attention (Crist, Wu, Karp, & Woldorff, 2008; Eimer, Holmes, & McGlone, 2003 2003; Holmes, Vuilleumier, & Eimer, 2003), casting doubts on the postulated top-down independence of faces. These findings are supported by neuroimaging studies with functional MRI, which reported activity modulations by attention in the FFA (Wojciulik, Kanwisher, & Driver, 1998), OFA and FFA (Chiu, Esterman, Han, Rosen, & Yantis, 2011) and OFA, FFA and STS (Cohen Kadosh et al., 2010). As stated earlier, visual bottom-up processing in general is under strong influence of top-down control at very early stages (Eason et al., 1969; J. M. Hopf & Mangun, 2000; McAlonan et al., 2008), so it would be surprising, if early face processing didn't show any cognitive penetrability. It is possible that these contrasting findings are caused by methodological issues. First, ERPs and ERFs are averages of brain signals, so the potentially useful single-trial variance of brain activity is likely to be neglected. Secondly, while all ERP/ERF and fMRI experiments are cleverly designed to link brain activity to a very specific cognitive process or brain region, most of them do not directly link the observed activity to the processed visual information. As mentioned before, one way to link visual information with behavioural and brain activity is *Bubbles* (Gosselin & Schyns, 2001).

4.4 How Bubbles can elucidate the processing of faces

Bubbles (Gosselin & Schyns, 2001) can be used to assess crucial and diagnostic visual information, even distinguishing between SF bands, by applying classification image techniques. Using *Bubbles*, Schyns et al. (2003) investigated further into the nature of the N170. By reverse-correlating the bubble-masks for each trial to the respective N170 single trial dipole amplitude, they found that more negative amplitudes are correlated to the eyes of a face suggesting that the N170 responds selectively to the eyes irrespective of task demands. Extending the analysis of the same data, Smith and colleagues (2004) found, that the P300, an ERP component thought to be related to "what" categorizations (Goodale & Milner, 1992), was highly correlated with features that drive categorization and was therefore sensitive to task demands. Looking at the EEG signal more closely, per electrode and time point within a trial, they could also show that occipitotemporal electrodes processed the respective contralateral eye at the time window of the N170, again irrespective of task demands. A feature-driven analysis with feature templates confirmed these results, both for first- and second order feature relations.

Smith et al. (2004) applied *Bubbles* to a facial expression categorization task for the first time. Examining the face as an expression transmitter and the brain as an expression decoder, they provided evidence that both the transmitting and the receiving ends work together to decorrelate the signal and minimize categorization errors. Categorization of facial expressions is therefore optimized by both the face as a transmitter as well as the brain as a decoder.

The question of how this decoding process works is addressed more closely in an EEG study by Schyns, Petro, & Smith (2007). Subjects performed an expression categorization task for the six basic expressions plus neutral, while their EEG was recorded. The authors showed that diagnostic facial information modulated categorization accuracy and EEG voltage, with SF bands being used flexibly depending on task demands. In addition, results showed that the N170 integrated these facial features over time, starting at the eyes around 50 ms prior to the N170 peak and, moving downwards in the face, ending with the diagnostic features for a given expression at the peak of the N170. Here, the N170 clearly distinguishes between expressions by processing expression-specific information. They reasoned that the N170 reflects a cognitive process, that is both automatic and goal-directed – automatic in that it always starts with the eyes and proceeds down the face, goal-directed (and top-down driven) in that it stops as soon as the information relevant for the correct categorization has been processed. These results have been corroborated with further analysis in Schyns et al. (2009). Again, using the same data set, van Rijsbergen and Schyns (2009) analyzed a longer time window of facial feature processing showing that after the N170, categorization specific information was trimmed down and even more task- and expression-specific. Furthermore, two studies have been published using *Bubbles* in conjunction with fMRI (F. W. Smith et al., 2008) and MEG (M. L. Smith, Fries, Gosselin, Goebel, & Schyns, 2009). Smith et al. (2008) were able to identify brain regions specifically sensitive to either the mouth or the eyes in either fearful or happy faces, identifying a widespread network of 18 feature-sensitive brain regions. Smith et al. (2009) examined feature-sensitivity in MEG sources for the eyes and the mouth in early face processing in two different categorization tasks (gender and expressiveness). Starting at 90 ms with sensitivity to isolated features, complexity of feature conjunctions increased with time and reached a maximum of information sensitivity with the M170. However, task effects in feature sensitivity were only observed at later stages (250 – 400 ms). This contradicts the results of Schyns et al. (2007) who observed a top-down influence on expression processing during the N170.

4.5 Summary

Face perception has been explained with different models, the two most influential of which both agree that early face processing can be divided into the processing of invariant and changeable features. Haxby et al.'s model (2000) identifies a neural core system in the brain, with the OFA and FFA being sensitive to invariant and the STS to changeable facial characteristics. Evidence for this is contradicting and the emergent picture tends to support a task-dependent involvement of these brain structures in face processing. Research on N170, M170 and fMRI data further corroborates the top-down influence on face processing, however, especially with highly time-resolved EEG and MEG data there is still some controversy. The reverse-correlation technique *Bubbles* has proven to be an effective method to study sensitivity to information in several different measures of brain activity (EEG, MEG, fMRI). Facial feature sensitivity correlations with EEG and MEG data have provided contradicting evidence of top-down control on feature processing during the N170 and M170.

5. Hypotheses

This thesis aims to resolve the issue of top-down influences on the N170 and M170 by asking six observers to perform two different face categorization tasks (Gender and Expression) on the same set of male and female faces, each displaying six possible expressions plus neutral. In both tasks, the stimulus set was the same, but observers were required to focus their attention to different task-relevant features of the faces, directly manipulating their feature-based attention. In Gender they would focus on features required to accurately resolve gender categorizations and in Expression they would focus on expressive features. By using the same stimulus set comparability across tasks was ensured and it was possible to attribute any information processing differences between the two tasks to top-down modulations.

I used *Bubbles* (Gosselin & Schyns, 2001) to model the information subtending behavioural decision and dynamical stimulus processing in the brain. On each trial of the experiment, *Bubbles* randomly sampled information from the input face. Across trials, I used Classification Image techniques and Mutual Information analyses with behavioural and brain measurements to estimate the facial features required for correct categorizations and their processing in the brain (using a single electrode approach with EEG and a source-based approach with MEG). Additional analyses were carried out on single-trial voxel activity using a mutual information approach (Schyns et al., 2011). If the N170 or M170 mark a divergence of feature processing that is sensitive to the behavioural task, then the N170 and M170 should integrate the diagnostic facial features of Gender, irrespective of those representing the expression of the same stimulus. Vice versa, in the Expression task I would expect an expression-specific integration of facial features that corresponds to expression-diagnostic features. Given that the original stimulus set is identical in both tasks, divergence of feature processing along the N170 and M170 time courses in either EEG sensors or MEG sources, would conclusively demonstrate a top-down, task-dependent influence on the N170 and M170 and thereby specify the timing and character of this influence.

II. Methods: Techniques and Experimental Procedures

To study face perception, I made use of two non-invasive neuroimaging techniques, EEG and MEG. This chapter will describe in detail the principles and workings of each technique. Furthermore, methodologies common to both studies presented in this thesis will be explained.

1. Electroencephalography: What is measured and how?

EEG is a non-invasive measure of electrical brain activity, recorded by placing electrodes at different locations on the scalp. The first human EEG recordings were conducted by Hans Berger between 1924 and 1931, during which time period he discovered nearly all main EEG findings regarding major cerebral diseases (including epilepsy) and EEG alterations in normal subjects during attention, sleep and narcosis (Berger, 1929; R. Jung & Berger, 1979). Since then, the technique has been much improved and standardized. The most commonly used electrodes are Ag/AgCl electrodes, because of their low resistance for DC and low frequency components. In addition, they produce very stable electrode potentials, which are fairly resistant to electrode movement artifacts (Kamp, Pfurtschneller, Edlinger, & Lopes da Silva, 2005). Whereas Berger only used two electrodes, one in the front and one in the back of the head, nowadays there is a positioning system in place that allows a comparable and standardised approach to EEG recording and analysis all over the world. The International 10-20 system (Jasper, 1958) specifies standard electrode positions in relation to fixed markers of the skull (the nasion just above the nose and the inion, a marked bony bump above the neck). It provides the basis for most commercial EEG systems, which usually contain more than the original 21 electrodes. Advanced technical possibilities provide for anything between 16 to over 300 electrodes, which are usually incorporated into electrode caps or nets. These caps/nets allow a fast, easy and standardized measurement of EEG activity for most head sizes (Niedermeyer & Lopes da Silva, 2005).

So, what is measured by the EEG exactly? In a recent review, Kirschstein and Koehling (2009) summarized old and new findings: the EEG registers neuronal activity within the brain. This activity reflects changes in the resting membrane potential relative to the extracellular space. These changes in membrane potentials are generally seen as action potentials (APs), which are the largest potential changes that occur in neurons intracellularly. However, extracellularly these potentials are much weaker and only last about 1 ms and thus are too short to sum up sufficiently to produce an EEG signal, which is registered on the scalp. The actual source of the EEG, Kirschstein and Koehling state, comes from cortical pyramidal cells, which form synapses at their dendrites. At these synapses, neuronal activity is transferred by a release of neurotransmitters. The activity is then integrated at the postsynaptic membrane and – if the depolarization reaches a certain threshold – elicits a postsynaptic potential that lasts up to several tens of milliseconds and can be recorded on the scalp. Depending on the synapse and neurotransmitter involved, this potential can be excitatory (Excitatory Postsynaptic Potential – EPSP) or inhibitory (IPSP). Due to charge carrier dynamics, a cortical EPSP from superficial gyri is usually reflected as negativity in the EEG, whereas an IPSP in superficial gyri is reflected as positivity. This is probably why the amplitude scale in graphs displaying EEG signals is often reversed, displaying excitatory potential changes upwards (Kirschstein & Koehling, 2009). However, for cortical sulci or slightly deeper sources, this pattern is usually reversed and potential amplitudes can be attenuated.

Finally, it is important to note that EEG always measures the difference between two electrodes. This means that one or more reference electrodes have to be placed at a strategic location on or close to the scalp. The reference electrodes should be in a location that is unlikely to pick up brain activity, but they should still be somewhat affected by the same general noise as the EEG electrodes, e.g. by eye blinks or other muscle artifacts or environmental noise. These electrodes can – for example – be placed on the earlobes, the tip of the nose or the mastoids (the bony structures right behind the ear; however see Van Petten & Kutas, 1988, on the disadvantages of two reference electrodes). Another method is to average the activity of all electrodes and use this signal as a reference (see Nunez & Srinivasan, 2006, for a discussion of the reference issue). The kind of reference used can have quite an effect on the EEG signal, so it is important to use the same reference for different experiments to ensure comparability. In addition, a ground electrode is placed among the recording electrodes, which is used as a reference for the amplifier. All information in this paragraph can be found in Niedermeyer & Lopes da Silva, (2005).

2. Magnetoencephalography: What is measured and how?

MEG is – like EEG – a non-invasive measure of brain activity; however, it measures the very weak magnetic field changes, which arise from neuronal activity. In analogy to EEG, MEG picks up the magnetic fields of pyramidal neurons when a postsynaptic potential is generated and behaves as a "current dipole". While EEG is mostly – but not exclusively – sensitive to currents perpendicular or radial to the scalp, MEG is sensitive to tangential currents only, as radial currents do not generate a magnetic field outside the head. Hence, MEG and EEG can be seen as complementary methods (Lopes da Silva, 2010).

Cohen (1968) pioneered in the development of MEG, but only recent advances in cooling techniques and the ability to use high-density sensor-grids have made MEG recordings useful, practicable, and affordable. MEG sensors are based on superconductors – materials that lose electrical resistance when cooled down below a critical temperature. The sensors used – Superconducting Quantum Interference Devices (SQUIDs) – are chosen for their very high sensitivity to magnetic fields (Parkkonen, 2010). The magnetic fields elicited by postsynaptic potentials are extremely weak (about a billion times smaller than the earth's static magnetic field); therefore it is important to shield the sensors from as much environmental magnetic noise as possible. The SQUIDs are kept below their critical temperature by liquid helium, which in turn means that the construction of an MEG dewar (the container which holds the sensors, the helium and eletronics) is fairly challenging in order to get the sensors as close as possible to the head of a person, but efficiently insulating the liquid helium at the same time. Because the SQUIDs are built very small to obtain greater sensitivity, their area of sensitivity is increased by flux transformers, which comprise a pick-up coil, an optional compensation coil and a signal coil, which are serially connected. The pick-up coil is closest to the brain, picks up the magnetic field and sends it to the signal coil, which then generates a magnetic field and flux to the SQUID. There are different configurations for flux transformers, like magnetometers and axial and planar gradiometers. Which of these are used depends on the kind of lead field wanted for the measurement, i.e. the sensitivity pattern to underlying sources. This, in turn, influences the way the MEG signal has to be interpreted. Similar to EEG, the first MEG measurements were done with only one channel. Following rapid improvements of the technical possibilities, nowadays, modern MEG systems have a multitude of sensors, usually ranging between 100 to 300 sensors. For an in-depth description of these and all other technical issues related to MEG measurements, see Parkkonen (2010).

As mentioned above, EEG and MEG measure complementary brain activity. They both measure synchronous postsynaptic activity of tens of thousands of neurons on a high-resolution temporal scale. However, while the quality of the electrical signal (i.e. mostly radial sources) is reduced by the conductivity of the skull, scalp, brain and other tissues and bodily fluids, the measurement of magnetic fields (tangential sources only) is significantly less distorted by these influences. It is primarily this fact that makes source localization using MEG far more accurate than EEG source localization. Hence, MEG has traditionally been designed to optimize for source localisation, whereas EEG was initially developed to allow for single electrode recordings (Hansen, Kringelbach, & Salmelin, 2010).

3. Experimental Procedures, Participants and Stimuli

In two very similar studies, I tested a total of six participants in the same experimental paradigm, three of them while recording their EEG signal and the other three while recording their MEG signal. Each participant completed two categorization tasks, Gender (2AFC) and Expression (7AFC), on the same set of FACS-coded expressive faces (six identities, three female), showing six different facial expressions (happy, surprised, fearful, disgusted, angry and sad) plus neutral (images are from the California Facial Expression database, CAFÉ, by Dailey, Cottrell, & Reilly, 2001). The tasks were always completed in the same order, with Gender preceding Expression, in order to avoid expression-specific carry-over effects into gender processing (as I expected expression processing to be more detailed and varied (also see Schyns & Oliva, 1999, for discussions). Each task consisted of 13 sessions (26 for both tasks); each session was divided into 10 blocks of 147 trials, amounting to a total of 19,110 trials per task. The total testing time for each participant and both tasks amounted to an average of three months.

Stimuli were presented using the Psychophysical Toolbox (Brainard, 1997) for MatLab (The Mathworks, Inc.), on a gray background with a vertical visual angle of 8.3 deg (this was kept constant in both studies, even though I was forced to adopt different viewing distances). On each trial, information from the presented face was decomposed into five non-overlapping spatial frequency bands (120–60, 60–30, 30–15, 15–7.5, and

7.5–3.8 cycles/face) and randomly sampled with Gaussian apertures using *Bubbles* (Figure 2.1). Each aperture (bubble) revealed six cycles per face. Bubble numbers were adapted online to maintain at least 75% correct categorizations for each combination of the seven expressions and the two genders. Observers indicated their response on labelled keyboard keys (EEG) or optically signalling button-boxes (MEG), however, expression/gender to finger mapping stayed constant for both studies. They were instructed to respond spontaneously, but in their own time, and to guess if they were unable to do the task.

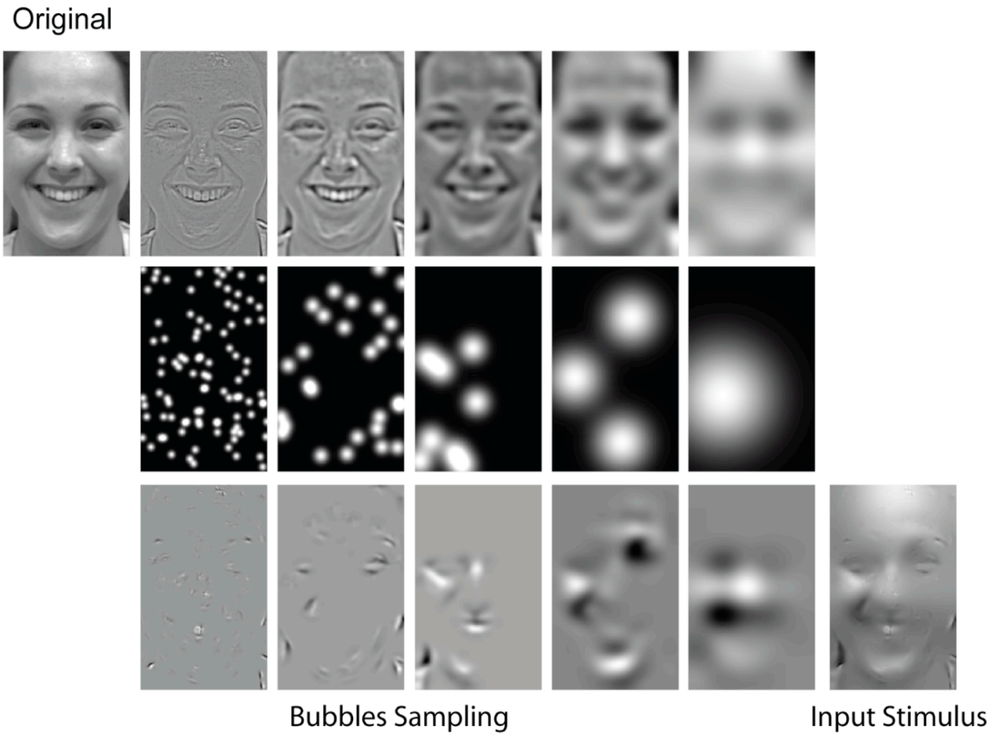

Figure 2.1: Illustration of the *Bubbles* sampling process (adapted from Schyns, Thut and Gross, 2011). First, the original face stimulus was decomposed into five non-overlapping SF bands of one octave each (top row; 120–60, 60–30, 30–15, 15–7.5, and 7.5–3.8 cycles/face). Then random bubble masks were generated for each band, containing Gaussian apertures spanning 6 cycles/face. These were combined with their corresponding SF face decomposition and the combination of all SF sampling images resulted in the final input stimulus.

In the EEG study I tested three right-handed females (observers E1, E2, E3), aged 27, 30 and 35, respectively. In the MEG study, I tested one right-handed male (aged 21) and two female participants (aged 28 and 26, left- and right -handed, respectively), who will be referred to as observers M1, M2 and M3. All participants had normal or corrected-to-normal vision and were paid a standard hourly rate of £6 as a compensation for their time. They signed a consent form, but were kept naïve with respect to the aim of the study until after the very last testing session, when they were offered a detailed explanation.

4. EEG procedures and pre-processing

In the first of the following two studies, I recorded the EEG of participants, while they performed two face categorization tasks, with 62 sintered Ag/AgCl electrodes, which were incorporated into an electrode cap (ANT, Waveguard) using linked mastoids as initial common reference and AFz as ground. The data was sampled at 1024 Hz. Data were recorded in five continuous blocks per testing session, hence pre-processing was performed separately for each recording block and saved as text files, which were subsequently read into and combined with MatLab for further analyses.

During pre-processing (using EEProbe, ANT), the data were re-referenced to an average reference, filtered with a band-pass filter from .1-30 Hz, and segmented into trial epochs of -200 to 500 ms around stimulus onset. A baseline correction was performed using the 200 ms pre-stimulus period as baseline. Because of the large number of single datasets (130 per participant), I used an automatic algorithm for the rejection of muscle and eye movement artifacts (implemented in EEProbe, ANT).

5. MEG procedures and pre-processing

In the second of the following two studies, I recorded participants' MEG signal while they performed the same two categorization tasks as in the EEG study. I used the Magnes®3600 WH system (4-D Neuroimaging, San Diego, CA, USA) with 248 magnetometers. Data was sampled at 1017 Hz and recorded in ten sepaprate blocks per testing session. Pre-processing was performed with the MatLab toolbox Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011).

The first pre-processing steps were performed on the recording block level. First, the data were segmented into epochs from -500 to 1000 ms around stimulus onset. Eye movement, muscle and jump artifacts (from SQUID jumps) were rejected using an automatic algorithm for each of the 260 single datasets for every participant. Even though manual artifact rejection is generally preferable to an automatic algorithm, manual rejection was not feasible for the large amount of data and was therefore only done for a sub-sample of data to ensure appropriate cut-off thresholds. In the next step, I denoised the data with Principal Component Analysis, using a Fieldtrip script written especially for MEG users at the CCNi (University of Glasgow). Lastly, the data were detrended to prepare for an Independent Component Analysis (ICA) to remove heartbeat artifacts. After detrending, the data were concatenated within each testing session and consequent analysis steps were carried out on the session level.

MEG is a highly sensitive technique and picks up much more than just the brain signal. Apart from artifacts like eye blinks and muscle tension, MEG (and to a lesser extent EEG) is also sensitive to blood flow in the brain, particularly its change in response to the heartbeat. Since the heartbeat is a very regular occurrence, it can be detected by performing an ICA on the electrophysiological or electromagnetic brain signal (Escudero, Hornero, Abasolo, Fernandez, & Lopez-Coronado, 2007; T.-P. Jung et al., 2001; T.-P. Jung et al., 2000; Makeig, Bell, Jung, & Sejnowski, 1996; J. E. Moran, Drake, & Tepley, 2004; Onton, Westerfield, Townsend, & Makeig, 2006). The ICA algorithm is based on the assumption that different brain signal generators are temporally independent and added in a linear fashion at each recording sensor. Hence, ICA works by disentangling or “unmixing” the brain signals of a number of sensors, each of which is only the linear combination of activity of different signal generators below the skull, into single independent signal components (Onton et al., 2006). This technique does not identify the signal generators, thus separating the problem of source identification from source localization (Makeig et al., 1996). ICA was applied to the preprocessed data per session and components relating to the heartbeat were removed from the data.

After the ICA, the analysis pipeline was split into two legs: For analysis on sensor-level (T.-P. Jung et al., 2001), the data were filtered with a lowpass filter of 35 Hz and downsampled to 256 Hz to reduce computation time. For the source analysis, the unfiltered 1017 Hz data were used.

In addition, for each MEG participant, I recorded an anatomical MRI scan and a functional face localizer. The face localizer required participants to look at grayscale faces, houses and noise in a block design and to respond with a button press to either a green or red tint of the stimulus. Both anatomical and functional data were analyzed using SPM8 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8/). The anatomical scan was used to project sources and source information sensitivity onto the brain. The functional data were analyzed, but are not reported due to the differences in stimuli and different attention and response demands between MEG and fMRI tasks.

III. How Bubbles can be used to extract information diagnosticity and sensitivity in the brain: basic analyses

1. Bubbles and Classification Images: Reverse Correlation

Bubbles was developed by Gosselin & Schyns (2001) with the aim to isolate visual features within the stimulus, which enable an observer to make a correct categorization (diagnostic information). It is a general technique that can be applied to any kind of visual stimuli (e.g. scenes, objects or faces). In addition, *Bubbles'* usage has since expanded from its original use of detecting diagnostic information to detecting information sensitivity of different kinds of brain measurements – like the BOLD signal (fMRI) and EEG or MEG data – and reaction time (Schyns et al., 2007; Schyns et al., 2009; F. W. Smith et al., 2008; M. L. Smith, Cottrell, Gosselin, & Schyns, 2005; M. L. Smith et al., 2004; van Rijsbergen & Schyns, 2009).

Bubbles works by randomly sampling the visual input space with Gaussian apertures. In this study, I added a spatial frequency dimension to the image dimensions to increase our control of the visual input space. The randomly visible information in the bubble mask of each trial was then reversely correlated with a measure of interest (e.g. performance accuracy, EEG single trial activity), resulting in a Classification Image (CI) (Murray, 2011). The CI shows the information, which modulated this measure in a specific way. For example, Gosselin and Schyns (2001) related the locations of the bubbles within the masks to performance accuracy during a categorization task, so that the resulting CI would show information that was diagnostic for making a correct categorization decision. In the following paragraphs I will describe in detail how these CIs are obtained and how they are interpreted in connection with accuracy, EEG and MEG signals.

2. Behavioural CIs as Indicators of Diagnostic Information

Behavioural CIs, as originally described by Gosselin and Schyns (2001), are computed using categorization accuracy by adding all bubble masks from correct trials (CorrectPlane) and dividing them by the sum of all bubble masks (TotalPlane) to obtain a ProportionPlane (Figure 3.1). In both studies reported in this thesis and for each observer, I computed such behavioural accuracy CIs for both categorization tasks, one CI for Gender (as it is a binary task) and seven CIs for each expression in the Expression task. The information revealed in any CI is diagnostic for the performed categorization, i.e. it is the information needed to perform a correct categorization (for example, the smiling mouth in “happy” or the wide open eyes in “fearful”). Behaviourally significant diagnostic facial features for both EEG and MEG experiments can be seen in Figure 3.2 ($p < .05$), multiplied with a spatial filter for each SF band and with an original stimulus face (compare Figure 3.4). It is obvious that the diagnostic features in both experiments corresponded closely to their counterparts in the other experiment (i.e. the smiling mouth was diagnostic for “happy” and the corners of the nose were diagnostic for “disgusted” in both EEG and MEG experiments), indicating – as assumed – that categorization behaviour was independent from brain imaging technique. Furthermore, diagnostic gender information always encompassed one or two eyes and the mouth, whereas the different expressions showed very specific and detailed diagnostic information: the smiling mouth in “happy”, the round mouth, open eyes and lifted eyebrows in “surprised”, the wide-open eyes and lightly opened mouth in “fearful”, the corners of the nose and lifted upper lip in “disgusted”, the frowning forehead and eyebrows and blown-up corners of the nose in “angry”, and the drawn eyebrows and corners of the mouth in “sad”.

In addition, behavioural CIs for each expression could also be computed for the Gender task. If expression diagnostic information also enabled correct gender categorizations, then I would see a similar pattern of diagnostic information as in the Expression task. Figure 3.3 shows the expression CIs for the Gender task for the three EEG participants. Even though I could occasionally detect parallels between diagnostic expression information (Figure 3.2, top) and expression information used to judge gender (Figure 3.3), this pattern is highly irregular and not consistent across participants. Note in Figure 3.3 for example, that the eyes in “fearful” were diagnostic for Gender for participants E1 and E2, but not for E3, whereas the reversed pattern can be seen in “happy” and “surprised” with the mouth (there was considerably less gender diagnostic mouth information in these expressions for E1 and E2, as compared to the expression diagnostic information). This noisy pattern of information use might well be caused by the different amount of information use in Gender, where participants generally require less bubbles (i.e. visible facial information) to correctly perform the gender categorizations, as compared to the number of bubbles they need for correct expression categorizations. Note that the differential use of bubbles and the number of bubbles used across tasks is a task-effect in itself (however see Appendix A). Another explanation for this effect could be that different participants found different expression information useful in order to perform the gender categorizations. Whatever the reason, this analysis demonstrates that the two categorization tasks evoked categorization-specific use of information on a behavioural level. These behavioural task effects suggest that the brain might apply task-dependent processing strategies during the face-selective N170 potential, which can be extracted using the same reverse-correlation technique with the amplitude of brain signals.

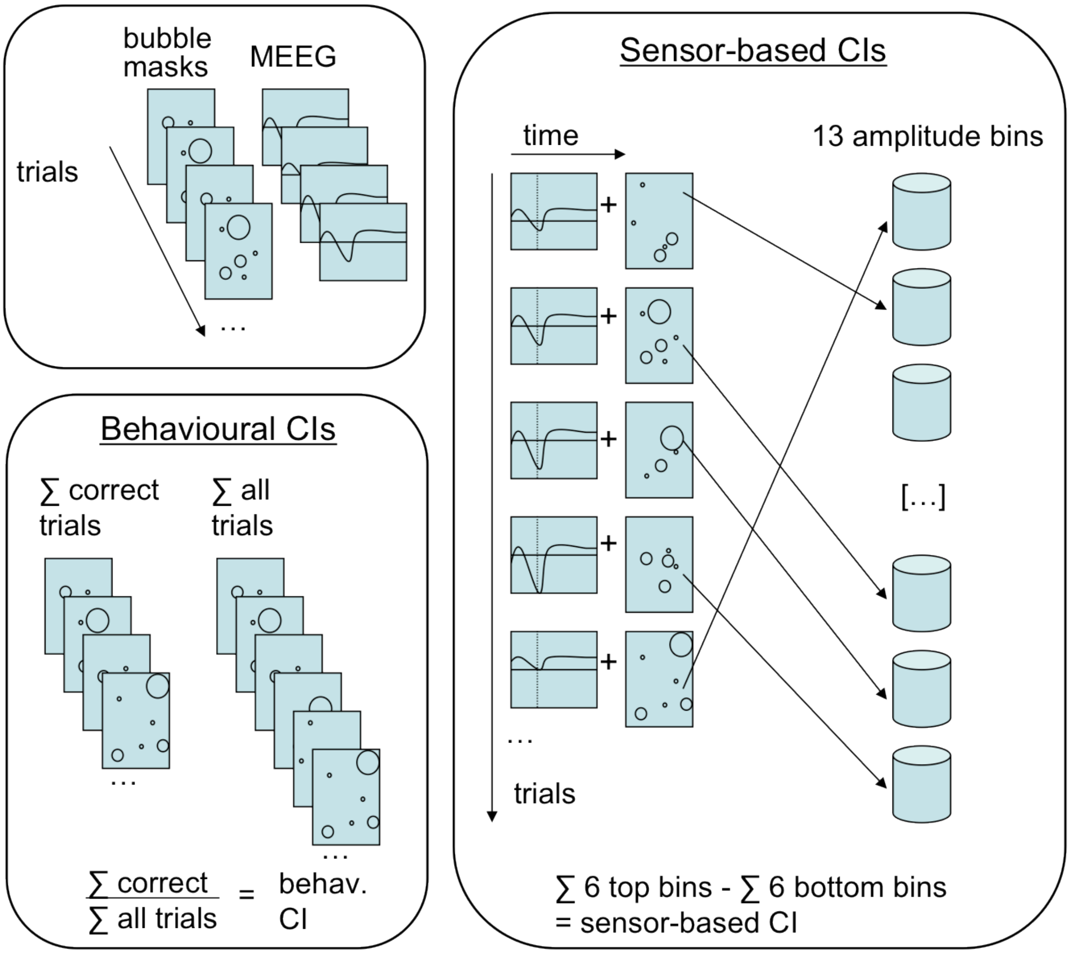

Figure 3.1: Computation of Classification Images. Top left panel: On each trial, the original stimulus face is overlaid with a randomly generated bubble mask. At the same time, the EEG or MEG is recorded, as well as the observer's response (correct/incorrect). For each expression/gender, all bubble masks of correct trials are added and divided by the sum of all bubble masks. This ratio yields the behavioural CI (bottom left panel). Right panel: For each condition and time point along the EEG, the signal amplitude is z-scored and divided into 13 amplitude bins. The bubble masks for the corresponding trials are sorted into these bins. The sum of the bottom six bins is subtracted from the sum of the top six bins. This difference makes up a sensor-based CI.

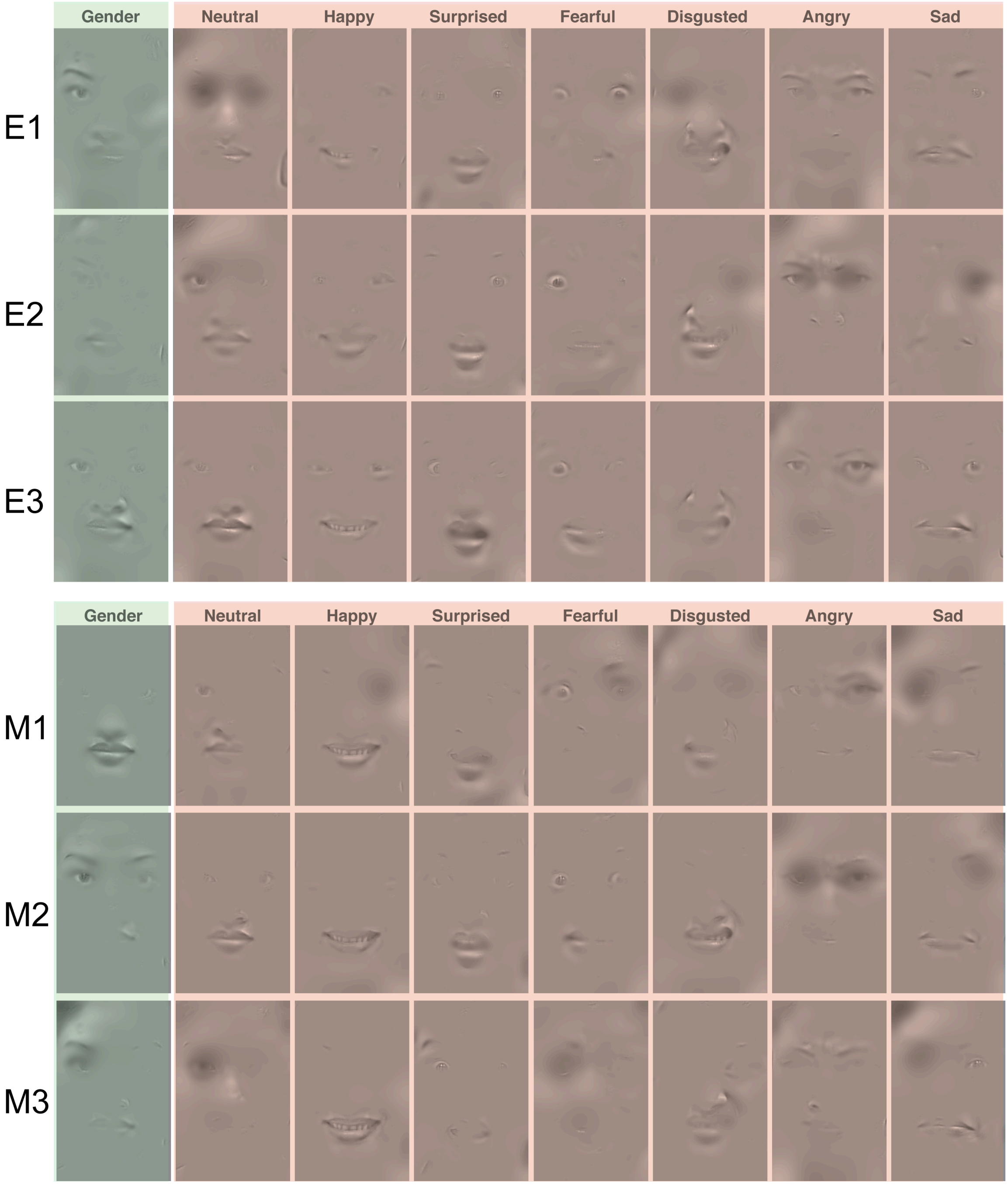

Figure 3.2: Behavioural CIs (effective images) for all six observers showing diagnostic information for each correct categorization decision. EEG observers are in the top panel, MEG observers at the bottom. Both eyes and the mouth are usually diagnostic for gender categorizations (green), whereas expression categorizations (red) require specific diagnostic sets of information, such as the smiling mouth in "happy" and the corners of the nose in "disgusted".

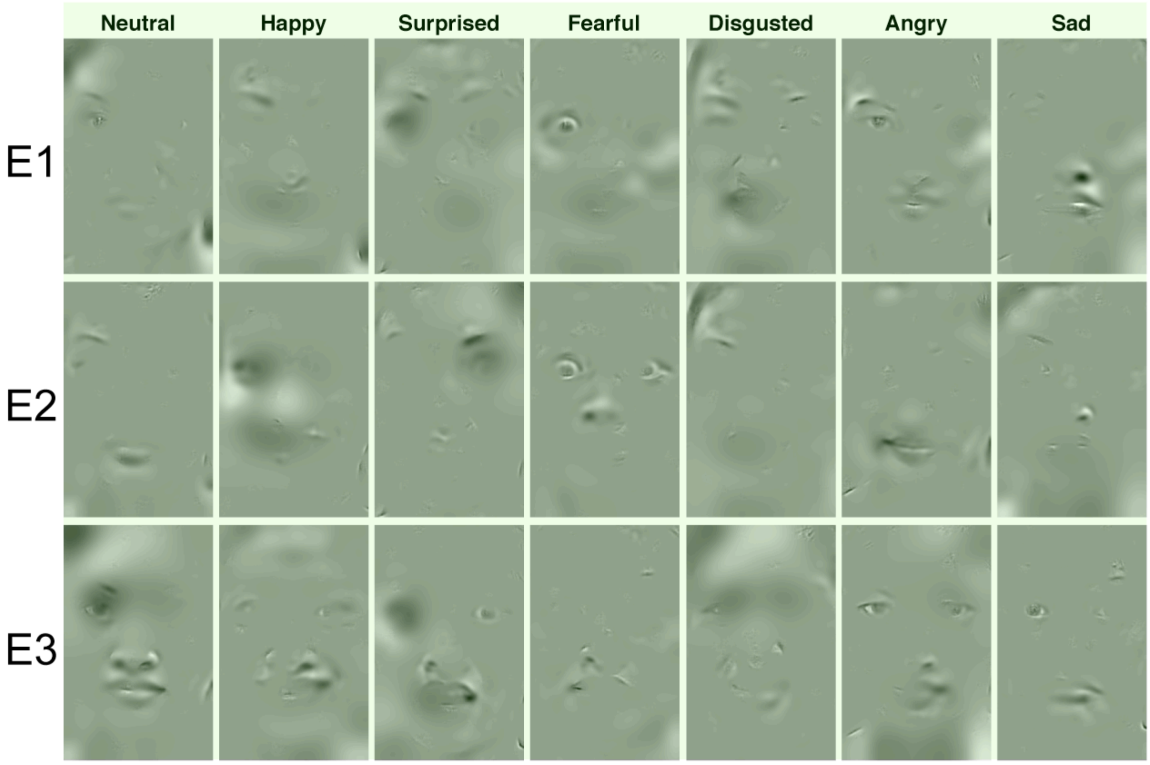

Figure 3.3: Behavioural CIs (effective images) for the EEG observers in the Gender task for each expression. In contrast to the same CIs for the Expression task, diagnostic information is much more varied across participants and doesn't necessarily correspond to the same information as in the Expression task (see text for possible explanations).

3. Sensor-based Classification Images: EEG

In order to correlate the single-trial EEG signal amplitudes to the observed visual information of each trial, I followed a well-established procedure (Schyns et al., 2003; Schyns et al., 2007; Schyns et al., 2009; M. L. Smith et al., 2004; M. L. Smith, Gosselin, & Schyns, 2006). First, for every time point along the N170 time window (starting 50 ms before and ending 25 ms after the average peak), I determined the mean and standard deviation of the amplitude distribution in the EEG signal. I then used this information to z-score and sort each trial into 13 amplitude bins, each comprising .5 SD and covering -2.75 to 2.75 SD around the amplitude mean. Next, I added all six bins below and above the middle bin and subtracted the bottom from the top bins, hence excluding the middle bin from further analysis (Figure 3.1, right panel). This procedure was repeated for every time point and every expression condition, so that I was able to obtain a time course of CIs, representing information the EEG signal was sensitive to, for each expression over the N170. I then z-scored and applied a threshold to each image ($p < .05$), extracting only information that was significantly correlated with the modulation of the EEG signal. These binary masks of significant information (for each SF band) were multiplied with a spatial filter (per SF band) and the original stimulus, resulting in so-called effective images. Effective images were only used for display purposes, whereas the raw, z-scored CIs were used for all further analyses. An example of this process and sensor-based CIs computed in this way can be found in Figure 3.4. Sensor-based CIs for the MEG data were computed in a very similar fashion, but are not reported here, as the final MEG analyses were done almost exclusively on the source level.

The CIs in Figure 3.4 are representative of all other EEG subjects and expressions and in this chapter their main purpose is to demonstrate different computation stages of CIs. However, they are also more or less representative of some general observations I made in relation to my hypotheses. The information integrated along the N170 for both tasks was very similar, yet there are some fine distinctions between tasks. When looking at the effective images, it becomes obvious that for “happy” in this example the mouth was the first feature integrated in the Expression task, whereas the eyes were integrated first in the Gender task (marked with a dotted circle for Gender and a dashed circle for Expression). Next followed a period of very similar information processing spanning the whole face. Yet, in the raw CIs (top panel), it can be seen that the focus of information processing was in the mouth in Expression, and in the eyes and the mouth in Gender. These observations led me to assume that there might be a difference in information processing along the N170 time window caused by the difference in categorization demands. However, these observations were merely descriptive and highlighted the need for further analyses.

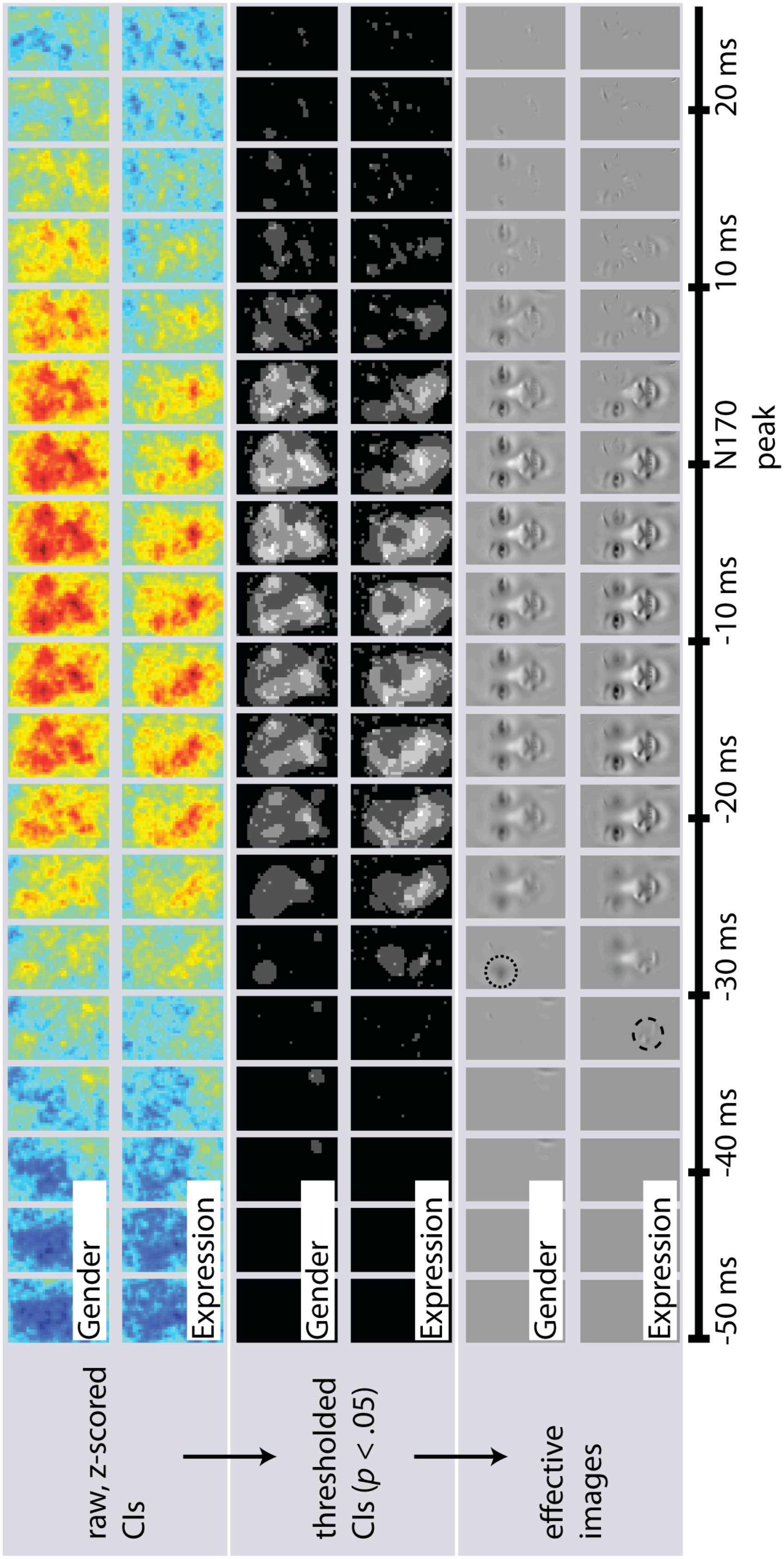

Figure 3.4: Illustration of different analysis stages of sensor-based CIs for “happy” (observer E3). All images are aligned to the average N170 peak and have a time resolution of 4 ms. The raw CIs (top) are z-scored across the entire time interval and can thus be thresholded to obtain significant pixels per SF (middle). The thresholded CIs are then multiplied with a spatial filter per SF and with the original stimulus face. These last CIs (bottom) are called effective images, as

they allow a better assessment of which features were integrated at a particular time point. However, their disadvantage is that the strength of sensitivity to each pixel is not represented. What can be seen in the effective images is that the mouth was integrated first in Expression (dashed circle), whereas the eyes were integrated first in Gender (dotted circle). However, they do not reveal that the subsequent focus of sensitivity stayed in the mouth in Expression and in the eyes and the mouth in Gender. This can be seen in the raw CIs (top) instead.

4. Summary and Conclusions

The diagnostic information in the behavioural CIs for both EEG and MEG experiments revealed a clear task-dependent information usage strategy. This was expected and replicates findings from previous studies (Schyns et al., 2007; M. L. Smith et al., 2005). For the sensor-based CIs, a similar pattern might have been present, but it was not immediately obvious. Visual inspection suggested a possible task-dependent visual processing strategy for each categorization task, but further analysis was required to corroborate this hypothesis.

IV. Evidence from EEG sensor-based classification images: How task demands influence information integration during the N170

The analyses detailed below were carried out separately for each observer (E1, E2, E3), task and expression. For each expression, I computed average ERPs to understand how the categorization task influenced the typical markers of the N170: its amplitude and latency. As is typical of ERP research, I computed ERPs bilaterally for all occipitotemporal electrodes, and then picked the electrode with the highest N170 amplitude for subsequent analyses (Picton et al., 2000; Sreenivasan et al., 2009). Also, see Appendix B for further EEG analyses.

1. ERP analyses reveal wider dispersion of N170 peaks and amplitudes in Expression

For all three observers and categorizations, electrode P8 had the highest N170 amplitude (see Figure 4.1). Visual inspection of the ERPs suggested wider dispersion of both peak amplitudes and latencies in Expression than in Gender. I used the robust MAD (median absolute deviation) to compare the dispersion between tasks for each observer. I obtained 95% confidence intervals for the MAD difference between tasks using the following single-trial percentile bootstrap technique: (1) First, I randomly sampled with replacement from the complete set of original trials across tasks, creating artificial expression conditions and tasks. (2) Then I averaged the EEG traces of each artificial expression condition and computed the MAD for each artificial task as a measure of dispersion between expressions for both the N170 peak latencies and amplitudes. (3)

Next I saved the MAD difference (Expression-Gender) and repeated the previous steps 999 times, resulting in a distribution of 1000 MAD differences based on chance. (4) Finally, I computed the 95% confidence interval for the bootstrap MAD differences. If the observed MAD difference of the original data was above the upper boundary of this CI, this difference was significantly larger than chance, indicating that the dispersion in Expression was larger than in Gender.

Both amplitudes and latencies for each observer varied significantly more in the Expression task (Table 4.1). *P* is the probability to obtain by chance an effect larger than the one observed. Wider dispersion of N170 peak latencies and amplitudes indicates that the categorization task influenced this early brain event, given that input stimuli were the same face set in both tasks. See Appendix A for evidence which rules out task difficulty as a confounding variable on these effects.

Peak amplitudes and latencies are brain correlates. As such, they do not provide direct evidence of a differential processing of facial information from the same faces. To directly address this, I turned to *Bubbles*. Specially, I sought to understand how the two categorization tasks differed in terms of (a) the information required from the face to produce correct categorization behavior and (b) how the EEG differentially processed this diagnostic information along the N170 time course.

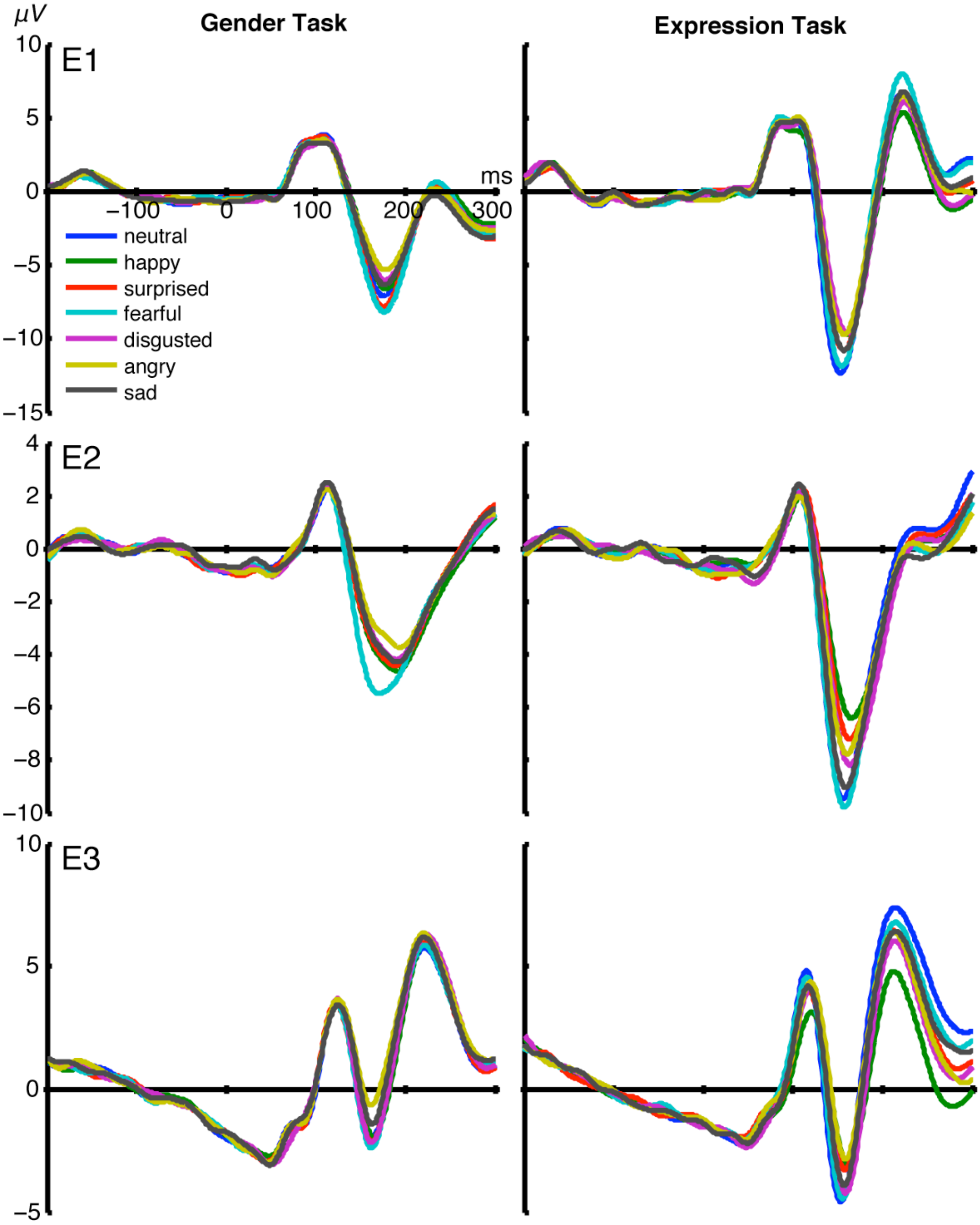

Figure 4.1: ERPs on P8 for all three observers (rows, E1, E2, E3) and both categorization tasks (columns). There was a clear N170 potential for all tasks and observers, however there were big modulations on both amplitudes and latencies for the different expressions. Specifically, N170 peak amplitudes and latencies appeared to have wider dispersion in the Expression task than in the Gender task. This effect was significant (see Table 4.1).

	ERP peak	MAD Δ Expression-Gender	95% Confid. Interval	*p* - value
Observer E1	amplitude	.491	[-.110 .219]	.000
	latency	2.000	[-1.000 1.000]	.000
Observer E2	amplitude	.858	[-.131 .156]	.000
	latency	1.000	[-1.000 1.000]	.014
Observer E3	amplitude	.395	[-.125 .128]	.000
	latency	1.000	[-1.000 1.000]	.000

Table 4.1: MAD differences between Expression and Gender tasks per observer, including 95% bootstrap confidence intervals and *p* values. *P* values revealed, that all MAD differences were significant, indicating wider dispersion of peak amplitudes and latencies in the Expression task.

2. Classification Images as measure of diagnostic and integrated information

The computation of behavioural and sensor-based EEG CIs has already been described in Chapter III. As a quick reminder, behaviourally, observers tended to use both the mouth and one or both eyes to classify gender, whereas they used expression-specific diagnostic information to categorize expressions, indicating a clear task effect for behavioural, diagnostic information usage (see Figure 3.2, Chapter III).

To understand the dynamic integration of facial information over the N170 time course I computed sensor-based EEG classification images for each expression, starting 50 ms prior to the N170 peak and ending 25 ms after the peak. Figure 4.2 illustrates EEG CIs (effective images) for the expressions “happy” and “fearful” for observer E3 in both Gender and Expression categorization tasks (aligned to the ERP peak of “happy”; peak images are surrounded by a black box). In both tasks, I found that feature sensitivity generally started in the eyes about 50 ms prior to the ERP peak (see black curves) and then moved down on the face to focus onto specific features around the N170 peaks (as in Schyns et al., 2007; also see the scan path analysis in Appendix B, 2.). Hence, the time window of interest to examine influences on feature processing started approximately 50 ms preceding the N170 peak. The greater dispersion of N170 latencies in Expression over Gender could have been driven by differential processing of features. To further examine this differentiated processing, I focused on the spatial frequency bands where such differences could be observed (i.e. SF bands 1 to 4, rejecting the lowest SF band 5, 7.5–3.8 cycles/face).[1]

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[1] The information content of the individual SF bands was determined by computing the CIs separately for each band and inspecting them visually. The lowest SF band consisted of “blobs” as big as the faces themselves, and thus was not feature specific and diagnostic at all. The “blobs” of the 4th SF band covered approximately half the face and were indicative for diagnostic information being either in the upper, middle or lower region of the face, and hence it was included in the analyses.

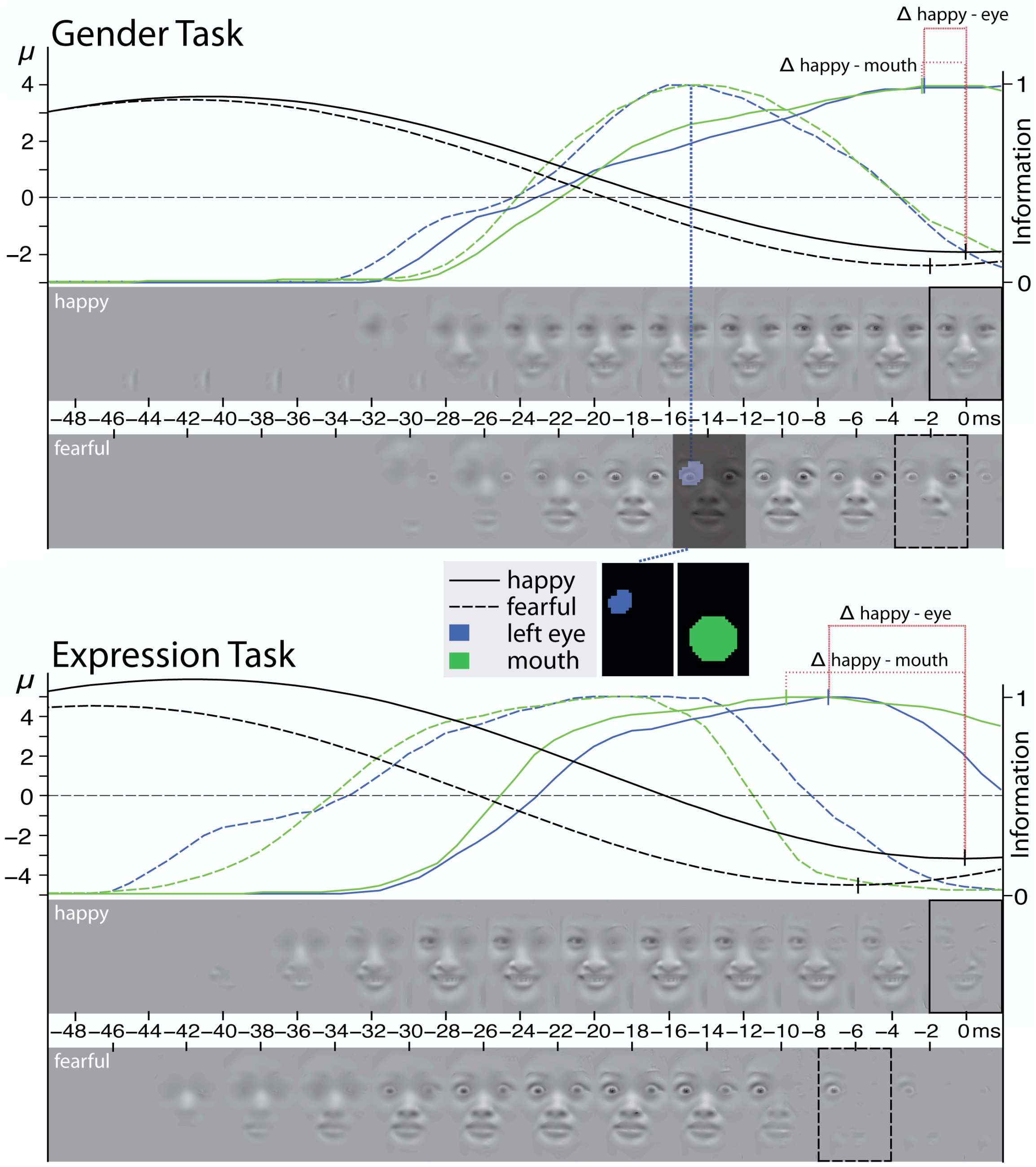


Figure 4.2: Information Integration Dynamics over the N170 for observer E3 in Gender and Expression for happy and fearful faces on occipito-temporal electrode P8. The gray-scale Classification Images depict - every 4 ms - the information within a stimulus face that elicited significantly more negative amplitudes in the EEG signal than other information at a given time point over the N170 (the CIs were thresholded and multiplied with the stimulus face after applying a spatial filter for each SF band). The black boxes depict the CIs at the time of the N170 peak. In order to relate the integrated information directly to the ERP (black curves), I derived a measure of information sensitivity directly from the CIs (coloured curves). To this effect, I intersected the CIs at each time point with two feature templates (see centre of figure) for the contralateral eye (blue) and the mouth area (green). By adding all significant pixels within the intersected area, I obtained the blue and green information curves. I then regressed the peaks of information with the peaks of the ERP, including all expressions, separately for each

categorization task and observer. I found significant correlations between the time the two features were integrated and the time the N170 peaked for the Expression categorization task only (see Table 4.2).

3. The Backus-Gilbert-Spread as measure of feature integration similarity

My hypothesis is that processing of features is more differentiated in Expression than Gender due to the requirement of integrating expression-specific features (e.g. the wide-opened eyes in “fear,” the corners of the nose in “disgust” or the wide-open mouth in “happy”). Computationally, a simple test of differentiation between expressions is to Pearson correlate, for each expression considered (e.g. “happy”), the classification images reflecting the EEG sensitivity with the corresponding classification images of all other expressions within one categorization task (e.g. “happy” with “sad”, “happy” with “angry”, “happy” with “disgusted etc.). To derive a single measure per subject for all expressions, I used an adapted version of the Backus-Gilbert Spread (BGS; Backus & Gilbert, 1967; adapted in Schyns et al., 2009). Specifically, every 4 ms of the N170, I cross-correlated the unthresholded (z-scored) classification images across expressions to produce a symmetric cross-correlation matrix. The BGS measures the distance of this cross-correlation matrix X to an identity matrix I (which represents a perfect decorrelation between expressions) (1).

$$1-\left[\sum_{i,j}(\mathbf{X}-\mathbf{I})^2/\sum_{i,j}(\mathbf{1}-\mathbf{I})^2\right] \quad (1)$$

BGS values will therefore range from 0 (perfect correlation) to 1 (perfect decorrelation) and I would expect higher decorrelation of the BGS when observers categorize expressions compared to when they categorize gender, due to the integration of specific expressive features in the former. Figure 4.3 plots the BGS along the N170 time course for the two categorization tasks and each observer (colour-coded for subjects). It is important to note that I aligned all time courses relative to the N170 peak of each expression prior to computing the BGS, to compare the critical feature integration preceding each peak. At first glance, the resulting curves seem to confirm the predicted higher decorrelations of the EEG classification images in the Expression task (red curves), compared with the Gender task (green curves). To test for significance, like in the ERP analysis, I computed data-driven 95% confidence intervals for each observer. (1) First I created a pool from all trials of both tasks and all expressions. (2) Then, in each bootstrap iteration, I randomly picked a sample of trials with replacement from the whole pool of trials for each expression and task using the sample size of the original sample of trials. (3) In the next step, I computed the EEG CIs for the random samples and calculated the BGS difference. This procedure was repeated 599 times, resulting in a BGS difference distribution for each time point along the N170 time window, which was used to determine the 95% confidence interval of the observed BGS difference (using the correction validated by Wilcox, 2005). The confidence interval (black dashed curves) and the observed difference (solid black) are plotted in Figure 4.3 below the BGS curves. Surprisingly, the confidence intervals for the null-hypothesis do not always contain 0. This indicates that there is a bias in the data, which might drive a BGS difference between the two tasks. The BGS is a very noise sensitive measure and because raw (and z-scored) CIs are noisier with decreasing trial numbers, it is possible that differences in trial numbers caused this bias in the observed and bootstrap data. When equating trial numbers on both the observed data and the random bootstrap samples, it is obvious that there is no effect of task on the similarity of feature integration at the critical time period before the N170 peak (Figure 4.3, b.). This came somewhat as a surprise, especially since visual inspection of the CIs suggested a difference in feature processing. A reason for this null-effect could be that features for gender and expressions are quite often overlapping, especially in expressions, which have eyes and mouth as diagnostic information (such as neutral, fearful, sad, and sometimes surprised and happy).

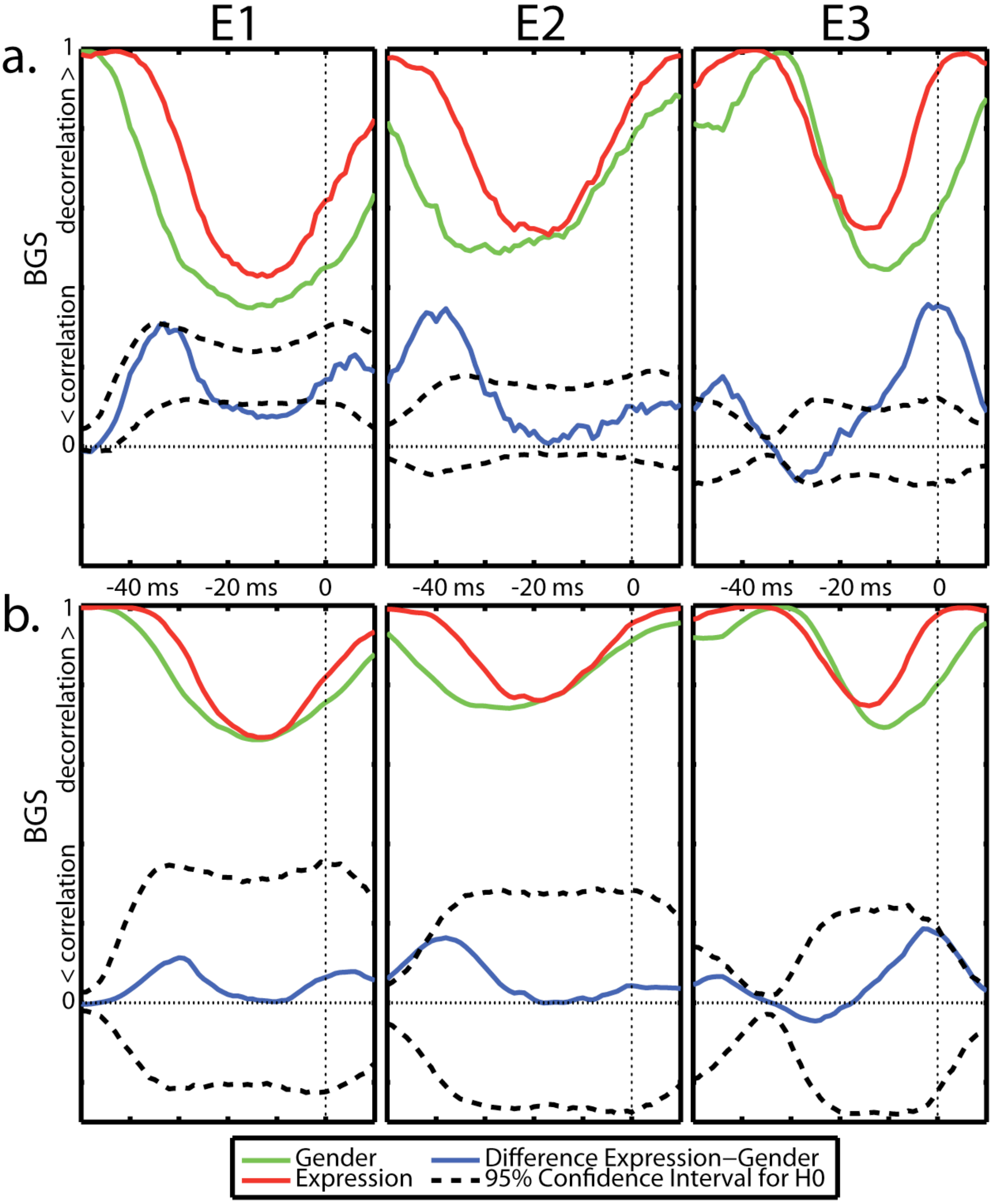


Figure 4.3: The Backus-Gilbert-Spread for all three observers (from left to right: E1, E2, E3), aligned to the N170 peak (at 0 ms). The green lines represent the Gender task, the red ones the Expression task, the blue ones the difference between the two tasks. The dashed lines denote the 95% confidence interval. a. The BGS of the real data. The confidence interval for the H0 does not contain 0, this suggests a bias in the data. b. When the same trial numbers are used for both tasks the confidence interval for the H0 is correct. The BGS and its difference in b. are an average bootstrap of the effect with equal trial numbers. See text for further discussion.

4. Intersection of CIs with diagnostic features reveals the integration of both expression and gender features during the N170 irrespective of categorization task

The BGS analysis revealed a rather similar processing of features between Gender and Expression during the N170. In the next step I therefore attempted to extract evidence for the integration of both expression and gender diagnostic features in both tasks. To this end, I examined the overlap of integrated facial information of both tasks. In order to determine significant facial features from the EEG CIs I first thresholded each EEG CI by using a z-score cut-off corresponding to $p < .05$. This was first done separately for each SF band, but then the images were flattened, setting all pixels that were significant in any band to 1 and all other pixels to 0, creating binary EEG information masks (see Figure 3.4, middle panel). The same procedure was applied to the behavioural CIs of each task, resulting in binary behavioural information masks. In the next step, I determined the overlap of integrated facial information in the EEG CIs by simply intersecting, time point by time point, the binary EEG information masks of both tasks. Next, I again intersected these images with the behavioural information masks for each expression and gender categorization. Adding all remaining significant pixels within the ensuing information images, resulted in two curves for each observer and expression, one revealing the amount of facial information that was jointly integrated in both tasks and diagnostic for the underlying expression and the other one revealing the joint information, which was diagnostic for gender categorizations in both tasks. Figure 4.4 displays the integrated facial information at the maxima of these information curves, showing that both gender and expression information were integrated in both tasks. As a result of the intersections, gender information was usually represented by the mouth and the left eye, whereas expression information was expression specific, just like the behavioural diagnostic information. This is especially obvious in “disgusted”, where the behaviourally diagnostic features (Figure 3.2) had only little overlap for either gender or expression categorizations. If feature processing was different and not overlapping for each task, there would be no or only little residual information left when intersecting the EEG information masks of both tasks. However, since Figure 4.4 clearly displays that both gender and expression diagnostic information were integrated in both tasks, it is likely that feature processing itself was not top-down modulated by the demands of each categorization task.

In this analysis step, I only regarded the overlap of features in both tasks, I did not take into account whether the integrated information in each task influenced the variability of the N170 peak. If both sets of information were processed in both tasks, then the question arises, why I found a task-dependent modulation of the ERP peaks.

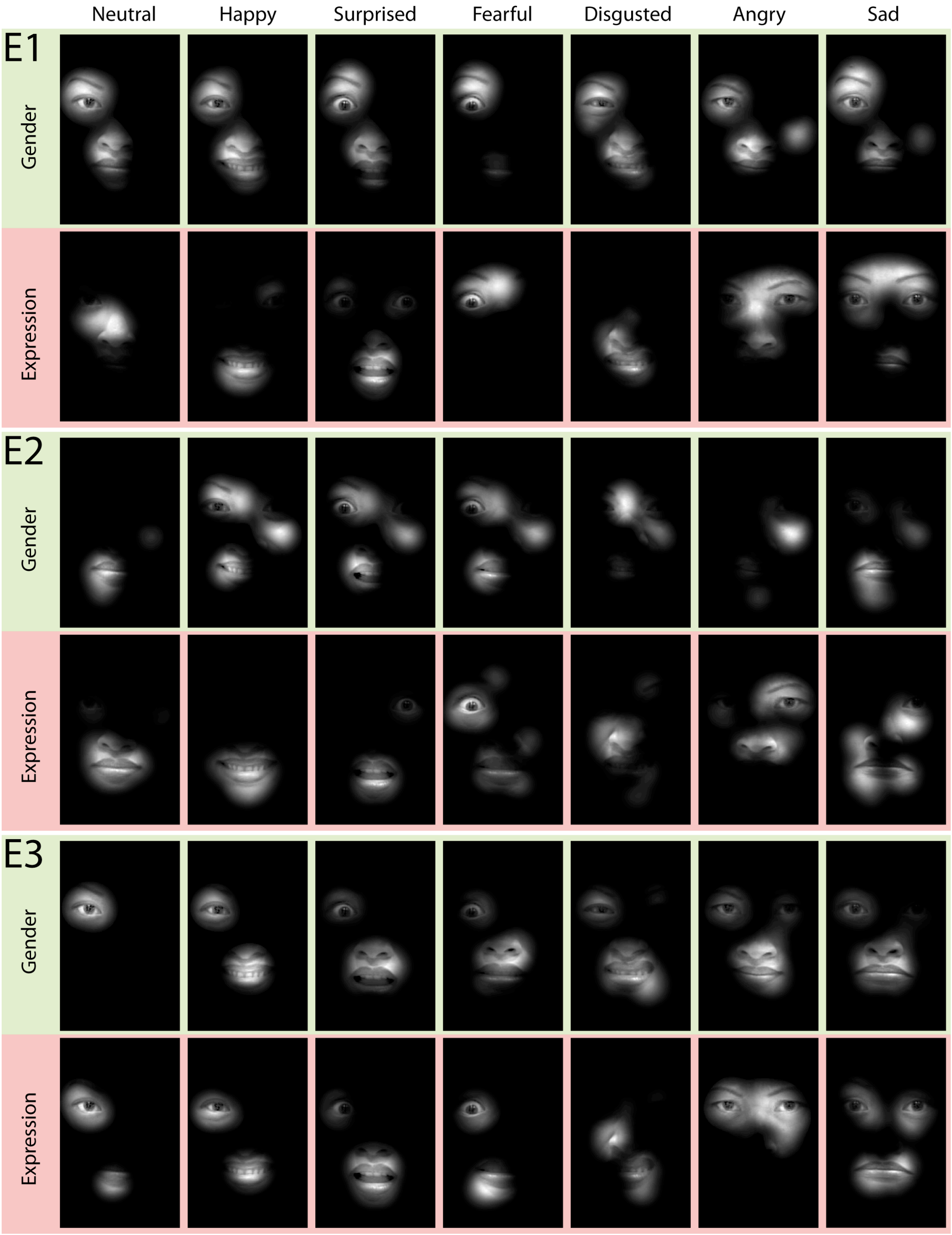


Figure 4.4: Diagnostic information for gender (green) and expressions (red) integrated in both categorization tasks for all three observers over the N170. The information images depict the integrated features at the maxima of diagnostic information sensitivity for each facial expression (in the order: ‘neutral’, ’happy’, ’surprised’, ’fearful’, ’disgusted’, ’angry’, ’sad’). Both tasks seem to integrate both gender and expression diagnostic features at the same time in the same EEG signal.

5. Peak feature sensitivity determines ERP peak in Expression, but not in Gender

The results so far suggest that both Expression and Gender tasks showed integration of both sets of diagnostic features for two different categorization tasks despite differing task demands. Here, I bring a closure to the question of task dependency of feature integration by relating the dispersion of the ERP latencies with the features integrated in each categorization task. Remember that the dispersion of N170 peak latencies and amplitudes was wider in Expression than in Gender. Next, I will demonstrate that greater dispersion of ERP peak latencies in judgments of expressions arose from a differentiated processing latency of features. In contrast, the more aligned processing of features across expressive faces in gender judgments resulted in more homogeneous ERP latencies.

We know from the behavioural classification images and the intersection analysis, that all observers used the left eye (contra-lateral to the right hemisphere electrode P8) and the mouth in Gender and in Expression for most expressions. I therefore declared these two features as regions of interest in the EEG CIs. I computed sensitivity to these features along the N170 time course by integrating the significant pixels, $p < .05$, that intersected with each feature of interest. I repeated this computation in Expression and Gender, independently for each expression. For each observer, I then regressed the time point of peak sensitivity to either the Left Eye or the Mouth (a measure of information latency) with the time point of the N170 peak (a measure of voltage latency), using the *robustfit* function in MatLab (compare Figure 4.2). Again, I used a bootstrap technique to obtain a 95% confidence interval for the slope of the regression for each observer and each feature of interest. This confidence interval constitutes a robust, data-driven statistical limit for a significant effect of each regression slope. (1) First, I sampled with replacement from each individual expression condition and task, keeping trials in the same original conditions. (2) Then I constructed, thresholded and binarised the classification images as described before, obtained the peak latencies of information sensitivity for each feature of interest and determined the N170 peak latencies. (3) I saved these latencies and repeated the previous steps 599 times. Eventually, I was able to compute a linear regression between information sensitivity peaks and ERP peaks for each sampling iteration, which left us with a distribution of six hundred regression slopes from which I was able to obtain a 95% confidence interval (again adjusting the interval boundaries as validated by Wilcox, 2005).

Table 4.2 reports the β coefficient estimates for the slope of the robust linear regressions, whereas Figure 4.5 illustrates both the robust regressions (right hand side) and the bootstrap distributions of slopes (left hand side). In Expression, there was a clear positive relationship between peak sensitivity to both features and N170 peak latency, whereas there was no such significant relationship in Gender. The only exception is the Left Eye in Expression for observer E2, which has a p-value of .097 and is therefore not significant.

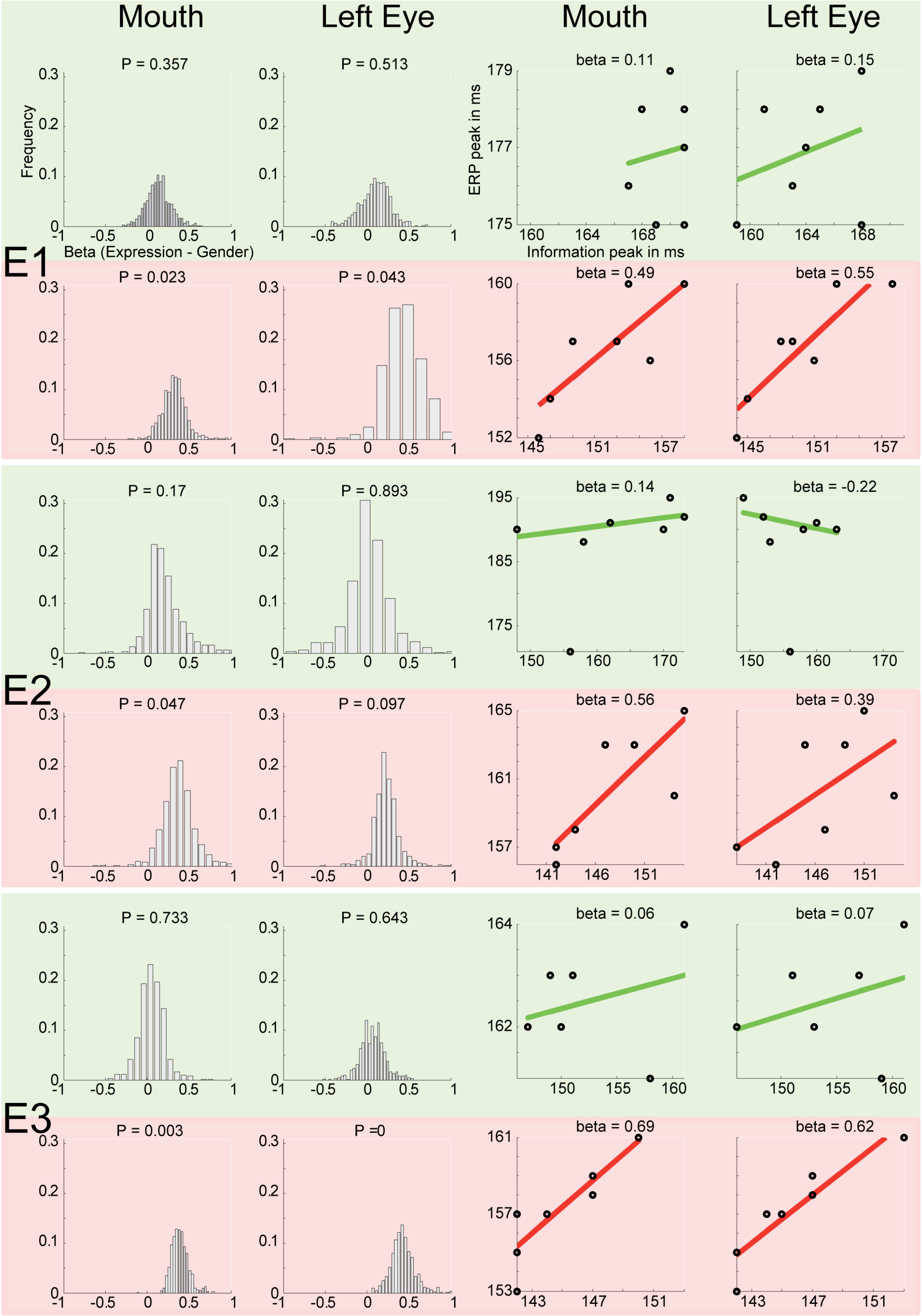


Figure 4.5: Robust regressions (left) and corresponding slope distributions* (right) obtained by a single-trial bootstrap procedure (Gender = green, Expression = red). The slope distribution of E3, Expression, left eye, has no values below 0, which causes the p-value to be 0 exactly.

*Note: The same number of bins was used to plot the histograms, however, due to uniform axis scaling, some bins appear to be larger than others.

		Gender		Expression	
		Left Eye	Mouth	Left Eye	Mouth
Observer E1	*β*	.146 [-.38 .51]	.108 [-.20 .54]	.545 [-.20 1.10]*	.488 [.00 .77]*
	p	.513	.357	.043	.023
Observer E2	*β*	-.224 [-.94 1.16]	.137 [-.22 .95]	.387 [-.20 .75]	.555 [-.14 .90]*
	p	.893	.17	.097	.047
Observer E3	*β*	.068 [-.33 .46]	.060 [-.36 .46]	.622 [.10 .86]*	.687 [.20 .70]*
	p	.643	.733	0	.003

Table 4.2: Results of the linear regressions, correlating peak feature sensitivity of the mouth and the left eye with the N170 peak latencies across expressions. Reported are the beta coefficient estimates of the slope of the regression [confidence intervals] and their bootstrap *p* values. A *p* value of zero means there is no overlap at all between the bootstrap distribution of beta-coefficients and zero (* significant at $p < .05$).

Finally, in order to confirm that the difference of regression slopes between categorization tasks is significant, I applied a shift function analysis to compare the distributions of bootstrapped beta-coefficients between tasks. Instead of relying only on one measure of central tendency to compare distributions, the shift function compares two distributions quantile by quantile using the Harrell-Davis estimator (hd) of quantiles one to nine. Specifically, the shift function is a measure of how much each quantile needs to be shifted to be comparable to the data of the same quantile in the other group. A bootstrap procedure is then used to obtain a 95% confidence interval for the difference between the hd estimators of the groups. If this confidence interval excludes zero, the difference is significant. I found that all quantiles of the distribution of bootstrapped differences of all observers for both the Mouth and the Left Eye were significantly different from zero, with the exception of the ninth quantile of the Left Eye for observer E2 (Figure 4.6). This confirms my hypothesis, that task-specific top-down control significantly modulates the N170, by shifting the N170 peak in relation to the time point of features integrated. Since all expressions have the same processing time line in relation to the N170 peak in Gender, but not in Expression, only Expression shows a clear relationship between maximum feature sensitivity and ERP peak.

On this basis, I can conclude that despite the great overlap of integrated information between categorization tasks, the timing of this information processing varies in Expression, but not in Gender, and thus only modulates the latencies of the N170 peaks in Expression, while the integration of features and the N170 peaks are aligned to the same point in time in Gender.

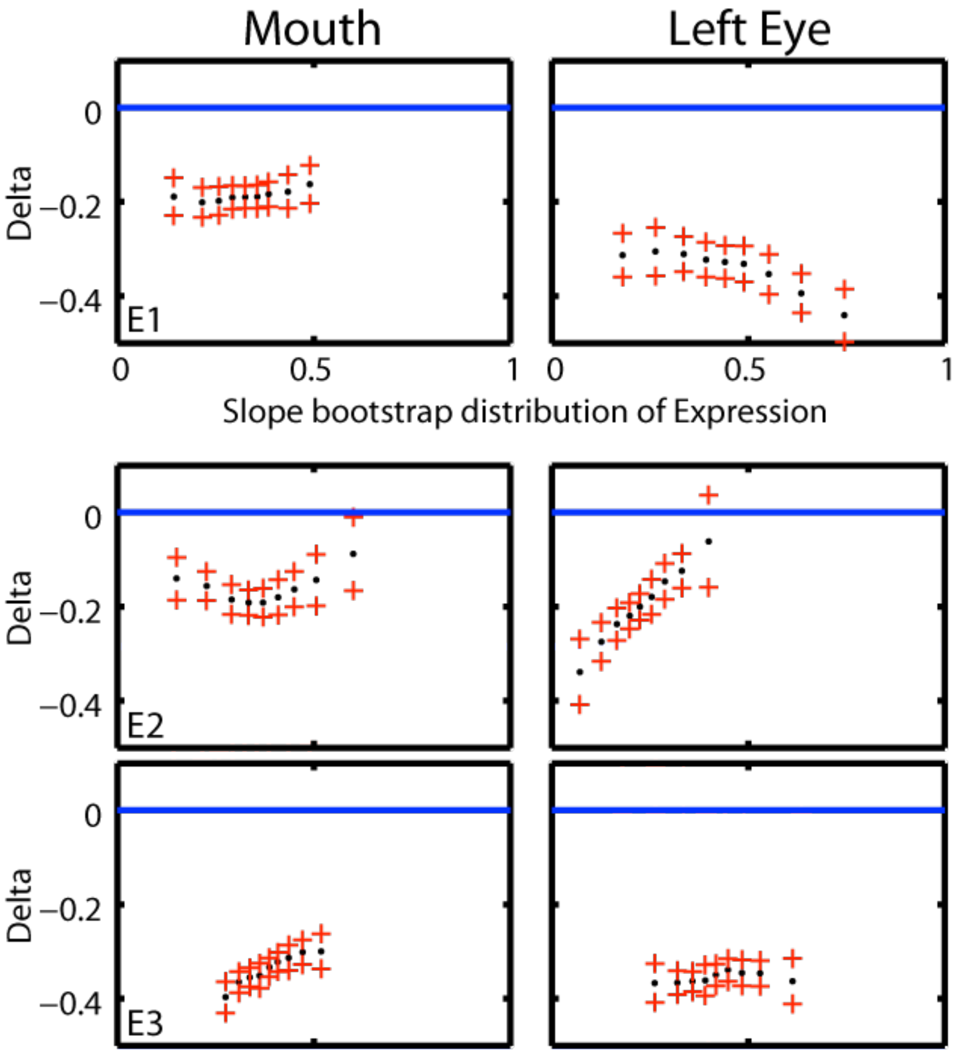


Figure 4.6: Results of the shift function analysis, which compares the Gender slope bootstrap distribution with the Expression slope bootstrap distribution for each observer – quantile by quantile – using the Harrell-Davis estimator (hd). The difference (Delta) between the quantiles of the distributions is significant, if the confidence intervals (marked by red plus-signs) exclude 0. This task effect is significant for all cases, except the 9^{th} quantile for E2, Left Eye.

6. Summary

The results of the EEG study allow several conclusions:

- Categorization task demands had a modulating top-down effect on peak amplitudes and latencies of the N170 ERP per expression. In Gender, ERPs for the expressions were more aligned in time and amplitude than in Expression, resulting in significantly wider latency and amplitude dispersion of the N170 peak in Expression.
- However, the integrated facial information per expression in both tasks was no more similar in Gender than Expression.
- In fact, the EEG signal carried the diagnostic information for both categorization tasks at the same time in relation to the N170 peak, independent of categorization task.
- Despite this overlap of integrated features with respect to the ERP peak, the N170 latency was modulated by peak feature sensitivity latency to either the Left Eye or the Mouth in all three observers in Expression, suggesting that task demands impacted on the timing of feature sensitivity. This effect is significant for Expression only, because top-down task demands modulate the timing of feature sensitivity differently for each expression, whereas the timing is the same for all expressions in Gender.

Finally, it can be concluded that top-down task demands had an impact on feature processing during the N170 in this experimental paradigm. However, I did not find this differential processing in the features themselves, only in their timing. Since I examined surface activity of the EEG signal, the question arises, whether the partial lack of differential feature processing between tasks was due to a lack of sensitivity of the EEG signal to such differences. A source-based analysis could potentially provide a more differentiated understanding of feature processing during the N170. Different features could be processed in different brain areas depending on task (Haxby et al., 2000). On the scalp surface, this signal would be mixed and lead to the results observed in this study, but on the source level, categorization tasks might indeed influence feature processing differently. The aim of my next study was precisely this: to examine facial feature processing in the same experimental paradigm on the source level using MEG data.

V. Evidence from MEG sensor and source activity: How task demands influence facial feature processing during the M170 in occipitotemporal sensors and voxels

As with the EEG data, all MEG analyses were carried out separately for each observer (M1-3), task and expression. Instead of just a single-sensor analysis as for the EEG data, I adopted an MEG specific approach: To extend the analyses from EEG sensors to MEG, in a first stage, I applied the previous EEG peak dispersion analysis to sensor MEG data. In a second stage, I proceeded to the source level, searching for voxels with sensitivity to face categories and diagnostic features to examine the differential processing of feature information between categorization tasks.

1. M170 peak analyses reveal a task effect of amplitude and latency dispersion

In analogy to the EEG analysis, I examined the sensors with the highest amplitude peaks for their dispersion in M170 peak latency and amplitude and compared the dispersions across tasks. In order to find sensors with the highest activation, I computed the (artificial) Planar Gradient (PG) of the Event-Related Fields (ERF). MEG magnetometers measure only radial/axial magnetic field changes (whereas EEG measures both radial and tangential sources). Due to the leadfield of the magentometers, activity on topographies is displayed on two sides of the source. To see the exact location of the underlying source it is practical to compute the PG as a measure of tangential/planar sources, as it has the highest signal directly above a source, by measuring the rate of change at each magnetometer ERF surface location. Figure 5.1

demonstrates this transformation for the time window of 170-180 ms for the averaged data of all trials of the Gender task for observer M3.

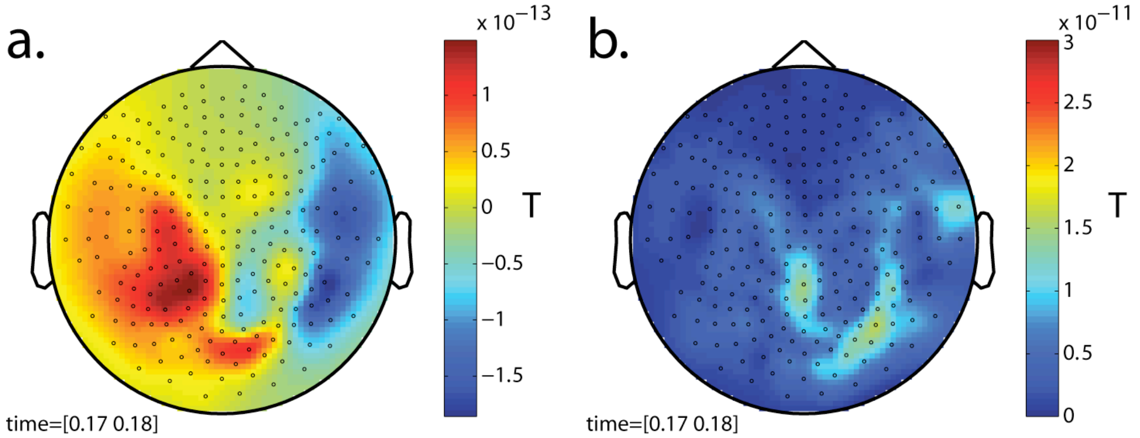


Figure 5.1: Topographies illustrating the transformation from (a.) Event-related fields as measured with magnetometers to their (b.) Planar Gradients (observer M3, Gender, 170-180 ms). It can be seen that the PG is high when there is a great change from positive to negative values in the ERF topography, depicting the area right above a source of activity.

As with the ERP peaks I expected a wider dispersion in the Expression task for both latencies and amplitudes due to more differential processing of expressions in the Expression task. I used the same single trial bootstrap procedure as described for the EEG data to obtain the data driven 95% confidence intervals for the task difference of the MAD on each sensor (a positive MAD difference denotes wider dispersion in Expression). I determined the relevant sensors by inspecting the PG topographies at the peak of the M170 and their average time courses and picking the five sensors with the highest M170 peak. For M1 I only picked four sensors, because no other sensors showed a clear M170. The sensor locations on the scalp are depicted in Figure 5.2. Results are reported in Table 5.1. For all observers I found sensors with significantly wider dispersion in either amplitude or latency of the M170 peaks in the Expression task (marked with *). For M1, one sensor was significant for both latency and amplitude dispersions (A187) and another one for latency dispersion only (A167). Observer M2 only had one significant MAD task difference for the peak amplitudes of sensor A183.

Observer M3 had two significant sensors for both amplitudes and latencies (A189, A190 and A206, A222, respectively). All sensors were significant at $p < .05$, corrected with Bonferroni for the number of comparisons (.0125 for M1 and .01 for M2 and M3). Hence, the effect observed for the N170 amplitude and latency dispersion appeared to be present for the M170 as well, however, this effect was spread over several sensors. This suggests again, that categorization task had a differential effect on averaged brain activity in occipitotemporal areas, with generally greater amplitude and latency dispersion in the Expression task during the face-preferential M170.

	Sensor	PG peak	MAD Δ Expression-Gender	95% Confidence Interval	*p* - value
Observer M1	1. A166	amplitude	1e-12 x .130	1e-12 x [-.311 .240]	.284
	2. A167		-.120	[-.289 .238]	.476
	3. A168		.001	[-.244 .191]	.830
	4. A187*		.302	[-.235 .165]	.006
	1. A166	latency	0	[-1.000 1.000]	.448
	2. A167*		2	[-1.000 1.000]	0
	3. A168		0	[-2.000 1.000]	.302
	4. A187*		1	[-1.000 1.000]	.002
Observer M2	1. A207	amplitude	1e-12 x .094	1e-12 x [-.230 .343]	.652
	2. A190		.015	[-.257 .306]	.922
	3. A201		.038	[-.269 .333]	.902
	4. A200		-.016	[-.251 .319]	.776
	5. A183*		.498	[-.272 .366]	.008
	1. A207	latency	1	[-1.000 2.000]	.058
	2. A190		0	[-1.000 2.000]	.562
	3. A201		-1	[-3.000 3.000]	.622
	4. A200		-2	[-7.000 7.000]	.630
	5. A183		-2	[-4.000 5.000]	.332
Observer M3	1. A189*	amplitude	1e-12 x 1.158	1e-12 x [-.270 .277]	0
	2. A206		.065	[-.276 .235]	.554
	3. A207		.256	[-.257 .228]	.034
	4. A190*		.358	[-.259 .240]	0
	5. A222		-.014	[-.196 .201]	.904
	1. A189	latency	0	[-1.000 1.000]	.488
	2. A206*		1	[-1.000 1.000]	.004
	3. A207		0	[-1.000 1.000]	.380
	4. A190		1	[-1.000 1.000]	.050
	5. A222*		1	[-1.000 1.000]	.002

Table 5.1 (previous page): Selected high amplitude MEG sensors for the M170 and their peak latency and amplitude MAD task differences (Expression minus Gender). Significance levels and confidence intervals were determined using a data-driven single-trial bootstrap technique. A *p* value of zero means there is no overlap at all between the bootstrap distribution of MAD differences and zero (* sensors significant at $p < .05$, corrected with Bonferroni). In Fig. 5.2, the sensors for each observer are shown on a topographic surface, numbered as in the table.

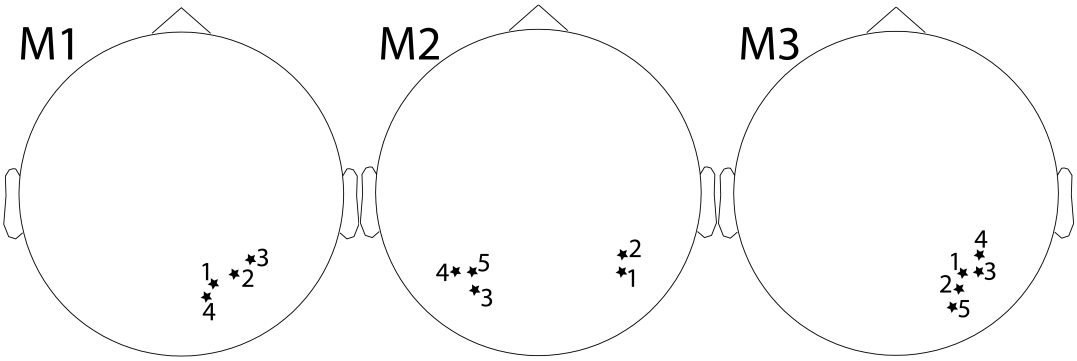


Figure 5.2: Scalp locations of high-amplitude sensors for each observer as referred to in Table 5.1.

2. Source analysis revealed higher occipitotemporal activity during both face categorization tasks

Even though the sensor-based EEG analysis found a task-effect in the timing of the N170 and related information sensitivity, it did not determine any definitive task effect specifically on information processing during the N170. One explanation for this non-result could be the fact that the analyses were carried out on surface brain activity only and therefore small differences in the sources active during each task would not be sufficient to reveal a difference at the sensor level using EEG sensor measurements. Hence, the purpose of the MEG analyses was to determine whether task differences existed at the more precise source level. In order to compare task differences in facial feature processing during the M170, it was crucial to identify sources that responded selectively to faces and at the same time to reduce activity elicited by general visual, attentional or motor processes. Determining source activity inside the brain from sensor data recorded at the surface of the brain is an inverse problem. This problem has been and still is discussed widely and there are many ways to approach it (Darvas, Pantazis, Kucukaltun-Yildirim, & Leahy, 2004; Faugeras et al., 2004; Haufe et al., 2011; Ilmoniemi, 1993; Mosher, Leahy, & Lewis, 1999; Niedermeyer, 1996). A classic approach of estimating MEG sources is the *Linearly Constrained Minimum Variance* beamformer technique (Van Veen, Drongelen, Yuchtman, & Suzuki, 1997). A beamformer is a spatial filtering technique, which separates overlapping signals from different spatial locations (Van Veen & Buckley, 1988). The applied spatial filter aims to pass the signal from one location, while attenuating activity from all other sources (Van Veen et al., 1997). The LCMV beamformer considers all possible locations without any prior assumptions as to where an active source might be. Instead of applying the filter to the raw signal, the LCMV uses the spatial covariance of the source activity (Van Veen et al., 1997). In the same article, Van Veen discusses how to best determine the spatial covariance. He states that one condition with the beamformer is, that the time window over which the source activity is to be determined, needs to contain at least as many data points as sensor locations to guarantee an acceptable amount of localization accuracy and to reduce the randomness of the data. In fact, he suggests, as a general rule of thumb, to use about 3-4 times as many data points as there are sensors. To obtain a sufficient amount of data points and to compare the results, he introduces different methods: a) to use one time window with an average of single trials, b) to use one (the same) data point from each single trial and c) to use all data points of all single trials. The author then generated artificial data with a single dipole, whose signal was made up of a sinusoid and added noise (making up either 80% or 20% of the signal). Method a) yielded the best localization results for both types of data tested, with localization peaks being very focal and accurate, method c) was second best, showing similar results for both types of data, with source peaks being slightly wider, but higher than for method a), whereas method b) only worked well for the high variance data. With respect to the hypothesis, I was specifically interested in the time window of the M170 to determine task effects on feature processing. In order to find face sensitive sources it is therefore crucial to restrict the time window used to compute the covariance matrix of the face sensitive period around the M170 peak (as determined by the ERF/PG). Obviously, with this rather short time window (~ 40 ms), the use of method a) would be inappropriate because there wouldn't be enough time points with respect to the number of sensor locations (> 200). Instead, I opted for method c) and used all time points of all single trials to compute the covariance matrix.

Van Veen et al. (1997) further state that source activity of interest is often masked and overlaid by noise activity in the brain yielding a low signal-to-noise ratio for effects due to experimental manipulations. A way to counteract this problem is to select a time period, such as the pre-stimulus baseline period, which should not elicit any face-selective activation and therefore only contain noise, and use it to separate the signal of interest from the noise component. This so-called *Neural Activity Index* (NAI) is computed by dividing the difference of the time period of interest and the noise period by the noise period. For the time window of the M170 (150 – 190 ms after stimulus onset), I computed the covariance matrix, the spatial filter, the power of source activity and the NAI for each observer, task and session, and then averaged over sessions to obtain a grand-average representation of source activity (NAI) for each observer and task. Figure 5.3 depicts horizontal slices of source activity for the M170 time window. All three observers show a higher NAI in occipitotemporal areas, such as STS/FFA (M1), FFA/OFA (M3) and OFA and Visual Cortex (M2). However, it is also obvious, that the individual differences between observers can be quite substantial, which justifies my single subject rather than an average subject approach. Since my aim is to find task differences in facial feature processing, the question arises now whether the observed source activity in both tasks is sensitive to task-relevant and irrelevant face categories for each observer.

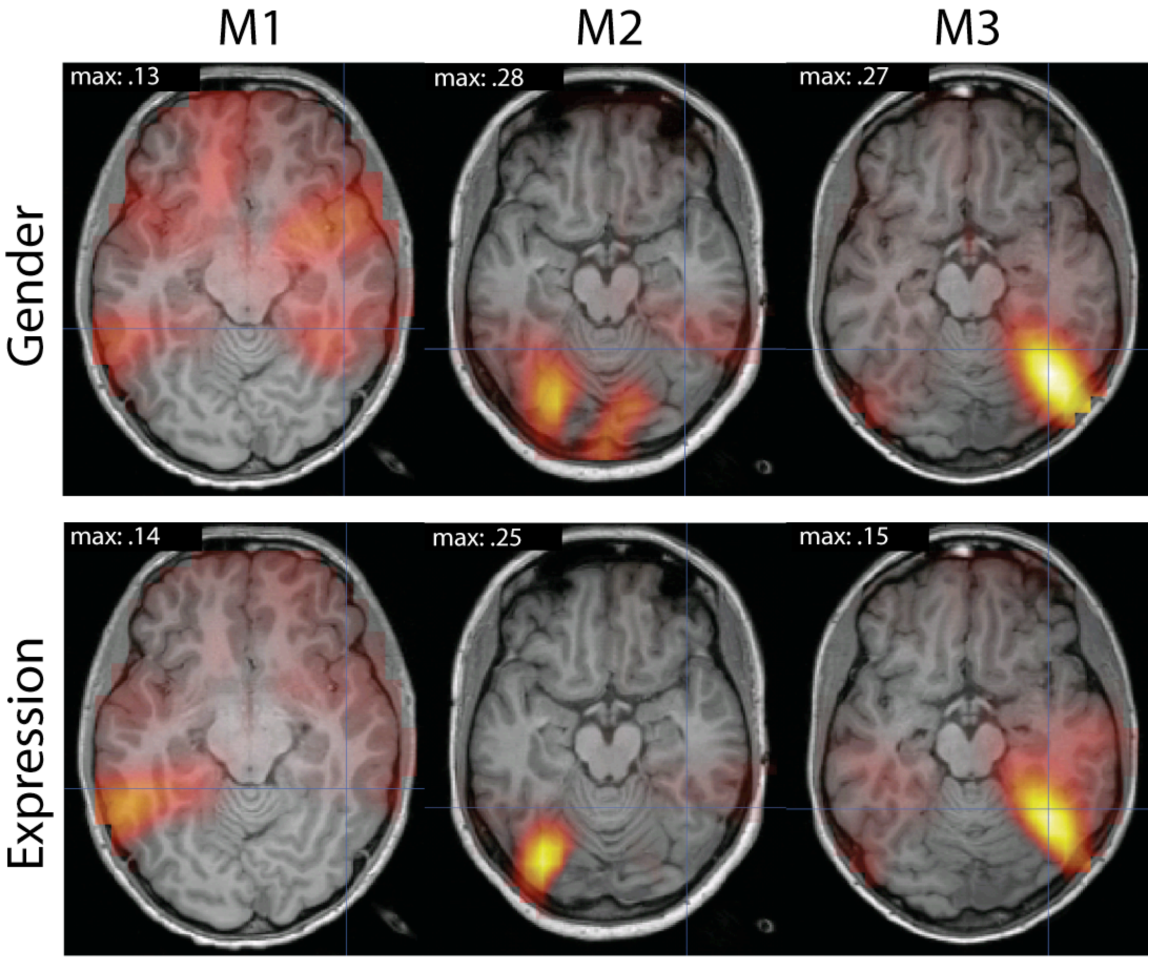


Figure 5.3: Horizontal brain slices showing the Neural Activity Index for the M170 time window from 150 – 190 ms after stimulus onset. Maximum NAI values of each image are in the top left corner of the image, minimum value is always 0.

3. Mutual Information reveals task-dependent differences in brain sensitivity to face category

If I was following the same analysis protocol as for the EEG study, the next logical step towards my aim of examining task differences in feature processing on the source level would be to compute CIs for each voxel along the ventral stream. This was indeed done for some voxels for one observer (M3). However, in the EEG study I did this for only one electrode, whereas for this study it would take great computational resources and a lot of time to compute CIs for more than 1000 voxels. Hence, for reasons of practicality, I turned towards Information Theory (IT) instead (Shannon, 1948). First I used IT to identify voxels in each categorization task, which responded selectively to either the gender category or the expression category of the stimuli.

In Information Theory (Shannon, 1948) the mutual dependence of two random variables is measured by Mutual Information (MI)[2]. According to Magri et al. (2009), MI can be used to identify components of brain activity that respond selectively to stimulus-based differences and cannot be explained by trial-by-trial response variability. The following equation defines the MI between two random variables X and Y in bits of information (Cover & Thomas, 2006, p. 20):

$$MI(X;Y) = \sum_{y \in Y} \sum_{x \in X} p(x,y) \log_2 \left(\frac{p(x,y)}{p(x)p(y)} \right) \qquad (2)$$

According to Schyns et al. (2011), MI measures the amount of bits of information shared by the two variables X and Y. If their joint probability p(x,y) is zero, then their MI becomes zero as well. Expressed in terms of entropy H, the uncertainty of a random variable, MI can also be computed with

$$MI(X;Y) = H(X) - H(X|Y) = H(Y) - H(Y|X) \qquad (3)$$

where H(X) is the entropy of X and H(X|Y) is the conditional entropy of X given Y (Cover & Thomas, 2006, p. 21). If both terms are the same, then knowing Y will not reduce the uncertainty of X and the MI will be 0. If, however, Y reduces the uncertainty

---

[2] MI has been used in EEG and vision research before (e.g. Lopes da Silva, Pijn, & Beoijinga, 1989, and Harel, 2007) for good examples of MI in EEG research). It has been used for decades for a variety of research questions and analyses, e.g. pattern recognition and matching (Uttley, 1976), which was extended to co-registration and alignment of brain images (Liao et al., 2007); MI as a neural coding principle in vision (Harel, Ullman, Epshtein, & Bentin, 2007; Lopes da Silva et al., 1989); in chemical physics (Sagar & Guevara, 2005); and in biophysics and neural networks (Friston, 2000; Manwani & Koch, 1999), to only name few.

of X, then their MI will be greater than 0 and Y can predict X to a certain extent. Figure 5.4 gives an overview of all computations of MI conducted in this study and the basic parameters. All bins were equi-populated. The number of bins for continuous measures, such as pixel values and source amplitude, was set to four, following the example of Schyns et al. (2011). Figure 5.5 describes a computation example for MI(source power, face category), the analysis step following next.

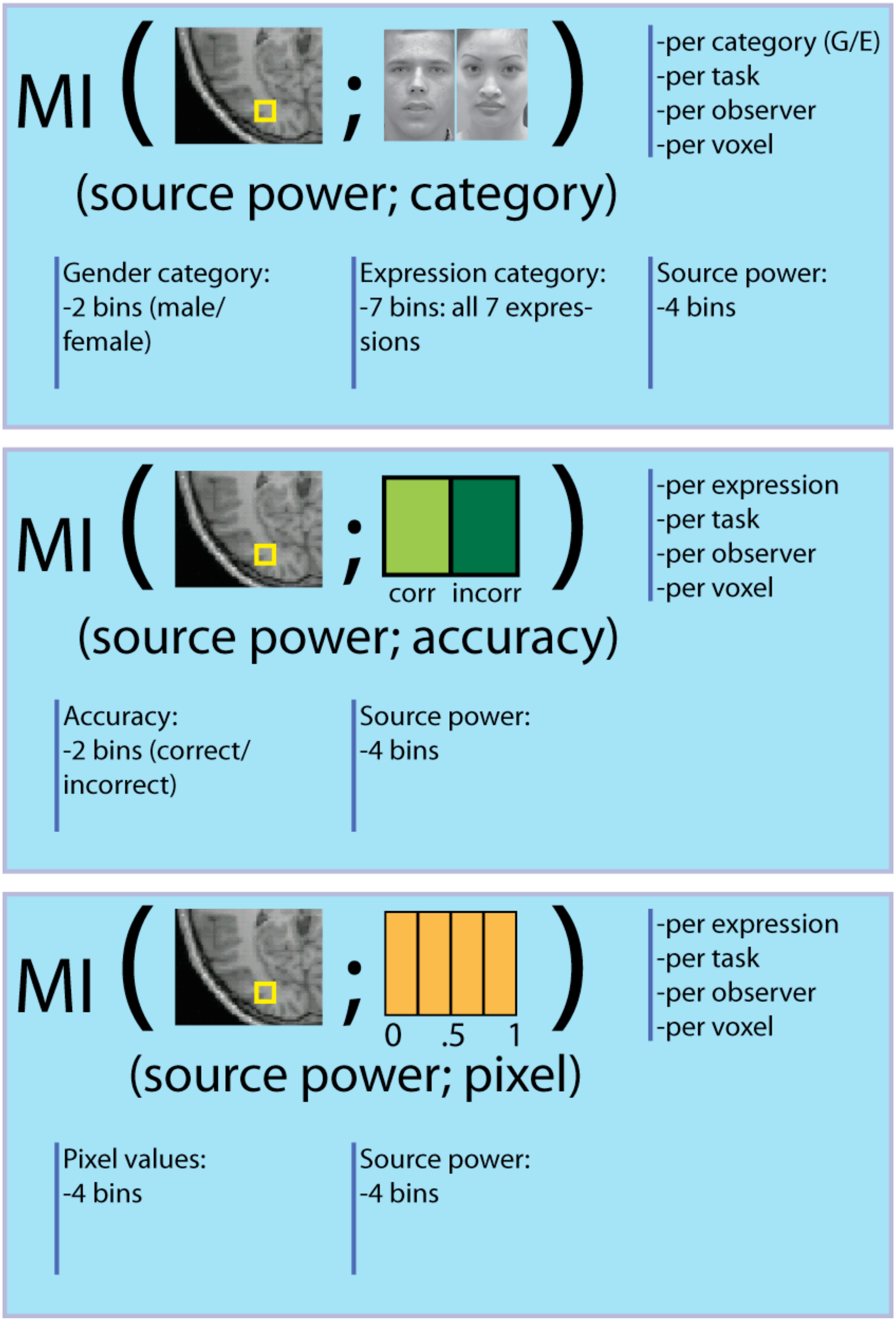
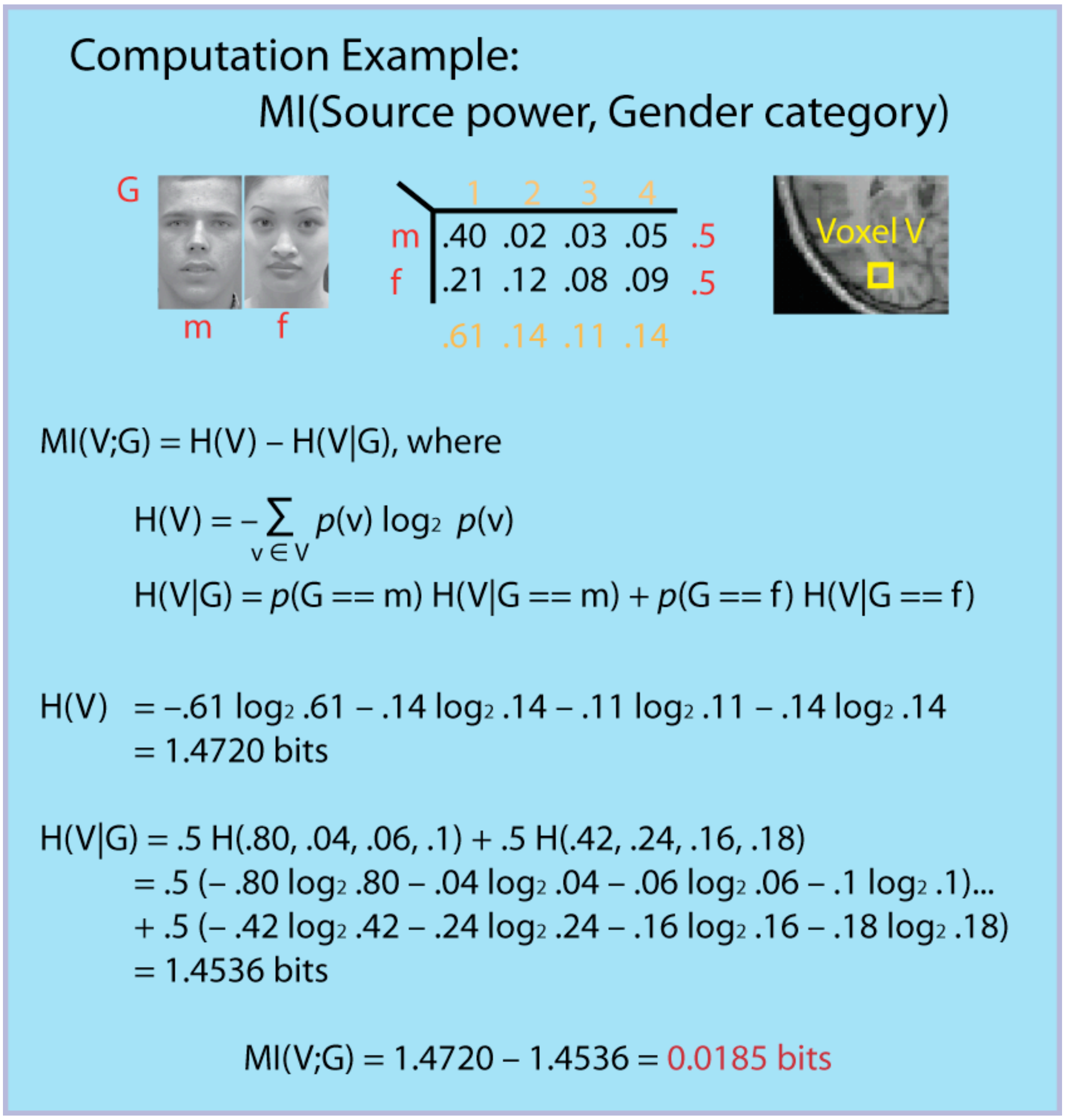


Figure 5.4 (previous page): The three kinds of MI computations used in this analysis. I first determined the MI between source power and (top) face category (either Gender or Expression), then (middle) with accuracy (correct vs. incorrect trials) and, finally (bottom), with the grey-values of each pixel of the bubble masks. Each panel describes the parameters of computation and the number of equi-populated bins applied for each measure.



Computation Example:
MI(Source power, Gender category)

	1	2	3	4	
m	.40	.02	.03	.05	.5
f	.21	.12	.08	.09	.5
	.61	.14	.11	.14	

$MI(V;G) = H(V) - H(V|G)$, where

$$H(V) = -\sum_{v \in V} p(v) \log_2 p(v)$$

$$H(V|G) = p(G == m)\, H(V|G == m) + p(G == f)\, H(V|G == f)$$

$$\begin{aligned} H(V) &= -.61 \log_2 .61 - .14 \log_2 .14 - .11 \log_2 .11 - .14 \log_2 .14 \\ &= 1.4720 \text{ bits} \end{aligned}$$

$$\begin{aligned} H(V|G) &= .5\, H(.80, .04, .06, .1) + .5\, H(.42, .24, .16, .18) \\ &= .5\,(-.80 \log_2 .80 - .04 \log_2 .04 - .06 \log_2 .06 - .1 \log_2 .1)\ldots \\ &\quad + .5\,(-.42 \log_2 .42 - .24 \log_2 .24 - .16 \log_2 .16 - .18 \log_2 .18) \\ &= 1.4536 \text{ bits} \end{aligned}$$

$$MI(V;G) = 1.4720 - 1.4536 = 0.0185 \text{ bits}$$

Figure 5.5: Computation example for MI(Source power, Gender category), adapted from Schyns, Thut & Gross, 2011. The table at the top displays the joint probabilities of all four bins (yellow) of the source power for one voxel (V) and the two bins for the Gender category G (m and f, in red). The MI is computed by subtracting the conditional entropy H(V|G) from the entropy H(V). Note, that for the Expression category I used seven bins (one for each expression) instead of the two for Gender. See Figure 5.4 for further details.

In the next step, I used MI to determine the mutual dependence between MEG source power of voxels in the ventral stream and either the expression category (e) or the gender category (g) of the face stimuli. This was done for both categorization tasks, Expression (E) and Gender (G), yielding four conditions of MI: explicit sensitivity to task relevant stimulus category, MI(G,g) and MI(E,e), and implicit sensitivity to task irrelevant stimulus category, MI(G,e) and MI(E,g). This design allowed me to compare the location and strength of sensitivity of voxels in both tasks to either implicit or explicit stimulus category. In order to compute these MI conditions, I applied the following steps:

(1) First, I selected a total of 1090 voxels (8 mm side length) that fell within the occipitotemporal area, ensuring that all areas of the core system of face processing and the visual cortex were included.

(2) For each voxel, I calculated the single trial source power for the time window of the M170 (150 – 190 ms after stimulus onset), by matrix-multiplying its spatial filter from the beamformer analysis with the single-trial time courses of all channels.

(3) Again for each voxel, I sorted the single trials by stimulus category: once, I sorted them by the seven expressions (e) and once by their gender (g).

(4) Then I calculated the MI between single trial source power of each voxel in each task (G and E) and the category of stimuli (e and g), using the MatLab-based *Information Breakdown Toolbox* by Magri et al. (2009). I used the following toolbox parameters for all MI computations: the direct method with quadratic extrapolation and equi-populated bins to maximise response entropy (Magri et al., 2009). These were the same parameters as used by Schyns et al. (2011). Trials for each bin amounted to 1363, 1077 and 1466 for M1, M2 and M3, respectively. This computation provided me with four time courses of MI between voxel activity and face category, effectively a measure of voxel sensitivity to either expressions or gender in each categorization task.

(5) Visual inspection of these sensitivity time courses indicated that some voxels responded more to either stimulus condition than others. In order to find voxels with significantly higher MI than others, I created a data-driven, artificial MI baseline by repeating the MI analysis, but this time randomizing the single trials for each voxel to break the link between source power and expression or gender category. I used this random MI time course from all voxels to create, time point by time point, a

data-driven 95% confidence interval for the null-hypothesis of MI effects, at the same time controlling for multiple comparisons.

(6) Finally, I interpolated the MI across voxels and plotted the significant MI sensitivities onto the anatomical MRI template of each observer, for each MI condition and separated into six time bins during the M170 time window. The results are shown in Figures 5.6, 5.7 and 5.8.

The results from this analysis have several implications with respect to my hypothesis. (1) First, the inter-individual differences, like in the source analysis, were substantial and imply that averaging over observers would result in great loss of information. (2) Second, categorization task had an effect on brain sensitivity to explicit face categories (see Table 5.2 for an overview of the following descriptions). In the explicit conditions, MI(G,g) and MI(E,e), all observers responded to the task-relevant face categories with different brain areas. Observer M2 (Figure 5.7) had a peak of explicit gender sensitivity in the right VC/OFA, whereas the peak of explicit expression sensitivity was located in the left STS/FFA. Observer M3's peak of explicit gender sensitivity was positioned in the right FFA/OFA, and the explicit sensitivity peak of expression in the right VC (Figure 5.8). Even though observer M1 (Figure 5.6) was sensitive to both explicit and implicit stimulus categories in the same brain areas, the peak of explicit gender sensitivity was in the right OFA, whereas explicit expression sensitivity peaked in VC. In addition, this observer showed another interesting effect in both implicit and explicit conditions: peak sensitivity to expressions happened slightly earlier (144 – 160 ms) than sensitivity to gender (168 – 184 ms). (3) Generally speaking, the sensitivity to the task-irrelevant, implicit stimulus category was weaker and less systematic than to the explicit category. Observer M2 showed hardly any implicit sensitivity to gender in the Expression task (a little in bilateral OFA), and implicit sensitivity to expressions in the Gender task was in a slightly different brain area (left

OFA/VC) than explicit sensitivity to gender (rVC/rOFA). Observer M3 also had only very little implicit sensitivity to gender in the Expression task (lVC/rOFA), whereas implicit sensitivity to expressions in the Gender task peaked in the right FFA/OFA, which – for this observer – was also the peak for explicit gender sensitivity. For an overview of these results and additional sensitive brain areas, see Table 5.2.

In summary, all three observers displayed a clear and individual task effect in the explicit sensitivity to the task-relevant face category. This task effect was manifested in differences in location or timing of sensitivity. Brain sensitivity to task-irrelevant face categories was much weaker and there was some overlap, but there were also some tendencies toward differences in timing and location of sensitivity, especially when taking into account not just the peak areas (compare Table 5.2).

This task effect can be explained in terms of bottom-up and top-down processing. When a particular face category is relevant to perform a categorization task, our bottom-up processing stream is modulated by top-down control in a particular way: The relevant category receives more sensitivity in the face network and this sensitivity is either spatially located in a different brain area or temporally located earlier or later along the processing stream than sensitivity to the task-irrelevant face category.

	Explicit Face Category		Implicit Face Category	
	MI(G,g)	MI(E,e)	MI(E,g)	MI(G,e)
M1	***r*OFA**	**VC**	***r*OFA**	**OFA**
	*r*STS	*l*STS	*r*FFA	VC
	*r*FFA	*r*OFA	*r*STS	*l*STS
	*r*VC			
M2	***r*VC/*r*OFA**	***l*STS/*l*FFA**	OFA	***l*OFA/VC**
	*l*VC	*l*OFA		*r*FFA
		VC		
M3	***r*FFA/*r*OFA**	***r*VC**	*l*VC	***r*FFA/*r*OFA**
		VC	*r*OFA	*r*STS
		OFA		VC
		*l*STS		

Table 5.2: Overview of brain areas sensitive to implicit and explicit face categories. Bold print indicates the main focus of sensitivity. If an area is sensitive bilaterally, it is not preceded by a laterality descriptor (*r* or *l*). Observers M2 and M3 revealed sensitivity to explicit face categories in entirely different brain areas for each task. While observer M1 showed an overlap in sensitive areas, the peak sensitivity was in different areas and the timing of categorical sensitivity to expression was earlier than to gender (also note that *r*FFA is sensitive to both implicit and explicit gender category, while not at all for the expression category). For sensitivity to the implicit face category, there is a fair amount of overlap in brain areas, however, a similar, but much weaker trend emerges, when comparing the images from Figures 5.6 – 5.8.

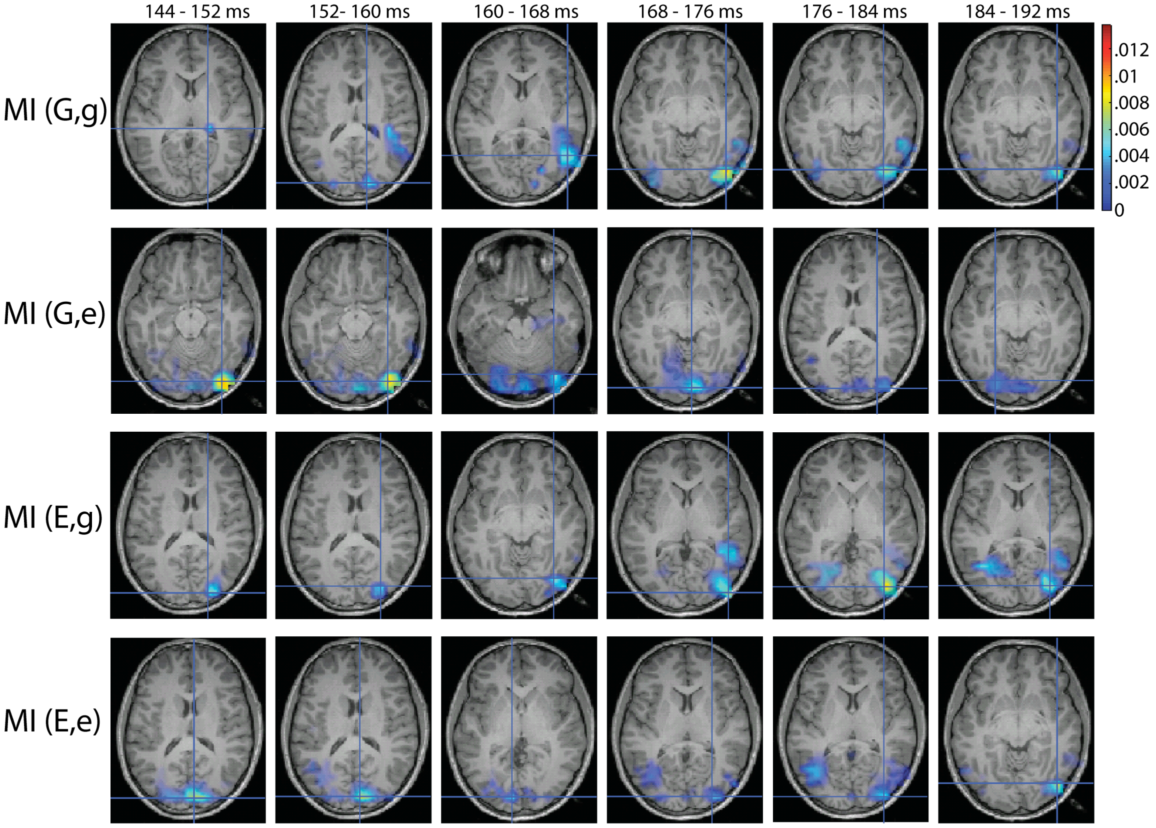
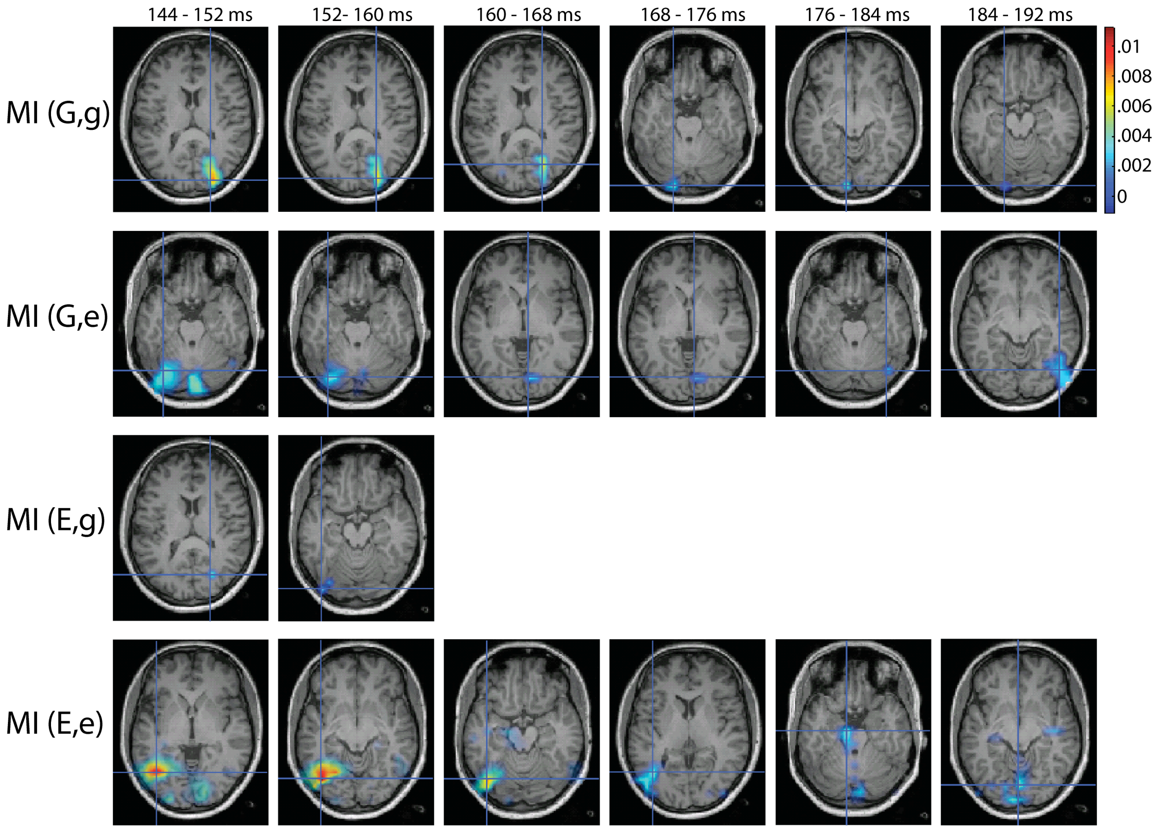
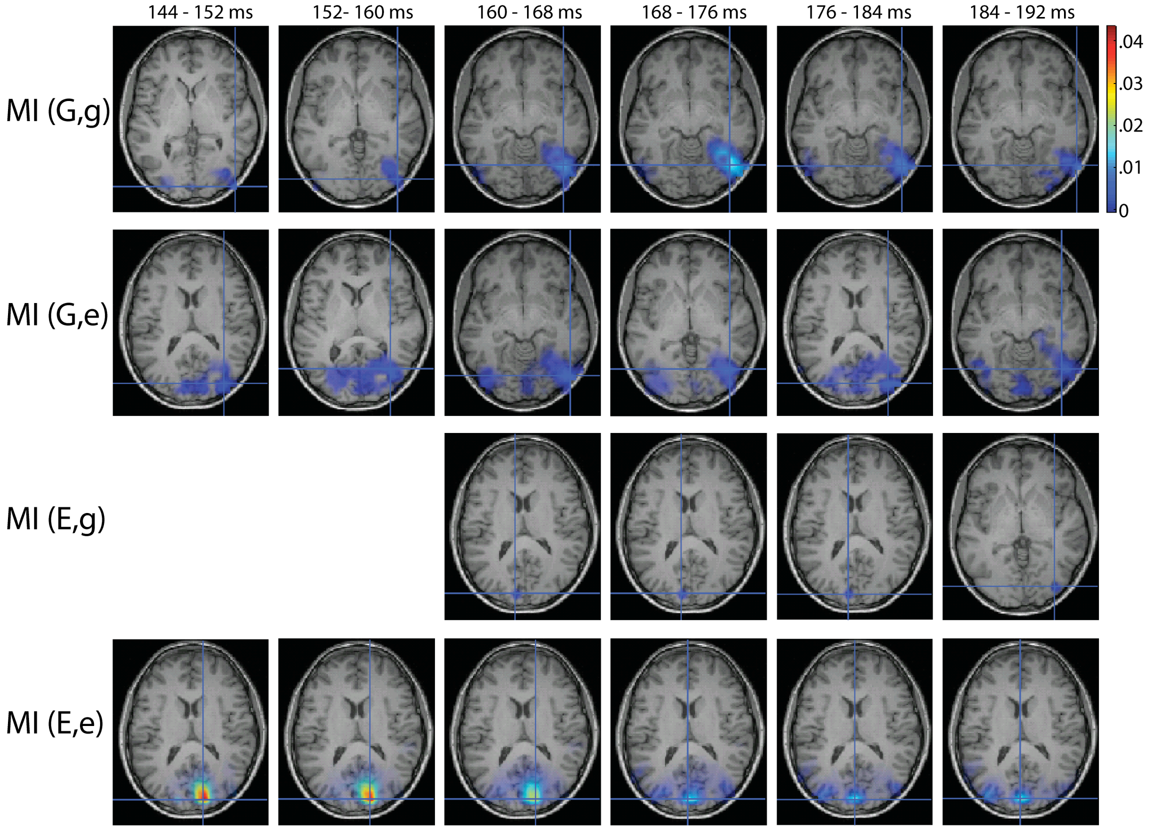


Figure 5.6: Mutual information between voxel power and stimulus category for observer M1. The top and bottom rows depict sensitivity of voxels to the explicit, task relevant stimulus category (MI(G,g) and MI(E,e)). The two middle rows depict sensitivity to the implicit stimulus categories. The sensitivity is displayed in bits; all images are on the same scale (top right).



Figures 5.7 (above) and 5.8 (below): Mutual information between voxel power and stimulus category for observer M2 (above) and M3 (below). See Figure 5.6 for descriptions.



4. Mutual Information reveals task-dependent diagnostic feature integration in behaviourally predictive, expression-sensitive voxels

Having established that the brain processes face categories differentially dependent on categorization demands, I was now left with the question, whether this sensitivity modulation to face category impacts on categorization accuracy and is represented in the integrated facial information. As mentioned in the EEG analysis, if feature processing differs in the two categorization tasks, then I would expect differential processing of expressions in the Expression task and similar processing of expressions in the Gender task. If the integrated information corresponds to the respective diagnostic information for each task (obtained with behavioural CIs, see Chapter III), there would be strong evidence that the categorization task manipulates differential feature processing in a top-down manner.

Again, I turned to the MI approach, this time to identify voxels, which share mutual information with the successful categorization of an expression or gender (compare Figure 5.4). This method was used to ensure, that integrated information in these voxels was linked to behaviour and could thus be compared to behavioural diagnostic information. For each observer, task and expression, and over the time window of the M170, I computed MI between the single trial source power of 1090 voxels (the same voxels as in the previous analysis step) and the behavioural response (correct/incorrect). I used exactly the same parameters as for the previous MI computation, using equi-populated bins with the same number of trials per condition for each observer. Because the response occurred in time after this sensitivity, these voxels were predictive of a correct or incorrect categorization decision. In order to visualize the significant voxels with their sensitivity strength and location, I plotted them in a 3D scatter plot (Figure 5.8). Significance thresholds for voxel sensitivity were again determined using the same data-driven 95% confidence interval (see step (5) in section 3 of this chapter). I plotted all voxels (the size of the marker represents strength of sensitivity) for six time bins of the M170 time window in one plot. A crude observation of the scatter plots revealed that there were usually clusters of voxels responding to the same expressions. In the Expression task, the clusters predicting correct categorization of "happy" were especially big and wide-spread. In the Gender task, it was usually other expressions (other than "happy") that predicted a correct gender categorization.

These clusters of voxels could now be used to determine the integrated facial features. Again, if voxels predicting a correct categorization of a certain expression in the Expression task corresponded to the diagnostic behavioural information, then there should be a greater variance of integrated information in Expression. And vice versa, voxels sensitive to expressions, but predicting correct gender categorizations should all integrate similar facial information that overlaps with the diagnostic information for gender.

In order to determine the integrated facial features, I computed the MI between every single pixel of all bubble masks for each expression and the single trial source power of all predictive voxels within one expression cluster of the previous analysis step (compare Figure 5.4). Again, I used the same computation parameters as in the first MI computation, with the same numbers of trials per observer and bin (see step 4). This analysis yielded images of the size of sensor-based CIs, each pixel representing a value of MI (see Appendix C for a comparison of voxel-based CIs and corresponding MI images). Figures 5.10 – 5.12 depict these MI images. For each expression and task, I chose the MI images from the six M170 time bins that had the highest values of MI. In some cases, if there was no sensitivity in a time bin to an expression from the previous analysis step, there was of course no such image available. Also, if there were images with peak values of less than .01 bits of information, they were excluded as well. For comparison purposes, each graph also contains the behavioural CIs for all expressions and gender. All images are overlaid onto an original stimulus face to ease interpretation of the depicted information.

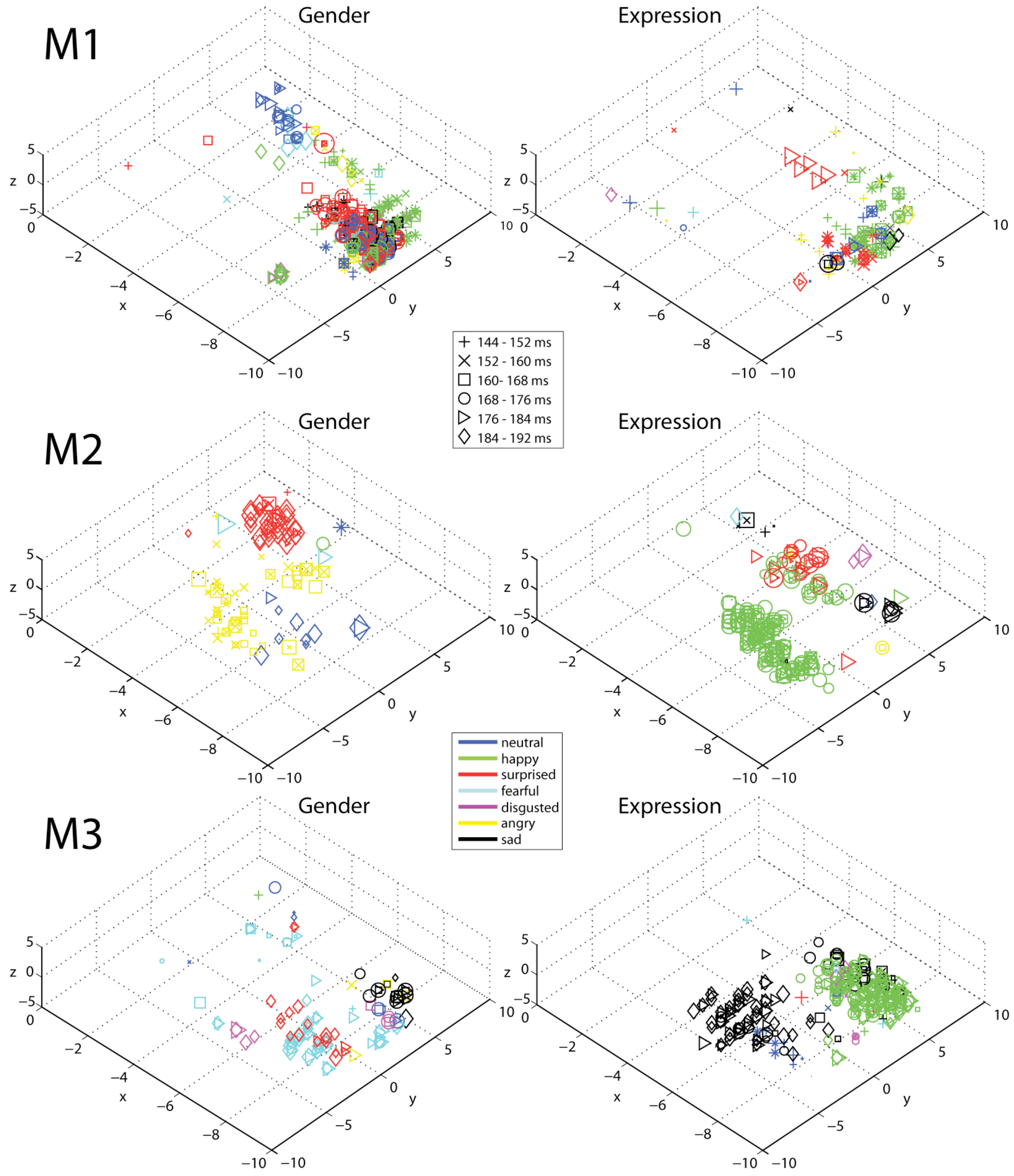


Figure 5.9: 3D scatter plots of voxels sensitive to expressions and predictive of categorization accuracy for each task and observer. The 3D space depicts the occipitotemporal brain with 1090 voxels (occipital is at the side of the y-axis). Each marker represents the strength of the sensitivity by its size (same scale for all plots), whereas the symbol of the marker represents the time bin of activation (see legend) and the colour the expression. See text for further discussion.

Again, several conclusions can be drawn from this analysis. Observers displayed their own pattern of information processing and behavioural sensitivity. For observers M1 and M3 there was a clear task effect of information processing, for observer M2, I found a weaker task effect. Observer M1 (Figure 5.10) was using the mouth for gender categorizations. In all expressions, the sensitive voxels integrated primarily the mouth in the Gender task. In contrast, in the Expression task, expression associated voxels integrated information that matched behaviourally diagnostic information from the respective expression. Even though there was an overlap between gender and expression diagnostic information (e.g. the mouth in "happy"), in the Expression task expressions included other diagnostic features as well, which were not present in the Gender task (eyes, wrinkles, eyebrows etc.). The only expression for M1, which contained expression diagnostic information in the Gender task, was "fearful".

Observer M3 (Figure 5.12) revealed a very similar pattern to observer M1. Instead of the mouth, M3 used primarily the left eye, left and right eyebrows and forehead. Again, these features could be found in most expression associated voxels in the Gender task. In the Expression task, I found expression diagnostic feature sensitivity in most expressions, but not all (none in "angry" and "fearful"). Again, there was one expression ("disgusted"), whose expression diagnostic information I also partially found in the Gender task.

Lastly, observer M2 only showed a weak effect, due to the MI images being very noisy. In fact, the images were originally so noisy, that I decided to use only the three most sensitive voxels of each cluster to reduce the variance of MI. So, depending on the total number of voxels in each cluster, the images in Figure 5.11 are the average of either one, two or three voxels. This decision was based on the assumption that it might be possible that different voxels integrated different information, which in turn led to the loss of individual information by averaging. The top three sensitive voxels are likely to lie close to each other and to integrate similar information; hence by restricting the number of voxels, I reduced the variance of information processing. Indeed, this strategy improved the images quite a bit, yet they were still not as clear as the other observers'. M2 used both eyes, eyebrows and the forehead for gender categorizations. These could be found in most of the expressions in the Gender task, though again not in all (no information in "disgusted" and "sad"). The same applied to the expression task with expression diagnostic information (however, no information overlap in "neutral"). Generally for this observer, however, the images are noisier and the MI values lower than for the other observers, so the observed task effect is weaker and less clear.

Finally, the overall conclusion from these results can be drawn, that categorization demands had a top-down modulatory effect on information processing in different voxels, which were sensitive to categorization accuracy. The behaviourally diagnostic information in Gender was replicated by most expression-associated voxels in the Gender task, leading to a more uniform and similar information processing across expressions. This contrasts results for the Expression task, where expression diagnostic information was processed by the different expression-associated voxels in the Expression task, leading to a more varied processing of information by voxels predictive of categorization accuracy. Hence, the results provide direct evidence for top-down control on facial feature integration during the time window of the M170.

5. Summary

The results of the MEG study have very clear implications. (1) I replicated the task effect on dispersion of peak amplitudes and latencies on the sensor-level, which I found in the EEG data, demonstrating the robustness of this effect. (2) I found very individual patterns of results for each observer, justifying a single subject approach. (3) Depending on task demands, sensitivity of brain areas to explicit, task-relevant face categories varies in either timing or location of sensitivity. This effect is present, but weaker for the implicit categories, indicating a preferential task-dependent allocation of category sensitivity. (4) The processed facial information in voxels predictive of categorization accuracy varies with categorization task and overlaps with the diagnostic information obtained from behavioural CIs for the task-relevant face category.

In conclusion, these results provide direct evidence for top-down modulation of the feature integration during the M170. There is more sensitivity to the face category that is relevant to the categorization task and this sensitivity occurs in different locations or time points. The integrated information itself overlaps with the information needed to successfully perform the categorization task at hand. This supports my hypothesis that face processing during the M170 is subject to top-down control.

Figures 5.10, 5.11 and 5.12 on the following pages: Comparison of images for MI(pixel/power) and behavioural CIs for clusters of voxels predictive of categorization accuracy for each expression, task and observer. The green box represents the Gender task, the red box the Expression task. On the left of the black line are the behavioural CIs, their most prominent diagnostic information marked with a circle (dotted for Gender, dashed for Expression). On the right of the black line are, for each expression, the MI images with the two highest MI values of all six time bins. Which time bin each image belongs to is marked at its top right corner using the same marker symbols for each bin as in Figure 5.6. Each MI image is also displayed with its own MI scale in bits for comparison (e.g. .04 = 4 bits of MI). Again, the circles correspond to the diagnostic information integrated. Note in Expression (red), this is the diagnostic information of the respective expression only.

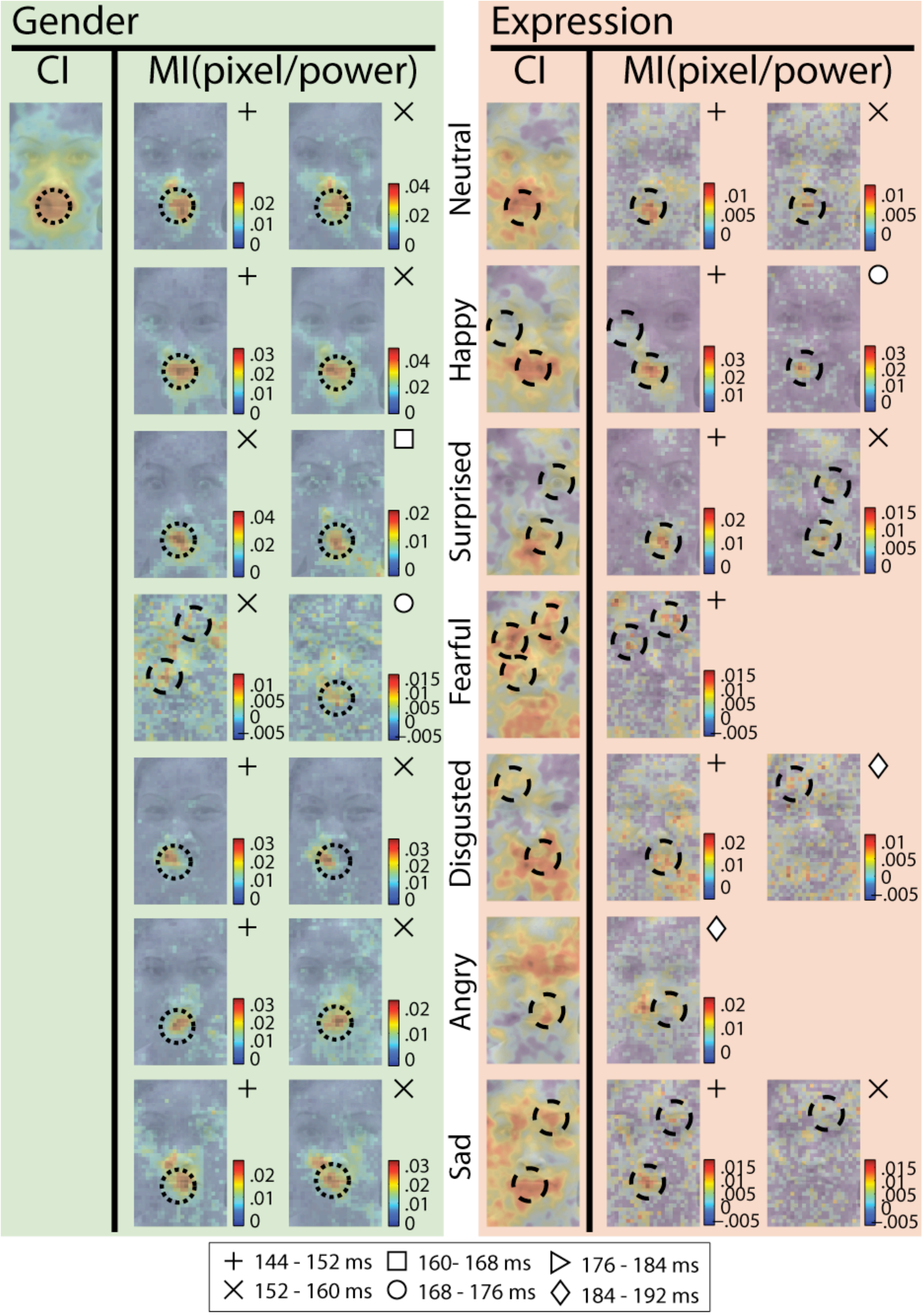


Figure 5.10: Observer M1.

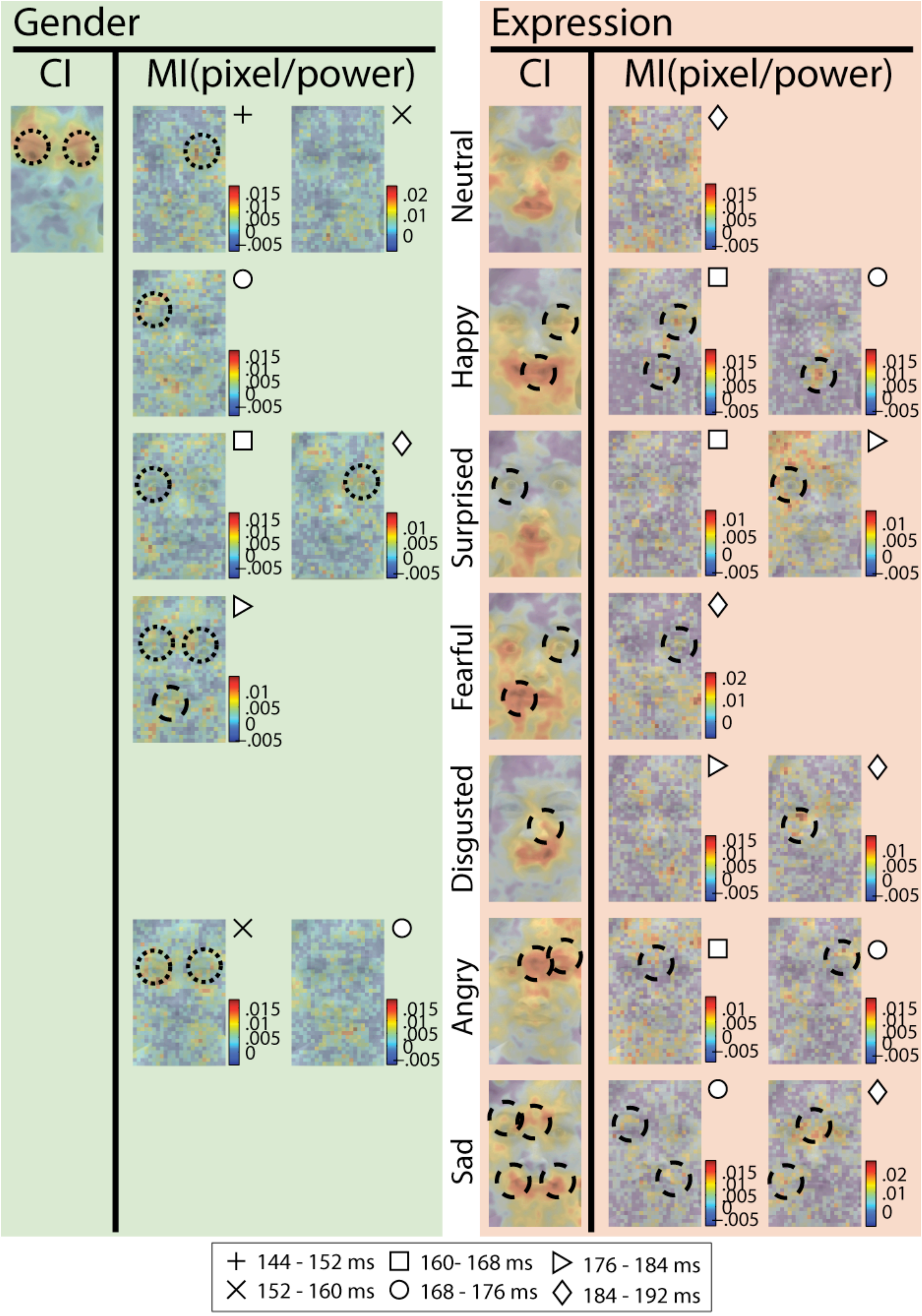


Figure 5.11: Observer M2. Each MI image represents the top three voxels of each cluster only.

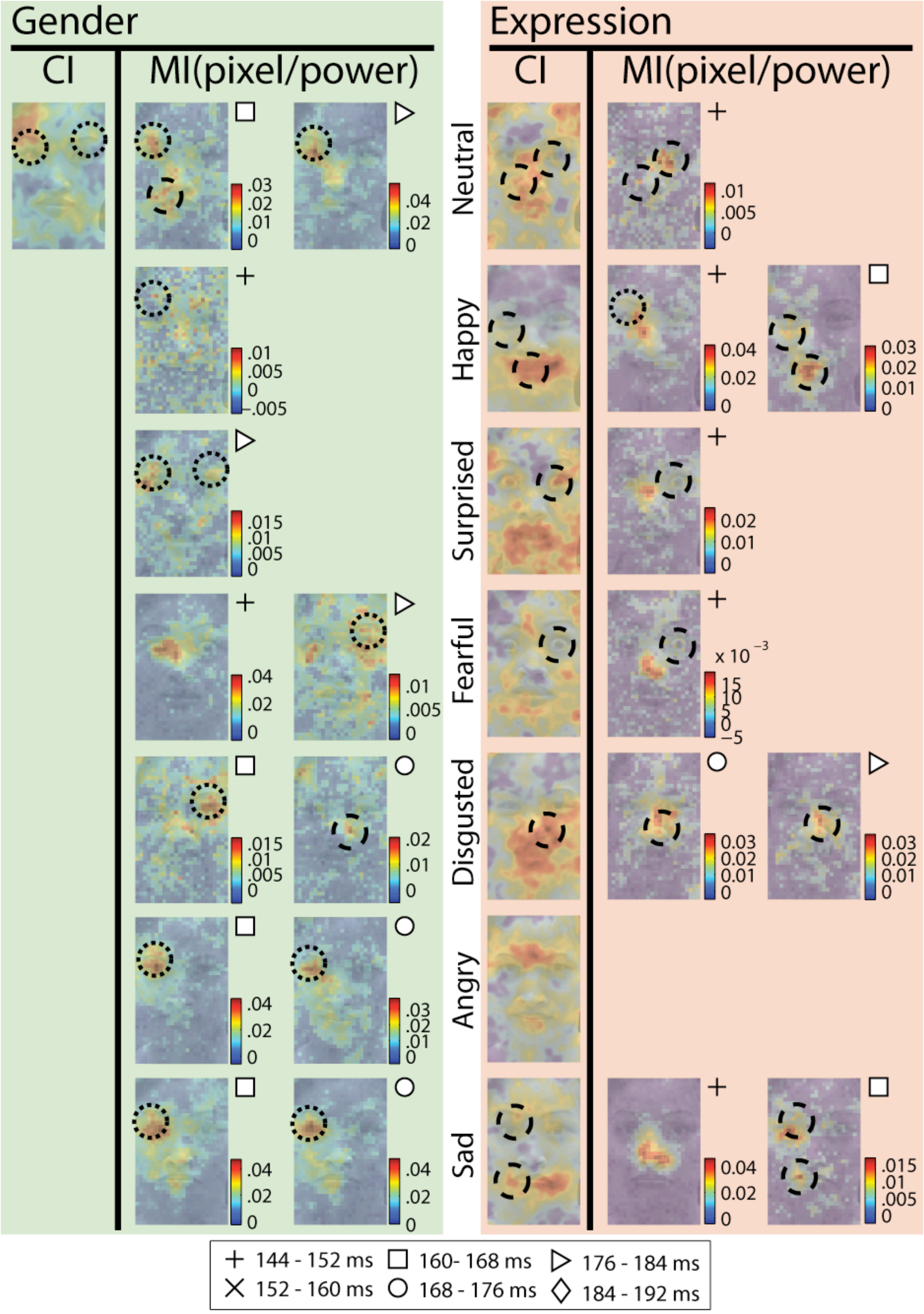


Figure 5.12: Observer M3.

VI. Discussion

The central aim of this thesis was to determine whether top-down control changes the way the brain integrates facial information during the time window of the N170 potential and M170 field. To this end I conducted two studies using the same experimental paradigm, while recording either their EEG or MEG activity. In the first study, I recorded participants' EEG signal while they categorized the same set of expressive faces by either gender (first task) or expression (second task). Behavioural analyses using Classification Image (CI) techniques and *Bubbles* exposed a task effect in the use of particular facial features to correctly perform gender or expression categorizations (diagnostic features). For example, in the Expression task observers used the smiling mouth to categorize "happy", while in the Gender task they used the eyes and only a small part of the mouth. A single sensor analysis revealed a significant task effect on the dispersion of both N170 peak latencies and N170 peak amplitudes of different expressions, with the dispersion of expressions being wider in the Expression task. Greater N170 peak differences of expressions in the Expression task suggested a possible expression specific processing of facial features. However, while this task effect was found in the timing and voltage of the peaks, a task difference in the processing of specific facial features using *Bubbles* and CI techniques with the N170 single-trial activity could not be determined. In fact, further analyses indicated that both sets of task-relevant and task-irrelevant diagnostic features were processed in both tasks at the same time. Yet, the wider dispersion found in the timing of N170 peak latencies was replicated in the timing of maximum feature sensitivity. From this, it can be concluded that despite the overlapping feature processing, the categorization task significantly modulated the timing of feature sensitivity of the N170. This modulation, in turn, impacted on the timing of the N170 peaks. This implies that the N170 reflects a function of visual feature processing and extraction (compare Schyns et al., 2007).

In the second study, participants performed the same two categorization tasks while their MEG activity was recorded. I was able to replicate the behavioural effects of task-dependent diagnostic feature use and the task effect of wider M170 peak dispersion of expressions in the Expression task. Instead of a single sensor analysis, I performed a source analysis. Next I determined brain areas sensitive to task-relevant, explicit or task-irrelevant, implicit face category (for each task) using a Mutual Information analysis. I found task differences in the timing and sources of sensitivity to both explicit and implicit face category. This indicated a top-down modulation of brain sensitivity to face categories depending on categorization demands. Next I determined the MI between the source power of voxels predictive of categorization accuracy and the corresponding bubble masks. Results revealed that the processed features in the voxel space overlapped with the behaviourally diagnostic features to a large extent. This provided strong evidence for a task-dependent, top-down modulation of information processing during the M170 time window.

In summary, top-down influences of task demands during the N170 and M170 changed:

- the timing of the processing of single expressions. The timing was more aligned for all expressions when they were task-irrelevant, and more differentiated when they were task-relevant.
- the focus and strength of brain sensitivity to the task-relevant face category.
- the facial information used by the brain to enable successful categorizations.

1. Reconciling conflicting results about top-down effects on the N170 and M170

As described in the introduction, the timing of top-down influences on face processing has been highly debated. While studies examining the timing of top-down effects on general visual bottom-up processing find differences as early as 70 ms (e.g. Eason et al., 1969), the N170 or M170 to faces was thought by some to be solely a reflection of basic, bottom-up, structural visual processing without top-down penetrability (Guillaume & Tiberghien, 2001; Cauquil et al., 2000; Carmel and Bentin, 2002; Lueschow et al., 2004; Furey, 2006; Philiastides et al., 2006; Rousselet et al., 2007; Rousselet et al., in press). In contrast, other studies found a top-down modulation of the N170 or M170 potential to faces (Sreenivasan et al., 2009; Mohamed et al., 2009; Okazaki et al., 2008; Holmes et al., 2003; Eimer, Holmes, McGlone, 2003; Crist et al., 2008; Wronka & Walentowska, 2011). All studies that found evidence opposing a top-down effect on the N170 or M170 have one feature in common (except Philiastides et al., 2006 and Rousselet et al., 2011, who used the same colour-tint paradigm): they compared the ERP to faces when faces were either targets or non-targets, while targets and non-targets were presented in different trials, i.e. never at the same time, but always at the same location. So, even if faces were task-irrelevant, they could have been processed as if they were targets for lack of a competing or distracting task-relevant stimulus. This would explain the lack of top-down effects on the N170 or M170 in these studies. Interestingly, studies that found top-down effects during the N170 or M170 either (1) had targets and non-targets superimposed onto each other, directing attention away from the faces, when they were non-targets (Sreenivasan et al., 2009; Mohamed et al., 2009; Okazaki et al., 2008), or (2) presented targets and non-targets at the same time, but not in the same location, again directing attention either to or away from faces (Crist et al., 2008; Eimer et al., 2003; Holmes et al., 2003). (3) A third kind of study used the same experimental paradigm as me, manipulating task-related feature-based attention (Wronka & Walentowska, 2011). This would suggest, that all three units of attention – feature-based, object-based and spatial attention – were able to modulate the N170 or M170 to faces when distractor stimuli were presented at the same time as the targets. My methods and results fit in nicely with this explanation: by manipulating task demands, I induced participants to attend to different diagnostic information within the same stimuli, manipulating their feature-based and/or spatial attention within the stimulus display and this resulted in a top-down modulation of N170 and M170 and facial feature processing latency, as well as a differential category and information sensitivity on the source level.

2. My results challenge some assumptions of Haxby et al.'s model of face perception

Haxby et al.'s (2000) anatomical and functional model of face perception makes certain claims as to the function of elements of the core system. Specifically, they posit, that the superior temporal sulcus (STS) is sensitive to changeable aspects of features, such as expression, whereas the fusiforma face area (FFA) is sensitive to invariant aspects, such as gender and identity. The occipital face area (OFA), in contrast, is supposed to be responsible for the simple scanning of all facial features. My results are not entirely in agreement with these hypotheses. In fact, sensitivity to both explicit and implicit face categories was already present in visual cortex (VC) and OFA for all participants. This places both gender and expression sensitivity slightly earlier – anatomically, not temporally – in the processing chain than assumed by Haxby et al. (2000). However, with respect to the OFA, this result is in line with Cohen-Kadosh et al. (2011), who found that TMS to the right OFA significantly impaired categorization of expression and identity of faces. Identity is – like gender – an invariant aspect of faces.

Furthermore, gender and identity are very strongly linked. My participants underwent long and intense testing. Hence, I have to take into account the possibility, that they learned the identities of the stimulus faces so well, that they performed an identity task to determine gender (although explicitly instructed not to). However, since both gender and identity are invariant aspects of faces, this possible task shift is of no practical consequence to my conclusions. The importance of the OFA for gender and expression categorization is further highlighted by a single-case lesion study (Steeves et al., 2006). Patient D.F., whose brain lesions overlap the OFA bilaterally, showed an increased response to faces in the FFA and performed normally in some face categorization tasks. However, she was severely impaired in categorizing identity, gender and expression. These results suggest, that the OFA plays a crucial role in the categorization of these three face categories in particular, and not only in the structural encoding of faces as suggested by Haxby et al. (2000).

In the MEG study, the FFA showed sensitivity to both gender and expressions, rather than just to invariant features (i.e. only gender). This is in line with results from several studies, using MEG and fMRI (Ganel, Valyear, Goshen-Gottstein, & Goodale, 2005; Halgren et al., 2000; Lewis et al., 2003). Surprisingly, in my results, the STS was also sensitive to both gender and expressions, but only for one observer (M2) the peak for explicit expression category was in the STS. It could be that my time window was too early for expression category sensitivity in the STS to reach a maximum for other participants as well. Had I included later time points, for example the P300 or a time window just after 200 ms, into my time window of interest, I might have found STS sensitivity to expressions in all participants (Furl et al., 2007).

The most puzzling result of the sensitivity localization is certainly the fact that I found sensitivity to different face categories in core visual areas (VC) during the N170 and M170 time window. While it is known that the VC, especially V1, V2 and V4, can be influenced by spatial attention (Bressler & Silver, 2010; Luck, Chelazzi, Hillyard, &

Desimone, 1997; J. Moran & Desimone, 1985), less is known about their categorical face sensitivity in response to task demands. There is, however, evidence for differential responses when categorizing the same stimuli by either patterns or colours (McClurkin & Optican, 1996), indicating a possible top-down influence in response to task demands on these core visual areas. In addition, further clues of face sensitivity in core visual areas are provided by Wilkinson et al. (2000). Specifically, they found that the human V4 was activated by faces to the same extent as the FFA. Both FFA and V4 were also activated by concentric sine patterns, however, V4 more so than FFA. Since faces contain a lot of concentric sine features, this overlap is not too surprising and could explain the face sensitivity I found during the M170 in VC[3]. However, my study extends the simple face sensitivity of core visual areas like V4 to sensitivity to task-relevant face categories, which implies that V4 (or other core visual areas) might also process semantic, categorical face information once low-level visual information like orientation, shapes etc. have been processed.

3. Why was there no task-differential feature processing in the EEG study?

When comparing the results of the two presented studies, the question arises why the EEG data did not yield a clear task effect of N170 feature processing. One very likely explanation is that the scalp N170, being the summation of the activity of several different brain sources, is too insensitive to distinguish between the sources' differential information sensitivity. The summation problem with scalp ERPs becomes even clearer,

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[3] The spatial resolution of our results is not detailed enough to distinguish well between different core visual areas (8 mm voxel size). However, regarding the evidence mentioned, V4 seems to be a likely candidate for the effects we observed in this general region, despite the fact, that some of the VC activation seems closer to the midline of the brain and therefore closer to V1 or V2.

when regarding all the different studies, which determined the source of the N170 – there is quite a variation in findings – including all three components of the core system of face processing (Haxby et al., 2000; Herrmann et al., 2005; Itier & Taylor, 2004; Schweinberger et al., 2007). In addition, my own results from the MEG study further corroborate this possibility. I found sensitivity to two different face categories during the M170 time window, and the focus of this sensitivity was in different brain areas. Since the source analysis was conducted using a very small time window around the M170, it is safe to assume that most information sensitivity found in occipitotemporal regions contributed to the M170 potential to a certain extent. If I presume that the EEG participants have displayed the same changes in brain sensitivity as the MEG participants, with sensitivity present to both explicit and implicit face categories during the N170 and M170, it is unsurprising that the ERP picked up on both sets of features.

It is possible that, had I extended the analyses to other electrodes, I would have found a task effect in some electrodes; especially since the brain areas found in the MEG study varied greatly in spatial location. Of course, my approach of picking the most active electrodes – an "electrode-of-interest" approach – even though widely-used (Picton et al., 2000; Rossion, Gauthier, et al., 2000; Sreenivasan et al., 2009), is not optimal. A great deal of information and variance in brain activity is lost when singling out sensors (Rousselet & Pernet, 2011). However, as explained before, reverse correlation and CI techniques take up a fair amount of processing time. A solution to this problem could be to apply a Mutual Information approach to all of the EEG sensor data, analogous to the approach used in the MEG voxel-based analysis. Using MI, one could obtain a topography of sensors, which could be more or less sensitive to either different face categories or correct categorizations, allowing then to look at feature processing at the sensors most active by pre-defined criteria.

Another problem I encountered with my EEG analysis was a fair amount of noise in the sensor-based CIs. On the one hand this was connected to lower trial numbers, but on the other hand this was probably also caused by issues of skull and tissue conductance impacting on the EEG signal (Hansen et al., 2010). Another option to reduce noise and increase focal activity of the EEG is to transform it into *Current Source Density* (CSD) by computing the surface Laplacian estimate of the electrophysiological topography (Nicholson & Freeman, 1975; Pernier, Perrin, & Bertrand, 1988). Not only is the CSD more focal and less smeared than the EEG potential (Pernier et al., 1988), it is also a reference-free measure, meaning that regardless of the EEG reference used, the CSD will always look the same (Kayser & Tenke, 2010). While Junghoefer et al. (1997) suggested using more than 100 electrodes to improve accuracy of the CSD, solutions have been found for low-density (< 64 electrodes) EEG data (Kayser & Tenke, 2006). It could be beneficial for the clarification of the results to check whether the use of the CSD in conjunction with the MI technique would improve the EEG signal to the extent that I would find task effects on the facial feature processing during the N170.

Despite and because of the lack of a task effect in the information processing of the N170, the EEG findings allow an important conclusion, that is further corroborated by the MEG results: both sets of task diagnostic features were integrated during the N170 and M170. While information processing during the N170 potential does not distinguish between the two tasks, indicating parallel, but possibly interacting feature processing, the N170 peaks and amplitudes for each task clearly do and the MEG results clarify, that sensitivity to both face categories was present, albeit much weaker for the task-irrelevant category. A further test (using the MEG data) of the integration of both sets of features would be to compare categorization-diagnostic voxels with voxels not predictive of task performance. Comparing their MI(power, pixel) could reveal whether the task-irrelevant diagnostic information was integrated in voxels not predictive of performance. Interestingly, one strand of face research has postulated that face recognition (e.g. identity or gender) is separate, but parallel to expression (Caharel, Courtay, Bernard, Lalonde, & Rebao, 2005). This assumption stems from Bruce and Young's model of face perception (1986). While some studies found no interaction between behaviour or ERP amplitudes when comparing tasks judging either variant or invariant face characteristics (Sergent, Ohta, Macdonald, & Zuck, 1994; Young, Newcombe, Haan, Small, & Hay, 1993), others, especially more recent studies, showed that the processing systems for variant and invariant face characteristics do indeed depend on each other to a certain extent (Aguado, García-Gutierrez, & Serrano-Pedraza, 2009; Baudouin, Gilibert, Sansone, & Tiberghien, 2010; Lander & Metcalfe, 2007; Martens, Leuthold, & Schweinberger, 2010). In light of this research background, it is not surprising, that both expression and gender diagnostic features were integrated at the same time during the N170/M170 time window and that the N170 and M170 reflected both processes. In fact, the reported (significant) greater dispersion of expression ERPs in the Expression task reflects a statistically significant interaction between expressions and categorization task. This could be interpreted in a sense, that gender either facilitates the processing of certain expressions or vice versa – that some expressions facilitate the processing of gender – or both. Evidence exists for both ways from research studying the influence of face familiarity on expressions (Dobel et al., 2008; Kaufmann & Schweinberger, 2004; Schweinberger & Soukup, 1998).

One result from the MEG analysis, that could provide further insight into this interaction, is the spatial and temporal pattern of voxels predictive of categorization performance (Figure 5.9). When comparing the diagnostic voxel patterns, there is a great difference across tasks per expression. Specifically, there was a greater bias in Expression for voxels to be diagnostic for “happy” (green), whereas in Gender, diagnostic voxels usually appeared for other and sometimes a greater number of different expressions. It is well known, that “happy” – being the only positive expression among negative ones – is usually easiest to categorize (Hugenberg, 2005). Hence I was wondering whether the greater number of diagnostic voxels for “happy” in Expression was related to categorization difficulty. I asked one observer (M3), who was the only one available, which expressions she found easiest to categorize. Without much thinking, she replied: “Happy and sad”. Interestingly, “happy” and “sad” (black) are the expressions represented by the most diagnostic voxels in the Expression task for this observer. While this is only incidental data, it could nevertheless be a hint towards the meaning of greater diagnostic voxel numbers for categorization performance. In the Expression task, it could indicate, which expressions were easiest to categorize. In contrast, in the Gender task, this information could uncover, which expressions contributed most usefully to gender categorizations in the Gender task. While observer M1 seemed to have benefited from all expressions in the Gender task, M2 and M3 did not show any diagnostic voxels related to “happy” and diagnostic for gender categorizations (while they do for expression categorizations). This could suggest, that “happy” is not very useful for the judging of gender, but more so for the categorization of expressions, revealing the possible nature of the interaction between expression shown and task performed. A study manipulating the task difficulty systematically would provide further insight into this interaction.

4. Methodological issues of these findings

A common criticism of experiments involving *Bubbles* is the small number of participants. While a lot of experiments in Psychology use a wide range of numbers of participants, it is generally agreed that three participants is too little. However, in addition to practical limitations (running one participant took about three months), there are other factors, which justify the use of fewer participants. Higher numbers of participants are generally recommended because experimenters are interested in group effects and averages across participants. Not only was I not aspiring a group comparison, the individual variance in these data also suggests, that averaging might result in the loss of individual task effects. Just as averaging the MEG or EEG signals results in a loss of single-trial variance, averaging across participants results in a loss of single-subject variance (Rousselet & Pernet, 2011). As demonstrated before, these and previous studies take into account the single trial variance and clearly show, that this variance does indeed carry meaningful information (Delorme, Makeig, Fabre-Thorpe, & Sejnowski, 2002; Mouraux & Iannetti, 2008; Rousselet et al., 2007; Schyns et al., 2007, Schyns et al., 2009). In addition, Rousselet and Pernet (2011) make a strong case for single-trial and single-subject analyses. Naturally, a single-subject approach per se cannot be used to justify a small number of participants. However, since I did not aspire group analyses, a smaller number of participants can be justified given the practical restraints.

Bubbles has also been criticised for other reasons; Murray and Gold (2004) pointed out two issues in particular. First, they stated that *Bubbles* does not fully characterise the LAM (Linear Amplifier Model) observer. This would make *Bubbles* inferior to other reverse correlation methods. Secondly, they identified a practical shortcoming: the Gaussian apertures would force observers to use the information available rather than let them apply their own natural pattern of information usage. This could result in misleading diagnostic information patterns, in turn reducing their ecological validity dramatically. The original authors respond to these claims in a reply article (Gosselin and Schyns, 2004). They address the first issue by pointing out that the LAM observer is an ideal model, but by no means an accurate model for a human observer. They state that the LAM observer represents a case that is an outlier in the real world, in all other cases *Bubbles* and other reverse correlation methods perform the same. As to Murray and Gold’s practical issue, Gosselin and Schyns (2004) refute their concerns by showing that results from a direct comparison of *Bubbles* and a Gaussian noise reverse correlation method are highly correlated, thus suggesting that *Bubbles* does not change observers’ information usage pattern. In summary, the most criticised issues of *Bubbles* are not problematic after all.

Finally, the fact that my findings fit in with the wider research context (e.g. the task effect in behavioural diagnostic information, the task difference in N170 peak dispersion, the top-down modulation of the N170 and M170, generally an influence of attention on early visual processing), additionally underline the validity of my analyses and results. Furthermore, rather than simply reporting task effects found in brain activity, I assigned visual information to the activity observed and was able to demonstrate task effects on the information level.

5. Scope and future directions

The presented analyses were restricted to a very narrow time window and only one general brain area (occipital and occipito-temporal regions). While this was useful in order to test my hypothesis, it would also be very informative to extend my analyses to all time points and brain voxels. That way it would be possible to determine, where and how the first sensitivity to faces and face categories emerges and when this information becomes decision relevant. The involvement of the extended system of face processing (Haxby et al. 2000) could possibly be mapped out. Liu, Harris and Kanwisher (2002) found, that activity in occipitotemporal areas as early as 100 ms after stimulus onset were already correlated with the perception and correct categorization of faces as compared to other objects. However, correct categorization of identity was only correlated to later activity during the M170. From these results I would predict from my data, that sensitivity to different face categories is not present at 100 ms, but develops subsequently and reaches a peak shortly before or at the N170 or M170 peak (also see M. L. Smith et al., 2009). The presented data could also be reanalyzed to address the question of how task impacts on processing after the N170 or M170. A much stronger category and diagnostic facial feature sensitivity could be hypothesized to emerge around 300 to 400 ms, corresponding to the time window of the P300, which is thought to be involved in decision making (Nieuwenhuis, Aston-Jones, & Cohen, 2005; Sutton, Braren, Zubin, & John, 1965; Sutton, Tueting, Zubin, & John, 1967). In addition, category related voxels that are associated with the fronto-parietal attention network (Sutton et al., 1967) might reflect top-down influences that are dependent on task. Using MI, this top-down category sensitivity could be mapped out in a temporally and spatially accurate manner, answering the question of how, when and through which mediating structures top-down control is exerted.

An area that has been thought to mediate top-down influences on the face processing system and that is also part of the extended system of Haxby et al.'s model is the amygdala (Adolphs, 1999; Pessoa, 2010). It is supposed to be especially involved in the evaluation of affective significance (Pessoa & Adolphs, 2010). The MI approach combined with *Bubbles* has the potential to elucidate, whether categorization task has an influence on the activity of the amygdala, especially in response to certain features, like the eyes, or expressions, like fear or anger (Adolphs, 1999). For example, because expressions are not task-relevant in the Gender task, the amygdala might not process "fear" preferentially in this task, only in the Expression task (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003). This would contrast findings from several studies demonstrating that the amygdala is independent of attention (Anderson et al., 2003; Dolan & Vuilleumier, 2003; Pessoa, Kastner, & Ungerleider, 2002), but also be in line with studies from Pessoa et al. (Pessoa, Kastner, et al., 2002; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002). Luo et al. (2010) suggest, that attention effects on the amygdala can only be observed after 280 ms, but before that the amygdala responds completely automatically and without top-down influences. Given these contrasting results, analysis of my data using MI and *Bubbles* might further elucidate this matter by extracting specific task-dependent facial information from activity in the amygdala.

6. Conclusions

The research presented in this thesis provides evidence for differential, task-dependent facial feature processing during the N170 and M170 time window. My findings corroborate findings from previous literature on task-dependence of the N170 and M170 and fit in nicely with findings from the wider literature about top-down effects on visual processing. By using *Bubbles* in conjunction with Classification Images and Mutual Information, I succeeded in extracting feature sensitivity correlated with brain activity, both on the scalp surface and on the source level of highly time-resolved neuroimaging data, in response to different categorization demands. These techniques have proven their usability and generate a wealth of information, which can and should be used to assess visual processing in the brain and to complement previous findings on an informational level.

VII. Appendix

A. The task effect of ERP dispersion is not caused by adaptive task differences in bubble numbers

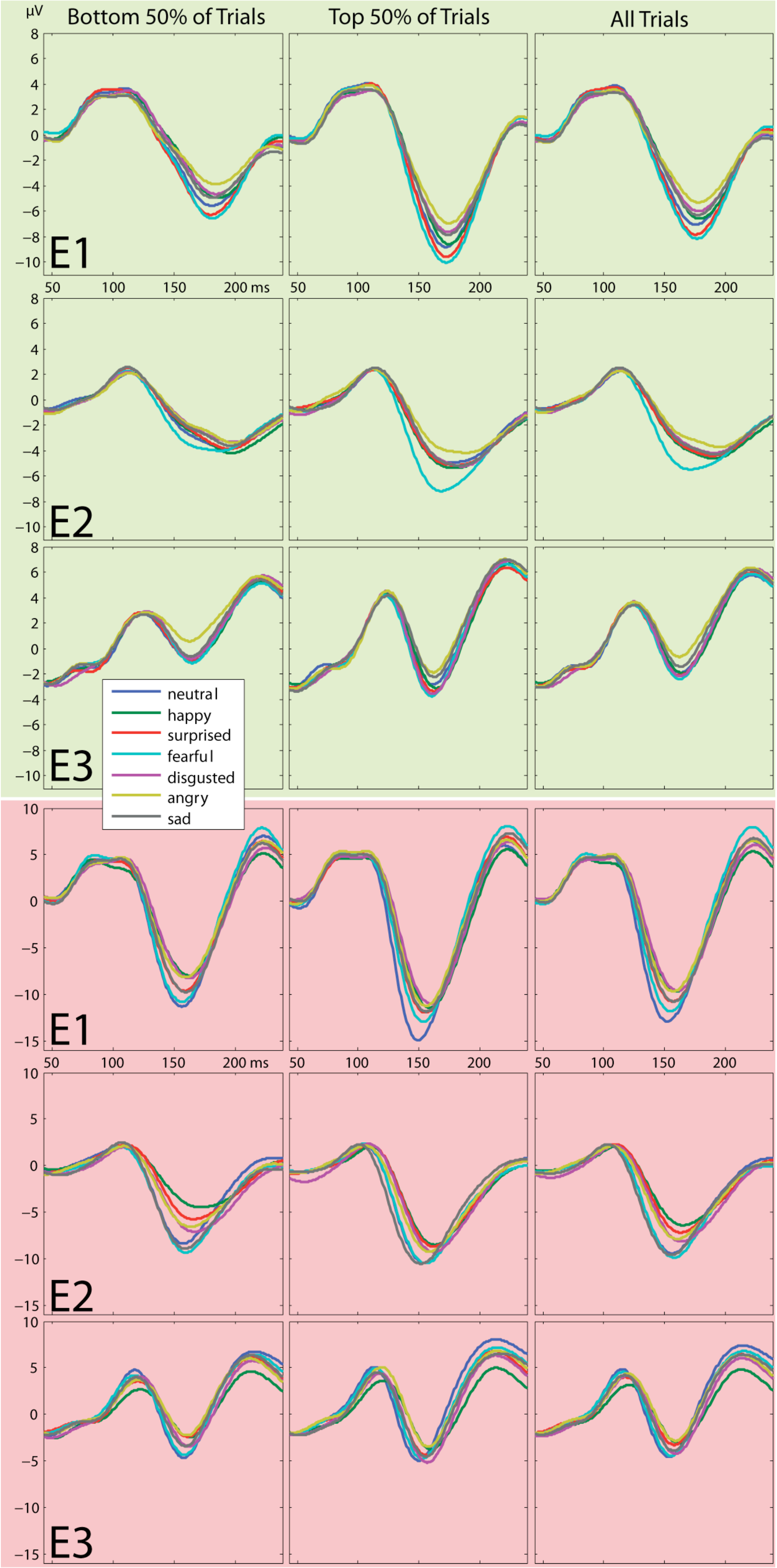
As mentioned in the Chapter II, bubble numbers were adapted online to maintain an accuracy threshold of 75% per condition. Due to the nature of the tasks, observers performed better in the Gender task, which led to lower bubble numbers in this task. Furthermore, bubble numbers were more varied in the Expression task due to the different degrees of difficulties in judging expressions. For example, “happy” generally had lower bubble numbers than “angry” or “sad”. The amount of bubble numbers in each trial is a direct correlate of facial information shown to the observer. Even though low-level sensory parameters of the image were kept constant, it was imperative to rule out the possibility, that the variation in the amount of meaningful information shown – and thus the task difficulty – did not cause the greater dispersion in ERP latencies in Expression.

To this end, I first plotted the ERPs for the bottom 50% of trials of the bubble number distribution and the top 50% of trials separately in groups. In either group there seemed to be the same kind of latency dispersion, i.e. lesser dispersion in the Gender task and higher dispersion in the Expression task (Figure A1). For the amplitudes, the picture was not so clear, but since my Regression Analysis (Chapter IV) was based on the latency rather than the amplitude dispersion, this finding is not problematic for the interpretation of my results.

In order to further corroborate the reliability of the ERP and regression analyses, which were based on the N170 latencies, I sorted all trials by their bubble numbers and plotted their EEG traces in one single image (Figure A2). If there had been a relationship of N170 latencies with bubble numbers, there should have been a clear latency decrease with increasing bubble numbers. However, it is obvious from the figure, that there was no decreasing ERP latency with increasing bubble numbers for any of the three observers. Additionally, there was also no systematic relationship between the N170 amplitude and the amount of bubble numbers, which would be represented in a decrease or increase in colour (white) with increasing bubble numbers.

These results suggest that the amount of bubble numbers (facial information shown to the observer) and thus the task difficulty had no direct effect on the N170 latency or amplitude. This rules out an alternative explanation for the task effect I observed in both N170 latency and amplitude dispersion and the regression analyses in the EEG study.

Figure A1 (page 120): ERPs for all three observers and tasks plotted separately in groups of trials with low bubble numbers (left column), high bubble numbers (middle) and all trials together (right). The peak latencies across expressions quite obviously are just as aligned (Gender, green panel) or varied (Expression, red panel) in both high and low bubble number trials compared to all trials. This provides evidence against an alternative explanation based on information shown and task difficulty for the differing ERP latency dispersion observed in each task.


μV
Bottom 50% of Trials
Top 50% of Trials
All Trials
8
6
4
2
0
−2
−4
−6
−8
−10
E1
E2
E3
50
100
150
200 ms
200
neutral
happy
surprised
fearful
disgusted
angry
sad
10
5
−5
−10
−15

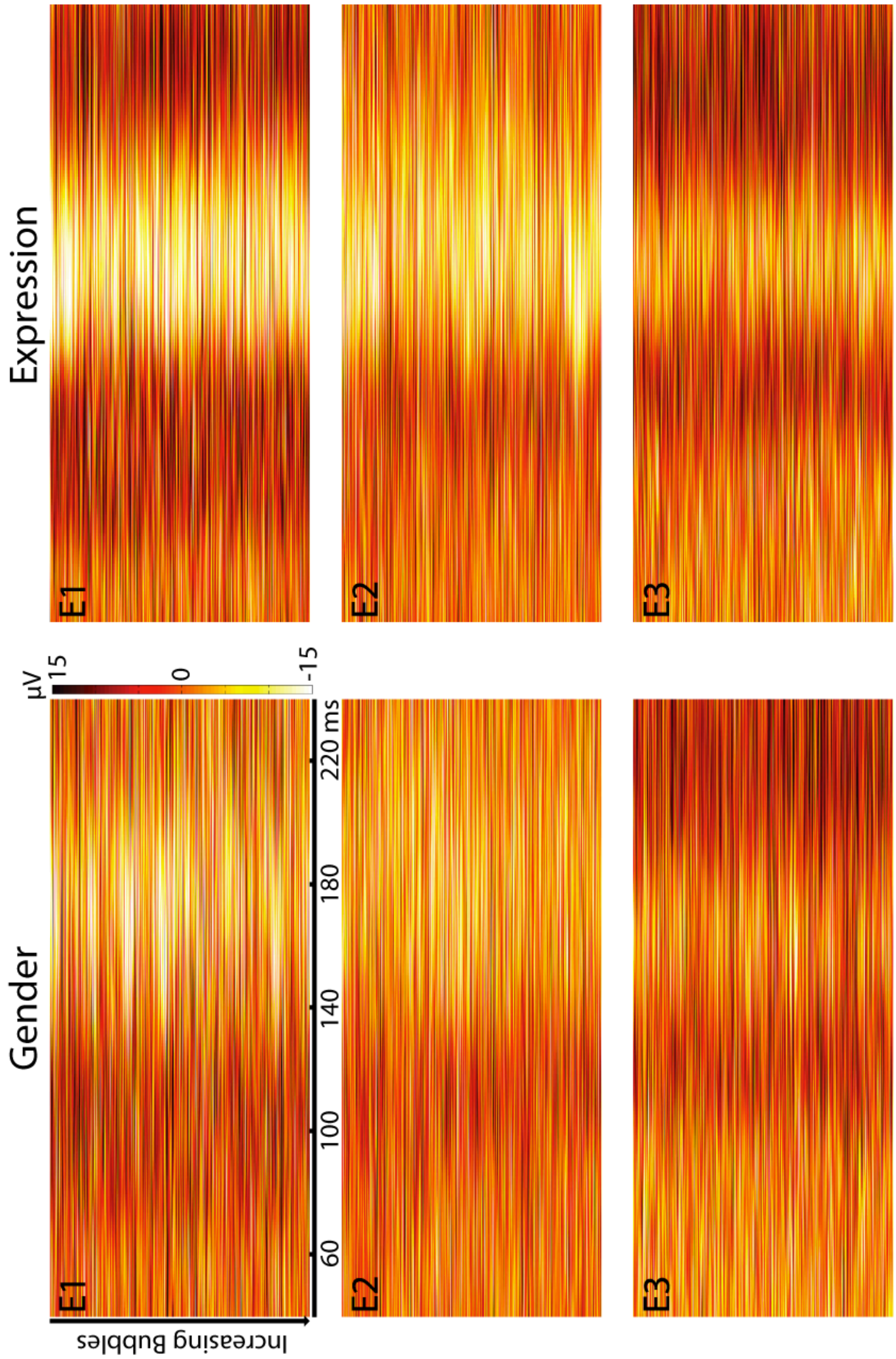


Figure A2: All trials per task are plotted in ascending order according to their bubble numbers, i.e. information shown. The rows represent observers in the usual order (E1-3). There is no systematic time shift of the N170 with increasing bubble numbers towards shorter N170 latencies. Similarly, N170 amplitudes are not higher or lower with increasing bubble numbers, suggesting that amplitude differences are not caused by differing amounts of facial information shown.

B. Additional analysis approaches for the EEG data

Since *Bubbles* is not a widely used technique, there are only a few established analysis steps, such as the computation of the various kinds of CIs. However, past the computation of CIs, there are no standard analyses. Consequently, many different analysis approaches were explored and tried before the final conclusions were drawn. This part of the appendix introduces two approaches that were adopted along the way, but turned out to be inferior to the final analyses (1.) or too inconclusive (2.) and were hence excluded from the main chapter. Other adopted approaches are not mentioned here, as they never reached a stage of presentability.

1. Sensor-based CI computation using EEG amplitudes as weights

As described in the Chapter III, CIs were computed by sorting bubble masks into amplitude bins and then subtracting the bottom from the top half of bins to gain information that preferentially elicited higher negative EEG amplitudes. This approach discretised the bubble mask distribution. At the start of the EEG analysis I decided to compare this discrete computation technique (method A) with a parametric computation technique (method B). For each time point along the N170 time window, I simply multiplied the (normalized) bubble masks with their corresponding amplitude value and added these weighted masks for all trials per expression. This allowed me to derive parametrically weighted CIs on the sensor level. I compared both sets of CIs visually and in addition analysed them in the same manner with some of the analysis approaches described in this thesis. Results were generally more stable and less noisy using method A. This was most likely caused by the greater sensitivity of method B to amplitude outliers, giving disproportionate weight to single bubble masks, whereas method A treated all outliers as belonging to the same amplitude bin, making CIs more robust.

2. A scan path analysis revealed individual and possibly task-dependent scanning patterns across observers

Schyns et al. (2007, 2009) found that the focus of facial feature sensitivity within one sensor-based CI of each observer and expression (the "scan path") followed a very specific pattern along the N170 time window. The integration would usually start in the eyes, then expand on and move downwards in the face towards the mouth. However, the integration process would end as soon as expression diagnostic information was integrated, for example the corners of the nose in "disgusted" or the mouth in "happy". According to the predictions of my hypothesis, I would expect the scan paths in the Gender task to be very similar across expressions, and in the Expression task to differ between expressions, especially towards the end, when the focus ends on the diagnostic information of each expression as opposed to the diagnostic information for gender.

I attempted to replicate their findings by plotting the y-coordinate of the maximum of information sensitivity within one sensor-based CI per time point against the time course of the N170. I cut off the scan path as soon as the maximum of information sensitivity was determined by activation outside the face area (as this indicates that noise sensitivity is greater than facial feature sensitivity). The results can be seen in Figure B1. Each observer represents one row of individual behavioural CIs for expression categorization. On each behavioural expression CI, I plotted the scan path of each task against the y-axis of the CI and the time scale of the N170 (Gender = green, Expression = red). Again, the N170 peaks were aligned and the white line denotes the point of the N170 peak (same for all images). My observers did not seem to follow the exact same eyes-to-mouth pattern that Schyns et al. (2007) suggested, instead there appeared to be a large variation across observers, tasks and expressions. While observer E1 showed the classic eye-to-mouth scanning pattern, Observer E3 showed the reverse (especially in Expression), generally starting with the mouth and then scanning upwards in the face. Observer E2, on the other hand started the scanning process either in the eyes, or the middle of the face.

The next question is now, whether the scanning process stopped and the N170 peaked when the diagnostic information was integrated. It is quite obvious that the scanning process didn't always stop right with the peak, but continued ~ 10 – 20 ms afterwards. However, most of the new information was integrated before the peak. For reference, Figure B1 plots the scan paths on top of the diagnostic information for expression. As a reminder, the diagnostic information for gender (see Figure 3.2) comprised the mouth and one or both eyes for all observers. Hence, within observers I would expect very similar scan paths across expressions for the Gender task and the scan paths would stop after the same information was integrated. The latter appeared to be true for all observers in most expressions. The N170 in Gender for observer E1 peaked after the eyes were integrated, but scanning often went down to the mouth just after the peak. For observer E2 it peaked after the mouth and/or the eyes were integrated and there was no new information after the peak. Observer E3 integrated both the mouth and the eyes before the peak (except in “sad”, where the mouth was integrated after the peak, and “disgusted”, which only included the eyes in the scan path). These results agree with Schyns et al.'s (2007) predictions of the N170 integrating diagnostic information. However, the great variation of scanning patterns within observers in the Gender task (especially E2 and E3) was in contrast to my hypothesis that Gender scan paths would be more similar than Expression scan paths.

For the Expression task, there was a similar picture. While there was a (predicted) large variation across expressions, the (red) scan paths nevertheless included all expression diagnostic features for

- five expressions in E1 – except “disgusted” and “sad”, where only the upper half of the face was scanned.

- four expressions in E2 – except “neutral”, “surprised” and “angry”, where scanning didn’t quite go up to the diagnostic eyes. However, bubbles in lower SF bands would have a radius that included the eyes at this point on the y-axis, so at least for “neutral” and “angry” the eyes would have been included in the scanned information (whereas “surprised” integrated the eyes in a high SF band).
- all expressions in E3.

While the above results indicate a replication of Schyns et al.’s results, the effects were difficult to quantify with respect to my hypothesis due to the great overlap of integrated information (for example compare the scan paths for “happy” across tasks) and the great variance over time within-observer, across-observer and within-task. Hence, it was impossible to interpret these descriptive results with respect to my hypothesis, which aimed to disambiguate different processing strategies with respect to the two categorization tasks.

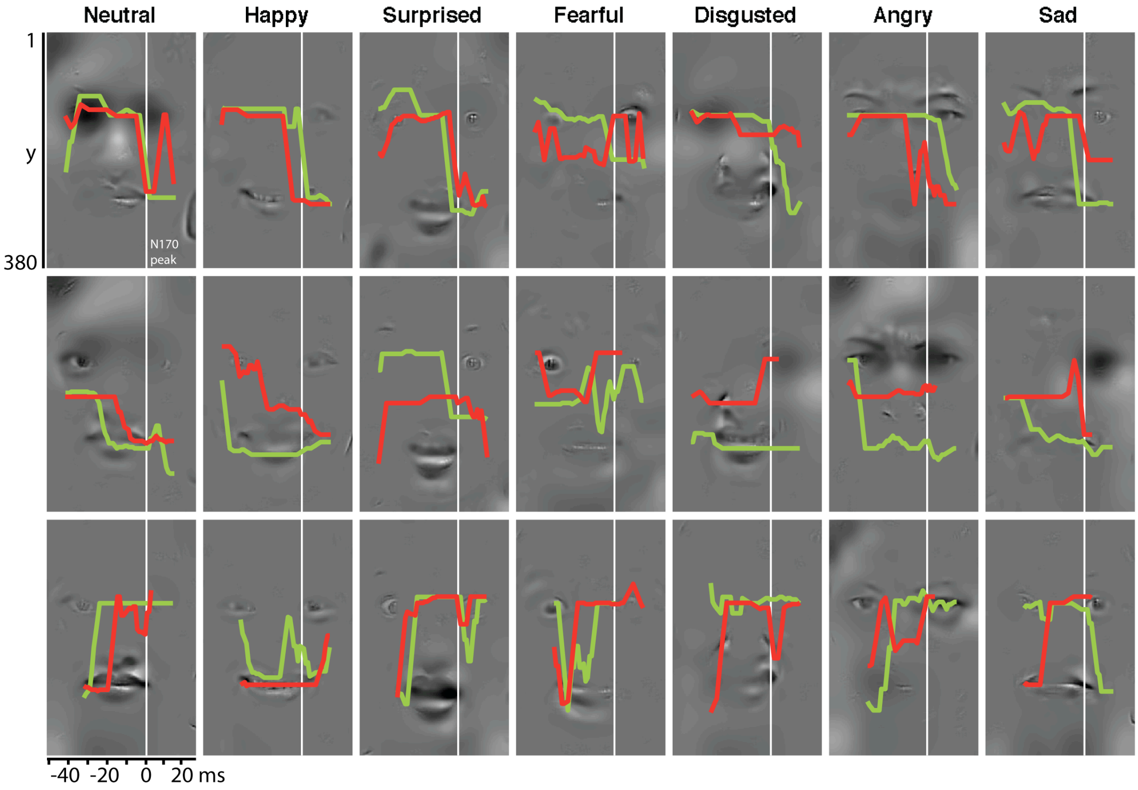


Figure B1 (previous page): Scan paths for all three subjects (rows, E1 at the top, E2 in the middle and E3 at the bottom) and seven expressions (columns) for Gender (green lines) and Expression (red lines). Scan paths are plotted on the background of behavioural CIs for expression categorizations to simplify interpretation of scan paths in relation to diagnostic expression information. The scan path denotes the maximum of information sensitivity on the y-axis of the sensor-based CI along the time window of the N170 (x-axis of each image). The scan paths are aligned to the N170 peak (white line). See text for further discussion.

C. Voxel-based CIs and their MI counterparts: a comparison

Instead of using the CI approach I used in the EEG study, I opted for the MI approach in the MEG study. The reasons for this were mainly of a practical nature. Instead of computing CIs for more than 1000 voxels, and looking at all of them to find voxels showing differential task-dependent feature integration, I instead used MI to find voxels sensitive to face categories and predictive of categorization accuracy per expression (the MI approach is more flexible in this respect). I then picked voxels of the latter group and computed images for sensitive voxels representing MI(source power/pixel), henceforth called MI images. In this step I could have computed CIs as well, but I chose the MI approach to stay consistent with my methodology within the MEG study. However, before making this decision, I compared, for a subset of voxels, MI images with voxel-based CIs (see Figure C1). Voxel-based CIs were computed in analogy to sensor-based CIs: Single-trial source power was reverse-correlated with corresponding bubble masks using the same binning procedure described in Chapter III.

From the comparison of voxel-based CIs with analogous MI images I drew three main conclusions:

1. MI images and CIs are sensitive to the same face information at the same time points in the same voxels.
2. MI images capture both positive and negative deflections in the CIs.
3. MI images might be slightly less noise sensitive than CIs, but they are also slightly less sensitive to real information.

Figure C1 shows two representative examples of the same time points in two voxels and two expressions, comparing both CIs and MI images. Both voxels illustrate nicely, that the focus of information sensitivity was on the same face areas in both CIs and MI images. While voxel A had meaningful positive deflections in the CIs and voxel

B negative ones, the MI images of both voxels captured either deflection as an increase in MI. Hence, using MI did not result in loss of information sensitivity, however, it did treat sensitivity to the presence and absence of features the same. Depending on the research question, this could lead to a problem, if one is interested to distinguish between these two cases. Yet, this is not the aim in my MEG study. I was interested in sensitivity to features depending on task, whether absent or present is irrelevant; either case makes a statement about voxel sensitivity in the context of top-down task effects.

Voxel A is a good example of the reduced noise sensitivity of the MI approach. At the first time point of “fearful” (x) there was a fairly high (slightly red) area in the bottom left corner of the CI, which was not present in the MI image at the corresponding time point (x*). However, the second time point (y) in “disgusted” showed a lower value (yellow) than x at the height of the left eye in the CI, but this information is present in the corresponding MI image y*. Also, MI images were generally more focused onto a certain feature, whereas CIs seemed to be more widespread in their sensitivity, leading me to the conclusion that CIs are generally more sensitive, but with a trade-off of higher noise sensitivity. Since one of the major problems in the EEG study was high noise in the CIs, the lower noise sensitivity of the MI technique is an advantage.

In conclusion, this comparison showed that MI images are a valid substitute for voxel-based CIs. They capture both positive and negative deflections of CIs, which can be an advantage or disadvantage depending on research question. In general, MI images are slightly less sensitive and more focused than CIs. This is a benefit compared to the much more noise sensitive CIs.

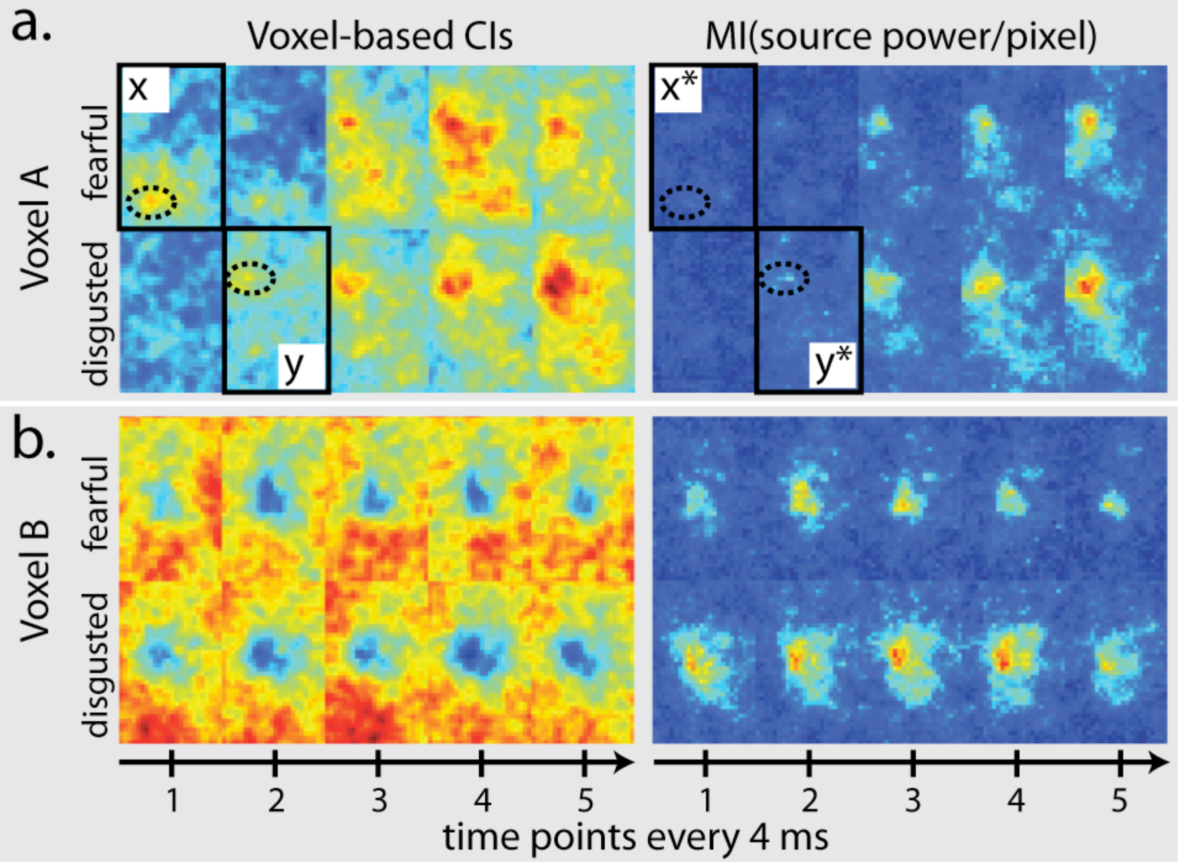


Figure C1: Comparison of voxel-based CIs and MI images displaying MI(source power/pixel). Both voxels show that MI images capture the same face information as CIs, be the CI deflection positive or negative. Also, MI images are less sensitive to noise: The fairly high values in x (circled) are not represented in x*, but the comparatively lower values in the left eye in y (circled) are represented in y*.

VIII. References

Adolphs, R. (1999). The Human Amygdala and Emotion. *Neuroscientist, 5*(2), 125-137.

Adolphs, R. (2002a). Neural systems for recognizing emotion. *Curr Opin Neurobiol, 12*(2), 169-177.

Adolphs, R. (2002b). Recognizing emotion from facial expressions: psychological and neurological mechanisms. *Behav Cogn Neurosci Rev, 1*(1), 21-62.

Afraz, S.-R., Kiani, R., & Esteky, H. (2006). Microstimulation of inferotemporal cortex influences face categorization. *Nature, 442*(7103), 692-695.

Aguado, L., García-Gutierrez, A., & Serrano-Pedraza, I. (2009). Symmetrical interaction of sex and expression in face classification tasks. *Attention, Perception, & Psychophysics, 71*(1), 9-25.

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: role of the STS region. *Trends in Cognitive Sciences, 4*(7), 267-278.

Anderson, A. K., Christoff, K., Panitz, D., De Rosa, E., & Gabrieli, J. D. E. (2003). Neural Correlates of the Automatic Processing of Threat Facial Signals. *Journal of Neuroscience, 23*(13), 5627-5633.

Arsalidou, M., Morris, D., & Taylor, M. (2011). Converging Evidence for the Advantage of Dynamic Facial Expressions. *Brain Topography*, 1-15.

Auckland, M. E., Cave, K. R., & Donnelly, N. (2007). Nontarget objects can influence perceptual processes during object recognition. *Psychonomic Bulletin & Review, 14*(2), 332-337.

Backus, G. E., & Gilbert, J. F. (1967). Numerical applications of a formalism for geophysical inverse problems. *Geophysical Journal International, Royal Astronomical Society, 13*, 247-276.

Bar, M. (2003). A Cortical Mechanism for Triggering Top-Down Facilitation in Visual Object Recognition. *Journal of Cognitive Neuroscience, 15*(4), 600-609.

Bar, M., & Aminoff, E. (2003). Cortical Analysis of Visual Context. *Neuron, 38*(2), 347-358.

Baudouin, J.-Y., Gilibert, D., Sansone, S., & Tiberghien, G. (2010). When the smile is a cue to familiarity. *Memory, 8*(5), 285-292.

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, v8*(n6), p551(515).

Bentin, S., & Deouell, L. Y. (2000). Structural Encoding and Identification in Face Processing: ERP Evidence for separate mechanisms. *Cognitive Neuropsychology, 17*(1), 35-55.

Berger, H. (1929). Ueber das Elektrenkehalogramm des Menschen. *Archiv fuer Psychiatrie und Nervenkrankheiten, 87*, 527-570.

Berman, R., & Colby, C. (2009). Attention and active vision. *Vision Research, 49*(10), 1233-1248.

Bichot, N. P., Rossi, A. F., & Desimone, R. (2005). Parallel and Serial Neural Mechanisms for Visual Search in Macaque Area V4. *Science, 308*(5721), 529-534.

Biederman, I., Mezzanotte, R. J., & Rabinowitz, J. C. (1982). Scene perception: Detecting and judging objects undergoing relational violations. *Cognitive Psychology, 14*(2), 143-177.

Bindemann, M., Burton, A. M., Langton, S. R. H., Schweinberger, S. R., & Doherty, M. J. (2007). The control of attention to faces. *Journal of Vision, 7*(10).

Bisley, J. W. (2011). The neural basis of visual attention. *The Journal of Physiology, 589*(1), 49-57.

Bötzel, K., Schulze, S., & Stodieck, S. R. G. (1995). Scalp topography and analysis of intracranial sources of face-evoked potentials. *Experimental Brain Research, 104*(1), 135-143.

Boynton, G. M. (2009). A framework for describing the effects of attention on visual responses. *Vision Research, 49*(10), 1129-1143.

Brainard, D. H. (1997). The Psychophisics Toolbox. *Spatial Vision, 10*, 433-436.

Bressler, D. W., & Silver, M. A. (2010). Spatial attention improves reliability of fMRI retinotopic mapping signals in occipital and parietal cortex. *NeuroImage, 53*(2), 526-533.

Broadbent, D. (1982). Task combination and selective intake of information. *Acta Psychologica, 50*, 253-290.

Broadbent, D., & Broadbent, M. (1987). From detection to identification: Response to multiple targets in rapid serial visual presentation. *Attention, Perception, & Psychophysics, 42*(2), 105-113.

Brockmole, J. R., Castelhano, M. S., & Henderson, J. M. (2006). Contextual cueing in naturalistic scenes: Global and local contexts. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 32*(4), 699-706.

Brown, J. M., & Narayanan, S. (2009). Visual streams and shifting attention *Progress in Brain Research* (Vol. Volume 176, pp. 47-63): Elsevier.

Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology, 77*(3), 305.

Caharel, S., Courtay, N., Bernard, C., Lalonde, R., & RebaÔ, M. (2005). Familiarity and emotional expression influence an early stage of face processing: An electrophysiological study. *Brain and Cognition, 59*(1), 96-100.

Calder, A. J., & Young, A. W. (2005). Understanding the recognition of facial identity and facial expression. *Nat Rev Neurosci, 6*(8), 641-651.

Campbell, F. W., & Robson, J. G. (1968). Application of fourier analysis to the visibility of gratings. *J Physiol, 197*(3), 551-566.

Carmel, D., & Bentin, S. (2002). Domain specificity versus expertise: factors influencing distinct processing of faces. *Cognition, 83*(1), 1-29.

Cauquil, A. S., Edmonds, G. E., & Taylor, M. J. (2000). Is the face-sensitive N170 the only ERP not affected by selective attention? *Neuroreport, 11*(10), 2167-2171.

Chiu, Y.-C., Esterman, M., Han, Y., Rosen, H., & Yantis, S. (2011). Decoding Task-based Attentional Modulation during Face Categorization. *Journal of Cognitive Neuroscience, 23*(5), 1189-1204.

Cohen, D. (1968). Magnetoencephalography: evidence of magnetic fields produced by alpha-rhythm currents. *Science, 161*, 784-786.

Cohen Kadosh, K., Henson, R. N. A., Cohen Kadosh, R., Johnson, M. H., & Dick, F. (2010). Task-dependent Activation of Face-sensitive Cortex: An fMRI Adaptation Study. *Journal of Cognitive Neuroscience, 22*(5), 903-917.

Cohen Kadosh, K., & Johnson, M. H. (2007). Developing a cortex specialized for face perception. *Trends in Cognitive Sciences, 11*(9), 367-369.

Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1990). Attentional Modulation of Neural Processing of Shape, Color, and Velocity in Humans. *Science, 248*, 1556-1559.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci, 3*(3), 201-215.

Corrigan, N., Richards, T., Webb, S., Murias, M., Merkle, K., Kleinhans, N., . . . Dawson, G. (2009). An Investigation of the Relationship Between fMRI and ERP

Source Localized Measurements of Brain Activity during Face Processing. *Brain Topography, 22*(2), 83-96.

Cover, T., & Thomas, J. A. (2006). *Elements of Information Theory* (2nd ed.). Hoboken, New Jersey: John Wiley & Sons, Inc.

Cowan, N. (2011). The focus of attention as observed in visual working memory tasks: Making sense of competing claims. *Neuropsychologia, 49*(6), 1401-1406.

Crist, R. E., Wu, C.-T., Karp, C., & Woldorff, M. G. (2008). Face Processing Gated by Visual Spatial Attention. *Frontiers in Human Neuroscience, 1*, 1-6. doi: 10.3389/neuro.09.010.2007

Dailey, M. N., Cottrell, G. W., & Reilly, J. (2001). CAlifornia Facial Expressions Database (CAFE). CAFE http://www.es.ucsd.edu/user/gary/CAFE/

Darvas, F., Pantazis, D., Kucukaltun-Yildirim, E., & Leahy, R. M. (2004). Mapping human brain function with MEG and EEG: methods and validation. *NeuroImage, 23*(Supplement 1), S289-S299.

Davenport, J. L., & Potter, M. C. (2004). Scene Consistency in Object and Background Perception. *Psychological Science, 15*(8), 559-564.

Deffke, I., Sander, T., Heidenreich, J., Sommer, W., Curio, G., Trahms, L., & Lueschow, A. (2007). MEG/EEG sources of the 170-ms response to faces are co-localized in the fusiform gyrus. *NeuroImage, 35*(4), 1495-1501.

Dehaene, S. (1989). Discriminability and dimensionality effects in visual search for featural conjunctions: a functional pop-out. *Perception & Psychophysics, 46*(1), 72-80.

Dekowska, M., Kuniecki, M., & Jaśkowski, P. (2008). Facing facts: Neuronal mechanisms of face perception. [Review]. *Acta Neurobiologiae Experimentalis, 68*, 229-252.

Delorme, A., Makeig, S., Fabre-Thorpe, M., & Sejnowski, T. J. (2002). From single-trial EEG to brain area dynamics. *Neurocomputing, 44-46*, 1057-1064.

Desimone, R. (1991). Face-Selective Cells in the Temporal Cortex of Monkeys. *Journal of Cognitive Neuroscience, 3*(1), 1-8.

Deutsch, J. A., & Deutsch, D. (1963). Attention: some theoretical considerations. *Psychological Reviews, 87*, 272-300.

Diamond, R., & Carey, S. (1986). Why faces are and are not special: an effect of expertise. *J Exp Psychol Gen, 115*(2), 107-117.

Dobel, C., Geiger, L., Bruchmann, M., Putsche, C., Schweinberger, S., & Junghöfer, M. (2008). On the interplay between familiarity and emotional expression in face perception. *Psychological Research, 72*(5), 580-586. doi: 10.1007/s00426-007-0132-4

Dolan, R. J., & Vuilleumier, P. (2003). Amygdala automaticity in emotional processing. *Ann N Y Acad Sci, 985*, 348-355.

Downing, C. J. (1988). Expectancy and visual-spatial attention: Effects on perceptual quality. *Journal of Experimental Psychology: Human Perception and Performance, 14*(2), 188-202.

Dricot, L., Sorger, B., Schiltz, C., Goebel, R., & Rossion, B. (2008). The roles of "face" and "non-face" areas during individual face perception: Evidence by fMRI adaptation in a brain-damaged prosopagnosic patient. *NeuroImage, 40*(1), 318-332.

Eason, R. G., Harter, M. R., & White, C. T. (1969). Effects of attention and arousal on visually evoked cortical potentials and reaction time in man. *Physiology & Behavior, 4*(3), 283-289.

Egner, T., Monti, J. M. P., Trittschuh, E. H., Wieneke, C. A., Hirsch, J., & Mesulam, M. M. (2008). Neural Integration of Top-Down Spatial and Feature-Based Information in Visual Search. *Journal of Neuroscience, 28*(24), 6141-6151.

Eimer, M. (2000). Effects of face inversion on the structural encoding and recognition of faces. Evidence from event-related brain potentials. *Brain Res Cogn Brain Res, 10*(1-2), 145-158.

Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face processing. *Neuroreport, 13*, 427-431.

Eimer, M., Holmes, A., & McGlone, F. P. (2003). The role of spatial attention in the processing of facial expression: an ERP study of rapid brain responses to six basic emotions. *Cognitive , Affective, & Behavioral Neuroscience, 3*(2), 97-110.

Ellis, H. D. (1975). Recognizing faces. *British Journal of Psychology, 66*(4), 409-426.

Eryilmaz, H. H., Duru, A. D., Parlak, B., Ademoglu, A., & Demiralp, T. (2007, 22-26 Aug. 2007). *Neuroimaging of Event Related Brain Potentials (ERP) using fMRI and Dipole Source Reconstruction.* Paper presented at the Engineering in Medicine and Biology Society, 2007. EMBS 2007. 29th Annual International Conference of the IEEE.

Escudero, J., Hornero, R., Abasolo, D., Fernandez, A., & Lopez-Coronado, M. (2007). Artifact Removal in Magnetoencephalogram Background Activity With Independent Component Analysis. *Biomedical Engineering, IEEE Transactions on, 54*(11), 1965-1973.

Farah, M. J., Wilson, K. D., Drain, M., & Tanaka, J. N. (1998). What is "special" about face perception? *Psychol Rev, 105*(3), 482-498.

Faugeras, O., Adde, G., Charpiat, G., Chefd'Hotel, C., Clerc, M., Deneux, T., . . . Wotawa, N. (2004). Variational, geometric, and statistical methods for modeling brain anatomy and function. *NeuroImage, 23*(Supplement 1), S46-S55.

Fei-Fei, L., & Perona, P. (2005). *A bayesian hierarchical model for learning natural scene categories.* Paper presented at the 2005 IEEE Computer Society Conference on Computer Vision and Pattern Recognition (CVPR '05), San Diego.

Freedman, D. J., Riesenhuber, M., Poggio, T., & Miller, E. K. (2006). Experience-Dependent Sharpening of Visual Shape Selectivity in Inferior Temporal Cortex. *Cerebral Cortex, 16*(11), 1631-1644.

Friston, K. (2000). The labile brain. III. Transients and spatio-temporal receptive fields. *Philosophical Transactions of the Royal Society B: Biological Sciences, 355*, 253-265.

Furey, M. L., Tanskanen, T., Beauchamp, M. S., Avikainen, S., Uutela, K., Hari, R., & Haxby, J. V. (2006). Dissociation of face-selective cortical responses by attention. *Proceedings of the National Academy of Sciences of the United States of America, 103*(4), 1065-1070.

Furl, N., van Rijsbergen, N. J., Treves, A., Friston, K. J., & Dolan, R. J. (2007). Experience-dependent coding of facial expression in superior temporal sulcus. *Proceedings of the National Academy of Sciences, 104*(33), 13485-13489.

Gainotti, G. (2007). Different patterns of famous people recognition disorders in patients with right and left anterior temporal lesions: A systematic review. *Neuropsychologia, 45*(8), 1591-1607.

Ganel, T., Valyear, K. F., Goshen-Gottstein, Y., & Goodale, M. A. (2005). The involvement of the "fusiform face area" in processing facial expression. *Neuropsychologia, 43*, 1645-1654.

Giesbrecht, B., Woldorff, M. G., Song, A. W., & Mangun, G. R. (2003). Neural mechanisms of top-down control during spatial and feature attention. *NeuroImage, 19*(3), 496-512.

Gilbert, C. D., & Sigman, M. (2007). Brain States: Top-Down Influences in Sensory Processing. *Neuron, 54*(5), 677-696.

Gobbini, M. I., & Haxby, J. V. (2007). Neural systems for recognition of familiar faces. *Neuropsychologia, 45*(1), 32-41. doi: 10.1016/j.neuropsychologia.2006.04.015

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences, 15*, 20-25.

Gordon, R. D. (2004). Attentional Allocation During the Perception of Scenes. *Journal of Experimental Psychology: Human Perception and Performance, 30*(4), 760-777.

Gosselin, F., & Schyns, P. G. (2001). Bubbles: a technique to reveal the use of information in recognition tasks. *Vision Res, 41*(17), 2261-2271.

Gosselin, F., & Schyns, P. G. (2004). No troubles with bubbles: a reply to Murray and Gold. *Vision Research, 44,* 471-477.

Greenberg, A. S., Esterman, M., Wilson, D., Serences, J. T., & Yantis, S. (2010). Control of Spatial and Feature-Based Attention in Frontoparietal Cortex. *Journal of Neuroscience, 30*(43), 14330-14339.

Grent-'t-Jong, T., & Woldorff, M. G. (2007). Timing and Sequence of Brain Activity in Top-Down Control of Visual-Spatial Attention. *PLoS Biol, 5*(1), e12.

Gronau, N., Neta, M., & Bar, M. (2007). Integrated Contextual Representation for Objects' Identities and Their Locations. *Journal of Cognitive Neuroscience, 20*(3), 371-388.

Groves, P. M., & Eason, R. G. (1969). Effects of Attention and Activation on the Visual Evoked Cortical Potential and Reaction Time. *Psychophysiology, 5*(4), 394-398.

Guillaume, F. C., & Tiberghien, G. (2001). An event-related potential study of contextual modifications in a face recognition task. *NeuroReport, 12*(6), 1209-1216.

Halgren, E., Raij, T., Marinkovic, K., Jousmaki, V., & Hari, R. (2000). Cognitive response profile of the human fusiform face area as determined by MEG. *Cereb Cortex, 10*(1), 69-81.

Hansen, P. C., Kringelbach, M. L., & Salmelin, R. e. (2010). *MEG: An Introduction to Methods.* USA: Oxford University Press.

Harel, A., Ullman, S., Epshtein, B., & Bentin, S. (2007). Mutual information of image fragments predicts categorization in humans: Electrophysiological and behavioral evidence. *Vision Research, 47*(15), 2010-2020.

Haufe, S., Tomioka, R., Dickhaus, T., Sannelli, C., Blankertz, B., Nolte, G., & Mueller, K.-R. (2011). Large-scale EEG/MEG source localization with spatial flexibility. *NeuroImage, 54*(2), 851-859.

Haxby, J. V., Grady, C. L., Horwitz, B., Ungerleider, L. G., Mishkin, M., Carson, R. E., . . . Rapoport, S. I. (1991). Dissociation of object and spatial visual processing pathways in human extrastriate cortex. *Proceedings of the National Academy of Sciences of the United States of America, 88*(5), 1621-1625.

Haxby, J. V., Hoffmann, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. [Review]. *Trends in Cognitive Sciences, 4*(6), 223-233.

Hein, G., & Knight, R. T. (2008). Superior Temporal Sulcus - It's My Area: Or Is It? *Journal of Cognitive Neuroscience, 20*(12), 2125-2136.

Heinze, H. J., Mangun, G. R., Burchert, W., Hinrichs, H., Scholz, M., Munte, T. F., . . . Hillyard, S. A. (1994). Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature, 372*(6506), 543-546.

Herrmann, M. J., Ehlis, A.-C., Muehlberger, A., & Fallgatter, A. J. (2005). Source Localization of Early Stages of Face Processing. *Brain Topography, 18*(2), 77-85.

Hollingworth, A. (1998). Does consistent scene context facilitate object perception? *Journal of Experimental Psychology: General, 127*(4), 398-415.

Holmes, A., Vuilleumier, P., & Eimer, M. (2003). The processing of emotional facial expression is gated by spatial attention: evidence from event-related brain potentials. *Cognitive Brain Research, 16*(2), 174-184.

Holmes, A., Winston, J. S., & Eimer, M. (2005). The role of spatial frequency information for ERP components sensitive to faces and emotional facial expression. *Cognitive Brain Research, 25*(2), 508-520.

Hopf, J.-M., Luck, S. J., Girelli, M., Hagner, T., Mangun, G. R., Scheich, H., & Heinze, H.-J. (2000). Neural Sources of Focused Attention in Visual Search. *Cerebral Cortex, 10*(12), 1233-1241.

Hopf, J. M., & Mangun, G. R. (2000). Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology, 111*(7), 1241-1257.

Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nat Neurosci, 3*(3), 284-291.

Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurones in the cat's striate cortex. *The Journal of Physiology, 148*(3), 574-591.

Hugenberg, K. (2005). Social Categorization and the Perception of Facial Affect : Target Race Moderates the Response Latency Advantage for Happy Faces. *Emotion, 5*(3), 267-276.

Ilmoniemi, R. J. (1993). Models of source currents in the brain. *Brain Topography, 5*(4), 331-336.

Itier, R. J., Herdman, A. T., George, N., Cheyne, D., & Taylor, M. J. (2006). Inversion and contrast-reversal effects on face processing assessed by MEG. *Brain Research, 1115*(1), 108-120.

Itier, R. J., & Taylor, M. J. (2004). Source analysis of the N170 to faces and objects. *NeuroReport, 15*(8), 1261-1265.

Japee, S., Crocker, L., Carver, F., Pessoa, L., & Ungerleider, L. G. (2009). Individual Differences in Valence Modulation of Face-Selective M170 Response. *Emotion, 9*(1), 59-69.

Jasper, H. H. (1958). The 10-20 electrode system of the International Federation. *Electroencephalography & Clinical Neurophysiology, 10*, 370-375.

Jemel, B., Coutya, J., Langer, C., & Roy, S. (2009). From upright to upside-down presentation: A spatio-temporal ERP study of the parametric effect of rotation on face and house processing. *BMC Neuroscience, 10*(1), 100.

Johnson, M. H., Dziurawiec, S., Ellis, H., & Morton, J. (1991). Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition, 40*(1-2), 1-19.

Jung, R., & Berger, W. (1979). Fiftieth Anniversary of Hans Berger's Publication of the Electroencephalogram

His First Records in 1924--1931. *Archiv fuer Psychiatrie und Nervenkrankheiten, 227*, 279-300.

Jung, T.-P., Makeig, S., McKeown, M. J., Bell, A. J., Lee, T.-W., & Sejnowski, T. J. (2001). Imaging Brain Dynamics Using Independent Component Analysis. *Proc IEEE Inst Electr Electron Eng, 89*(7), 1107-1122.

Jung, T.-P., Makeig, S., Westerfield, M., Townsend, J., Courchesne, E., & Sejnowski, T. J. (2000). Removal of eye activity artifacts from visual event-related potentials in normal and clinical subjects. *Clinical Neurophysiology, 111*(10), 1745-1758.

Junghöfer, M., Elbert, T., Leiderer, P., Berg, P., & Rockstroh, B. (1997). Mapping EEG-potentials on the surface of the brain: A strategy for uncovering cortical sources. *Brain Topography, 9*(3), 203-217.

Kadosh, K. C., Walsh, V., & Kadosh, R. C. (2011). Investigating face-property specific processing in the right OFA. *Social Cognitive and Affective Neuroscience, 6*(1), 58-65.

Kamp, A., Pfurtschneller, G., Edlinger, G., & Lopes da Silva, F. H. (2005). Polygraphy. In E. Niedermeyer & F. H. Lopes da Silva (Eds.), *Electroencephalography: Basic Principles, Clinical Applications, and Related Fields* (5th ed.). Philadelphia: Lippincott, Williams & Wilkins.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The Fusiform Face Area: A Module in Human Extrastriate Cortex Specialized for Face Perception. *J. Neurosci., 17*(11), 4302-4311.

Kanwisher, N., & Wojciulik, E. (2000). Visual attention: Insights from brain imaging. *Nat Rev Neurosci, 1*(2), 91-100.

Kaufmann, J. M., & Schweinberger, S. R. (2004). Expression influences the recognition of familiar faces. *Perception, 33*(4), 399-408.

Kayser, J. r., & Tenke, C. E. (2006). Principal components analysis of Laplacian waveforms as a generic method for identifying ERP generator patterns: II. Adequacy of low-density estimates. *Clinical Neurophysiology, 117*(2), 369-380.

Kayser, J. r., & Tenke, C. E. (2010). In search of the Rosetta Stone for scalp EEG: Converging on reference-free techniques. *Clinical Neurophysiology, 121*(12), 1973-1975.

Kirschstein, T., & Koehling, R. (2009). What is the Source of the EEG? *Clinical EEG and Neuroscience, 40*(3), 146-149.

Kloth, N., Dobel, C., Schweinberger, S. R., Zwitserlood, P., Bölte, J., & Junghöfer, M. (2006). Effects of personal familiarity on early neuromagnetic correlates of face perception. *European Journal of Neuroscience, 24*(11), 3317-3321.

Koch, C., & Ullman, S. (1985). Shifts in selective visual attention: towards the underlying neural circuitry. *Human Neurobiology, 4*, 219-227.

Lander, K., & Metcalfe, S. (2007). The influence of positive and negative facial expressions on face familiarity. *Memory, 15*(1), 63-69.

Langton, S. R. H., Law, A. S., Burton, A. M., & Schweinberger, S. R. (2008). Attention capture by faces. *Cognition, 107*(1), 330-342. doi: 10.1016/j.cognition.2007.07.012

Laycock, R., Crewther, D. P., & Crewther, S. G. (2008). The advantage in being magnocellular: A few more remarks on attention and the magnocellular system. *Neuroscience & Biobehavioral Reviews, 32*(8), 1409-1415.

Laycock, R., & Crewther, S. G. (2008). Towards an understanding of the role of the [`]magnocellular advantage' in fluent reading. *Neuroscience & Biobehavioral Reviews, 32*(8), 1494-1506.

Laycock, R., Crewther, S. G., & Crewther, D. P. (2007). A role for the [`]magnocellular advantage' in visual impairments in neurodevelopmental and psychiatric disorders. *Neuroscience & Biobehavioral Reviews, 31*(3), 363-376.

Lazebnik, S., Schmid, C., & Ponce, J. (2006). *Beyond bags of features: spatial pyramid matching for recognizing natural scene categories.* Paper presented at the 2006 IEEE Computer Society Conference on Computer Vision and Pattern Recognition (CVPR'06), New York.

Lewis, S., Thoma, R. J. C. A., Lanoue, M. D., Miller, G. A., Heller, W., Edgar, C., . . . Canive, J. M. (2003). Visual processing of facial affect. *Neuroreport 14*(4), 1841-1845.

Li, F. F., VanRullen, R., Koch, C., & Perona, P. (2002). Rapid natural scene categorization in the near absence of attention. *Proceedings of the National Academy of Sciences of the United States of America, 99*(14), 9596-9601.

Liao, Y.-L., Sun, Y.-N., Guo, W.-Y., Chou, Y.-H., Hsieh, J.-C., & Wu, Y.-T. (2007, 22-26 Aug. 2007). *A Comparison between the Surface-Based and Mutual-Information-Based Methods for Co-registering SPECT and MR Images.* Paper presented at the Engineering in Medicine and Biology Society, 2007. EMBS 2007. 29th Annual International Conference of the IEEE.

Liu, J., Harris, A., & Kanwisher, N. (2002). Stages of processing in face perception: an MEG study. *Nat Neurosci, 5*(9), 910-916.

Liu, J., Higuchi, M., Marantz, A., & Kanwisher, N. (2000). The selectivity of the occipitotemporal M170 for faces. *Neuroreport, 11*(2), 337-341.

Liu, T., Larsson, J., & Carrasco, M. (2007). Feature-Based Attention Modulates Orientation-Selective Responses in Human Visual Cortex. *Neuron, 55*(2), 313-323.

Lopes da Silva, F. H. (2010). Electrophysiological Basis of MEG Signals. In P. C. Hansen, M. L. Kringelbach & R. Salmelin (Eds.), *MEG: An Introduction to Methods* (pp. 5-27). USA: Oxford University Press.

Lopes da Silva, F. H., Pijn, J. P., & Beoijinga, P. (1989). Interdependence of EEG signals: linear vs. nonlinear associations and the significance of time delays and phase shifts. *Brain Topography, 2*(1-2), 9-18.

Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural Mechanisms of Spatial Selective Attention in Areas V1, V2, and V4 of Macaque Visual Cortex. *Journal of Neurophysiology, 77*(1), 24-42.

Lueschow, A., Sander, T., Boehm, S. G., Nolte, G., Trahms, L., & Curio, G. (2004). Looking for faces: Attention modulates early occipitotemporal object processing. *Psychophysiology, 41*(3), 350-360.

Luo, Q., Holroyd, T., Majestic, C., Cheng, X., Schechter, J., & Blair, R. J. (2010). Emotional Automaticity Is a Matter of Timing. *The Journal of Neuroscience, 30*(17), 5825-5829.

Luu, P., Geyer, A., Fidopiastis, C., Campbell, G., Wheeler, T., Cohn, J., & Tucker, D. M. (2010). Reentrant Processing in Intuitive Perception. *PLoS ONE, 5*(3), e9523.

Magri, C., Whittingstall, K., Singh, V., Logothetis, N., & Panzeri, S. (2009). A toolbox for the fast information analysis of multiple-site LFP, EEG and spike train recordings. *BMC Neuroscience, 10*(1), 81.

Makeig, S., Bell, A. J., Jung, T.-P., & Sejnowski, T. J. (1996). Independent Component Analysis of Electroencephalographic Data. *Advances in Neural Information Processing Systems, 8*, 145-151.

Manwani, A., & Koch, C. (1999). Detecting and Estimating Signals in Noisy Cable Structures, I: Neuronal Noise Sources. *Neural Computation, 11*, 1797-1829.

Marois, R., & Ivanoff, J. (2005). Capacity limits of information processing in the brain. *Trends in Cognitive Sciences, 9*(6), 296-305.

Martens, U., Leuthold, H., & Schweinberger, S. R. (2010). Parallel processing in face perception. *Journal of Experimental Psychology: Human Perception and Performance, 36*(1), 103-121.

McAlonan, K., Cavanaugh, J., & Wurtz, R. H. (2008). Guarding the gateway to cortex with attention in visual thalamus. *Nature, 456*(7220), 391-394.

McClurkin, J. W., & Optican, L. M. (1996). Primate striate and prestriate cortical neurons during discrimination. I. simultaneous temporal encoding of information about color and pattern. *Journal of Neurophysiology, 75*(1), 481-495.

McKone, E., Kanwisher, N., & Duchaine, B. C. (2007). Can generic expertise explain special processing for faces? *Trends in Cognitive Sciences, 11*(1), 8-15.

Menz, M. D., & Freeman, R. D. (2004). Temporal Dynamics of Binocular Disparity Processing in the Central Visual Pathway. *Journal of Neurophysiology, 91*(4), 1782-1793.

Merigan, W. H., & Maunsell, J. H. R. (1993). How Parallel are the Primate Visual Pathways? *Annual Review of Neuroscience, 16*(1), 369-402.

Mohamed, T. N., Neumann, M. F., & Schweinberger, S. R. (2009). Perceptual load manipulation reveals sensitivity of the face-selective N170 to attention. *NeuroReport, 20*(8), 782-787.

Moran, J., & Desimone, R. (1985). Selective Attention Gates Visual Processing in the Extrastriate Cortex. *Science, 229*, 782-784.

Moran, J. E., Drake, C. L., & Tepley, N. (2004). ICA Methods for MEG Imaging. *Neurology and Clinical Neurophysiology, 72*.

Mosher, J. C., Leahy, R. M., & Lewis, P. S. (1999). EEG and MEG: forward solutions for inverse methods. *Biomedical Engineering, IEEE Transactions on, 46*(3), 245-259.

Mouraux, A., & Iannetti, G. D. (2008). Across-trial averaging of event-related EEG responses and beyond. *Magnetic Resonance Imaging, 26*(7), 1041-1054.

Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the Shape, Size, and Orientation of Objects for Grasping in Neurons of Monkey Parietal Area AIP. *Journal of Neurophysiology, 83*(5), 2580-2601.

Murray, R.F. & Gold, J.M. (2004). Troubles with Bubbles. *Vision Research, 44*, 461–470.

Murray, R. F. (2011). Classification images: A review. *Journal of Vision, 11*(5).

Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology, 9*(3), 353-383.

Nicholson, C., & Freeman, J. A. (1975). Theory of current source-density analysis and determination of conductivity tensor for anuran cerebellum. *Journal of Neurophysiology, 38*(2), 356-368.

Niedermeyer, E. (1996). Dipole theory and electroencephalography. *Clinical Electroencephalography, 27*(3), 121-131.

Niedermeyer, E., & Lopes da Silva, F. H. (2005). *Electroencephalography: Basic Principles, Clinical Applications, and Related Fields* (5th ed.). Philadephia: Lippincott, Williams & Wilkins.

Nieuwenhuis, S., Aston-Jones, G., & Cohen, J. D. (2005). Decision making, the P3, and the locus coeruleus--norepinephrine system. *Psychological Bulletin, 131*(4), 510-532.

Nothdurft, H. (1993). The role of features in preattentive vision: comparison of orientation, motion and color cues. *Vision Research, 33*(14), 1937-1958.

Nunez, P. L., & Srinivasan, R. (2006). *Electric Fields of the Brain: the Neurophysics of EEG*. New York: Oxford University Press.

O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature, 401*(6753), 584-587.

Okazaki, Y., Abrahamyan, A., Stevens, C. J., & Ioannides, A. A. (2008). The timing of face selectivity and attentional modulation in visual processing. *Neuroscience, 152*(4), 1130-1144.

Oliva, A., & Schyns, P. G. (1997). Coarse blobs or fine edges? Evidence that information diagnosticity changes the perception of complex visual stimuli. *Cognit Psychol, 34*(1), 72-107.

Oliva, A., & Torralba, A. (2007). The role of context in object recognition. *Trends in Cognitive Sciences, 11*(12), 520-527.

Onton, J., Westerfield, M., Townsend, J., & Makeig, S. (2006). Imaging human EEG dynamics using independent component analysis. *Neuroscience & Biobehavioral Reviews, 30*(6), 808-822.

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational Intelligence and Neuroscience*.

Palermo, R., & Rhodes, G. (2007). Are you always on my mind? A review of how face perception and attention interact. *Neuropsychologia, 45*(1), 75-92.

Palmer, S. E. (1975). The effects of contextual scenes on the identification of objects. *Memory & Cognition, 3*(5), 519-526.

Parkkonen, L. (2010). Instrumentation and Data Preprocessing. In P. C. Hansen, M. L. Kringelbach & R. Salmelin (Eds.), *MEG: An Introduction to Methods* (pp. 29-69). USA: Oxford University Press.

Parr, L. A., Dove, T., & Hopkins, W. D. (1998). Why faces may be special: evidence of the inversion effect in chimpanzees. *Journal of Cognitive Neuroscience, 10*(5), 615-622.

Pegna, A. J., Khateb, A., Michel, C. M., & Landis, T. (2004). Visual recognition of faces, objects, and words using degraded stimuli: Where and when it occurs. *Human Brain Mapping, 22*(4), 300-311.

Pernier, J., Perrin, F., & Bertrand, O. (1988). Scalp current density fields: concept and properties. *Electroencephalogr Clin Neurophysiol, 69*(4), 385-389.

Pessoa, L. (2010). Emotion and cognition and the amygdala: From "what is it?" to "what's to be done?". *Neuropsychologia, 48*(12), 3416-3429.

Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. *Nat Rev Neurosci, 11*(11), 773-783.

Pessoa, L., Kastner, S., & Ungerleider, L. G. (2002). Attentional control of the processing of neutral and emotional stimuli. *Cognitive Brain Research, 15*, 31-45.

Pessoa, L., McKenna, M., Gutierrez, E., & Ungerleider, L. G. (2002). Neural processing of emotional faces requires attention. *Proceedings of the National Academy of Sciences, 99*(17), 11458-11463.

Philiastides, M. G., & Sajda, P. (2006). Temporal Characterization of the Neural Correlates of Perceptual Decision Making in the Human Brain. *Cerebral Cortex, 16*(4), 509-518.

Picton, T. W., Bentin, S., Berg, P., Donchin, E., Hillyard, S. A., Johnson, R., . . . Taylor, M. J. (2000). Guidelines for using human event-related potentials to study cognition: Recording standards and publication criteria. *Psychophysiology, 37*(2), 127-152.

Pitcher, D., Walsh, V., & Duchaine, B. (2011). The role of the occipital face area in the cortical face perception network. *Experimental Brain Research, 209*(4), 481-493.

Pizzagalli, D. A., Lehmann, D., Hendrick, A. M., Regard, M., Pascual-Marqui, R. D., & Davidson, R. J. (2002). Affective Judgments of Faces Modulate Early Activity (~160 ms) within the Fusiform Gyri. *NeuroImage, 16*(3, Part 1), 663-677.

Polk, T. A., Drake, R. M., Jonides, J. J., Smith, M. R., & Smith, E. E. (2008). Attention Enhances the Neural Processing of Relevant Features and Suppresses the Processing of Irrelevant Features in Humans: A Functional Magnetic Resonance Imaging Study of the Stroop Task. *Journal of Neuroscience, 28*(51), 13786-13792.

Posamentier, M. T., & Abdi, H. (2003). Processing Faces and Facial Expressions. *Neuropsychology Review, 13*(3), 113-143.

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology, 32*, 3-25.

Price, C. J. (2010). The anatomy of language: a review of 100 fMRI studies published in 2009. *Annals of the New York Academy of Sciences, 1191*(1), 62-88.

Pylyshyn, Z. (1999). Is vision continuous with cognition? The case for cognitive impenetrability of visual perception. *Behavioral and Brain Sciences, 22*, 341-423.

Rees, G. (2009). Visual Attention: The Thalamus at the Centre? *Current Biology, 19*(5), R213-R214.

Reynolds, R. I. (1981). Perception of an illusory contour as a function of processing time. *Perception, 10*(1), 107-115.

Rhodes, G., Michie, P. T., Hughes, M. E., & Byatt, G. (2009). The fusiform face area and occipital face area show sensitivity to spatial relations in faces. *European Journal of Neuroscience, 30*(4), 721-733.

Roelfsema, P. R. (2005). Elemental operations in vision. *Trends in Cognitive Sciences, 9*(5), 226-233.

Rossion, B., de Gelder, B., Pourtois, G., GuÈrit, J. M., & Weiskrantz, L. (2000). Early extrastriate activity without primary visual cortex in humans. *Neuroscience Letters, 279*(1), 25-28.

Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., & Crommelinck, M. (2000). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. *Neuroreport, 11*, 69-74.

Rossion, B., Joyce, C. A., Cottrell, G. W., & Tarr, M. J. (2003). Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *NeuroImage, 20*(3), 1609-1624.

Rousselet, G. A., Gaspar, C. M., Wieczorek, K. P., & Pernet, C. R. (in press). Modelling single-trial ERP reveals modulation of bottom-up face visual processing by top-down task constraints (in some subjects). [Original Research]. *Frontiers in Psychology, 2*. doi: 10.3389/fpsyg.2011.00137

Rousselet, G. A., Husk, J. S., Bennett, P. J., & Sekuler, A. B. (2007). Single-trial EEG dynamics of object and face visual processing. *NeuroImage, 36*(3), 843-862.

Rousselet, G. A., & Pernet, C. (2011). Quantifying the time course of visual object processing using ERPs: it's time to up the game. *Frontiers in Psychology, 2*.

Saenz, M., Buracas, G. T., & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nat Neurosci, 5*(7), 631-632.

Saenz, M., Buracas, G. T., & Boynton, G. M. (2003). Global feature-based attention for motion and color. *Vision Research, 43*(6), 629-637.

Sagar, R. P., & Guevara, N. L. (2005). Mutual information and correlation measures in atomic systems. *The Journal of Chemical Physics, 123*(4), 044108.

Said, C. P., Moore, C. D., Engell, A. D., Todorov, A., & Haxby, J. V. (2010). Distributed representations of dynamic facial expressions in the superior temporal sulcus. *Journal of Vision, 10*(5).

Said, C. P., Moore, C. D., Norman, K. A., Haxby, J. V., & Todorov, A. (2010). Graded representations of emotional expressions in the left superior temporal sulcus. [Original Research]. *Frontiers in Systems Neuroscience, 4*. doi: 10.3389/fnsys.2010.00006

Schoenfeld, M. A., Hopf, J. M., Martinez, A., Mai, H. M., Sattler, C., Gasde, A., . . . Hillyard, S. A. (2007). Spatio-temporal Analysis of Feature-Based Attention. *Cerebral Cortex, 17*(10), 2468-2477.

Schweinberger, S. R., Kaufmann, J. r. M., Moratti, S., Keil, A., & Burton, A. M. (2007). Brain responses to repetitions of human and animal faces, inverted faces, and objects -- An MEG study. *Brain Research, 1184*, 226-233.

Schweinberger, S. R., & Soukup, G. R. (1998). Asymmetric relationships among perceptions of facial identity, emotion, and facial speech. *Journal of Experimental Psychology. Human Perception & Performance, 24*(6), 1748-1765.

Schyns, P. G., Goldstone, R. L., & Thibaut, J. P. (1998). The development of features in object concepts. *Behav Brain Sci, 21*(1), 1-17; discussion 17-54.

Schyns, P. G., Jentzsch, I., Johnson, M., Schweinberger, S. R., & Gosselin, F. (2003). A principled method for determining the functionality of brain responses. *Neuroreport, 14*(13), 1665-1669.

Schyns, P. G., & Oliva, A. (1994). From Blobs to Boundary Edges: Evidence for Time- and Spatial-Scale-Dependent Scene Recognition. *Psychological Science, 5*(4), 195-200.

Schyns, P. G., & Oliva, A. (1997). Flexible, diagnosticity-driven, rather than fixed, perceptually determined scale selection in scene and face recognition. *Perception, 26*(8), 1027-1038.

Schyns, P. G., & Oliva, A. (1999). Dr. Angry and Mr. Smile: when categorization flexibly modifies the perception of faces in rapid visual presentations. *Cognition, 69*(3), 243-265.

Schyns, P. G., Petro, L. S., & Smith, M. L. (2007). Dynamics of visual information integration in the brain for categorizing facial expressions. *Curr Biol, 17*(18), 1580-1585.

Schyns, P. G., Petro, L. S., & Smith, M. L. (2009). Transmission of Facial Expressions of Emotion Co-Evolved with Their Efficient Decoding in the Brain: Behavioral and Brain Evidence. *PLoS ONE, 4*(5), e5625.

Schyns, P. G., & Rodet, L. (1997). Categorization Creates Functional Features. *Journal of Experimental Psychology: Learning, Memory, & Cognition., 23*(3), 681-696.

Schyns, P. G., Thut, G., & Gross, J. (2011). Cracking the Code of Oscillatory Activity. *PLoS Biol, 9*(5), e1001064.

Serences, J. T., & Boynton, G. M. (2007). Feature-Based Attentional Modulations in the Absence of Direct Visual Stimulation. *Neuron, 55*(2), 301-312.

Sergent, J., Ohta, S., & Macdonald, B. (1992). Functional Neuroanatomy of Face and Object Processing. *Brain, 115*(1), 15-36.

Sergent, J., Ohta, S., Macdonald, B., & Zuck, E. (1994). Segregated processing of facial identity and emotion in the human brain: A pet study. *Visual Cognition, 1*(2), 349-369.

Shannon, C. (1948). A mathematical theory of communication. *Bell Systems Technical Journal, 27*, 379-423.

Shulman, G. L., Ollinger, J. M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Petersen, S. E., & Corbetta, M. (1999). Areas Involved in Encoding and Applying Directional Expectations to Moving Objects. *Journal of Neuroscience, 19*(21), 9480-9496.

Simon, D., Craig, K. D., Miltner, W. H. R., & Rainville, P. (2006). Brain responses to dynamic facial expressions of pain. *Pain, 126*(1-3), 309-318.

Smallman, H. S. (1995). Fine-to-coarse scale disambiguation in stereopsis. *Vision Research, 35*(8), 1047-1060.

Smith, F. W., & Muckli, L. (2010). Nonstimulated early visual areas carry information about surrounding context. *Proceedings of the National Academy of Sciences, 107*(46), 20099-20103.

Smith, F. W., Muckli, L., Brennan, D., Pernet, C., Smith, M. L., Belin, P., . . . Schyns, P. G. (2008). Classification images reveal the information sensitivity of brain voxels in fMRI. *NeuroImage, 40*(4), 1643-1654.

Smith, M. L., Cottrell, G. W., Gosselin, F., & Schyns, P. G. (2005). Transmitting and decoding facial expressions. *Psychol Sci, 16*(3), 184-189.

Smith, M. L., Fries, P., Gosselin, F., Goebel, R., & Schyns, P. G. (2009). Inverse Mapping the Neuronal Substrates of Face Categorizations. *Cerebral Cortex, 19*(10), 2428-2438.

Smith, M. L., Gosselin, F., & Schyns, P. G. (2004). Receptive fields for flexible face categorizations. *Psychological Science, 15*(11), 753-761.

Smith, M. L., Gosselin, F., & Schyns, P. G. (2006). Perceptual moments of conscious visual experience inferred from oscillatory brain activity. *Proc Natl Acad Sci U S A, 103*(14), 5626-5631.

Sreenivasan, K. K., Goldstein, J. M., Lustig, A. G., Rivas, L. R., & Jha, A. P. (2009). Attention to faces modulates early face processing during low but not high face discriminability. *Attention, Perception, & Psychophysics, 71*(4), 837-846.

Steeves, J. K. E., Culham, J. C., Duchaine, B. C., Pratesi, C. C., Valyear, K. F., Schindler, I., . . . Goodale, M. A. (2006). The fusiform face area is not sufficient for face recognition: Evidence from a patient with dense prosopagnosia and no occipital face area. *Neuropsychologia, 44*(4), 594-609.

Stigchel, S. V. d., Belopolsky, A. V., Peters, J. C., Wijnen, J. G., Meeter, M., & Theeuwes, J. (2009). The limits of top-down control of visual attention. *Acta Psychologica, 132*(3), 201-212.

Stoppel, C. M., Boehler, C. N., Sabelhaus, C., Heinze, H.-J., Hopf, J. M., & Schoenfeld, M. A. (2007). Neural mechanisms of spatial- and feature-based attention: A quantitative analysis. *Brain Research, 1181*, 51-60.

Streit, M., Dammers, J. r., Simsek-Kraues, S., Brinkmeyer, J. r., Wolwer, W., & Ioannides, A. (2003). Time course of regional brain activations during facial emotion recognition in humans. *Neuroscience Letters, 342*(1-2), 101-104.

Sutton, S., Braren, M., Zubin, I., & John, E. R. (1965). Evoked-potential correlates of stimulus uncertainty. *Science, 150*, 1187-1188.

Sutton, S., Tueting, P., Zubin, J., & John, E. R. (1967). Information delivery and the sensory evoked potential. *Science, 155*(1436-1439).

Tanskanen, T., Nasanen, R., Montez, T., Paallysaho, J., & Hari, R. (2005). Face recognition and cortical responses show similar sensitivity to noise spatial frequency. *Cereb Cortex, 15*(5), 526-534.

Taylor, M. J., Bayless, S. J., Mills, T., & Pang, E. W. (2011). Recognising upright and inverted faces: MEG source localisation. *Brain Research, 1381*, 167-174.

Taylor, M. J., Mills, T., Smith, M. L., & Pang, E. W. (2008). Face processing in adolescents with and without epilepsy. *International Journal of Psychophysiology, 68*(2), 94-103.

Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature, 381*(6582), 520-522.

Torralba, A. (2003). Contextual Priming for Object Detection. *International Journal of Computer Vision, 53*(2), 169-191.

Torralba, A., & Oliva, A. (2003). Statistics of natural image categories. *Network: Computation in Neural Systems, 14*(3), 391-412.

Torralba, A., Oliva, A., Castelhano, M. S., & Henderson, J. M. (2006). Contextual guidance of eye movements and attention in real-world scenes: The role of global features in object search. *Psychological Review, 113*(4), 766-786.

Tovee, M. J. (1998). Is Face Processing Special? *Neuron, 21*(6), 1239-1242.

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology, 12*(1), 97-136.

Treue, S., & Martinez-Trujillo, J. C. (2007). Attending to Features inside and outside the Spotlight of Attention. *Neuron, 55*(2), 174-176.

Uttley, A. M. (1976). A two-pathway informon theory of conditioning and adaptive pattern recognition. *Brain Research, 102*(1), 23-35.

van Rijsbergen, N. J., & Schyns, P. G. (2009). Dynamics of Trimming the Content of Face Representations for Categorization in the Brain. *PLoS Comput Biol, 5*(11), e1000561.

Van Petten, C., & Kutas, M. (1988). The use of event-related potentials in the study of brain asymmetries. *The International Journal of Neuroscience, 39*(1-2), 91-99.

Van Veen, B. D., & Buckley, K. M. (1988). Beamforming: A Versatile Approach to Spatial Filtering. *IEEE ASSP Magazine, 5*, 4-24.

Van Veen, B. D., Drongelen, W. v., Yuchtman, M., & Suzuki, A. (1997). Localization of Brain Electrical Activity via Linearly Constrained Minimum Variance Spatial Filtering. *IEEE Transactions on Biomedical Engineering, 44*(9), 867-880.

Van Voorhis, S., & Hillyard, S. (1977). Visual evoked potentials and selective attention to points in space. *Perception & Psychophysics, 22*, 54-62.

Vandenberghe, R., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2001). Location- or Feature-Based Targeting of Peripheral Attention. *NeuroImage, 14*(1), 37-47.

Vuilleumier, P., & Pourtois, G. (2007). Distributed and interactive brain mechanisms during emotion face perception: Evidence from functional neuroimaging. *Neuropsychologia, 45*(1), 174-194.

Walther, D. B., Koch, C., & Paul Cisek, T. D. a. J. F. K. (2007). Attention in hierarchical models of object recognition *Progress in Brain Research* (Vol. Volume 165, pp. 57-78): Elsevier.

Weissman, D. H., Mangun, G. R., & Woldorff, M. G. (2002). A Role for Top-Down Attentional Orienting during Interference between Global and Local Aspects of Hierarchical Stimuli. *NeuroImage, 17*(3), 1266-1276.

Wiese, H., Schweinberger, S. R., & Neumann, M. F. (2008). Perceiving age and gender in unfamiliar faces: Brain potential evidence for implicit and explicit person categorization. [10.1111/j.1469-8986.2008.00707.x]. *Psychophysiology, 45*(6), 957-969.

Wilcox, R. R. (2005). *Introduction to Robust Estimation and Hypothesis Testing* (2nd ed.). San Diego, CA: Academic Press.

Wilkinson, F., James, T. W., Wilson, H. R., Gati, J. S., Menon, R. S., & Goodale, M. A. (2000). An fMRI study of the selective activation of human extrastriate form vision areas by radial and concentric gratings. *Current Biology, 10*(22), 1455-1458.

Wojciulik, E., & Kanwisher, N. (1999). The Generality of Parietal Involvement in Visual Attention. *Neuron, 23*(4), 747-764.

Wojciulik, E., Kanwisher, N., & Driver, J. (1998). Covert Visual Attention Modulates Face-Specific Activity in the Human Fusiform Gyrus: fMRI Study. *Journal of Neurophysiology, 79*(3), 1574-1578.

Woldorff, M. G., Liotti, M., Seabolt, M., Busse, L., Lancaster, J. L., & Fox, P. T. (2002). The temporal dynamics of the effects in occipital cortex of visual-spatial selective attention. *Cognitive Brain Research, 15*(1), 1-15.

Wolfe, J. M., Cave, K. R., & Franzel, S. L. (1989). Guided search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance, 15*(3), 419-433.

Wronka, E., & Walentowska, W. (2011). Attention modulates emotional expression processing. *Psychophysiology*. doi: doi: 10.1111/j.1469-8986.2011.01180.x

Yamasaki, H., LaBar, K. S., & McCarthy, G. (2002). Dissociable prefrontal brain systems for attention and emotion. *Proceedings of the National Academy of Sciences of the United States of America, 99*(17), 11447-11451.

Young, A. W., Newcombe, F., Haan, E. H. F. d., Small, M., & Hay, D. C. (1993). Face perception after brain injury. *Brain, 116*(4), 941-959.

Zanto, T. P., Rubens, M. T., Bollinger, J., & Gazzaley, A. (2010). Top-down modulation of visual feature processing: The role of the inferior frontal junction. *NeuroImage, 53*(2), 736-745.