DIAGNOSTIC INFORMATION USE TO UNDERSTAND BRAIN MECHANISMS OF FACIAL EXPRESSION CATEGORIZATION

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THESIS SUBMITTED TO THE

UNIVERSITY OF GLASGOW FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

JULY 2010

Containing studies performed in the
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For Cops, Mum, Dad & baby Hannah.

SUMMARY

Proficient categorization of facial expressions is crucial for normal social interaction. Neurophysiological, behavioural, event-related potential, lesion and functional neuroimaging techniques can be used to investigate the underlying brain mechanisms supporting this seemingly effortless process, and the associated arrangement of bilateral networks. These brain areas exhibit consistent and replicable activation patterns, and can be broadly defined to include visual (occipital and temporal), limbic (amygdala) and prefrontal (orbitofrontal) regions. Together, these areas support early perceptual processing, the formation of detailed representations and subsequent recognition of expressive faces. Despite the critical role of facial expressions in social communication and extensive work in this area, it is still not known how the brain decodes nonverbal signals in terms of expression-specific features. For these reasons, this thesis investigates the role of these so-called diagnostic facial features at three significant stages in expression recognition; the spatiotemporal inputs to the visual system, the dynamic integration of features in higher visual (occipitotemporal) areas, and early sensitivity to features in V1.

In Chapter 1, the basic emotion categories are presented, along with the brain regions that are activated by these expressions. In line with this, the current cognitive theory of face processing reviews functional and anatomical dissociations within the distributed neural "face network". Chapter 1 also introduces the way in which we measure and use *diagnostic* information to derive brain sensitivity to specific facial features, and how this is a useful tool by which to understand spatial and temporal organisation of expression recognition in the brain. In relation to this, hierarchical, bottom-up neural processing is discussed along with high-level, top-down facilitatory mechanisms.

Chapter 2 describes an eye-movement study that reveals inputs to the visual system via fixations reflect diagnostic information use. Inputs to the visual system dictate the information distributed to cognitive systems during the seamless and rapid categorization of expressive faces. How we perform eye-movements during this task informs how task-driven and stimulus-driven mechanisms interact to guide the extraction of information supporting recognition. We recorded eye movements of observers who categorized the six basic categories of facial expressions. We use a measure of task-relevant information (diagnosticity) to discuss oculomotor behaviour, with focus on two findings. Firstly, fixated regions reveal expression differences. Secondly, by examining fixation sequences, the intersection of fixations with diagnostic information increases in a sequence of fixations. This suggests a top-down drive to acquire task-relevant information, with different functional roles for first and final fixations.

A combination of psychophysical studies of visual recognition together with the EEG (electroencephalogram) signal is used to infer the dynamics of feature extraction and use during the recognition of facial expressions in Chapter 3. The results reveal a process that integrates visual information over about 50 milliseconds prior to the face-sensitive N170 event-related potential, starting at the eye region, and proceeding gradually towards lower regions. The finding that informative features for recognition are not processed simultaneously but in an orderly progression over a short time period is instructive for understanding the processes involved in visual recognition, and in particular the integration of bottom-up and top-down processes.

In Chapter 4 we use fMRI to investigate the task-dependent activation to diagnostic features in early visual areas, suggesting top-down mechanisms as V1 traditionally exhibits only simple response properties. Chapter 3 revealed that diagnostic features modulate the temporal dynamics of brain signals in higher visual areas. Within the hierarchical visual

system however, it is not known if an early (V1/V2/V3) sensitivity to diagnostic information contributes to categorical facial judgements, conceivably driven by top-down signals triggered in visual processing. Using retinotopic mapping, we reveal task-dependent information extraction within the earliest cortical representation (V1) of two features known to be differentially necessary for face recognition tasks (eyes and mouth). This strategic encoding of face images is beyond typical V1 properties and suggests a top-down influence of task extending down to the earliest retinotopic stages of visual processing. The significance of these data is discussed in the context of the cortical face network and bidirectional processing in the visual system.

The visual cognition of facial expression processing is concerned with the interactive processing of bottom-up sensory-driven information and top-down mechanisms to relate visual input to categorical judgements. The three experiments presented in this thesis are summarized in Chapter 5 in relation to how diagnostic features can be used to explore such processing in the human brain leading to proficient facial expression categorization.

ACKNOWLEDGEMENTS[1]

First of all, thank you to the Suit. Thank you Philippe for giving me this opportunity. It was invaluable to observe at the start of my career your integrity of work and depth of knowledge. I enjoyed our chats too!

Thank you to Lars, for lessons in science and beyond, and for inspiring me. You helped me refine my interests, and in doing so never once told me to stop asking questions. You taught me the trouble was worth it.

Big thanks to the Smiths, Marie and Fraser, without whom this experience would have been very different. I value working with you greatly, and your friendship more. Look forward to visiting you in your own labs soon!

Babydavid, Gordon and Phil – thank you for making work a nice place to be and for keeping me smiling. Miss you already.

Thank you Ingram – my fellow WIP, without whom I may never have realised that it is possible to be an academic AND to be fabulous. 17 gins to celebrate…? Bring the Haun.

Morv, Eils, KJ, Vaz, Monique, Marie - I'm back. Thanks for always being there. See you in New York.

Ross, Eils, Hannah, Jonnie, Sylvia, Ottie and all our extended family – fun times with you provided some much-needed balance. Ross, thank you for lessons over the years, for teaching me things I don't need to know and things I probably shouldn't ever know. Invaluable.

Mum, Dad, Chriss & Joe - I am forever grateful. Your support and encouragement goes beyond that which could ever be expected.

Finally, Cops. Thesis. Done. On we go together. The sheep heart seems like only yesterday. As wives do, I gave ample critique of your thesis, and as husbands do, you have been so patient with mine. Couldn't have done it without you.

[1] This thesis was funded by an Economic & Social Research Council postgraduate research studentship.

AUTHOR'S DECLARATION

I declare that this thesis is my own work unless indicated otherwise in the text, carried out under the normal terms of supervision. All collaborators are duly acknowledged.

This thesis has been composed by the undersigned. It has not been submitted or accepted in any previous application for any degree at this or any other university.

Lucy S. Petro

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[*] Chapter corresponds to: **Petro, L.S.,** Miellet, S. & Schyns, P.G. (2009) Top-Down Control of Fixations in the Categorization of Facial Expressions. *Cognition, under revision.*

† Chapter corresponds to: Schyns P.G., **Petro, L.S.** & Smith, M. L. (2007) Dynamics of Visual Information Integration in the Brain for Categorizing Facial Expressions. *Current Biology*, 17, 1580-1585. License Agreement between Lucy S. Petro and Elsevier provided by Copyright Clearance on Centre July 12th 2010.

‡ Chapter corresponds to: **Petro, L.S.,** Smith, F.W., Schyns, P.G. & Muckli, L. (2009) Top-Down Modulation of the Cortical Representation of Face Features in V1. *Journal of Neuroscience, under revision.*

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ABBREVIATIONS

EEG	Electroencephalography
ERP	Event-related potential
FFA	Fusiform face area
FMRI	Functional magnetic resonance imaging
HSF	High spatial frequency
IOG	Inferior occipital gyrus
LOC	Lateral occipital cortex
LSF	Low spatial frequency
MEG	Magnetoencephalography
OFA	Occipital face area
OFC	Orbitofrontal cortex
PFC	Prefrontal cortex
STS	Superior temporal sulcus
TMS	Transcranial magnetic stimulation

CHAPTER ONE

RECOGNIZING EMOTION FROM FACIAL EXPRESSIONS

1.1. FACIAL EXPRESSIONS: A KEY COMMUNICATION CHANNEL

Faces are a rich source of information, and humans have become highly adept at extracting information about identity, gender, race, age, and emotion. The complex arrangement of bilateral brain networks supporting the detection of this rich and varied biological information, the comprehension of which is vital for successful interpersonal relations, exhibit consistent and replicable activation patterns, and can be broadly defined to include visual, limbic and prefrontal regions.

In the context of social interaction, perhaps the most significant subset of information conveyed by a face is the emotional status of an individual, revealed by their facial expression. In part as a consequence of primates developing more complex social groups, the primate face has developed into an extremely efficient communicator of affect. This rising complexity of facial musculature and innervation is coupled with an increasingly sophisticated neural representation of facial signals in the brain, explored in this thesis using task-relevant (or diagnostic) features. In line with its significance, facial expression processing is the focus of extensive research, employing behavioural, single-cell, electrophysiological and neuroimaging techniques to detail emotional processing, spanning molecular, cellular, systems, behavioural and cognitive levels of analysis from early developmental stages through to adulthood.

1.1.1. Development of expression recognition systems

Expression recognition is one of the earliest communicative abilities we acquire and it develops at a time when the hard wiring of cells remains very intense. It has therefore been studied from early stages of development, revealing remarkable discrimination at a very young age (Walker-Andrews, 1997). Children as young as a few months old can differentiate happy and sad faces from surprised faces, and can discriminate between different intensities (i.e., mild versus intense happy faces, Nelson & De Haan, 1997). From the perspective of brain function and anatomy, central to this is how expression recognition development is shaped by the maturation of neural networks predetermined to mediate this skill. This development may be modulated by factors such as gender, socio-economic status, verbal capabilities and IQ and therefore the contribution of these should be considered in studies correlating cerebral maturation with augmented regulation of emotional behaviour.

1.1.2. Gender differences in expression recognition

The traditional view is that females are generally more proficient in expression recognition, empathy, and emotional understanding (Hall, 1984; Hall et al., 2000). The female advantage has been shown for nonverbal (auditory and visual) and verbal stimuli, and implies differential cognitive processing to that of males. This could be related to development, for example, there are gender differences in the activity of gonadal hormones in the amygdala (which contributes to expression recognition in adults) prior to birth (Roselli & Resko, 1986). For this reason, research on gender differences in expression processing is moving from perceptual and behavioural patterns to more integrative theoretical models that highlight the interaction with biological factors in development. Both gender differences in expression recognition, and the increasing proficiency with age, provide support for a specialized neural system for decoding the emotional content of faces.

1.1.3. BASIC FACIAL EXPRESSIONS

Although humans have acquired the capabilities of spoken language, the role of facial expressions in social interaction remains considerable. Irrespective of whether facial expressions are inextricably linked to the internal emotion and therefore part of a structured emotional response, or whether cultures develop their own expressions, a facial expression is a visible manifestation, under both automatic and voluntary neural control, that can be measured. The Facial Action Coding System (FACS) details the anatomical basis of facial movement to describe how facial signals are exhibited based on the muscles that produce them. Ekman & Friesen (1978) developed FACS by determining how the contraction of each facial muscle transforms the appearance of the face, and how muscles act both singly and in combination to produce cognitive categories of expressions. Over the past 30 years, Paul Ekman has pioneered many other studies on the role of facial expressions in both communication and emotional reaction, and how they have evolved to inform conspecifics of internalised emotion. Ekman & Friesen (1975) concluded expressions could be reliably assigned into six basic emotions, and a number of characteristics differentiate them from moods or emotional traits. For example, the basic emotions are thought to benefit from a degree of universality, to engage specific physiological mechanisms (via the autonomic nervous system), share commonalities in the experience which calls forth the emotion, have a rapid onset and brief duration, and evoke specific memories and images. Although Ekman's approach has received criticism because the kinds of expressions seen in his photo stimuli are posed, they remain the most common stimuli in face processing studies. With general agreement on the basic emotions, the following six expressions are used in this thesis to investigate the role of task-relevant (diagnostic) information in expression categorization: happy, surprise, fear, disgust, anger and sad. Accurately decoding each

expression requires the brain to precisely and rapidly tease apart the information within each one (Smith et al., 2005; Schyns et al., 2009).

1.2. A MODEL OF FACE PROCESSING – THE 'DISTRIBUTED CORTICAL NETWORK'

Faces are one of the most frequent visual stimuli we encounter, thus it follows that specialized processing networks support face perception. Due to common activation patterns the neural signature of face processing is now well defined. Support for the neuropsychological basis of this comes from lesion data, for example, a specialized system is implied by prosopagnosic patients, who have focal brain damage to ventral occipitotemporal cortex (Damasio et al., 1982; Sergent & Signoret, 1992) and are selectively impaired in their ability to recognize familiar faces, but not in their ability to recognize other objects (Hecaen & Angelergues, 1986; McNeil & Warrington, 1993). Experiments on perceptual processing specific to faces provide evidence for cognitive mechanisms of face perception. For example, differences in face pairs (but less so for other non-face stimuli, see Bentin et al., 1996; Rossion et al., 2000; Rebai et al., 2001) are harder to detect if the images are inverted (Yin, 1969). Such phenomena suggest faces receive, at least to an extent, processing more specialized than that of general object recognition.

Bruce and Young (1986) described the dominant cognitive model of face processing over the last 20 years. Within this, early low-level processes represent face images, whilst later specialized areas carry out the processing of dissociable information such as expression. Converging evidence suggests that this network (with a right hemisphere dominance) consists of the inferior occipital gyrus ("occipital face area", OFA), middle fusiform gyrus ("fusiform face area", FFA), (posterior) superior temporal sulcus (STS), inferior frontal gyrus and orbitofrontal cortex, as well as subcortical contributions from the amygdala. Even the mere percept of a face (without an explicit task) induces activation in this network (Ishai et al., 2005). Bruce and Young (1986) described a dissociation between

expression and identity recognition, and Haxby et al's (2000) influential neuroanatomical account of the "distributed human neural system for face perception", supports this by differentiating within the *core system* a response to invariant and variant face aspects i.e. fusiform gyrus and superior temporal sulcus respectively (and also describes the *extended system* involved in cognitive functions related to face processing, Figure 1.1.). Striking support for this comes from the double-dissociation in impaired (either in expression *or* identity) individuals. There remains interest in where expression and identity systems separate i.e. before or after perceptual representations have been formed. It seems that evidence so far would suggest a relative rather than absolute dissociation (see Calder & Young, 2005 for review).

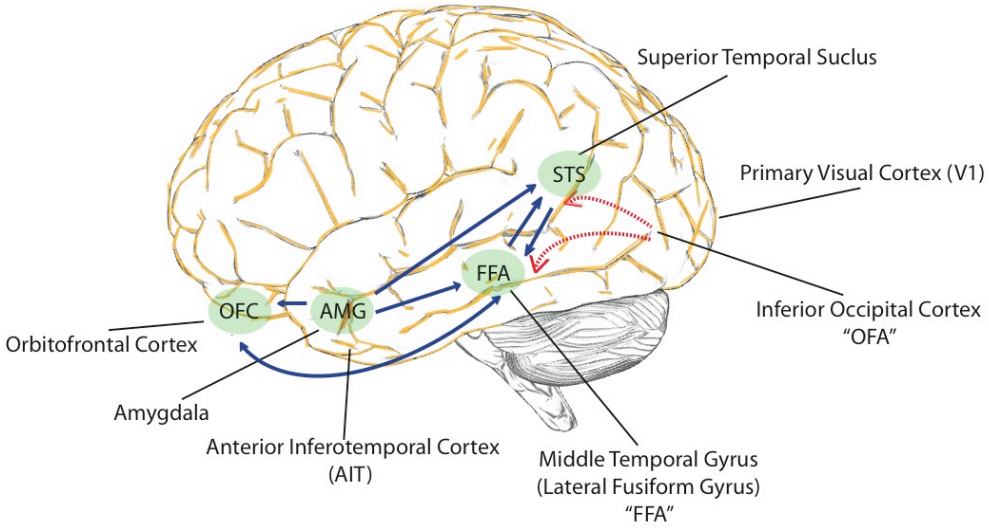


Figure 1.1. The Distributed Face Network. Visual facial information is processed from the primary visual cortex (V1) to inferior occipital cortex (OFA), to the middle fusiform gyrus (FFA) for identity processing and to the superior temporal sulcus (STS) for expression analysis (red arrows). The inferior occipital cortex lies adjacent to the lateral fusiform region ventrally and the superior temporal sulcal region dorsally, suggesting it inputs to both of these temporal face-sensitive regions (Haxby et al., 2000). The extended system is represented in part by the transparent green circles: amygdala (AMG) and orbitofrontal cortex (OFC). Blue arrows show some anatomical connections within the face network (see text).

1.2.1. CORE SYSTEM

Visual processing of faces relies on functional specialization in regions of temporal cortex in the ventral visual stream. Evidence for this comes from electrophysiological studies in non-human primates showing face-selective neurons in the temporal cortex. The core system comprises three bilateral regions in occipitotemporal visual extrastriate cortex (Kanwisher et al., 1997; McCarthy et al., 1997; Halgren et al., 1999; Haxby et al., 1999; Ishai et al., 1999; Hoffman & Haxby, 2000): the inferior occipital gyrus (occipital face area, OFA), lateral fusiform gyrus (fusiform face area, FFA) and superior temporal sulcus (STS). Face perception studies tend to focus upon the FFA, whilst those of social cognition and emotion include the STS (and amygdala). As mentioned, differential roles for these regions have been proposed and anatomical connections suggest the inferior occipital cortex feeds directly to both the lateral fusiform gyrus for processing identity (Sergent et al., 1992; George et al., 1999; Hoffman & Haxby, 2000), and to the superior temporal sulcus which is sensitive to changeable face aspects (Puce et al., 1998; Hoffman & Haxby, 2000).

Inferior occipital cortex

The role of the OFA in face processing is less defined than that of the FFA and STS. Models of face perception suggest the OFA is involved in early stages of processing and therefore modulated by the physical information in stimuli rather than high-level categorizations such as expression. This is in line with hierarchical models of visual processing in which facial information reaches the FFA or STS *via* the OFA. A recent transcranial magnetic stimulation (TMS) study by Pitcher et al., (2007) demonstrated that repeated stimulation of the right OFA disrupted accurate discrimination only of face parts and not of the spacing between parts, confirming the role of the OFA in early stages of face processing (i.e. in generating an initial representation before later processing of expression

or identity).

Fusiform cortex

While there is agreement on the anatomical correlates of face processing, there remains controversy over the precise neurofunctional role of the FFA; that is, whether this region is *specialized* for face processing or *activated* during face processing (and thus specialized for visual expertise). The domain-specificity hypothesis describes the former, and suggests that there exists a "face-system" activated only by faces (Kanwisher et al., 1997). The latter argument suggests we are experts at face discriminations, and that faces undergo robust categorizations in the same manner as various object classes (Gauthier et al., 1999), therefore neurons in this region are involved in visual expertise. In recent studies, stronger expertise effects have been observed in the lateral occipital cortex (LOC) than the FFA, suggesting this perceptual expertise is not specific to the FFA (Rhodes et al., 2004; Moore et al., 2006; Op de Beeck et al., 2006; Yue et al., 2006). Whether the preference of the FFA is confounded by expertise or not is a long and ongoing debate.

The involvement of the FFA (and anterior temporal regions, Quian Quiroga et al., 2005; Kriegeskorte et al., 2008) in identity judgments is well-supported; not only do lesions lead to deficits in recognizing individuals (Damasio et al., 1982), but increased activity is observed to a sequence of different individuals as opposed to the same face presented repeatedly (Gauthier et al., 2000; Andrews & Ewbank, 2004). Interestingly, Ganel et al., (2005) performed an fMRI investigation to examine the role of the FFA in expression processing and actually observed higher activation in the FFA when judging expression over identity although the theory of dissociable systems would assume it plays no or little role. Ganel et al observed FFA sensitivity to variations in expression even when attention was aimed at identity, and higher activation in the FFA during passive viewing of faces when expression was varied compared with when it remained constant. The authors

proposed that expressions are the variant aspects of invariant faces; thus the way an individual expresses emotion is constrained by their identity. Indeed several other studies highlight an increased response in the FFA to fearful as opposed to neutral faces (Pessoa et al, 2002; Vuilleumier et al., 2001). Such findings are interesting with regard to whether information also proceeds indirectly to the STS via the FFA, and if expressions are processed interactively recruiting the FFA.

Superior temporal sulcus

Haxby et al (2000) proposed a route leading from the inferior occipital cortex to the superior temporal cortex, in which changeable aspects of faces resulting from movements of facial musculature are represented. This receives support from single-cell recordings in both monkeys (Hasselmo et al., 1989) and humans (Ojemann et al., 1992). The idea of a functional division between regions of the face network that process changeable or static aspects of the face is consistent with the processing of visual information from the retina into the high-resolution parvocellular stream and lower resolution, motion-sensitive magnocellular stream. The ventral and dorsal visual streams, that support object recognition and spatial orientation respectively (Ungerlieder & Mishkin, 1982), reflect the mapping of these parvo- and magnocellular inputs (Merigan, 1991). This dissociation of processing is not absolute however; even though V1 segregates magnocellular, parvocellular (and koniocellular) input from the LGN, which has parvo cells terminating in layer 4Cβ and the upper portion of layer 6, and magno cells in layer 4Cα and lower layer 6 (Livingstone & Hubel, 1988), the intracortical wiring of thalamic input within V1 is very complex. Recent research suggests geniculate pathways are elaborately combined prior to exiting primary visual cortex (Sincinch & Horton, 2005). During the processing of *dynamic* expressive faces, motion information may be transmitted primarily by the dorsal stream to the STS, while static features may be processed in the ventral stream before projecting to the STS to

integrate information about form and movement (with both streams having undergone computations with the other in V1, Oram & Perret, 1996; Cusick, 1997). The perception of static images that *imply* motion can also activate the STS (Kourtzi & Kanwisher, 2001). With regard to STS connectivity within the face network, it sends reciprocal connections to the amygdala, which in turn sends reciprocal projections to the orbitofrontal cortex (OFC, Amaral et al., 1992). In addition, the STS directly connects with the OFC (Barbas, 1988), and STS neurons could be exposed to feedback from the amygdala (presumably later than initial STS activation) to enhance the response of pyramidal cells in this region to feed-forward processing.

That the STS responds to changeable face aspects, and more specifically, for certain aspects of faces such as head or eye-orientation, is supported by substantial empirical evidence (Baylis et al., 1987; Hasselmo et al., 1989; Perret et al., 1984, 1985, 1990, 1992; Bonda et al., 1996). Engell & Haxby (2007) recently revealed that the human STS shows dissociable but overlapping neural representations to facial expression and averted gaze (the overlap could represent a region for the integration of the two) and implicates the STS as a region responsible for neuropsychological evidence suggesting that impairments in facial expression recognition and gaze-perception co-exist (Campbell et al., 1990).

1.2.2. EXTENDED SYSTEM

Outwith the extrastriate regions that make up the core system, that is the "face perception" areas, the extended system processes the "social cognition" aspects of facial expression recognition, for example to evoke an emotional response in the perceiver, to judge intentions, to direct attention to what the transmitter also attends, or to process speech.

Amygdala

It has long been suggested that emotion involves the limbic system (Papez, 1937, Le

Doux, 1996). The amygdala is probably the most well studied brain region in terms of its contribution to social behaviour, although there still exists controversy over its precise role, partly due to its disproportionate association with "fear" or threat-related stimuli. This subcortical region of the limbic system is positioned medially to the temporal lobes and is ideally located to send diffuse connections to the cortex. Anatomically, the amygdala sends projections to all visual processing stages in the ventral stream, including primary visual cortex V1 (Amaral et al., 1992). Visual processing could engage top-down modulation of information being passed "upstream" and anatomical studies show the primate amygdala receives substantial input from temporal visual areas (Iwai et al., 1987) suggesting extrastriate face-processing regions could functionally interact with the amygdala. That it receives considerable input of highly processed cortical information and also benefits from subcortical input suggests in might participate in various aspects of expression recognition over variable time scales.

The role of the amygdala in facial expression processing is complemented by single-cell evidence in humans (Fried et al., 1997) and non-human primates (Leonard et al., 1985), where cells were shown to respond differentially to faces. Although the role of the amygdala in the processing of facial expressions is probably underrated and not completely understood at present, much evidence as accumulated so far, often in relation to lesions. Patient SM who suffers from bilateral calcification and atrophy of the amygdala displayed less intense ratings of fear than controls, was unable to draw a fearful face and her ratings of afraid faces correlated poorly with normal ratings (Adolphs, 1994; 1995). Another study of a patient also supports the role of the amygdala in the recognition of emotion; especially fear (Anderson & Phelps, 2000). The authors describe a patient with bilateral amygdala damage who is impaired in her ability to recognize fear in the faces of others but displays a fearful face herself and recognizes it as such. This suggests that its role should be thought

of as linking perception of facial expressions with some constructs of conceptual knowledge. A recent study by Hoffman et al., (2007) demonstrated using monkey fMRI that facial expressions and eye gaze/head orientation are processed differentially in distinct portions of the amygdala, the former engaging the basolateral complex, and the latter the lateral extended amygdala. The authors observed increased activation to threat stimuli, but the role of the lateral amygdala is less clear as there are no major projections from the STS to the lateral extended amygdala. It is possible that limited projections from the STS to the central nucleus (part of the lateral extended amygdala) carry gaze information. These results are extremely pertinent with regard to the extension of this to the human neural basis of emotion perception, in which the role of the amygdala remains somewhat ambiguous even though a large number of studies show amygdala activity correlates with enhanced responses to visual stimuli in the visual cortex (Morris et al., 1998; Pessoa et al., 2002; Sabatinelli et al., 2005).

Orbitofrontal cortex

It has been suggested that there is also a facial expression-selective region in the inferior frontal cortex (Sprengelmeyer et al., 1998; Nakamura et al., 1999; Kolb & Taylor, 2000), in particular the orbitofrontal cortex, which is intimately connected to the amygdala. The primate orbitofrontal cortex is located on the ventral surface of the frontal cortex, and can be physically defined by being the prefrontal region that receives projections from the magnocellular medial nucleus of the mediodorsal thalamus (Fuster, 1997). This is in contrast to other parts of the prefrontal cortex which receive projections from other parts of the mediodorsal thalamus, such as the dorsolateral prefrontal cortex which receives projections from the parvocellular lateral part of the mediodorsal thalamic nucleus and the frontal eye fields (Brodmann's area 8).

As well as being closely associated with the subcortical regions, the prefrontal cortex receives dense connections from the temporal visual cortex (Seltzer & Pandya, 1989, rhesus monkey). This provides a plausible mechanism for orbitofrontal regions to contribute to expression recognition via feedback to temporal areas. Tsao et al., (2008) found three functionally distinct face-selective patches in the ventral prefrontal cortex of the monkey, one strongly lateralized to the right hemisphere. These prefrontal regions could form centres devoted to retrieving and responding to facial information, and likely communicate with face-selective areas in the inferotemporal cortex. Emery and Amaral (1999) suggested that the prefrontal cortex might provide contextual modulation of the amygdala during the processing of facial expressions.

Cingulate cortex

Driven by lesion studies in humans and animals, the anterior cingulate cortex has been related to the processing of expression. Based on cytoarchitecture and connectivity, the anterior cingulate cingulated (ACC) can be divided in to dorsal and rostral-ventral parts, and is also part of the limbic system. The dorsal part is thought to be involved in cognitive processes including attention, motor control, motivation, and errors in information processing. The rostral ventral part regulates emotional processing with Bush et al., (2000) suggesting the ACC forms part of a circuit involved in a form of attention that subserves cognitive and emotional processing, and so is modulatory in its role.

Effective connectivity for face processing

To understand processing within the face network, Fairhall and Ishai (2007), used fMRI with dynamic causal modelling (DCM). To determine the most probable pattern of effective connectivity within the three core regions, they defined prototype models of: OFA (inferior occipital gyrus) projecting to FFA (fusiform gyrus) to STS; OFA to STS to FFA; OFA to FFA *and* STS; or the OFA to FFA *and* STS with the addition of uni- or

bidirectional processing also between the STS and FFA. They found evidence suggesting direct and separate influence of the OFA on the STS and FFA in both left and right hemisphere core systems. With regard to the extended system, viewing expressive faces increased effective connectivity through the FFA to amygdala, which is interesting in terms of the role the FFA may play in expression processing but is surprising this was not also observed for the STS. They argue that the STS activation can be somewhat unreliable across subjects and tasks, and that it makes sense that during the processing of expressive faces it is the fusiform gyrus driving the dynamic interaction with limbic areas. They concluded both that the core system is hierarchically organized in a principally feed-forward manner and that the central influence on the extended system is the fusiform gyrus, the ventral part of the core system. It could also be that STS would exert a stronger influence when viewing dynamic faces, i.e. during biological motion.

1.3. Specificity of Brain Regions for Expression Processing

To appreciate the emotional content of facial expressions commands a distributed network of neurons that construct detailed representations of expressive faces and encode perceptual information about the emotion, creating options for responding to such stimuli (Rolls, 1999), illustrating the privileged status of emotional stimuli for the brain (Davidson et al., 2004). Moreover, several studies suggest not only that there might be a right hemisphere dominance for this, but also that additional, specific brain regions exhibit specialized functioning for emotional operations. I will only briefly review these regions as this thesis is concerned with the ventral stream cortical sensitivity (early visual and occipitotemporal areas) to diagnostic features during expression categorization (up to 200ms).

1.3.1. HEMISPHERIC LATERALIZATION

The right and left brain hemispheres are not entirely symmetric. Functional and anatomical asymmetries exist throughout cortical and subcortical structures. This suggests that affective and cognitive functions may be supported by partially distinct systems, which undergo computations localised to only one hemisphere. Two general hypotheses for expression recognition asymmetry have been proposed, both of which yield support largely from patient studies.

Right hemisphere model

A correlation between expression processing and the right hemisphere was made nearly a century ago. Mills (1912a, b) noted that a unilateral right-sided lesion was linked to deficits in emotional expression. The involvement of the right hemisphere is suggested by studies showing a left perceptual bias in relation to the observer (i.e. right hemisphere/left visual field) when processing face information using chimeric stimuli (Levy et al., 1983). This involves a composite stimulus of half a happy face and half a neutral face (down the vertical meridian); observers are forced to judge if the left or right smiling face is happier. Studies of brain-damaged patients reveal that individuals with right-hemisphere lesions perform worse in expression recognition than patients with left-hemisphere lesions (Etcoff, 1986; Adolphs et al., 1996; Borod et al., 1998), and a number of electrophysiological and neuroimaging studies lend further support to this idea (Kestenbaum & Nelson, 1992; Munte et al., 1998; Narumoto et al., 2001; Sato et al., 2004).

Valence model

The valence hypothesis claims the right hemisphere is specialized for negative emotion and that the left hemisphere is specialized for positive emotion (Silberman &Weingartner, 1986; Ehrlichman, 1987). For example, patients are more likely to have difficulty perceiving negative versus positive emotion following right hemisphere lesion

(Adolphs et al., 1996; Borod et al., 1998), and in fact can retain the ability to perceive happy faces. An extensive review of the literature by (Borod et al., 1997) combined the results of 49 experiments to conclude that the left hemiface is more influential than the right when expressions are transmitted, and left-side asymmetries (defined as the expression intensity or muscular involvement on one side of the face relative to the other) are more common in negative expressions – taken together this could implicate the right hemisphere in negative emotion processing and the left in positive emotion processing. The extent to which each hemisphere is involved in emotion processing is still unclear, but most evidence continues to grow for the right hemisphere theory (Sato et al., 2004). Furthermore, this primarily refers to later stages of processing beyond the early activation of the ventral temporal stream dedicated to the analysis of faces.

1.3.2. Specific Neural Substrates

Clinical, neurophysiological and neuroimaging studies contribute to the theory of (at least partly) dissociable neural systems for the recognition of specific expressions. The focus of this thesis is on the sensitivity to expression in the visual face processing system (occipital and temporal cortex) but a number of other regions are highlighted in the literature, and likely serve to link the perceptual representations of expressions with prior conceptual knowledge. In this sense, the contribution of areas outside the core face network exhibit indirect expression effects – that is, they are not directly involved in face processing per se. Indeed, studies of this type generally make demands on additional processes such as attention or memory. Therefore, in the studies mentioned below, the brain regions highlighted are not necessarily directly related to the extraction of emotion from faces. For example, amygdala activation to fearful faces could be related to attentional mechanisms driven by salience, and insula activation to disgusted faces is confounded by the fact that insular cortex is gustatory (suggesting this is not a "face response" as such).

There are generally few reported cases of impaired recognition of happy in brain-damaged patients (although see Anderson & Phelps, 2000 for a slight deficit after amygdala lesion). Adolphs et al., (1996) reported a deficit in recognizing surprise following (bilateral amygdala) lesion, Schroeder et al., (2004) found increased activation of the right posterior parahippocampal gyrus compared to neutral and disgusted faces. The amygdala has long been linked with a preferential activation by fearful faces (e.g. Morris et al., 1996; Philips et al., 1997; Whalen et al., 2001). Evidence for a region sensitive to disgusted faces came from studies of Huntington's patients, who exhibit fairly robust deficits in recognition (Spregelmeyer et al., 1996). The pathology of Huntington's disease involves the basal ganglia, and also the insular cortex. This association is supported by neuroimaging studies of healthy controls (Philips et al., 1997, Sprengelmeyer et al., 1998; Schroeder et al., 2004) who exhibit insula activation in response to judging disgusted faces. Interestingly, the anterior insula is described as gustatory cortex in primates (Rolls et al., 1994), containing neurons that respond to pleasant and unpleasant tastes (Yaxley et al., 1988); Harmer et al., (2001a) used transcranial magnetic stimulation to disrupt the processing of angry faces. When TMS was applied to the medial frontal cortex, observers were significantly slower at recognizing anger than when TMS was applied to the medial parietal control region. Blair et al., (1999a,b) suggested the processing of sad facial expressions involves the amygdala. This is supported by some lesion studies (Anderson & Phelps, 2000) but not others (Adolphs et al., 1994; Calder et al., 1996). Furthermore, Philips et al., (1997) and Kesler-West et al., (2001) found no activation of the amygdala for sad compared with neutral faces. There is a lack of consistency for a "sad-specific" neural system, as amygdala responses to sad faces may be confounded by concurrent autonomic responses (Blair et al., 1999a,b) linked to empathic feelings. Sadness, as with other basic expressions apart from

fear and disgust, lacks a strong correlation with any one specific brain region, mainly owing to insufficient data not allowing for a direct causal relationship.

Neurotransmitter involvement

Empirical evidence suggests that pharmacological interventions alter the processing of expressions in different ways. More specifically, serotonergic manipulations affect the processing of fearful and happy faces (Harmer et al., 2001b), noradrenergic manipulations affect the processing of sad faces (Harmer et al., 2001c) and GABAergic manipulations affect the processing of angry faces (Blair & Curran, 1999b). Specific neurotransmitter involvement in the processing of facial expressions is a function of the different brain regions recruited, but is interesting in terms of pharmacological intervention to improve social deficits (e.g. slow or incorrect categorization of expressions) in clinical disorders such as bipolar disorder (which is associated with abnormal activation of the ventral anterior cingulate cortex).

1.4. NEURAL MECHANISMS OF EXPRESSION PRECEPTION FROM FACES

The ability to recognize facial expressions relies on finely tuned neural mechanisms engaging specific neural circuits. Extensive research has been done on how perceptual and cognitive aspects of expression processing interact, providing a framework within which we should consider the representation of diagnostic features in the brain. Compton et al, (2003) suggest that the modification of visual processing by emotional significance of stimuli is how the brain evaluates stimuli as more salient than others. Below certain aspects of how face perception and attention cooperate are discussed, such as, whether certain aspects of face processing are automatic (in that they are unconsciously performed); how rapidly expressions are registered and discriminated; why facial expression categorization should be cast in terms of spatial frequency sensitivity; and how attentional resources are deployed to aid visual processing of expressions.

1.4.1. NON-CONSCIOUS EXPRESSION PROCESSING – SUBCORTICAL VISUAL PATHWAY

Since the discovery of the blindsight phenomenon (Weiskrantz, 1986), it has been apparent that visual processing can occur without primary visual cortex. This involves projections from the retina to the superior colliculus to the pulvinar nucleus of the thalamus to the amygdale and extrastriate cortex, and may be responsible for coarse (low spatial frequency, LSF), automatic processing of facial expression. Blindsight patients are though to be able to discriminate facial expressions (de Gelder et al., 1999), although in the absence of awareness. In other words, patients can discriminate expressions presented to them in their blind visual field. Although it is premature to assume normal recognition of facial expressions can occur in the absence of striate cortex (in blindsight patients regions of extrastriate cortex are likely to be engaged), some interesting evidence has arisen from studies of subliminally processing fearful faces.

Functional imaging data supports that the subcortical route to the amygdala is automatically recruited in the processing of facial expressions and that it may be preferentially activated by fear (LeDoux, 1996; Morris et al., 1998). Animal studies that indicate a direct short-latency pathway from the thalamus to the amygdala (Le Doux 1996) suggest the amygdala might evaluate emotionally valenced stimuli without awareness. In accordance with this theory, studies on humans by Öhman (1992) have demonstrated skin conductance responses to emotionally valenced facial expressions conditioned to predict an aversive electrical shock even when these expressions were presented in a manner that prevented awareness (i.e., facial expressions are presented for a very short time and are followed by a mask presented for a longer time so subjects report only having seen the mask and not a face). Whalen et al., (1998) used functional magnetic resonance imaging (fMRI) techniques to investigate whether the amygdala is activated in humans in response to implicit emotional stimuli. Although subjects reported seeing only neutral faces (as

expressive faces were only presented for 33ms) the blood oxygen level-dependent (BOLD) fMRI signal in the amygdala was significantly higher during viewing of masked fearful faces than during the viewing of masked happy faces.

Although some experiments imply perceptual processing adequate enough to differentiate particular expressions via circuits that largely involve subcortical structures, the underlying neural mechanisms supporting amygdala enhancement of emotional activation of visual cortices is not yet clear, and the idea that certain facial expressions are given precedence in neural processing systems remains a controversial issue. However, converging behavioural, physiological, neuroimaging and neuropsychological evidence does suggest that humans are subjectively unaware of facial expressions yet they can modulate activity in the amygdala. Therefore, it is possible that facial expressions that are not consciously perceived are processed to some extent by subcortical pathways—pathways that are able to distinguish emotional from unemotional faces but are unable to attach categorical labels to the face without cortical input.

1.4.2. ATTENTIONAL RESOURCES FOR EXPRESSION PROCESSING

To efficiently interact with the environment, the human visual system exerts attentive control in order to process some information more thoroughly whilst not attending to that which does not require detailed analysis. Corbetta & Shulman (2002) suggest that certain stimuli gain precedence in attracting attention due to a hard-wired brain mechanism by "learning, development or genetics". In the sense of being extremely salient stimuli, faces have emotional significance and therefore might benefit from preferential visual attention processes. Enhanced processing by selective attention results from the modulation of sensory cortex, the source of which is thought to be in frontoparietal regions (Kastner & Ungerleider, 2000). Corbetta & Shulman (2002) dissociate between a dorsal frontoparietal system that is related to both current task-demands and the salience of external stimulation,

and a ventral frontoparietal system that directs attention to behaviourally relevant stimuli.

Emotion and attention act interactively to modulate visual face processing, and are also highly dependent on task demands. Indeed much evidence has accumulated that expressive faces preferentially capture spatial attention. When attention is directed to faces, V1 activation is increased for fearful over neutral faces (Vuilleumier et al, 2001; Pessoa et al., 2002) as is activity in temporal and orbitofrontal cortices (Vuilleumier et al, 2001; Winston et al., 2003; Yamasaki et al; 2002). Thus throughout the cortical face network from early visual areas to the extended system, attention seems to enhance neural activation to expressive faces, although conflicting evidence arises from amygdala studies; amygdala responses to fearful faces has been shown to be unaffected by spatial attention (Vuilleumier et al., 2001), whilst other studies show attentional modulations of amygdala activation by happy or fearful faces (Pessoa et al., 2002). In fact, Pessoa et al. (2002) found that responses in all brain regions responsive to expression, including the amygdala and FFA, were eliminated when the faces were not attended, and concluded that facial expression processing is neither obligatory nor capacity-free. In contrast, the majority of studies manipulating both attention and emotion, show that diverting attention away from fearful faces leads to responses in the FFA that are reduced but not eliminated; and moreover that amygdala activation is maintained, suggesting that cortical processing needs some resources whereas amygdala activation is both mandatory and resource-independent (Vuilleumier et al., 2001; Anderson et al., 2003; Williams, et al., 2005). Expressive faces may be processed somewhat pre-attentively, but also preferentially engage attentional mechanisms compared to other object categories.

1.4.3. SPEED OF EXPRESSION DISCRIMINATION AND THE N170

ERPs recorded with EEG and MEG are used to investigate the millisecond temporal window of facial expression processing, with recent evidence suggesting there may be early

and late phases of emotional face processing, although the precise neural sources of these are still undefined. Evidence has accumulated for activation in inferotemporal cortex around 150-200ms, as indexed by the N170. The N170 has been used to investigate the neural mechanisms of face processing faces for several years. A large volume of research on the bilateral occipitotemporal N170 demonstrates some fairly consistent findings. Face stimuli appear to elicit a much larger amplitude N170 than object categories such as cars (Bentin et al., 1996; Rossion et al., 2000; Itier &Taylor, 2004), true even when stimuli are controlled as much as possible for low-level parameters such as size and luminance (Rousselet et al., 2005, 2007) which are known to influence the amplitude of early visual potentials (Regan et al., 1989). Furthermore, there is ample evidence that high-level processes drive the N170; Mooney faces elicit a reduced N170 when the face is no longer perceived as a face (Latinus & Taylor, 2005), suggesting this potential reflects face processing. The N170 is delayed and enhanced by face inversion (Jacques & Rossion, 2007; Rossion et al., 1999, 2000, 2003), although the nature of this is not yet completely clear. The timing of the N170 coincides with the vertex positive potential (VPP), which is also sensitive to faces and is thought to reflect the positive counterpart of the equivalent dipoles underlying the N170 (Botzel & Grusser, 1989). The larger N170 for faces likely reflects a synchronized increase in postsynaptic neural activity time-locked to faces as compared to objects. The N170 has been used to investigate the sensitivity of face processing to various stimulus and task manipulations including size (Jeffreys et al., 1992), isolated features (Bentin et al. 1996), spatial attention (Holmes et al., 2003) and task diagnosticity (Joyce et al., 2006). With regards to emotional modulation of the N170, there is evidence both for (Pizzigalli et al., 2002; Batty & Taylor, 2003; Eger et al., 20003) and against (Halgren et al., 2000; Eimer & Holmes et al., 2002).

ERP and MEG studies suggest that expressive faces are actually registered as early as 80ms after stimulus onset. Occipital regions differentiate fearful from happy faces at 90 ms (Pourtois et al., 2004), and happy from sad faces from 110 ms (Halgren et al., 2000). Frontal regions discriminate fearful from neutral faces beginning at 100 ms (Eimer & Holmes, 2002; Holmes et al., 2003) and fearful from happy faces from 120 ms (Kawasaki et al., 2001). Furthermore, several ERP studies have suggested that expressive faces are discriminated at *later* stages, for example over the P300 ERP (Schupp et al., 2004), as yet the significance of this has not been fully explained although it is often associated with more complex cognitive processes triggered by expressive stimuli.

Faces are detected and categorized extremely rapidly by the visual system. Facial expression recognition involves activation in a distributed network of brain regions over a consistent temporal pattern, which allows for interactions and feedback within the network. Basic expression discrimination can occur from 100 ms post-stimulus onset, but fine-grained cortical representations necessary to recognize identity and discriminate between emotion categories are computed within an additional 70 ms. There is also a later, parietal stage of encoding at 300ms related to perceptual decisions. Whether threatening faces are detected more rapidly than other expressions and whether this is aided by subcortical processing is difficult to determine because of limitations in our ability to measure latency responses in subcortical structures. Current evidence provides only some support for claims that rapid threat detection is mediated by purely subcortical pathways, or that threat is detected more rapidly than other expressions. With regards to the temporal aspect of the amygdala's contribution, neither EEG nor MEG can discriminate easily between activity here from that in surrounding cortex because they lack the required spatial resolution to do so. (In turn, fMRI lacks the temporal resolution). Some studies suggest the amygdala is activated after the initial feed-forward sweep of processing in occipitotemporal cortices, at

around 120ms (Halgren et al., 1994). Furthermore, using magnetoencephalography (MEG), judging expression elicited a stronger response than simple face detection in posterior superior temporal cortex over 140–170ms and later in the right amygdala at 220ms, suggesting an interaction between these regions (Streit et al., 1999).

1.4.4. SPATIAL FREQUENCIES AND EXPRESSION PROCESSING

Visual images are composed of a number of spatial frequencies, i.e. the frequency with which light-dark transitions repeat across an image, and psychophysical research shows the perceptual systems analyse this input via a number of channels preferentially tuned to a particular frequency (De Valois & De Valois, 1990). This spatial filtering is a basic mechanism to be considered during the processing of facial expressions. Each channel is tuned to a preferential frequency band, with declining sensitivity to increasingly different frequencies. A ‘‘bandwidth’’ characterizes the range of frequencies to which a channel is sensitive, and channel bandwidths are mostly in the range of 1 to 1.5 octaves– where an octave is a doubling of frequency, e.g., from 2 to 4 cycles per deg (c/deg) of visual angle, 4 to 8 c/deg, 16 to 32 c/deg and so forth. In total, approximately six channels constitute the bank of spatial filters analyzing the retinal input (Sowden & Schyns, 2006). At the centre of the research agenda is the debate of how high-level cognition interacts with inputs from low-level spatial frequency channels to extract information relevant for visual categorization. Top-down control implies that the visual system can actively modulate information extraction from one, or a combination of spatial frequency channels for stimulus encoding and categorization. For example, if categorization of ‘‘fear’’ requires extraction of the wide-opened eyes (Smith et al., 2005) from the retinal input, and because the wide-opened eyes are fine scale features, their accurate encoding should draw information from higher spatial frequency filters. In contrast, the wide-opened mouth of ‘‘happy’’ is a large-scale feature allowing encoding to be more distributed across the filters.

Top-down control of spatial frequency channels, often cast in terms of modulated attention, implies such flexible tuning of the visual system to encode the combination of spatial channels representing categorization-relevant information (with e.g., involvement of different channels for ‘‘the eyes’’ and ‘‘the mouth’’).

The effects of categorization task on information use, and the top-down control of spatial frequency channels pose very interesting questions. Work on hybrid images (Schyns & Oliva, 1999) suggests that task can tune an observer to the specific band (s) from which they can extract diagnostic features. Furthermore, observers perform worse when detecting a grating at a specific spatial frequency when it is randomly intermixed with gratings of differing spatial frequencies, as opposed to when it is presented with gratings of the same spatial frequency. These uncertainty effects can be eliminated if the observer is cued (e.g. with an auditory tone, Hubner, 1996; Davis et al., 1983). Oliva & Schyns (1997) showed that observers are not aware of a face that is presented in the spatial frequency band they are non-sensitized to in a face hybrid. Taken together this evidence would suggest that one can select spatial frequencies, rather than objects which happen to have a certain spatial frequency content.

Several researchers have argued for a special role of the low frequency bands in face processing (e.g. Harmon & Julesz, 1973; Goffaux et al., 2003) particularly so in the categorization of facial expressions. However, the low spatial frequency advantage for face processing is somewhat questionable; Halit et al., (2006) showed that faces containing both high and low spatial frequencies are detected more quickly and accurately than those containing predominantly low spatial frequencies. Some considerable evidence suggests that brain structures that are sensitive to emotional content such as the amygdala are preferentially sensitive to low spatial frequency (LSF) content in fearful faces. The subcortical structures superior colliculus and pulvinar nucleus of the thalamus (Vuilleumier

et al., 2003) that are more sensitive to low spatial frequencies, could directly activate the amygdala in response to fearful faces represented at low spatial frequencies. This is in line with anatomical and functional properties of the visual system such that the amygdala receives input from magnocellular cells (Schiller et al., 1979). Parvocellular inputs on the other hand, more sensitive to high spatial frequency (HSF) content project to ventral visual cortex for processing fine details. Vuilleumier et al also noted a sensitivity of the fusiform cortex to higher spatial frequency ranges, but an implied dissociation of subcortical and cortical pathways to process SF information remains debatable (Winston et al., 2003). The idea of a coarse, fast representation via low spatial frequencies (Schyns & Oliva, 1994) finds echo in Bar et al (2003, see later) who suggest a fast feedforward pathway to orbitofrontal cortex, which in turn directs precise, high spatial frequency information extraction in the visual input via the fusiform gyrus (see also Bullier, 2001). So, not only are spatial frequency bands important because they represent the building blocks of visual representations; spatial frequency bands also appear to play a central role in emotion processing in the brain. The demands imposed by perceptual tasks can bias spatial frequency information use, shown in many psychophysical studies of face processing (Schyns & Oliva, 1999; Morrison & Schyns, 2001; Schyns & Gosselin, 2003). For example, when judging if a face is expressive or neutral requires LSFs (below 2 cycles/degree; 8 cycles/image) perhaps because the composition of large scale features such as the mouth is sufficient to perform this task. On the other hand, the categorization of a particular expression seems to rely on higher SFs (above 6 cycles/degree; 24 cycles/image; Schyns and Oliva, 1999) possibly because finer details are required to disambiguate between expressions.

In terms of how spatial frequency information can be used for categorization, one common thought is that processing of coarse information precedes that of finer information

(Parker et al., 1992, 1996; Schyns & Oliva, 1994). Under this assumption, processing of lower spatial frequency information occurs faster to create a firm depiction of the face before increasingly higher spatial frequency information is required for more precise categorical decisions. Another hypothesis states that usage of spatial scale information is flexible, and is dictated by usefulness of information at different scales depending on the task (Oliva & Schyns, 1997; Schyns & Oliva, 1999). Categorisation can dictate the usage of different spatial scales according to the presence of task-dependent information, informing mechanisms of attention and perception.

1.5. USE OF DIAGNOSTIC INFORMATION

Different regions of the face are important for the recognition of different expressions (Hanawalt, 1944; Plutchik, 1962; Nummenmma, 1964; Bassili, 1979; Cunningham et al., 2005). For example, Bassili et al., (1979) showed that upper or lower portions are useful for particular emotions using point light displays. Thus different expressions require different features to be optimally represented in the visual system. During face processing, hierarchical models of visual cortex typically rely on a feed-forward sweep of information processing, but theories of visual recognition also depend on top-down processing in the cortex that is dependent on task. The Bubbles technique (Gosselin & Schyns, 2001) allows one to determine the specific visual information on which expression judgements are based. Furthermore these features that modulate behavioural response can be compared to the features modulating brain signals, shedding light on top-down influences in visual categorization.

1.5.1. BUBBLES IN THE BRAIN

Crucial to understanding the function of regions within the face-processing network is to establish the information they are sensitive to, and how this changes over spatial and temporal domains during the categorization of facial expressions. Sigala and Logothetis

(2001) investigated the neural mechanisms of visual categorization in the monkey, and revealed sensitivity of temporal neurons to features critical for the task. Facial expressions, as with other complex visual stimuli, elicit a response that must be correctly interpreted in order to relate it to perception and cognition. A critical part of the facial expression recognition process is identifying the features of the stimulus that inform perception. Bubbles (Gosselin & Schyns, 2001) occludes varying regions of a stimulus in an unbiased manner to ascertain a reliable association between stimulus information and observer response. As the stimulus is sampled through a noise field that contains randomly located Gaussian apertures, or 'bubbles', the input to the brain is a few small fractions of a signal. Observers are forced to make discriminatory categorizations of stimuli in which only randomly sampled regions are visible from within the masked stimulus (see Figure 3.1). Performance improves when information revealed is salient for resolving the task, meaning Bubbles can determine if different information from the same stimulus is used for particular tasks. Across extensive trial numbers, the data demonstrate differential significance across particular stimulus information, resulting in an image exposing the information that is diagnostic – that is, information that is sufficient to successfully perform that task.

This methodology works because within a stimulus, not all the available information contributes equally to the observer's ability to make judgements. The reaction of the system is an attempt to identify the signal, and the result of the experiment is a classification image, which illustrates the correlation between the noise contrast at each stimulus location and the system's responses. A classification image can thus be thought of as representing how each spatial location of the stimulus contributes to the system's attempts to identify the signal. A behavioural classification image resulting from the sampling of the stimulus with Bubbles is attained in the following steps: The bubble mask sampling the stimulus is different on each trial – this will result either in a correct response

if diagnostic information is revealed through the mask or an incorrect response if no task-dependent useful information is presented on that trial. Summing together the information leading to correct categorizations, and subtracting the information leading to incorrect responses, results in a behavioural classification image. This is equivalent to performing a least-square multiple regression between the sampled information and response. The pixel values are then z-scored and thresholded for classification images which reveal the significant visual information used to perform the given task, and constitute the minimal information that the brain must process in order to perform said task.

A further challenge is to attribute specific information content to measurable parameters of brain activity, for example in oscillatory networks that could support processing in distributed systems such as that dedicated to face processing (Fries, 2005). Bubble masks can also be correlated with brain signals to interpret them in terms of the visual features driving their activity. While traditional paradigms inform which regions may exhibit a greater activation to one expression over another, it is useful if we can then understand the content of information processing in that region. Furthermore, sensitivity to diagnostic features in a given region assumes a degree of top-down control in visual information processing.

1.5.2. TOP-DOWN MODULATION OF VISUAL PROCESSING

Visual categorization involves the bottom-up extraction of information in the context of top-down expectations, or task requirements. The model of face processing is hierarchical, however, there are numerically the same, if not more, feedback connections in the cortex, carrying top-down modulatory signals. Frontal regions have received much focus in demonstrating how top-down signals guide activation in sensory regions responsible for categorizing visual stimuli. In other words, frontal areas are thought to contain regions that functionally connect with face-sensitive temporal cortex to modulate

incoming sensory information (Summerfield et al., 2006). How top-down facilitation enhances cortical sensitivity to diagnostic information remains unclear, however Bar et al., (2006) observed orbitofrontal activity 50ms earlier than in temporal areas. Furthermore, this activity was modulated by LSF content of the images, suggesting that a coarse representation of the stimulus is projected from early visual areas to prefrontal cortex where predictions interact with temporal regions to facilitate visual analysis.

Another source of top-down control comes from visual attention. It has been the subject of extensive study over recent years owing to its contribution to visual processing in general. Sources of this modulation arise from frontoparietal regions. One key question concerns how early in the visual processing stream attention can exert its effect, i.e. once expressive facial feature information has impinged on the retina, how soon can attention aid the representation of emotion? The central visual pathway prior to the cortex connects the retina to the lateral geniculate nucleus (LGN) of the thalamus, which in turn sends projections to V1. A large number of electrophysiological and neuroimaging experiments (see Kanwisher & Wojciulik, 2000 for review) would suggest that in fact neural responses to visual stimulation can be modulated at extremely early stages, including at the LGN. Therefore during experiments considering the cortical response to expressive visual information (but not directly modulating attention), as in this thesis, one can assume attention likely plays a role, and may act even earlier in the visual processing stream than in temporal regions.

1.5.3. CONTROL OF EYE MOVEMENTS

Visual cognition is concerned with how information from the visual world is represented by the brain's cognitive systems in order to instruct behaviour. The visual system must actively and efficiently seek out information that is necessary for further processing from visually busy environments. This is achieved by performing saccadic eye

movements, which bring the eye to rest (or fixation) during which time information is processed at the region of greatest acuity, the fovea. Eye movements are therefore an interesting way to observe how task-dependent information is acquired during facial expression processing. Indeed a huge number of studies have investigated the correspondence between oculomotor behaviour and cognition (Henderson & Hollingworth, 1998; Henderson 2003; Henderson & Ferreira, 2004). Saccades towards diagnostic information would be considered as having top-down, task-related contributing factors, which are dissociable from bottom-up, stimulus-driven contributions to gaze behaviour. As previous studies have shown a need to attend to diagnostic features (in the absence of eye movements, see Chapter 3), it would seem likely that under free-viewing conditions observers would fixate diagnostic features, although this has never been shown for all basic expressions. Eye movement studies indicate that both primates and humans fixate upon the facial features, especially the eyes and mouth, of expressive faces (see Green & Phillips, 2004), although this was not related to behavioural judgements. In contrast, patient S.M. with early, bilateral amygdala damage and impaired recognition of fearful expressions appears to abnormally scan expressive faces and does not fixate the eyes (Adolphs et al., 2005). When explicitly informed to look at the eyes, this deficit was overcome suggesting that her inability may not be in recognizing fearful expressions per se but rather in attending to facial features that aid recognition of fear.

1.6. SUMMARY

From the huge number of studies outlined in the literature, a potential model for how the face network supports facial expression categorization is now fairly well-defined anatomically, although less so in terms of functionality. Face perception activates early visual cortices (V1, V2, V3) upwards in the cortical hierarchy to regions in the ventral temporal cortex, which provide a detailed analysis of visual properties at around 170ms, i.e.

function as recognition modules. For this reason, the ventral visual stream remains the crucial pathway for expression processing, but may receive contributions from subcortical pathways. The dorsal visual stream (middle superior temporal area) is likely to be recruited if facial expression processing involves motion signals and may feed into ventral temporal areas. This activation of fusiform and superior temporal cortices provides a foundation upon which limbic and frontal areas (i.e. the "cognitive system") can support the conceptual representation of the expression being signalled. It is worthwhile noting that some or all of these regions/stages of processing are likely subjected to feedback processing meaning that regions can participate in both early perceptual and later recognition-based mechanisms. In addition to feedback modulation via the amygdala, top-down influences imposed by the frontoparietal attentional systems and facilitatory prefrontal regions may affect processing in temporal cortex, suggesting multiple sources of control to extract feature representation.

Subcortical structures, namely the superior colliculus and pulvinar nucleus of the thalamus (which could be specialised for rapid and automatic processing, including temporally transient signals of facial expressions) pass information from the pulvinar thalamus to the amygdala, which also receives highly-processed cortical input from the temporal lobe, which in turn also projects to frontal areas. If the limbic and frontal areas are involved in conceptual representations of expressive faces, the amygdala and orbitofrontal cortex respectively could function in a variety of ways. They could modulate the formation of perceptual representations formed in temporal areas via feedback mechanisms to fine-tune or allocate attention to features. They may project to the hippocampus to induce memory-based knowledge of facial expressions. They may also be involved in generating a simulatory emotional response via connections with motor areas and hypothalamus.

The efficient processing of facial expressions is vital for us to appreciate social

situations. The Bruce and Young (1986) model of face processing still guides current studies of this, as does Haxby's (2000) model, which incorporates neuroimaging data from both humans and monkeys (although homology between visual cortical areas is still somewhat unclear). The independence of systems for the processing of expression and identity has been addressed using a variety of approaches, but more recent evidence suggests that these two aspects of face processing might not be as separate as was once thought, but rather the interaction between regions is what is critical. Although the STS appears central to the processing of expressive faces, contrary to its widely perceived role in identity processing, neurons in the FFA very likely also contribute to the affective representation of faces, by a modulation of attention and/or emotion, or even by inputs from the amygdala as well as intrinsic cortical processing.

There continues to be a great deal of research to address how humans effectively interpret changeable aspects of the face such as facial expressions. Increasing sophistication of brain measurements and interpretation moves us towards an understanding of properties of regions as determined by their response patterns and also functional connectivity to other regions (Friston, 1994; Summerfield et al., 2006; Fairhall& Ishai, 2007). Previous experiments have successfully correlated electroencephalographic signals to features that are diagnostic for a given face categorization (see Schyns et al., 2003; Smith et al., 2004) but never has this been applied to judgments of all basic expressions. The representation of diagnostic features in the brain has also never been explored at the earliest cortical stage of visual processing, V1. The studies presented over the next three chapters of this thesis (outlined in Table 1.1.) describe how the use of diagnostic information (which is goal-directed and thus under top-down control) contributes to current understanding of facial expression categorization, beginning with how spatiotemporal inputs via eye fixations reflect diagnostic feature extraction.

	Chapter 2 "Top-Down Control of Fixations in the Categorization of Facial Expressions"	**Chapter 3** "Dynamics of Visual Information Integration in the Brain for Categorizing Facial Expressions – an EEG Study"	**Chapter 4** "Top-Down Modulation of the Cortical Representation of Facial Features in V1 – an fMRI Study"
Hypothesis	Fixations extract diagnostic features	N170 sensitive to expression as a function of diagnosticity	Early visual areas are sensitive to diagnostic features
Method	Eye movements during expression categorization during free-viewing of unsampled expressive face stimuli	Behavioural and EEG classification images to infer feature extraction dynamics in occipitotemporal areas	Retinotopic mapping of diagnostic features in V1 & fMRI BOLD signal in these regions to expressions compared
Conclusion	Diagnostic information extraction increases with fixations performed	N170 encodes diagnostic features from the eyes downwards until behavioural information is processed	Cortical representation of diagnostic features is modulated by categorization task

Table 1.1. Summary of experimental chapters.

CHAPTER TWO

TOP-DOWN CONTROL OF FIXATIONS IN THE CATEGORIZATION OF FACIAL EXPRESSIONS

2.1. TOP-DOWN CONTROL OF EYE MOVEMENTS

Inputs to the visual system dictate the information distributed to cognitive systems during the seamless and rapid categorization of expressive faces. How we perform eye-movements during this ecologically relevant task informs how task-driven and stimulus-driven mechanisms interact to guide the extraction of information supporting recognition. In the current study, we recorded eye movements of observers who categorized the six basic categories of facial expressions. We used a measure of task-relevant information (*diagnosticity*) to discuss oculomotor behaviour, with focus on two findings. Firstly, fixated regions reveal expression differences. Secondly, examining fixation sequences, the intersection of final fixations with diagnostic information is greater than on first fixations. Our data suggest a top-down drive to acquire task-relevant information, with different functional roles for first and final fixations.

2.1.1. DIAGNOSTIC FEATURES SUPPORT EXPRESSION RECOGNITION

It is well established that the allocation of visual attention and guidance of eye movements is an important stage in the information-processing stream (Rayner et al., 2007; Rayner, 2009). What remains less clear is how eye movements are driven to rapidly extract information supporting categorical decisions. Current thinking (Henderson, 2003) would suggest a loop of saccadic control built upon an integral cognitive model, whereby

planning, attention, task and memory influence the sequence of spatiotemporal inputs to the visual system (most likely in combination with bottom-up, stimulus-driven factors).

Here, we framed such a closed loop model in the context of the biologically relevant task of facial expression categorization. We use this process as an avenue to explore a central issue in visual cognition: the interaction between top-down and bottom-up processing in saccadic control. Consider that saccadic movements are tuned to rapidly provide the visual system with information at the highest resolution. Consider also that saccades are guided to information that subserves the task. It then follows, in visual categorization tasks, that top-down control must guide, at least in part, the direction of saccades towards task-relevant information.

Facial expression recognition provides a strong foundation upon which to study the control of eye movements for two reasons. Firstly, from the top-down perspective, it is a proficient visual ability of humans, and benefits from neural networks specialized in processing information supporting this as well as other categorizations such as identity (Adolphs et al., 1996; Haxby et al., 2000). When emotion recognition is impaired, for example in amygdala damaged patients, the categorization deficit can be rectified with specific instructions for eye guidance (e.g. instructing to look at the eyes restored a normal categorization of "fear," in an amygdala damaged patient, Adolphs et al., 2005). Secondly, diagnostic information, as obtained with the Bubbles technique (Gosselin & Schyns, 2001, tells us expressive signals are not evenly distributed within the face (Smith et al., 2005, Schyns et al., 2007, 2009). Controlled guidance might be required for its extraction at high resolution in the fovea.

An important question therefore arises as to the functional role of eye movements. Several studies suggest eye movements are informative in terms of cognitive processing mechanisms during face processing (e.g. Yarbus, 1967; Walker-Smith et al., 1977;

Henderson et al., 2005; Barton et al., 2006; Buchan et al., 2007; Guo et al., 2006, 2007). Other evidence suggests that specific features of a stimulus underlie its correct categorization (Gosselin & Schyns, 2001). And these features are represented in the input image and in the brain at different spatial resolutions (i.e. across different spatial frequency bands, see Sowden & Schyns, 2006, for a review; and see also Schyns et al., 2007, 2009; Van Rijsbergen & Schyns, 2010 for electrophysiological evidence). On this basis, we predicted that diagnostic features are fixated prior to categorical decision and that foveated regions reflected the spatial frequency composition of the diagnostic features (Smith & Schyns, 2009).

In the experiment, we placed observers in an ecologically valid situation of categorization (distinguishing between six Ekman-coded facial expressions of emotion plus neutral) and recorded their eye movements while they performed the task. To understand the relationships between fixations in the face, diagnostic features, and spatial frequency composition of features, we merged the analysis of the typical fixation maps with the maps of diagnostic information (here across spatial frequencies) as computed in Bubbles. For each fixation in a series between stimulus presentation and behaviour, we computed whether this fixation extracted information from a diagnostic feature and if so, at what spatial resolution.

2.2. Experimental methods

2.2.1. Participants

Five female participants with normal vision from Glasgow University were paid to take part in the experiment. They gave written informed consent prior to involvement and the protocol was approved by the Faculty ethics committee.

2.2.2. STIMULI

Face stimuli were greyscale images of five females and five males taken under standardized illumination, each displaying the basic facial expressions ("happy," "surprise," "fear," "disgust," "anger," "sad") and "neutral." All 70 stimuli (normalized for the location of eyes and mouth) complied with the Facial Action Coding System (FACS) (Ekman & Friesen, 1978) and form part of the California facial expressions (CAFE) database (Dailey et al., 2001). The images were 240 x 380 pixels in size and viewed at a distance of 70cm, subtending 14.65° degrees of visual angle vertically and 9.15° degrees of visual angle horizontally. This represents roughly the size of a real face (approximately 19 cm in height) at a natural distance during interaction.

2.2.3. APPARATUS

Eye movements were recorded at a sampling rate of 1000 Hz with the SR Research Desktop-Mount EyeLink 2K eyetracker (with a chin/forehead rest), which has an average gaze position error of about 0.25°, a spatial resolution of 0.01° and a linear output over the range of the monitor used. Only the dominant eye of each participant was tracked although viewing was binocular. The experiment was implemented in Matlab (R2006a), using the Psychophysics (PTB-3) and EyeLink Toolbox extensions (Brainard, 1997; Pelli, 1997; Cornelissen et al., 2002). Stimuli were displayed at a resolution of 800*600 pixels on a Dell P1130 on NVIDIA Quadro FX 540, with a screen refresh rate of 120Hz. Chin and forehead rests maintained viewing distance at 70cm from the stimulus display monitor.

2.2.4. PROCEDURE

Prior to testing, observers learned to categorize the stimuli into the seven expression categories. Upon achieving a 95% correct classification criterion, observers performed 6 sessions of 350 trials (totalling 2100 trials) of the expression categorization task (300 trials per expression, randomly distributed across sessions). Calibration of eye fixations was

conducted at the beginning of the experiment using a nine-point fixation procedure as implemented in the EyeLink API (see EyeLink Manual) and using Matlab software. Calibration were then validated with the EyeLink software and repeated when necessary until the optimal calibration criterion was reached. At the beginning of each trial, participants were instructed to fixate a dot at the centre of the screen to perform a drift correction. If the drift correction was more than 0.5°, a new calibration was launched to insure an optimal recording quality. This was followed by the presentation of a face image, on a light-gray background, in the centre of a monitor. Stimuli remained on screen until response. Observers were asked to respond quickly and accurately by providing a verbal response for accuracy measures and a single key-press response as a measure of reaction time. Fixation acquisition terminated at the button press.

2.2.5. Extraction of Diagnostic Fixations

Computational Analyses of Fixations

The aims of our work are (a) to determine if fixations contribute to the extraction of diagnostic information on the face and (b) to examine how this extraction happens over a sequence of fixations.

A. Computation of diagnostic information per fixation. Smith et al., (2005) and Schyns et al., (2007, see Schyns et al., 2009 for the meta-analysis of this data used in the current experiment) used *Bubbles* to extract the diagnostic information when observers resolved the same task on the same stimuli as those used in the current experiment (7 alternative forced-choice categorization of the six basic expressions plus neutral). This diagnostic information comprised information represented at five different spatial resolutions from coarse to detailed (Figure 2.2.a). This information constitutes a diagnostic "spatial filter" (Figure 2.2.a) that can be apposed on the facial expression to reveal its diagnostic features (Figure 2.3.a).

We used these diagnostic filters to compute whether a given fixation lands on the diagnostic information, and if so, quantify the detail of diagnostic information each fixation "sees". The level of detail that is typically required from the features of expressive faces is shown in Figure 2.2.a. For example, a fixation landing on the right corner of the mouth in "happy" would receive a high score (of 1, represented in white in Figure 2.2.a), reflecting the fact that observers typically require this information at full spatial resolution (i.e. from five spatial frequency bands, summing the non-linear weights reflecting the number of cycles present at each band—with weights = 0.548, 0.314, 0.092, 0.043 and 0.003, from the finest to the coarsest SF band). In contrast, a fixation on the centre of the eye for the same expression would receive a lower score of 0.862 (equal to 0.548 + 0.314), because fewer spatial frequencies (specifically HSF bands 1 and 2) compose this feature. Using this information, we analysed "fixation diagnosticity" in the following two steps:

B. 1. *Distribution of diagnostic information and fixations in upper and lower face.* A cursory inspection of Figure 2.2.a reveals a distribution of diagnostic information in the top and the low part of the face. From this, we can derive a measure to predict where diagnostic fixations should land in the face, as a function of each expression (i.e. more in the lower part in "happy;" more in the upper part in "anger").

To this end, for each expression we segmented the face into its upper region (including the eyes) and its lower region (including the mouth, see the horizontal dividing line in Figure 2.2.b), integrated the number of cycles per face present in the areas of diagnostic information across the five spatial frequency bands and divided the resulting number by the total of diagnostic information across the two regions to derive weight values for the upper and lower face regions between 0 and 1. To illustrate, in "surprise", the lower region had a higher weight of 0.98 indicating that diagnostic information is very much local to the mouth for this expression, but the weights in "sad" were more even (0.59

and 0.41) indicating that diagnostic information was more distributed between the higher and lower face regions. In addition, for each expression, we separately computed the number of fixations landing in the upper and lower face regions (Figure 2.2.b).

B. *2. Increase in diagnostic information per fixation.* A fixation map misses important information: the temporal sequence of fixations. To remediate this, for each observer and expression, we combined in independent fixation maps all first fixations, all second, all third and all fourth fixations. We smoothed these fixation maps with a Gaussian kernel (sigma=10 pixels) and multiplied them with the diagnostic masks of figure 2.2.a, providing a measure of diagnostic information acquired in each fixation in a sequence. Across fixations 1 to 4, we can compute how each individual fixation contributes to the overall extraction of novel diagnostic information for behavioral decision (with the precaution of subtracting in fixation map n+1 the diagnostic information already present in fixation map n). The colour-coded plots of Figure 2.3.b illustrate the integration of this measurement for 2, 3 and 4 fixation sequences.

In addition, again by intersecting fixation maps with diagnostic masks, we computed an average diagnosticity measure per fixation (in other words, we weighted fixations by the number reflecting the level of diagnostic detail that is typically required from that region) and performed a linear regression of fixation and diagnostic information (Figure 2.4).

2.3. RESULTS

2.3.1. BEHAVIOUR

Accuracy

Analysis was performed on 1-, 2-, 3- and 4-fixation trials as these accounted for an average of 87% of data across observers. Observers completed a learning phase requiring a 95% performance and so categorization accuracy was high across all expressions (happy –

100%; sad – 96.8%; neutral – 95.2%; anger – 94.3%; disgust – 93.9%; fear – 93.8%; surprise – 89.7%, across observers). At both group and observer levels, the percentage of correct categorization did not significantly differ between expressions. However within observers, surprise and fear generally led to the numerically poorest performance, whilst happy was perfectly recognized.

Reaction Time

A one-way repeated-measures ANOVA revealed a significant effect of expression on Reaction Time (RT): $F(6, 28) = 9.79$, $p<0.001$, (Figure 2.1.). Pairwise comparisons between all expressions showed a faster categorization of "happy" compared with "surprise" and "disgust," and a slower categorization of "fear" compared with "sad" (Bonferroni-corrected t-test, $p<0.0083$).

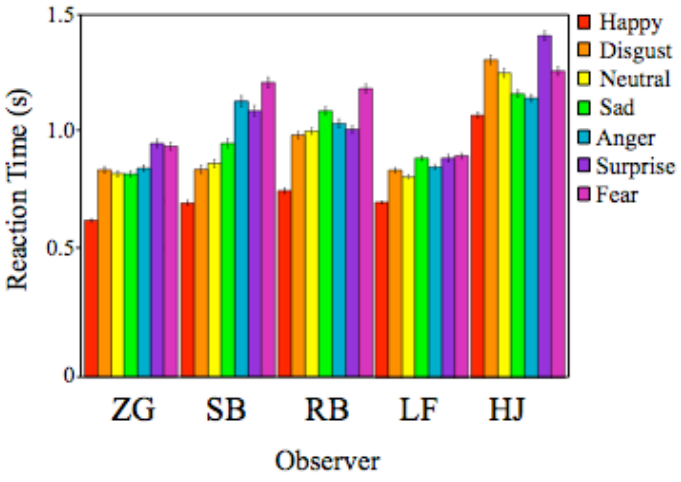


Figure 2.1. Mean reaction times per expression and observer (error bars report standard errors).

Number of Fixations

A one-way repeated-measures ANOVA on the mean number of fixations per expression also revealed a significant effect, $F(6, 28) = 15.69$, $p<0.001$. Mean (and standard deviation) number of fixations per expressions and collapsed across observers was "happy", 1.52 ± 0.22; "disgust", 2.13± 0.30; "sad", 2.14 ± 0.29; "anger", 2.16 ± 0.28; "neutral", 2.16 ±

0.42 ; “surprise”, 2.39 ± 0.38 ; “fear”, 2.53 ± 0.33. Pairwise comparisons between all expressions showed that “happy” was categorized with fewer fixations than “sad” and “fear” (Bonferroni-corrected t-test, $p < 0.0083$).

Number of Fixations and Reaction Time

If some expressions require the extraction and integration of more diagnostic information samples to produce correct categorization behaviour then their RTs should be slower. To test this hypothesis, we performed a robust linear regression that confirmed a linear increase between RT and fixation numbers ($y = 0.1853*x+640$, $R^2 = 0.4014$, $p<0.01$).

An interesting question arising from the linear relationship between number of fixations and RTs is the reason for systematically more fixations in specific facial expressions. This could stem from the distribution of facial features in the face. For example, the wide opened mouth in “happy” is a large feature confined to the bottom half of the face. In contrast, the features of sad and fear are distributed across the face, at finer resolutions around the eyes and the corners of the mouth. Extraction of diagnostic information might therefore require few fixations in “happy” (because the smiling mouth is a large scale, prevalent diagnostic feature) but the distribution of information over the face in “sad” (or “fear”) could lead to more fixations to integrate diagnostic information at high spatial resolutions. The following section explains how we tested this hypothesis.

2.3.2. Diagnosticity of Fixations and their Functional Roles

Fixation patterns reveal expression differences. To show that fixations reflect diagnostic information use, and thus reveal expression differences, we quantified and compared the distribution of both diagnostic information and fixations in the upper and lower parts of the face (divided equally in half). We show in Figure 2.2.b smoothed fixation maps for all expressions across observers. Overlaid are bar plots showing both the proportion of diagnostic information (green bars and Figure 2.2.a) and fixations (orange bars) in the

upper and lower portions of the face. Visual inspection shows that for all expressions apart from surprise and fear, these two proportions correspond well. That neither "surprise" nor "fear" share common distributions of diagnostic features and fixation locations is not unexpected given the poor behavioural performance with these two expressions. Both display wide-open eyes but "surprise" is also characteristic of a wide-open mouth, thus they might require fixations to the mouth *and* eyes to disambiguate. A two-way repeated measures ANOVA reveals a significant interaction with expression and region of face (upper/lower) in which fixations land, ($F(4, 65), = 32.7$, $p < 0.001$), with happy receiving significantly more fixations to the lower face than neutral, anger and sad (Bonferroni-corrected t-test).

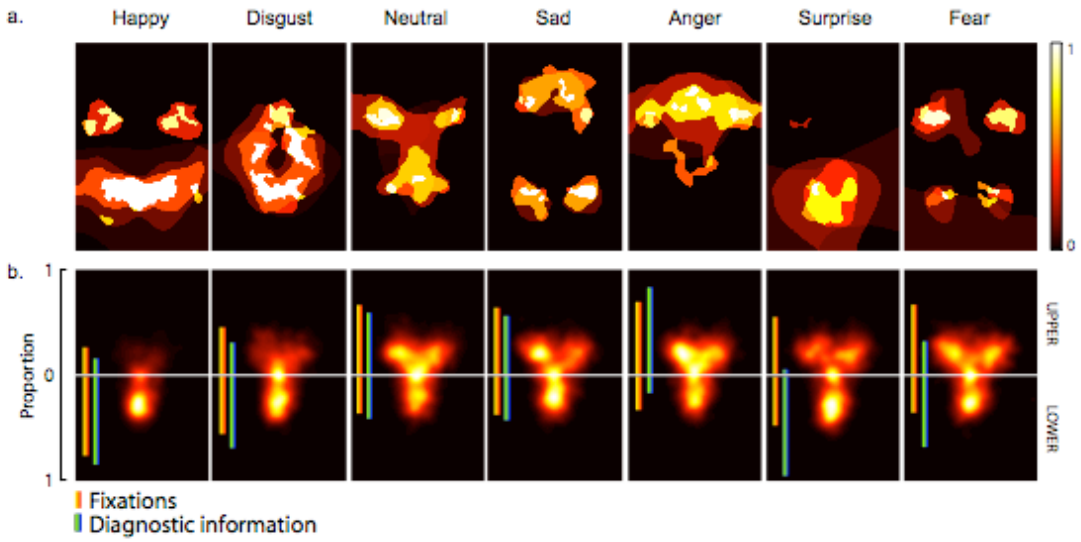


Figure 2.2a. A meta-analysis of the diagnostic information sampled by Smith et al., (2005) & Schyns et al., (2007, see Schyns et al., 2009) comprised information at five different spatial resolutions from detailed to coarse. The range of colours reveals the different level of detail of diagnostic information per expression. b. Smoothed fixation distribution maps for the seven expressions collapsed across observers, ordered by reaction time. Orange bars correspond to the proportion of fixations in the upper and lower parts of the face, and green bars to the proportion of diagnostic information (in 1a) within the upper and lower face (indicated by the white line).

Increase in diagnostic information per fixation. Figure 2.3.a is designed to illustrate, colour-coded per observer, the relationship between the order of a fixation in the sequence leading to behaviour (represented as rows) and the location of diagnostic features in the face for this expression (from Schyns et al., 2009). For all fixations in a sequence, we intersected the fixation maps with the diagnostic mask (represented in Figure 2.2.a) and computed the increase in diagnostic information in the sequence of two-, three- and four-fixations trials (Figure 2.3.b). Figure 2.2b reveals that diagnostic information acquisition increases with fixations performed. This suggests a large enough increase must occur in order that behavioural response can be achieved. The accumulation of information when only two fixations are performed is typically at least as great as when three or four fixations are performed, implying information acquisition is key to categorization. Generally, the information accumulated during "surprise" judgments is somewhat lower than that for other expressions. The diagnostic information for this expression is the mouth, but observers typically fixate the eyes and mouth. Again, this could be related to the high confusability with "fear".

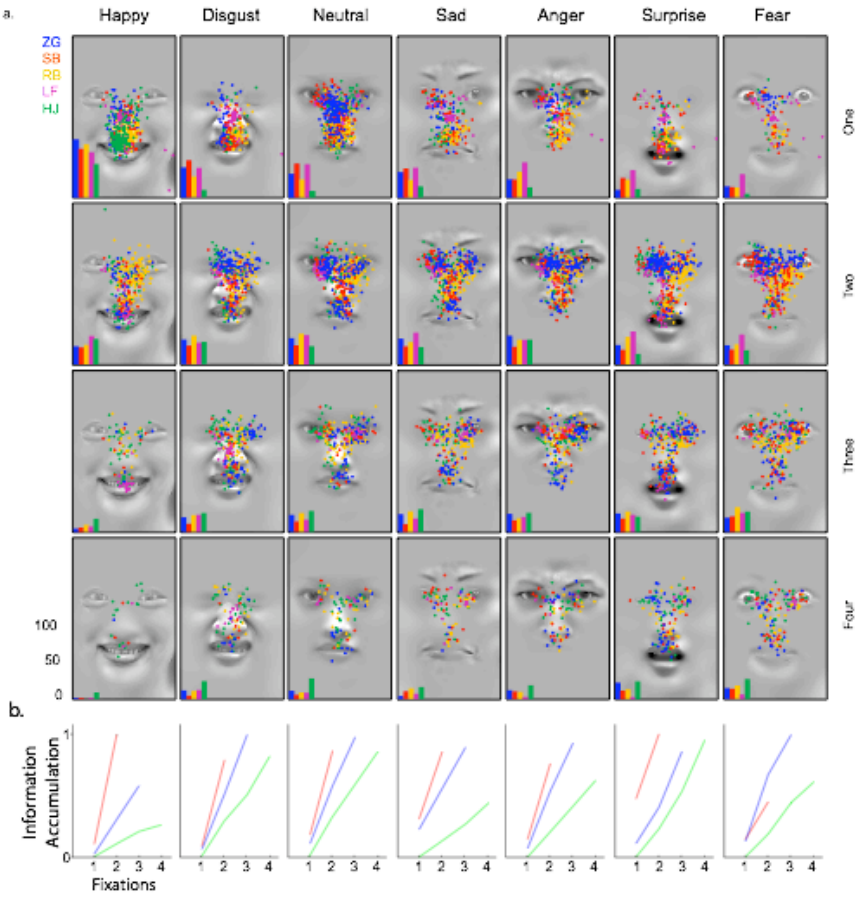


Figure 2.3a. Greyscale images: For each expression, classification images reveal the significant (p < .001, corrected, Chauvin et al. 2005) sum of the five spatial frequency bands required for 75% correct categorization of each of the seven expressions. **Fixation maps:** distribution of fixations (colour-coded for observer) grouped according to fixation number in the sequence per trial. Histograms (colour-coded for observer) reveal per expression the proportion of trials that were of one, two, three or four fixations. **b.** Per expression, the average increase in diagnostic information is integrated over fixations for sequences of two-, three- and four-fixation trials (normalized between 0 and 1).

A multiple linear regression revealed that the average diagnosticity of fixations significantly increased from first to final fixations (Figure 2.4). This suggests that information acquired in the final fixation is more informative for the task than that of the first fixation (Figure 2.4.). Some trials required only one fixation; this implies that the measure of diagnosticity of the single fixation should be significantly greater than the intersection of first fixations when more than one fixation was performed. A two-way

repeated measures ANOVA (expression x fixation) confirmed this prediction, $F(4, 65) = 7.0$, $p<0.05$.

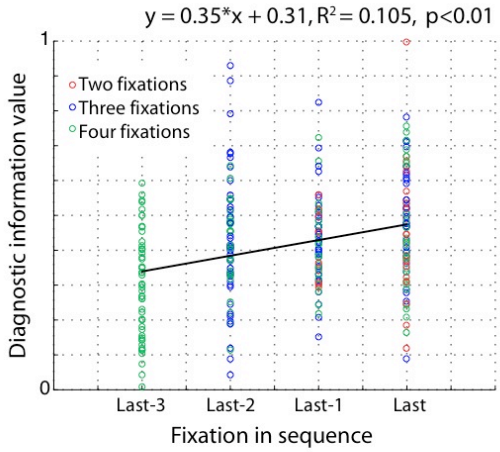


Figure 2.4. Average diagnostic information of fixations across expressions. Multiple linear regression using least mean squares of fixation in the sequence (x-axis) and diagnostic information value (y-axis, normalized between 0 and 1). Data were pooled across expression and observer.

2.4. FIXATIONS EXTRACT DIAGNOSTIC INFORMATION

Saccadic eye movements inform how spatial information is used for components of cognitive behaviour. In the context of facial expression categorization, we make three independent points. We show that the number of fixations required for correct categorization differs across expression. We show that the number of fixations positively correlates with reaction times. Finally, we show that fixations land on diagnostic features, with an increase in diagnosticity between first and final fixations. These results confirm facilitation by cognitive mechanisms to guide saccades to diagnostic inputs (Malcolm et al., 2008), channelling high-resolution task-relevant features from stimulus (Castelhano et al., 2009) to higher areas for efficient decoding of emotional content.

It is more recently assumed that saccadic control relies upon an integral cognitive model (Findlay & Gilchrist, 2001; Henderson, 2003; Chen & Zelinsky, 2006; Zelinsky et

al., 2006; Henderson, 2007), modulated by attention, task, planning and working memory (Hollingworth et al., 2008; Hollingworth & Luck, 2009). Indeed, a significant input to saccadic control centres is of cortical origin (Schiller & Tehovnik, 2005), where such cognitive functioning occurs. It is interesting to consider how these higher influences diagnostically tune eye movements. With regard to attention, if observers exploit task-constraints to attend information for recognition (Schyns, 1998; Smith et al., 2005; Schyns et al., 2007, 2009), and eye movements indicate attentional mechanisms, the visual system may seek this information in free-viewing conditions. In order to accomplish this, frontoparietal regions may be recruited in the cognitive selection of visual features (see Corbetta & Shulman, 2002 for discussion), though this remains to be explicitly tested in a rigorous context.

Two outstanding questions should be a focus of eye movement research. The first concerns the respective contribution of bottom-up and top-down information in guiding saccades. Our measure of fixation diagnosticity leaves little doubt that fixation location is strongly constrained by the top-down requirement to encode diagnostic, task-dependent information, given the considerably higher probability to land in any other face region if the saccadic guidance was random. One could argue that bottom-up information such as high contrast guides the next fixation in the sequence, but we argue this is unlikely for several reasons. First, observers know they are extracting information from a face, and unlike other objects and scenes, faces have an almost singular regularity in the organization of their components (most of us have two eyes, a nose and a mouth forming a configuration with little variance—certainly less so than the buildings forming a city). So, observers tend to know, in a top-down manner, where and how far features are from the features they are currently fixating. Second, and this is clear from Figure 2.3a, regions of high contrast are not necessarily correlated with features of high diagnosticity (see Henderson et al., 2007;

Kreiger et al., 2000; Tatler et al., 2005, for discussion of image properties and fixation location). For example, the contours of the face, or the hairline, tend to be regions of high contrast, but they receive few, if any fixations. So, in this context of "high information" the threshold for parafoveal cues could be lowered and their role considerably diminished compared with, e.g., typical outdoor scenes (Torralba et al., 2006). Furthermore, the features that diagnose facial expressions (with the notable exception of the broad smiling mouth in "happy") are represented at a fine scale (e.g. the wrinkly frown in sadness, the white of the eyes in "fear", Smith & Schyns, 2009) which require encoding at High Spatial Frequencies, themselves requiring foveation of the information. This presents a prime example of a situation where the image representation of diagnostic cues interact with the information requirements of the task to "diagnostically" allocate fixations to specific face regions. One might also consider how eye movements towards diagnostic regions reflect the speed of visual processing (Kirchner & Thorpe, 2006; Bacon-Macé et al., 2007), and how this supports the transition from visual perception to categorization response (and often to the programming of additional saccades).

A second question of interest concerns what happens during a fixation. This can be broken down into several sub-questions: What specific information is extracted and encoded by the visual system? How is this information integrated with that already encoded and memorized from previous fixations? And then, critically, when and how does the system decide that sufficient diagnostic information has been accrued to warrant accurate categorization behaviour? These are questions for further research but our data suggest a few interesting points. For example, at least in facial expressions, features are bilaterally symmetric `(left and right wide opened eyes in "fear"; left and right corner of the mouth in "happy"; left and right involving the eyebrows in "sad"; the left and right corners of the nose in "disgust;" and so forth). As far as eye information is concerned, it is

puzzling to notice that observers tend to fixate one eye, then the next eye, when this information is redundant—i.e. one eye would suffice. For example, in "fear" and "surprise," two expressions mostly confused, an optimal strategy would be to combine one eye with the mouth, but observers tend to integrate both eyes and the mouth.

To conclude, the evidence of a top-down determination of fixations reported here raises many questions. The advantage of faces over other stimuli to address them is that the spatial location of features is stable, enabling the system to use this knowledge to guide information extraction. This provides a useful platform to address questions relating to cortical networks supporting the extraction, encoding and integration of information that supports categorization.

CHAPTER THREE

DYNAMICS OF VISUAL INFORMATION INTEGRATION IN THE BRAIN FOR CATEGORIZING FACIAL EXPRESSIONS – AN EEG STUDY

3.1. COMPUTATIONAL BRAIN DYNAMICS OF EXPRESSIVE FACE PROCESSING

In the previous chapter, we computed the increase in diagnostic information over successive fixations, during free viewing of expressive faces. That diagnostic information increases with fixations performed suggests that diagnostic feature extraction is a motivation for saccadic eye movements. An interesting question arises here, in that each diagnostic input must be compared with some internal representation to determine if more information is required. (This likely involves mechanisms of working memory and attention). It is therefore pertinent to address how early expression-specific information is dissociated in the brain. The results of a large number of face recognition studies reveal bilateral activation in inferotemporal cortex at around 170ms; this negative potential is referred to as the N170. Studies of this ERP reveal consistent findings, making it a standard marker of face processing in the brain. Although there is ample evidence that high-level processing underlies the N170, there remains uncertainty as to how expression modulates it.

Key to understanding visual cognition is to determine when, how, and with what information the human brain distinguishes between visual categories. So far, the dynamics of information processing for categorization of visual stimuli has not been elucidated. By using an ecologically important categorization task (seven expressions of emotion), we demonstrate, in three human observers, that an early brain event (the N170 Event Related

Potential, occurring 170 ms after stimulus onset (Bentin et al., 1996; De Hann et al., 1998; Rossion et al., 1999; Eimer, 2000; Lui et al., 2000; Rossion et al., 2000; Sagiv & Bentin, 2001; Tanaka & Curran, 2001; Taylor et al., 2001; Eimer & Holmes, 2002; Rossion et al., 2002; Batty & Taylor, 2003; Gauthier et al., 2003; Rossion et al., 2003; Itier & Taylor, 2004; Maurer et al., 2005) integrates visual information specific to each expression, according to a pattern. Specifically, starting 50 ms prior to the ERP peak, facial information tends to be integrated from the eyes downward in the face. This integration stops, and the ERP peaks, when the information diagnostic for judging a particular expression has been integrated (e.g., the eyes in fear, the corners of the nose in disgust, or the mouth in happiness). Consequently, the duration of information integration from the eyes down determines the latency of the N170 for each expression (e.g., with ‘‘fear’’ being faster than ‘‘disgust,’’ itself faster than ‘‘happy’’). For the first time in visual categorization, we relate the dynamics of an important brain event to the dynamics of a precise information-processing function.

We instructed three observers to resolve seven biologically relevant face categorizations (‘‘happy,’’ ‘‘fear,’’ ‘‘surprise,’’ ‘‘disgust,’’ ‘‘anger,’’ ‘‘sad,’’ and ‘‘neutral’’) of FACS-coded faces (Ekman & Friesen, 1975; 1978) (five males and five females) displaying each expression of emotion (for a total of 70 original stimuli). The experiment sought to establish a one-to-one correspondence between random samples of facial information presented on each trial (sampled from the original faces, with Gaussian windows smoothly revealing information from five non-overlapping spatial frequency—SF–bandwidths; see Figure 3.1.) and behavioural (Gosselin & Schyns, 2001; Schyns et al., 2002; Smith et al., 2005) and brain responses to this facial information (Schyns et al., 2003; Smith et al., 2004; Smith et al., 2006). With classification image techniques, we estimated, for each observer, across the 21,000 trials of the experiment (3000 trials per expression)

how facial information modulated behaviour (categorization accuracy) and brain responses (modulations of EEG voltage over the time course of the N170).

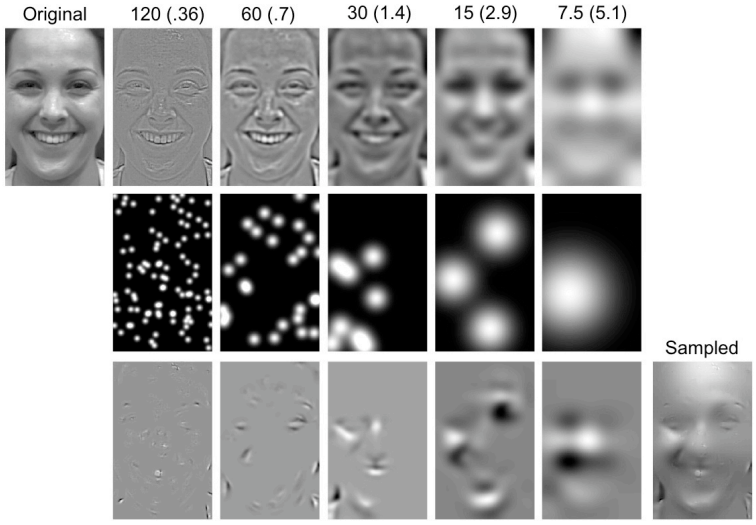


Figure 3.1. Stimulus Generation Process. First row: On each trial a randomly chosen original stimulus is decomposed into 5 non-overlapping Spatial Frequency (SF) bands of one octave each (120-60, 60-30, 30-15, 15-7.5 and 7.5-3.8 cycles/face). Second row: Gaussian apertures each revealing 6 cycles, irrespective of SF band, are randomly positioned (standard deviations of the bubbles were 0.36, 0.7, 1.4, 2.9, 5.1 cycles/degree of visual angle from the fine to the coarse SF band). Third row: The SF-band facial information from the first row is sampled with the Gaussian apertures of the second row. The addition of the randomly sampled face information from each SF band produces one stimulus image.

3.2 EXPERIMENTAL METHODS

3.2.1. PARTICIPANTS

Three female participants from Glasgow University, UK, were paid to take part in the experiment. All had normal vision and gave informed consent prior to involvement. Glasgow University Faculty of Information and Mathematical Sciences Ethics Committee provided ethical approval.

3.2.2. STIMULI

Original face stimuli were greyscale images of five females and five males taken under standardized illumination, each displaying seven facial expressions. All 70 stimuli (normalized for the location of the nose and mouth) complied with the Facial Action

Coding System (FACS, Ekman & Friesen, 1978) and formed part of the California facial expressions (CAFE) database (Dailey et al., 2001). Stimuli were then sampled using the Bubbles technique (Gosselin & Schyns, 2001), to ascertain a measure of specific visual input modulating the identification of each expression. To this end, a bubble mask randomly samples the stimulus on each trial – this will result either in a correct response if diagnostic information is revealed or an incorrect response if no useful information is presented on that trial. Summing together the information leading to correct categorizations, and subtracting the information leading to incorrect responses, results in a behavioural classification image. Bubble masks can also be correlated with EEG amplitudes to derive the information modulating brain signals. Because facial information is represented at multiple spatial scales, on each trial we exposed the visual system to a random subset of spatial frequency (SF) information contained within the original face image. To this end, we first decomposed the original image into five non-overlapping SF bands of one octave each (120–60, 60–30, 30–15, 15–7.5, and 7.5–3.8 cycles/face; see Figure 3.1.). To each SF band, we then applied a mask punctured with Gaussian apertures. These were positioned in random locations trial by trial, approximating a uniform sampling of all face regions across trials. The size of the apertures was adjusted for each SF band, so that six cycles per face was revealed. In addition, we adjusted the probability of a bubble in each SF band so as to maintain constant the total area of face revealed across trials (SDs of the bubbles were 0.36, 0.7, 1.4, 2.9, and 5.1 cycles/degree of visual angle from the fine to the coarse SF band). We performed calibration of the sampling density (i.e., the number of bubbles) online on a trial-by-trial basis to maintain the observer's performance at 75% correct categorization independently for each expression. The stimulus presented on each trial comprised the randomly sampled information from each SF band summed together.

3.2.3. PROCEDURE

Prior to testing, the three observers learned to categorize the 70 original images into the 7 expression categories. Upon achieving a 95% correct classification criterion of the original images, observers performed a total of 15 sessions of 1400 trials (for a total of 21,000 trials) of the sampled facial expressions categorization task (i.e. 3000 trials per expression, happy, sad, fearful, angry, surprised, disgusted and neutral faces, randomly distributed across sessions), whilst we concurrently recorded their EEG. Short breaks were permitted every 100 trials of the experiment. In each trial a 500 ms fixation cross (spanning 0.4º of visual angle) was immediately followed by the sampled face information, as described before. Stimuli were presented on a light gray background in the centre of a monitor; a chin-rest maintained a fixed viewing distance of 1 m (visual angle 5.36º x 3.7º forehead to base of chin). Stimuli remained on screen until response. Observers were asked to respond as quickly and accurately as possible by pressing expression-specific response keys (7 in total) on a computer keyboard. The stimuli were displayed on a CRT (Sony Trinitron) with a 1280 x 1024 pixel resolution and 75Hz refresh rate. The experiment was programmed with the Psychophysical toolbox (Brainard, 1997; Pelli, 1997) and we explicitly waited for the monitor to be synchronized before issuing the command to send the stimulus data to the screen buffer.

We used sintered Ag/AgCl electrodes mounted in a 62-electrode cap (Easy-Cap) at scalp positions including the standard 10-20 system positions along with intermediate positions and an additional row of low occipital electrodes. Linked mastoids served as initial common reference, and electrode AFz as the ground. Vertical electro-oculogram (vEOG) was bipolarly registered above and below the dominant eye, and the horizontal electro-oculogram (hEOG) was registered at the outer canthi of both eyes. Electrode impedance was maintained below 10 kΩ throughout recording. Electrical activity was continuously sampled at 1024 Hz. Analysis epochs were generated offline, beginning 500

ms prior to stimulus onset and lasting for 1500 ms in total. We rejected EEG and EOG artifacts by using a [230 mV; + 30 mV] deviation threshold over 200 ms intervals on all electrodes. The EOG rejection procedure rejected rotations of the eyeball from 0.9° inward to 1.5° downward of visual angle—the stimulus spanned 5.36° x 3.7° of visual angle on the screen. Artifact-free trials were sorted with EEProbe (ANT) software, and narrow-band notch filtered at 49–51Hz and re-referenced to average reference. For each observer we selected a left and right occipitotemporal electrode on the basis of those electrodes recording the highest amplitude of the N170 peak.

3.2.4. COMPUTATION: BEHAVIORAL CLASSIFICATION IMAGE

On each trial of a categorization task, the randomly located Gaussian apertures make up a 3D mask that reveals a sparse face. Observers will tend to be correct when this sampled SF information is diagnostic for the categorization of the considered expression. For identifying SF features used for each facial expression categorization, across trials the probability of being correct was computed by summation of the aperture masks leading to correct categorizations and division of the result by the sum of all aperture masks shown (for correct and incorrect categorizations) for that expression. This is analogous to performing a least-square multiple regression. We then transformed these probabilities into Z scores to locate the statistically significant regions ($p < .05$, corrected, Pixel Test Chauvin et al., 2005) corresponding to the features used to accurately perform the categorization of each expression. The procedure was repeated independently for each one of the five SF bands, representing in the three dimensions of stimulus sampling the combination of SF bands and image features diagnostic for the categorization of each expression. Filtering the original stimulus with the diagnostic information represented in each SF band produces the effective stimulus for each expression as represented in ‘‘Behaviour’’ in Figures 3.2-4. for the spatial frequency decomposition.

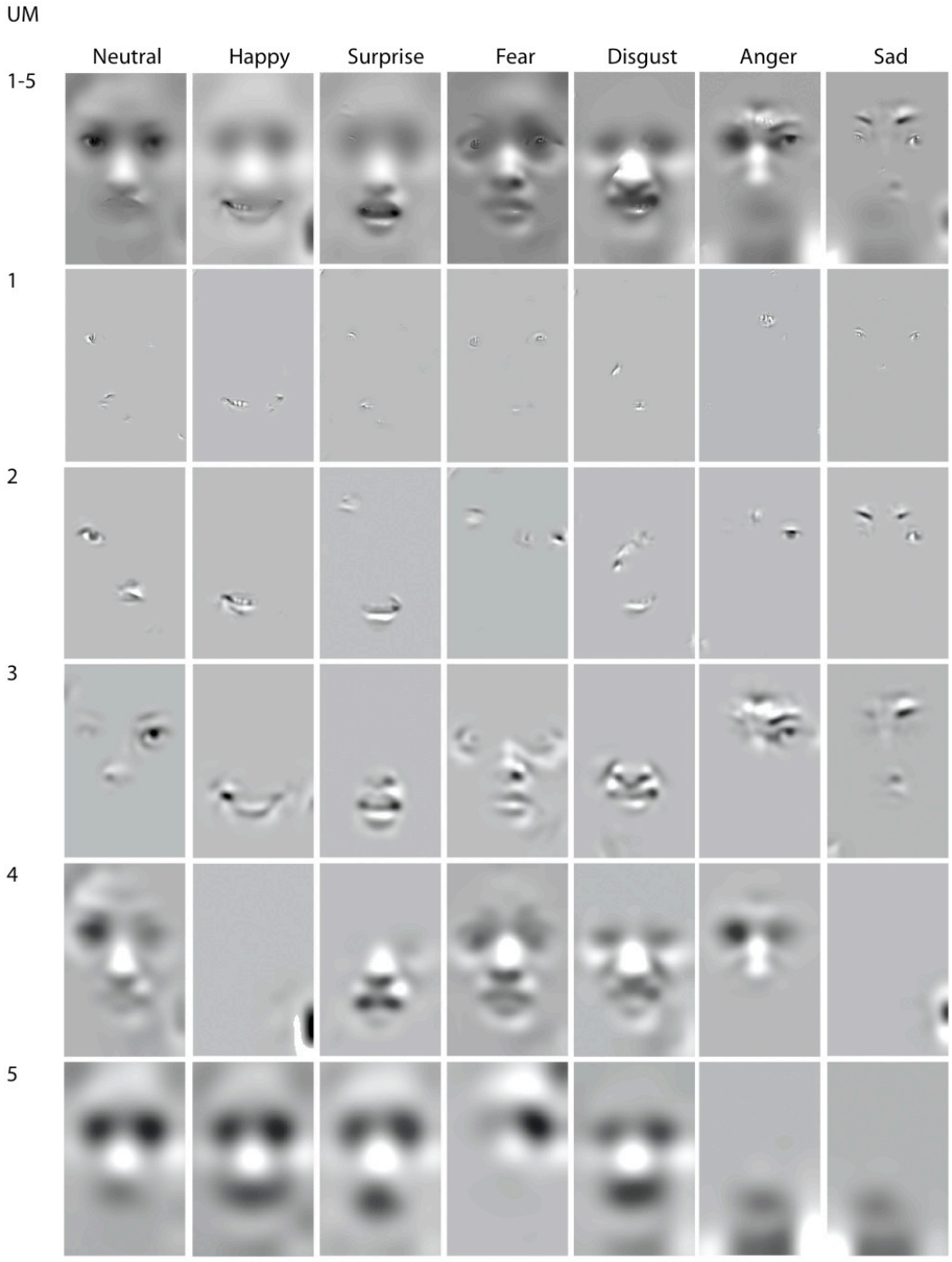


Figure 3.2. Behavioral Classification Image (UM) and their decomposition into five Spatial Frequency bands. Row 1-5. The behavioral classification image represents the diagnostic Spatial Frequency information, collapsed across the five Spatial Frequency bands sampled during the experiment, that observer UM used to correctly classify each expression. Rows 1 to 5. Each row of images represents the specific features that the observer used from this particular Spatial Frequency band. They illustrate that perceptual judgments of expressions depend on very specific and localized image features represented across a range of spatial frequency bands.

Figure 3.3. Behavioral Classification Image (LP) and their decomposition into five Spatial Frequency bands. See Figure 3.2. for caption.

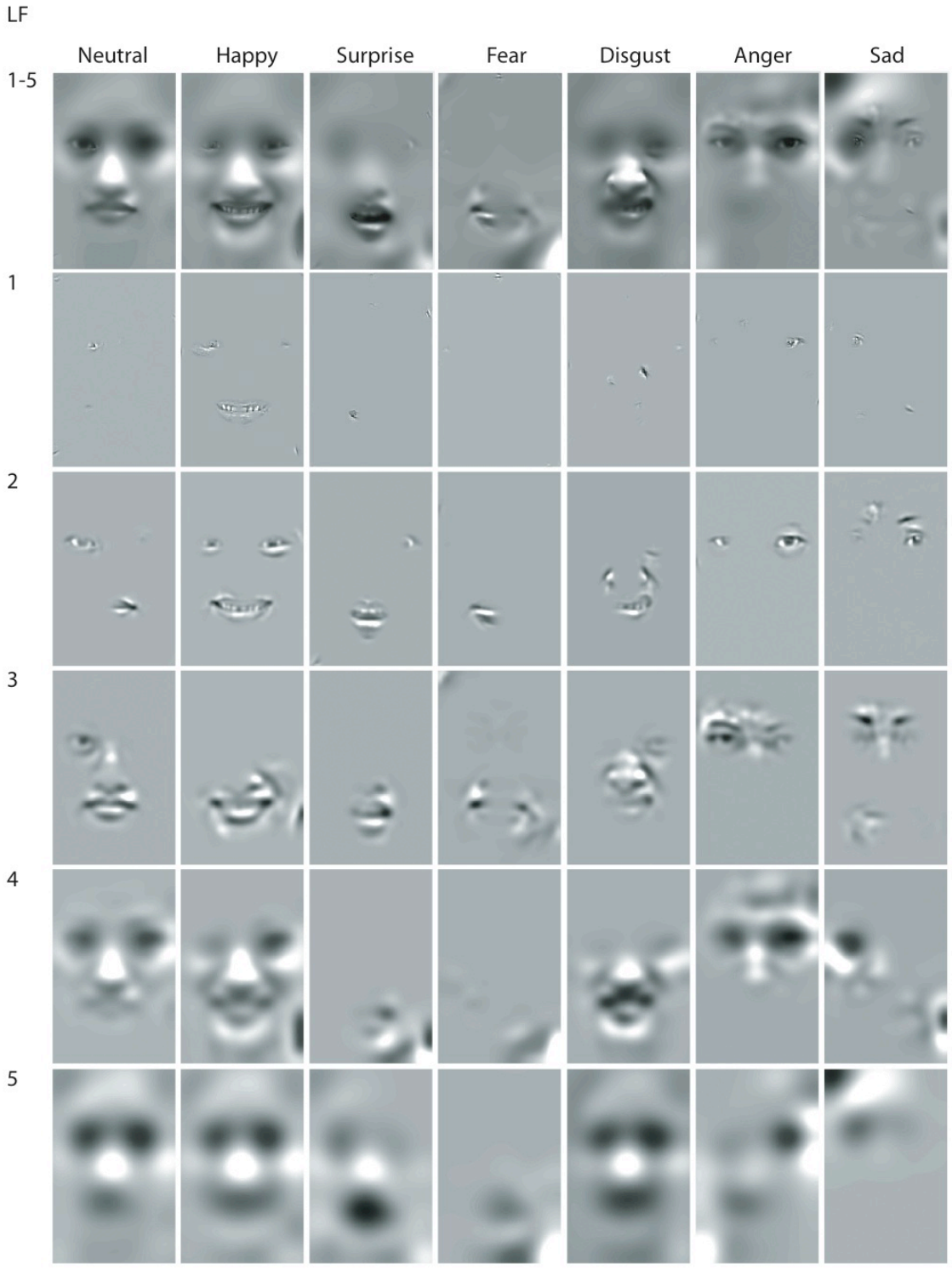


Figure 3.4. Behavioral Classification Image (LF) and their decomposition into five Spatial Frequency bands. See Figure 3.2. for caption.

3.2.5. COMPUTATION: SENSOR-BASED EEG CLASSIFICATION IMAGES

To ascertain the facial information systematically correlated with modulations of the EEG signal, we applied Bubbles to single-trial raw electrode amplitudes (Schyns et al., 2003; Smith et al., 2004; Smith et al., 2006). For each observer, we selected a left and a right occipitotemporal electrode (henceforth, OTL and OTR, respectively) on the basis of those electrodes recording the highest amplitude of the N170 peak on the left and right hemispheres. This corresponded to electrodes P8 and PO7 for each observer. On each trial and for each electrode of interest, we measured the brain's response to the corresponding bubble mask, by sampling the EEG signal every 4 ms, over 1 s (500 ms prestimulus). In each time window, independently for each expression and SF band, we estimated the facial features correlated with modulations of EEG amplitudes as follows: We computed the mean EEG over a 4 ms time window and summed together the bubble masks leading to amplitudes above (versus below) the mean. The procedure was repeated independently for each one of the five SF bands, each one of the seven expressions, and each one of the 250 time points. Subtracting the bubble masks above and below the mean leads to one classification image per SF band, time point, and expression. This classification image represents the significant ($p < .05$, Pixel Test) facial information (if any) that is correlated with modulations of the EEG for that SF band, time point, and expression. Repeating these operations for each electrode (OTR, OTL), time window, and expression resulted in a dynamic mapping of the use of facial information in the brain. We focused analyses on the time course of the N170 (i.e., 140–220 ms) independently for each observer. The gray-level movies of information sensitivity in Figure 3.5-7. illustrate such time courses for electrodes OTR and OTL and expressions ‘‘fear,’’ ‘‘disgust,’’ and ‘‘happy’’ for all observers.

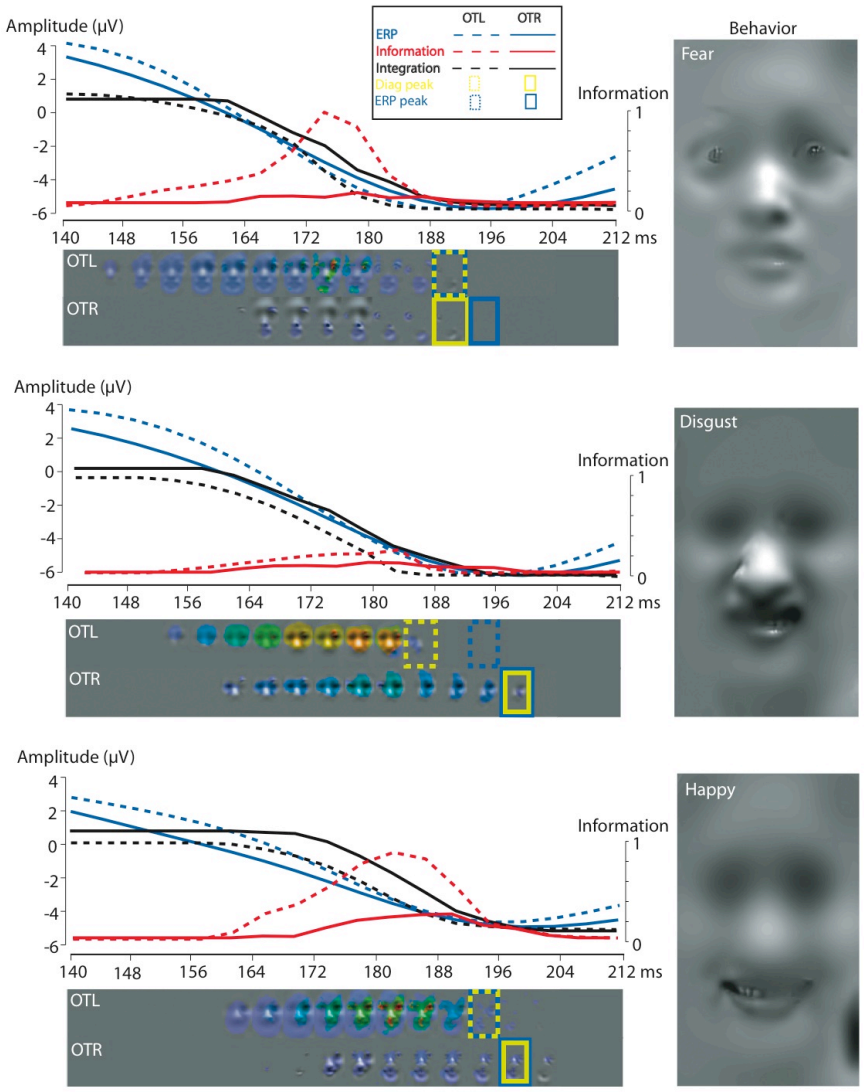


Figure 3.5. The N170 Integrates SF Facial Information (UM, "fear," "disgust," "happy"). Behavior. Representation of the facial SF features required for correct behavior. **Left Panel.** For Left and Right occipitotemporal electrodes (OTL and OTR, OTL dashed lines), the blue curves indicate the typical N170 negative deflection. With 'Bubbles', we derive, "in a movie" of classification images, the dynamics of the sensitivity of the N170 for any facial information (see the OTL and OTR classification images, time resolution is 4 ms). Note that this analysis concerns strictly the EEG: It is not related to behavior at this stage. The red curves quantify this sensitivity to facial information, which peaks for each expression and electrode before the ERP peak (indicated with blue boxes). The color-coding of the classification images localizes this SF information in the face, with red indicating higher information values and blue lower information values. The black curves integrate the red curve over time–they are negated and rescaled to the ERP peak for comparison purposes—demonstrating that the N170 reflects a process that integrates facial features over time. The dashed yellow boxes indicate the maximum of the integration of the information required for categorization behavior (the diagnostic information).

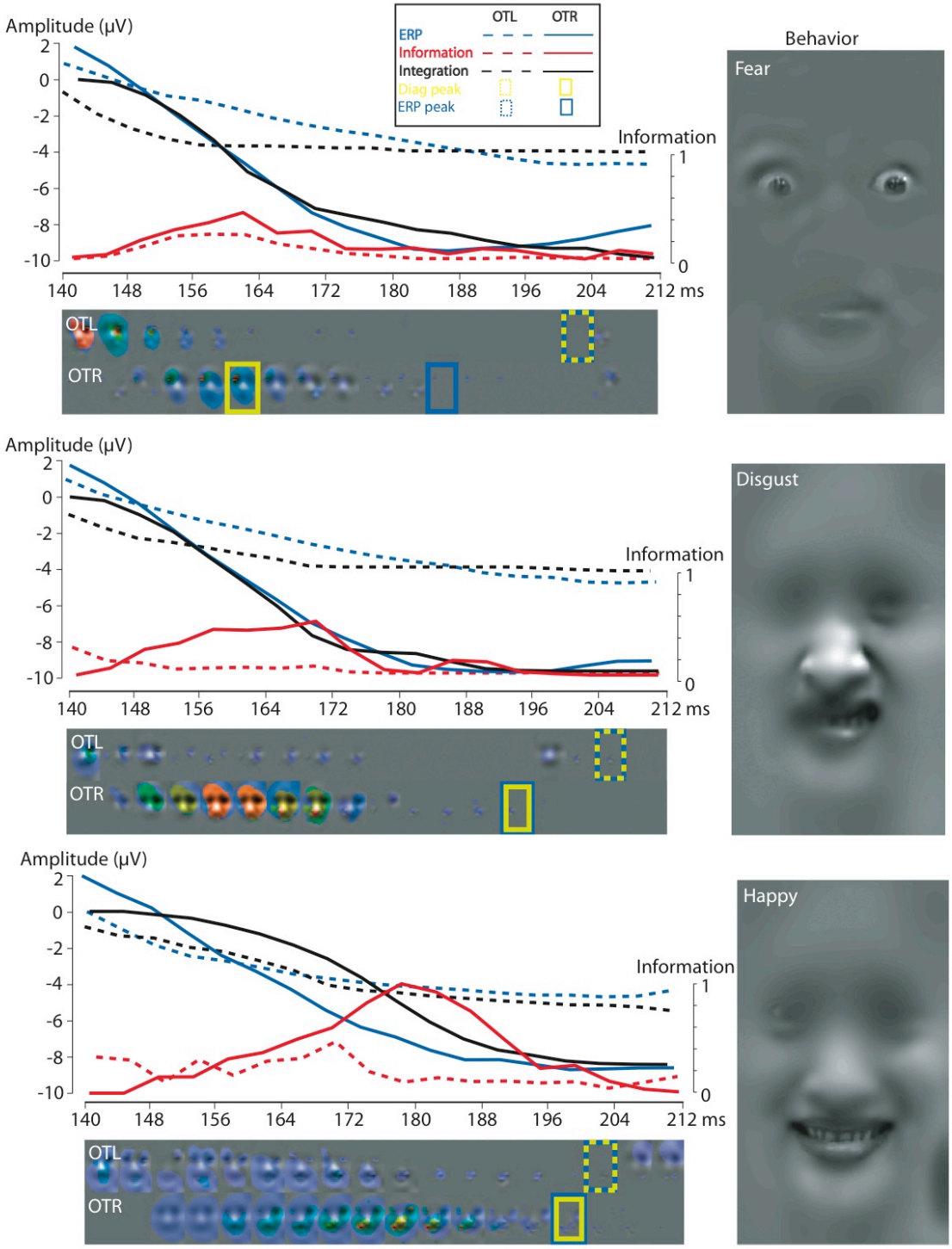


Figure 3.6. The N170 Integrates SF Facial Information. Illustration for LP and expressions ‘‘fear,’’ ‘‘disgust,’’ ‘‘happy.’’ See Figure 3.5. for caption.

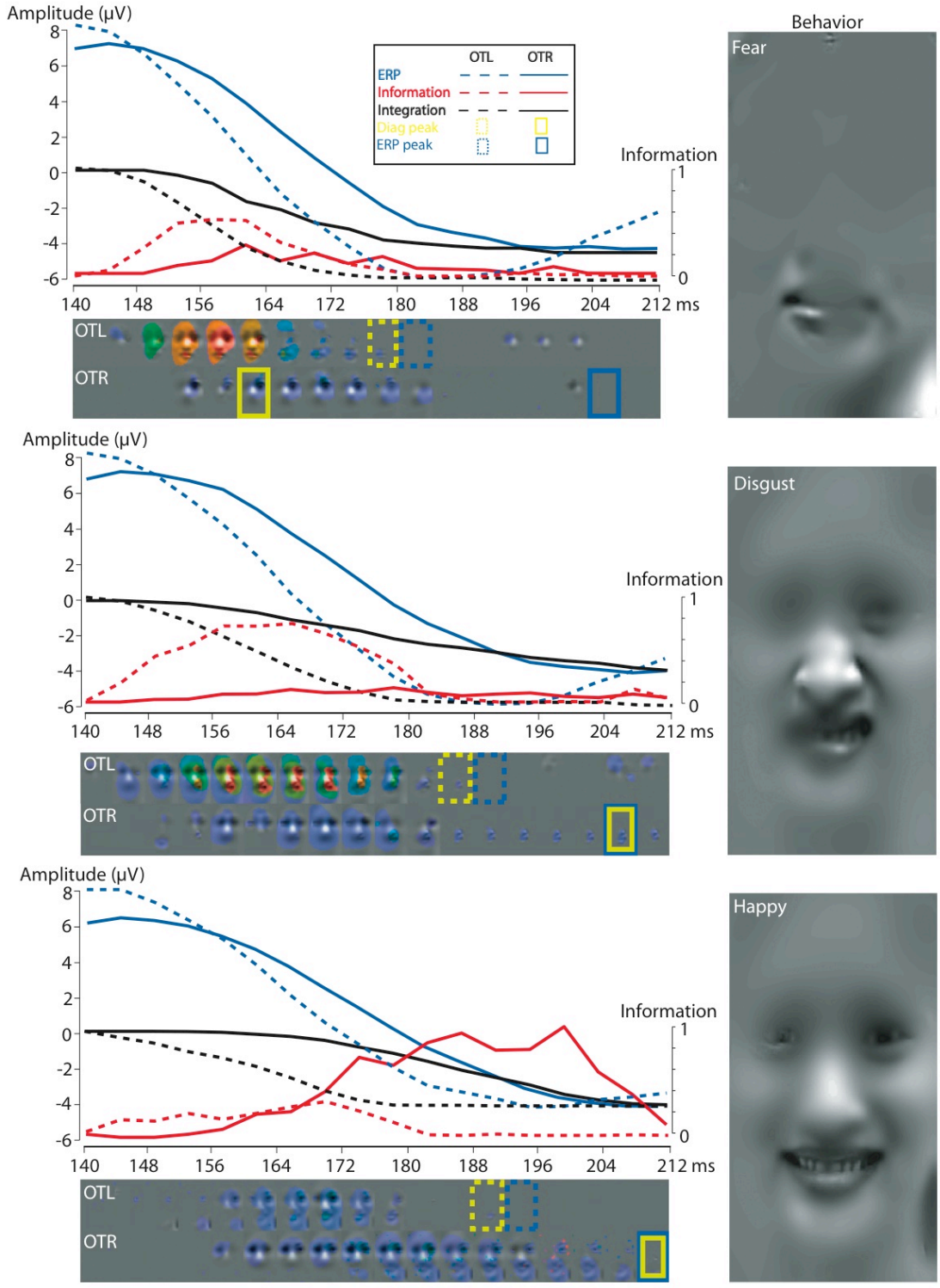


Figure 3.7. The N170 Integrates SF Facial Information. Illustration for LF and expressions ‘‘fear,’’ ‘‘disgust,’’ ‘‘happy.’’ See Figure 3.5. for caption.

SF information measurement over the time course of the ERP & its integration

For every 4 ms time window, each EEG classification image reveals the sensitivity of the EEG to face information in five different SF bands. For each time window, we computed, within each SF band, the total number of cycles represented in the statistically significant regions of the classification image and summed cycles per face across the five SF bands (the pixels comprising the information in each band are summed before dividing this by the number of pixels in one cycle, per band, to give a normalised measure of information in each classification image). We repeated this operation across time windows, expressions, and OTL and OTR electrodes and normalized the cycles per face measurements to obtain for each time point, electrode, and expression a measure of SF information varying between 0 and 1 for each observer. In Figures 3.5-7, the red curves (dashed for OTL) plot the resulting information function for each electrode and expression. The black curves (dashed for OTL) represent the temporal integration of the red curves, negated and normalized for each expression so that the maximum of the black curve (i.e., the maximum of SF integration) coincides with the ERP peak.

3.2.6. FURTHER CHARACTERIZATION OF FACIAL INFORMATION INTEGRATION

1) Time course of the N170 in the 2D image space

To further characterize the integration of facial information over the time course of the N170, we summed at each 4 ms time point the classification images over all seven expressions (per electrode and observer) and SF bands. We then summed each classification image along the x dimension and located the y coordinate (i.e., the location of information within the image space in the vertical dimension) of the maximum of SF information. We thereby obtained a single number for each time point, corresponding to the y location of the maximum of SF information. We linearly regressed (least-mean square) this coordinate of maximum facial information with the dynamics of the N170 signal (N170

latency at successive points over the interval of the ERP), for each observer, pooling OTR and OTL data (i.e., resulting in two y coordinates per time point of the N170 time course). Figure 3.8. presents these regressions for the three observers.

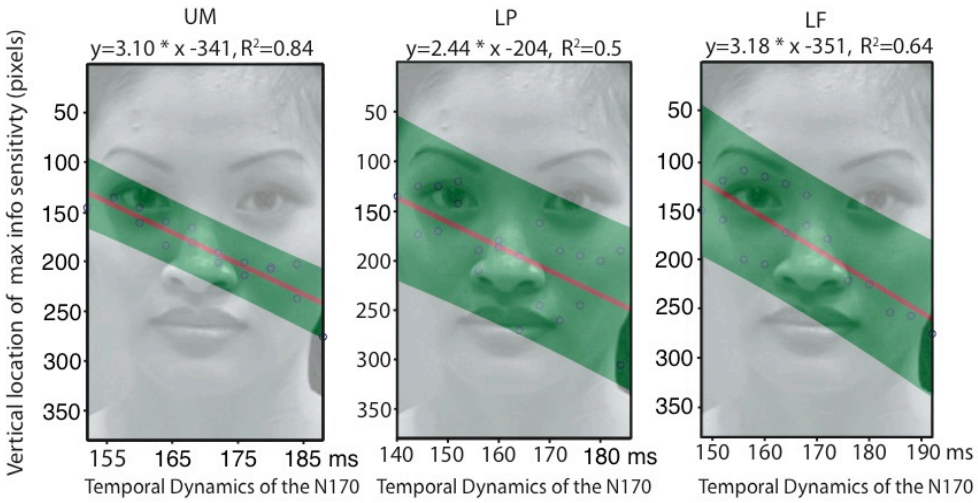


Figure 3.8. The Integration of Facial Information Tends to Proceed from the Eyes Down to the Bottom of the Face. For each observer (UM, LP and LF), Least-Mean Square linear regression of the location of the maximum of SF information (summed by time window over all 7 expressions) within the image space in the vertical dimension (Y axis of each figure) with the temporal dynamics of the N170 signal (X axis of each Figure). For each observer, we pooled data over electrodes OTR and OTL, for a total of two data points per time point. Blue circles indicate individual data points (N170 latency, Y coordinate of maximum SF information). The red line indicates the linear regression of the data points and the flanking green boxes the confidence intervals ($p < .05$) on the Y-axis. Note that the scanpaths are undefined outside the time points indicated on the X-axis of the Figure.

2) Time course of the N170 and diagnostic information.

To test the hypothesis that ERP latencies are related to the latency of integration of the diagnostic information required for behaviour (e.g., the mouth in ‘‘happy,’’ see ‘‘Behaviour’’), we performed the following analysis: At each 4 ms time point, we intersected the thresholded classification images of behaviour (one per SF band for each expression) with the corresponding thresholded classification images of the EEG (the behavioural image at each SF band is multiplied by the EEG classification image at each

band, this new measure of information that is common to both behavioural and EEG classification images is computed as before using the number of cycles per band). For each time point, this isolated the information from behaviour that is represented in the EEG classification image. We computed how much SF information was represented in each image and integrated this SF information over time. The maximum of the integrated intersection (information common to both behavioural and EEG classification images computed by multiplying the two) over the time course of the N170 is indicated with a yellow dashed box in Figure 3.2. - e.g., for ‘‘happy,’’ it coincides with the N170 peaks on OTR and OTL. To demonstrate that ERP latency correlates with the latency of the maximum of diagnostic information integration, we linearly regressed (least-mean squares) these two measurements, by pooling data across all observers, electrodes, and expressions (see Figure 3.9).

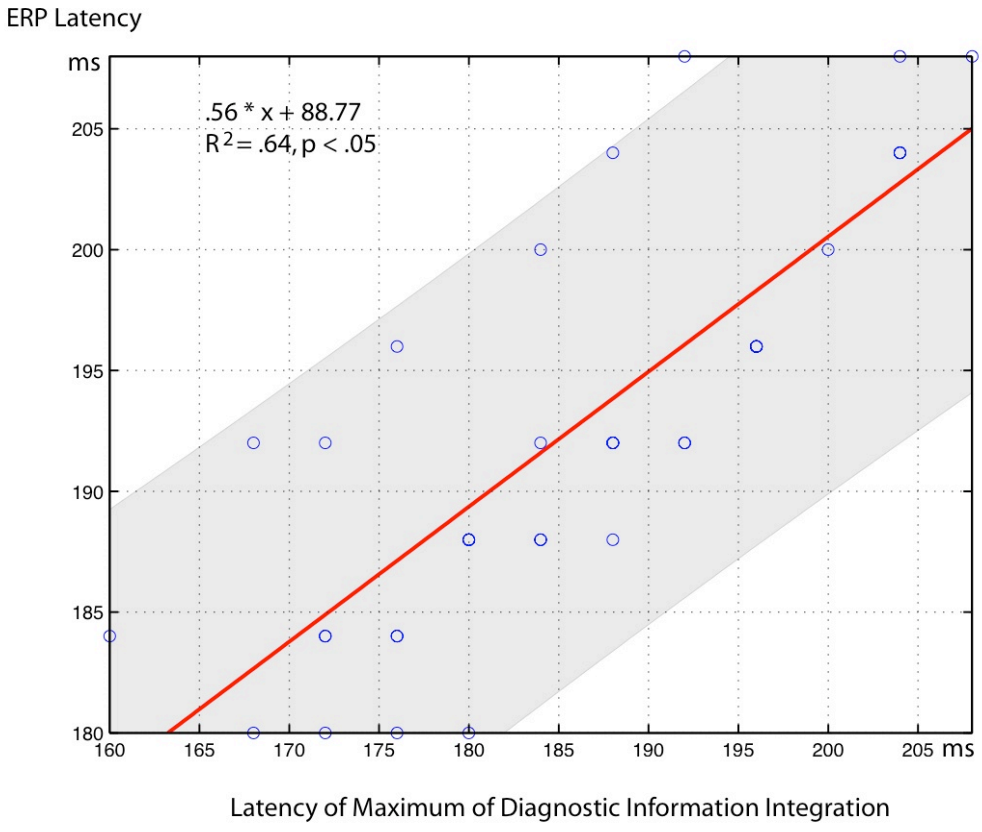


Figure 3.9. The integration of facial information stops, and the N170 peaks, when diagnostic information has been integrated. Least-Mean Square linear regression of the ERP latencies (X axis) with latency of maximum of diagnostic SF integration (Y axis). Blue circles indicate individual data points (N170 latency, latency of maximum of diagnostic SF integration). The red line indicates the linear regression of the data points and the flanking grey boxes the confidence intervals ($p < .05$). Data were pooled across 3 observers, 2 electrodes and 7 expressions, for a total of 42 (maximum of diagnostic information, ERP latency) coordinates.

3.3. Diagnostic Information Use

3.3.1. Facial information modulates categorization accuracy

Using the classification image techniques discussed, we first analyzed for each observer, expression and spatial frequency band the diagnostic facial features associated with categorization accuracy. We then rendered the facial features diagnostic of each expression with an effective image to reveal the diagnostic features (Figures 3.2-4). To illustrate, the facial features diagnostic of "fear" are primarily the wide opened eyes, whereas the region around the wrinkled nose is diagnostic of "disgust," and the smiling mouth diagnostic of "happy."

3.3.2. Facial information modulates EEG voltage

Again using the classification image techniques discussed, we analyzed, at a 4 ms resolution, for each observer, expression and spatial frequency band the facial features associated with modulations of EEG voltages—measured on the Right and Left occipitotemporal (OTR and OTL) electrodes with the largest negative deflection within the 140-212 ms time interval of the N170 (see Figure 3.10. below). For each expression and OTR and OTL electrode, Figures 3.5-7. represent the EEG classification images at each time step. Together, they form "movies" representing over time the dynamics of the sensitivity of the EEG to facial features. To illustrate, the grey-level OTR and OTL movies for "disgust" on Figure 3.5. reveal that the dynamics of sensitivity of the EEG moves from

the location of the eyes progressively towards the lateral sides of the wrinkled nose over the N170 time course.

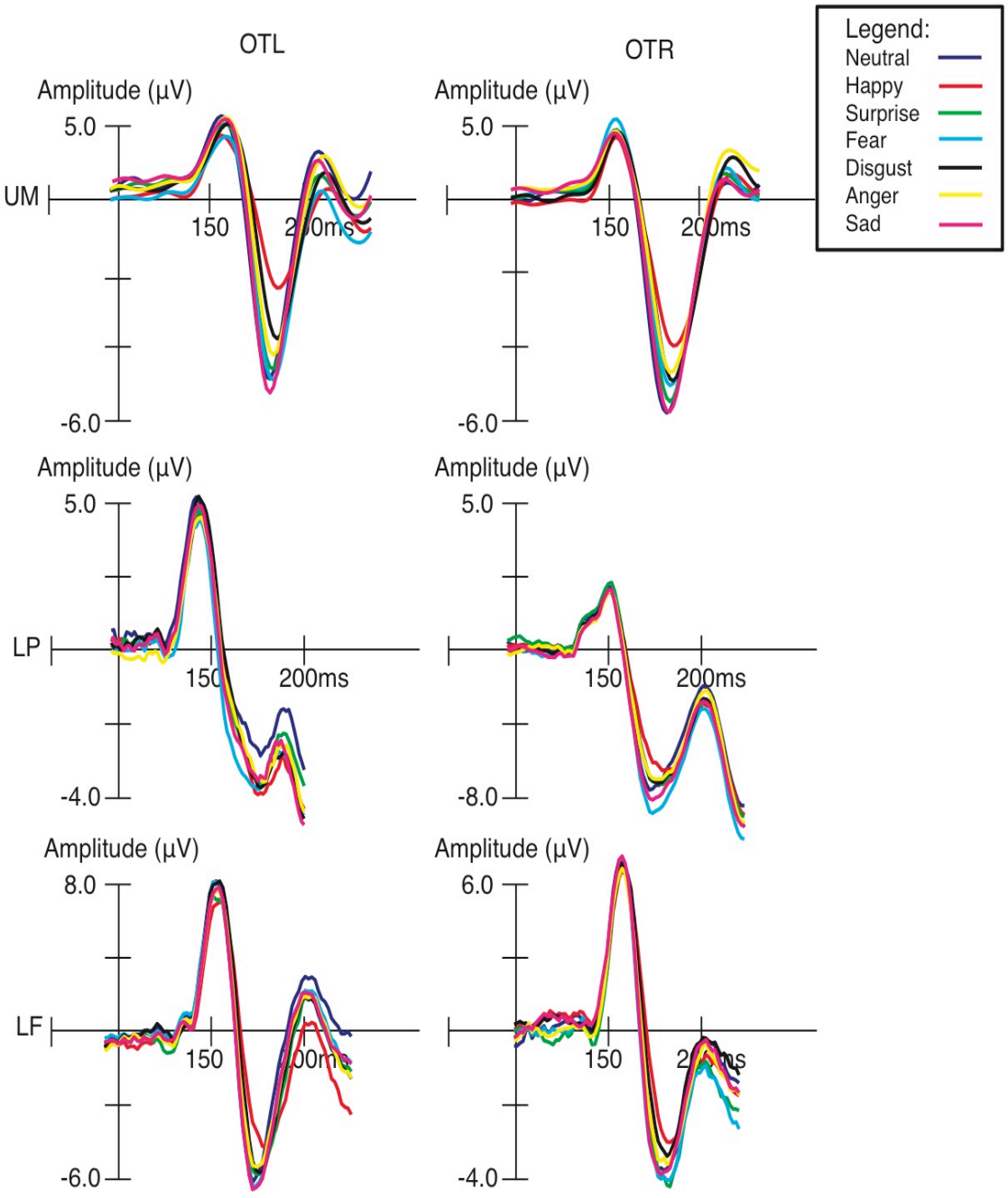


Figure 3.10. OTR, P8, and OTL, PO7, ERPs for Illustrated for UM, LP, and LF

3.4 THE N170 INTEGRATES FEATURES OVER TIME

To frame the function of the N170, every 4 ms we computed on OTR and OTL electrodes the overall quantity of SF information to which the EEG was sensitive. The red curves in Figures 3.5-7. (dashed for OTL) report this measure. It is immediately apparent that an almost monotonic increase in SF information sensitivity is followed by an almost monotonic decrease, itself followed by the ERP peak (indicated with a blue box in Figures 3.5-7.). This shape of the information sensitivity curve characterized all seven expressions and three observers, both on OTL and OTR (n = 42). The red curves reflect a dynamic of information sensitivity characteristic of the derivative of an integrated function: The instantaneous slope of the ERP would closely reflect the slope of an information accumulation function. To test this hypothesis, we integrated the red curves over time to produce the black curves (see Figures 3.5-7., OTL dashed) and correlated, independently for each observer and electrode the resulting integrated function with the ERP curve of each expression (represented in blue in Figures 3.5-7., OTL dashed). We computed confidence intervals using a bootstrap with replacement, 999 resampling trials, at $p < 0.05$. Table 3.1. presents the correlations averaged across expressions, for each observer and OTL and OTR electrodes. The high correlations suggest that the unfolding of the N170 on both electrodes closely reflects processes of integration of SF information starting from about 50 ms before the N170 peaks.

	OTL		OTR	
	m	std	m	std
UM	0.98	0.02	0.97	0.03
LP	0.93	0.06	0.97	0.02
LF	0.93	0.04	0.98	0.01

Table 3.1. Observer (UM, LP and LF) mean correlations (n = 7 expressions) and standard deviations between the ERP curves and the function of integration of SF facial information, on electrodes OTL and OTR.

3.4.1. THE INTEGRATION OF FACIAL INFORMATION PROCEEDS FROM THE EYES & MOVES DOWN THE FACE

Information integration across expressions was similar on both electrodes, for all observers. To illustrate, consider Figure 3.8. in which three plots represent a different observer. The X coordinate of each plot indicates the time interval of the ERP on both electrodes; the Y coordinate represents the Y face coordinate of the maximum of SF information present in the EEG classification images, summed across all expressions. At each time step, two points (one for OTL, one for OTR, see blue circles) illustrate the relationship between the dynamics of the N170 and the information that is being integrated - the background face should only be used to facilitate the Y coordinate localization of the facial features corresponding with the SF information maxima. Linear regressions (performed collapsing OTL and OTR coordinates) indicate linear relationships between the two factors ($p < .05$, confidence interval indicated in green). Thus, OTL and OTR N170s tend to integrate facial features from the top of the face (i.e. the eyes), progressively downwards on a vertical axis to the bottom of the face (see also Figure 3.11. for

illustrations of OTR and OTL Scanpaths for Observers UM, LP and LF, with Expressions ‘‘Fear,’’ ‘‘Disgust,’’ and ‘‘Happy’’. Shown under ‘‘Behaviour’’: Classification images revealing the significant ($p < .05$) spatial frequency features required for 75% correct identification of each expression).

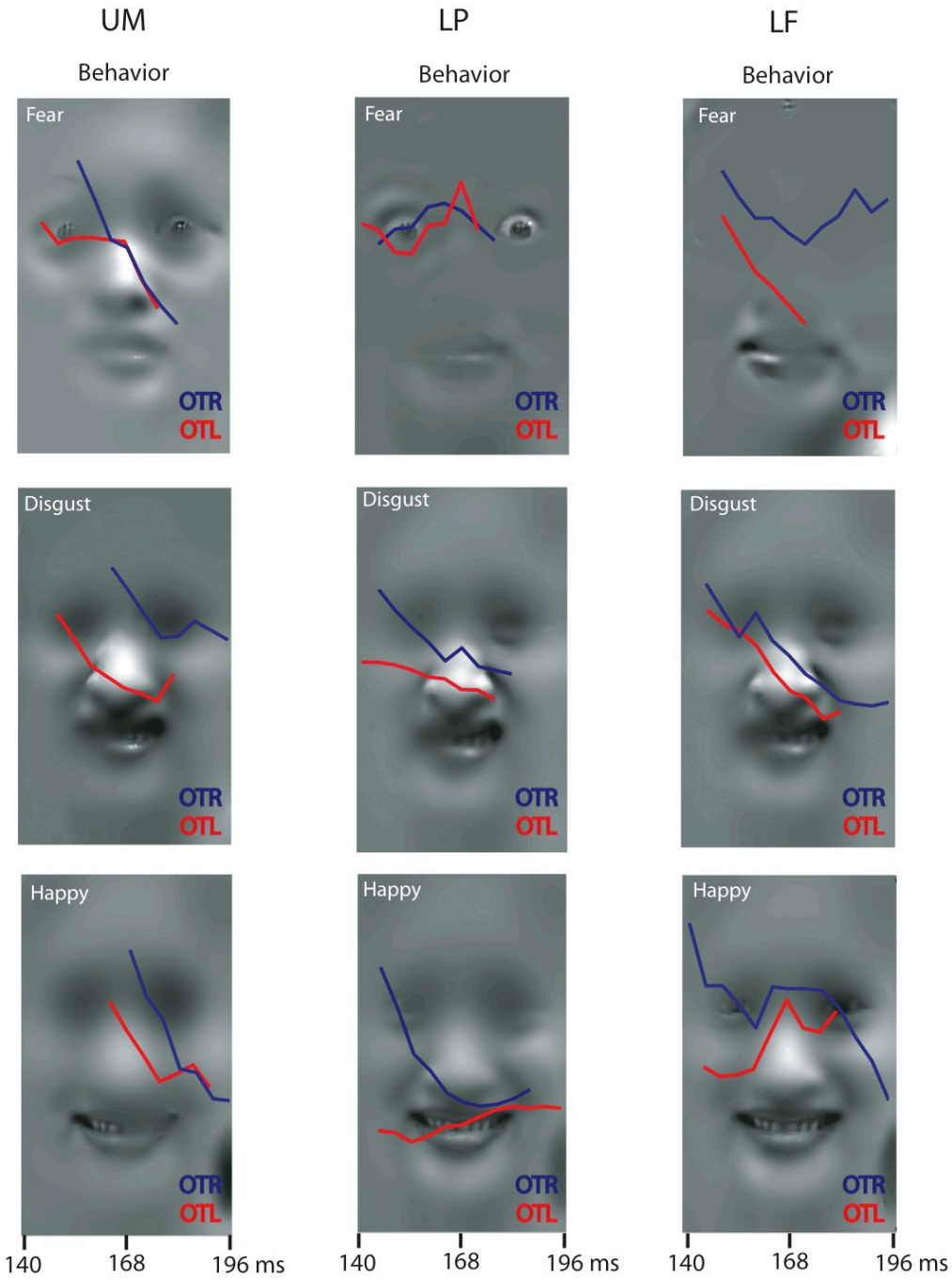


Figure 3.11. Illustration of OTR and OTL Scanpaths for Observers UM, LP and LF, with Expressions ‘‘Fear,’’ ‘‘Disgust,’’ and ‘‘Happy’’. Shown under ‘‘Behaviour’’: Classification images revealing the significant ($p < .05$) spatial frequency features required for 75% correct identification of each expression. OTR, OTL. Time courses of the y (face) coordinate of the maximum of information over the time course (140–196 ms) of the ERP for each expression. There is a trend for information integration to start around the location of the eyes and then move down in the face. The underlying classification images of behaviour illustrate that the integration of information moves down in the face toward the location of the expression-specific diagnostic information.

3.4.2 THE INTEGRATION OF FACIAL INFORMATION STOPS & THE N170 PEAKS WHEN DIAGNOSTIC INFORMATION IS REACHED

The integration scanpath on the face suggests that the latency of each ERP could depend on the vertical distance of the expression-specific diagnostic information from the two eyes. In this case, the eyes in “fear” would lead to an early ERP and the mouth in “happy” to a later ERP. We tested this hypothesis for each observer, electrode and expression ($n = 42$) by extracting the SF information common to the behavioral and to the EEG classification images—i.e. by computing an intersection between the thresholded behavioral and EEG classification images (i.e. the information common to both behavioural and EEG classification images). The resulting function reflects only the integration of diagnostic, behavior-relevant information over time. We computed the maxima of this integration over the time course of each ERP (maxima are rendered with yellow boxes in Figures 3.5-7.) and regressed them with the ERP latencies. In Figure 3.8., the resulting regressions present a linear relationship between the timing of the maximum integration of diagnostic information and the latency of the ERP. Thus, the N170 latency marks then end of a process that integrates SF facial features, starting at the location of the eyes and ending at the location of the expression-specific diagnostic information. This explains why ‘fear’ (involving mostly the eyes) peaks earlier than ‘disgust’ (involving the corners of the nose) and ‘happy’ (involving the mouth). It also implies that the information processed over the N170 conveys sufficient information to predict categorization behavior.

We have shown in three observers that the dynamics of the N170 wave, on the left and right occipitotemporal regions, closely correlate with a function integrating facial features over time. This integration proceeds over a 50 ms time window prior to the N170 peak, in a scan path starting from the location of the eyes downwards in the face. We have shown that the vertical distance between the two eyes and the facial location of the expression-specific diagnostic information (e.g. the mouth in 'happy') determines the latency of the N170 for this expression.

3.5. THE N170 ERP REFLECTS A COGNITIVE PROCESS

There has been considerable debate regarding the nature of category effects on the N170. The evidence reported here demonstrates that the N170 reflects a process under cognitive control, not a low-level effect. To recapitulate, the N170 curve (on OTL and OTR) integrates SF information over time with evidence for a mixture of automatic and goal-directed control. It is automatic because it tends to start with the eyes and then integrates information downwards on the Y-axis of the face plane. It is goal-directed because the downward integration stops when the diagnostic features have been integrated. Thus, claims to the effect that low-level properties might explain modulations of the N170 will need to be revised (Bentin et al., 2007). Specifically, if a process integrates information, including diagnostic information, extrapolating from our data, variations in the location of this information in the stimulus will have an impact on the shape of the N170—as demonstrated here between the early ERP to the eye information, in 'fear' and the late ERP to the mouth information, in 'happy.' However, as we have shown, it is the knowledge of the location of the information used in the image, together with an understanding of the dynamics of the overall processing of this information (here from the eyes to the mouth) that enable specific predictions about the shape of the N170 ERP.

3.5.1. AUTOMATIC & GOAL-DIRECTED CONTROL OF INFORMATION INTEGRATION

An important question for future research concerns the precise nature of the 'automatic' vs. 'goal-directed' aspect of the SF integration process. Crucial to this is the suggestion that Pre-Frontal Cortex (PFC) is involved in task-dependent, adaptive coding in working memory, attention and control (Duncan et al., 2001). The difficult question is how these different regions interact to process the visual and semantic information leading to different categorizations of a given stimulus. Recent thinking (Duncan et al., 2001; Bar et al., 2003) suggests that top-down expectations from PFC become coupled with the visual occipital cortex and the fusiform gyrus to progressively construct task-dependent representations for recognition. The evidence of information integration reported here also suggests a progressive integration of information over the left and right occipitotemporal region. For control, we would predict a strongly overlapping fronto-occipito-temporal network responsible for the implementation of top-down expectations that allow for the effective integration (i.e. encoding and retention) of visual categorization information over short periods of time.

Implications of Diagnostic Information

We demonstrated that the integration of the expression-specific diagnostic information occurs just before the N170 peaks, on the left and right occipitotemporal electrodes. Consequently, in a time window ranging from about 160 to 205 ms, there is enough information in the brain (though split between two hemispheres), to determine the emotional category of the input stimulus, a category-specific effect. The idea of category-specific effects on the N170 has never been conclusively associated with the specific information of a behavioral categorization response. Our findings extend those demonstrating that inferior temporal cortex neurons in nonhuman primates are sensitive to

diagnostic object properties (Logothetis et al., 1995; Freedman et al., 2003; Neilsen et al., 2006). They also open the interesting prospect of predicting behavior, from a brain signal measured as early as 160-200 ms following stimulus onset, a critical finding for 'mind-reading' (Philiastides et al., 2006). However, there is considerable lateralization of the diagnostic information observed over the N170. This raises the question of whether inter-hemispheric integration of diagnostic information, following its extraction over the N170 time-course, is required for perceptual decision. A better understanding of the dynamics of information processing, from its lateralized extraction to its integration for perceptual decision will be critical to understand categorization processes.

CHAPTER FOUR

TOP-DOWN MODULATION OF THE CORTICAL REPRESENTATION OF FACIAL FEATURES IN V1– AN FMRI STUDY

4.1. EARLY VISUAL SENSITIVITY TO DIAGNOSTIC INFORMATION DURING THE PROCESSING OF FACIAL EXPRESSIONS

Natural social interaction assumes we are proficient at categorizing faces, extracting and decoding cues supporting judgements such as gender and expression. These cues are termed the diagnostic features and have been shown to enhance behavioural performance. Previous studies reveal that diagnostic features also modulate the spatial (Smith et al., 2008) extent and temporal dynamics (Schyns et al., 2007, Chapter 3) of brain signals in higher visual areas. However, in the context of top-down signals active in the visual system, it is unknown to what degree higher visual areas engage early visual areas (V1/V2/V3) in the processing of diagnostic features. To investigate this top-down interaction, Chapter 4 describes how we identified the cortical representation of two features using retinotopic mapping that are task-dependently encoded during face processing: the mouth and eyes. With a general linear model (GLM), we contrasted BOLD activation in these regions of interest to happy and fearful faces, during gender and expression tasks. We reveal for the first time that task-dependent activation exists within the earliest cortical representation (V1 to V3) of diagnostic features. This strategic encoding of face images is beyond typical V1 properties and suggests top-down influences extending to early retinotopic stages of processing.

4.1.1. THE CORTICAL FACE NETWORK AND V1

Faces hold great biological significance hence we categorize them easily. To perform judgements such as gender or expression, we extract specific subsets of information. Techniques using reverse correlation (e.g. Bubbles, Gosselin and Schyns, 2001; Smith et al., 2005) are used to reveal these diagnostic features driving behavioural performance.

Previously we have shown that diagnostic features activate higher visual areas. With time-resolved (4ms) electroencephalographic signals, Schyns et al., (2007; 2009, Chapter 3) demonstrated a systematic integration of diagnostic features in occipitotemporal regions during the face-sensitive N170 event-related potential. This was extended to spatially and temporally resolved magnetoencephalographic signals by Smith et al., (2009), to reveal complexity of feature use corresponds to cortical location: sensitivity to isolated features was observed at 90ms in occipital extrastriate regions but more complex combinations of features drive the signal in occipitotemporal regions over 170ms. Using functional magnetic resonance imaging, Smith et al., (2008) revealed voxel-based sensitivity to diagnostic features in regions activated in expression processing (anterior cingulate, Bush et al., 2000; Britton et al., 2006; anterior/posterior cingulate, Winston et al., 2003) and face perception (right middle temporal gyrus and left inferior occipital gyrus, Haxby et al., 2000). Activation in these areas is typical of the cortical face network, in which there is no functional emphasis on early visual areas (Haxby et al., 2000, Ishai, 2008).

Early visual areas classically do not represent complex visual categorizations. Instead functional properties of brain areas at higher levels support category-selectivity (Kanwisher et al., 1997, Epstein and Kanwisher 1998; Levy et al., 2001; Hasson et al., 2003). However, it is well established that higher visual areas can have a modulatory top down influence

(Bar 2007; Bressler et al., 2008, Beck and Kastner, 2009) stretching to V1 (Kastner and Ungerlieder, 2000; Muckli et al., 2005; Silvanto et al 2005). For example, in contrast to the small receptive fields and simple response properties of V1 (Grill-Spector and Malach, 2004), it also displays responses outside the classical receptive field (Angelucci at al., 2002; Harrison et al., 2007), and modulation by attention (Kanwisher and Wojciulik 2000) and apparent motion in non-stimulated areas along the illusory path (Muckli et al., 2005), implying it gains considerable information from higher areas. This suggests the high resolution spatial map provided by V1 acts as a foundation upon which top-down influences improve task-driven visual stimulus discriminations by targeting early stages of processing (Ahissar and Hochstein, 2002).

We sought to investigate sensitivity to facial features in the BOLD signal of early visual areas. We retinotopically-mapped "mouth" and "eye" regions of interest in V1, V2 and V3, and revealed task-specific differential processing of happy and fearful faces. As gender and expression categorizations typically require different diagnostic information, we were able to investigate effects in V1 as a function of the task and independently of stimulus properties.

4.2. EXPERIMENTAL METHODS

4.2.1. PARTICIPANTS

Nine subjects (21–29 years, five males) with normal vision gave their informed consent and were screened for potential health risks (procedures approved by local ethics committee).

4.2.2. STIMULI

Face stimuli were greyscale images of five males and five females taken under standardized illumination, displaying happy, fearful and neutral expressions. Neutral was included to maintain a level of difficulty i.e. to minimize the chance of subjects performing the task using only one feature, e.g. a "happy" or "not happy" decision using the wide open mouth.

Stimuli were normalized for location of mouth and eyes and comply with the Facial Action Coding System (Ekman and Friesen, 1978; California Facial Expressions database, Dailey et al., 2001). Face stimuli spanned 19° x 13° of visual angle (Figure 4.1.A). For retinotopic mapping of the mouth and eyes, contrast-reversing checkerboards (4 Hz) were presented in the location at which these features appeared during face trials. Mouth checkerboard spanned 2.8° x 7.2°, and eye checkerboards 2.8° x 3.6°. Vertical distance from the bottom of the eye checkerboard to the top of the mouth checkerboard was 4.9°. Total pixel area of the mouth checkerboard was the same as the two eye checkerboards together.

4.2.3. Design and Procedure

Face Categorization & Retinotopic Mapping of Features Prior to scanning, subjects practised the classification of gender and expression until they reached a performance exceeding 95% accuracy. Stimuli were generated using Presentation software (version 10.3. Neurobehavioral Systems, Inc.) and presented using an MR-compatible binocular goggle system (NordicNeuroLab [NNL], Bergen, Norway; Engström et al., 2005). Eye movements of the right eye were monitored using the NNL Eyetracking Camera, and data collected using a ViewPoint EyeTracker® by Arrington Research. The rapid event related fMRI experiment consisted of trials of one of six conditions on a grey background: happy, neutral, or fearful face, mapping of eyes or mouth, and fixation baseline. Subjects were instructed to keep fixation on the central fixation checkerboard (subtending 0.44° x 0.46°) throughout the whole experiment. Face and mapping conditions were presented for 1s, and were preceded by 3 seconds of fixation (Figure 4.1.A). Conditions were presented randomly with equal frequency. Subjects performed 720 trials split into 6 functional runs. Runs alternated between gender and expression tasks. A button pad was used for response. No response was required for mapping or fixation only conditions. Although the faces were

centred and normalised for location of features and illumination, and are presented at a constant size and view, we expect them to induce slightly different activation patterns in V1 due to different low-level properties (e.g. higher contrast of the eyes in "fear"; of the mouth revealing white teeth in "happy"). To ensure that activation was not solely driven by these properties, subjects performed both expression and gender tasks in which diagnostic information is typically extracted from different locations within the face.

Retinotopic Mapping of Early Visual Areas. Early visual areas were mapped using a standard phase-encoded polar angle protocol (Sereno et al., 1995, Figure 4.1.B) using standard parameters employed in our lab (Muckli et al. 2005, 2009).

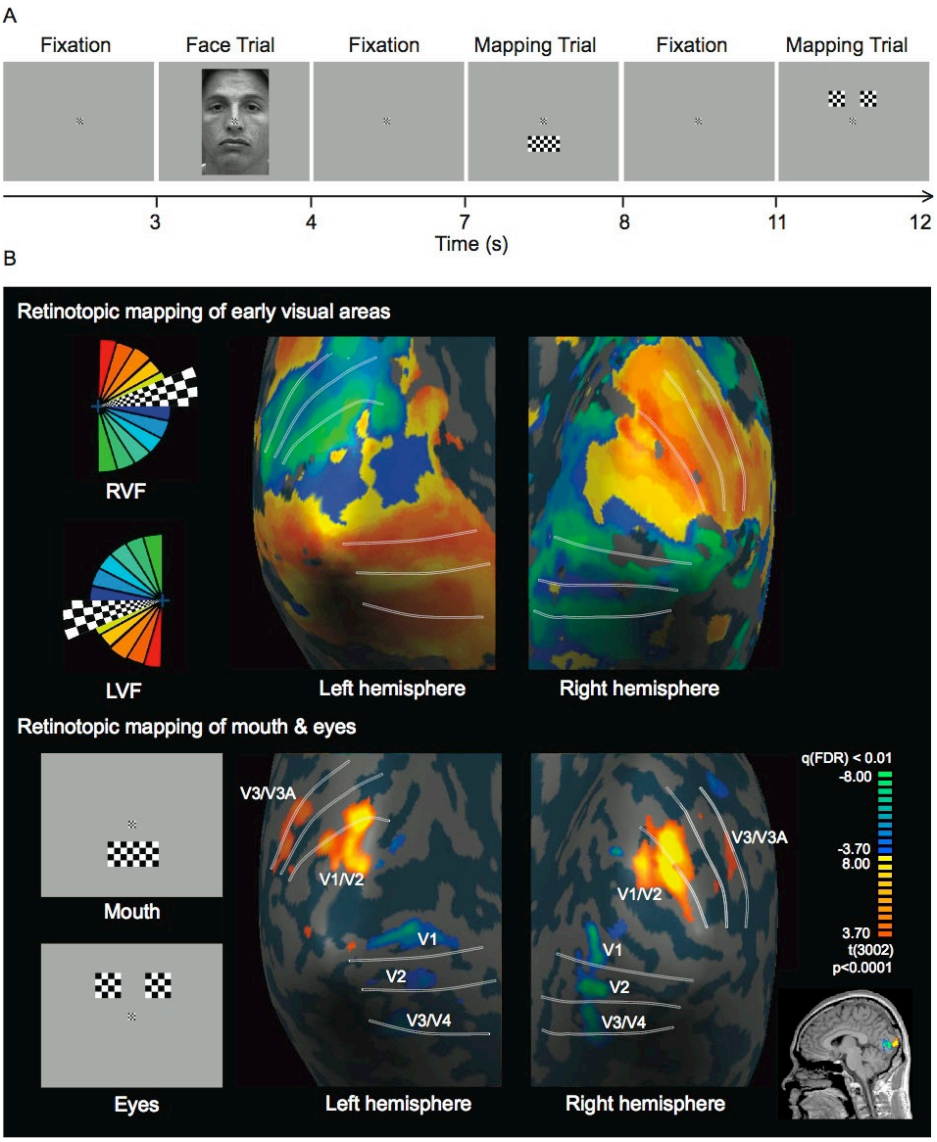


Figure 4.1.A. Time line of stimulus sequence. Neutral face, mapping of mouth and eyes, and fixation conditions were presented for 1s, preceded by 3s of fixation. B. Borders between early visual areas indicated by white lines in one subject in both inflated hemispheres, defined by retinotopic mapping. The cortical representation of the mouth in V1/V2 and V3/V3a (red to yellow), and eyes in each of V1, V2 and V3/V4 (blue to green), mapped using checkerboards over the location of the mouth and eyes respectively. Faces were scaled such that the mouth and eyes mapped to the upper and lower calcarine sulcus respectively (see sagittal plane for same subject).

4.2.4. MRI PROCEDURES

Imaging. Subjects were scanned in a 3T-SiemensTimTrio with a 12-channel head coil, at the Centre for Cognitive Neuroimaging, Glasgow. A gradient-recalled echoplanar imaging sequence was used for parallel imaging with an IPat factor of 2 and the following parameters: 17 slices, oriented to cover visual cortex; TR, 1s; TE, 30 ms; FA, 62°; FOV, 210 mm; resolution isotropic voxel size 2.5mm; slice thickness, 2.5mm; and gap thickness, 10% (0.25mm), PACE motion correction. In addition, T1-weighted anatomical scans were acquired for all subjects (TR, 2s, TE, 4.38ms, FA 15°, FOV, 240, isotropic voxel size, 1 mm^3).

Data Analysis. Analysis was performed using BrainVoyager software 1.10.4 (Brain Innovation) and Matlab 2007b (The Mathsworks Inc.). The first two volumes of each run were discarded due to T1 saturation effects. Standard pre-processing was as follows: slice scan time correction was performed using sync interpolation based on the TR of 1000ms and on the ascending, interleaved order of slice scanning. Standard three dimensional motion correction to adjust for head movements was performed as well as linear-trend removal and temporal high-pass filtering at 0.006Hz. After alignment with the anatomical scan, all individual datasets were transformed into Talairach space (Talairach and Tournoux, 1988).

Retinotopic Mapping. A cross-correlation analysis was used for the retinotopic-mapping experiment. We used the predicted hemodynamic signal time course for the first $1/8^{th}$ of a

stimulation cycle (32 volumes/4 volumes per predictor) and shifted this reference function slowly clockwise in time (4 volumes corresponding to 45° visual angle). Data were projected to the surface (Figure 4.1.B) with colours corresponding to the lag value that resulted in the largest cross-correlation (location in the visual field of the rotating checkerboard ray at which the maximal voxel response was obtained). This identified the boundaries of early visual areas V1, V2, V3/V3A and V4. Data contributing to behavioural analysis included 8 of the 9 subjects due to technical reasons.

Cortical Surface Reconstruction & ROI Definition. The high-resolution T1-weighted anatomical data were used for surface reconstruction of both cortical hemispheres for all nine subjects (Kriegeskorte and Goebel, 2001). Inhomogeneity correction of signal intensity was followed by segmentation of the white and grey matter border. Functional data were projected onto the inflated hemispheres allowing the borders between early visual areas to be identified (Muckli et al., 2005, 2009). Mouth and eye checkerboard mapping data were then used to identify the cortical representation of the mouth and eyes in each early visual area.

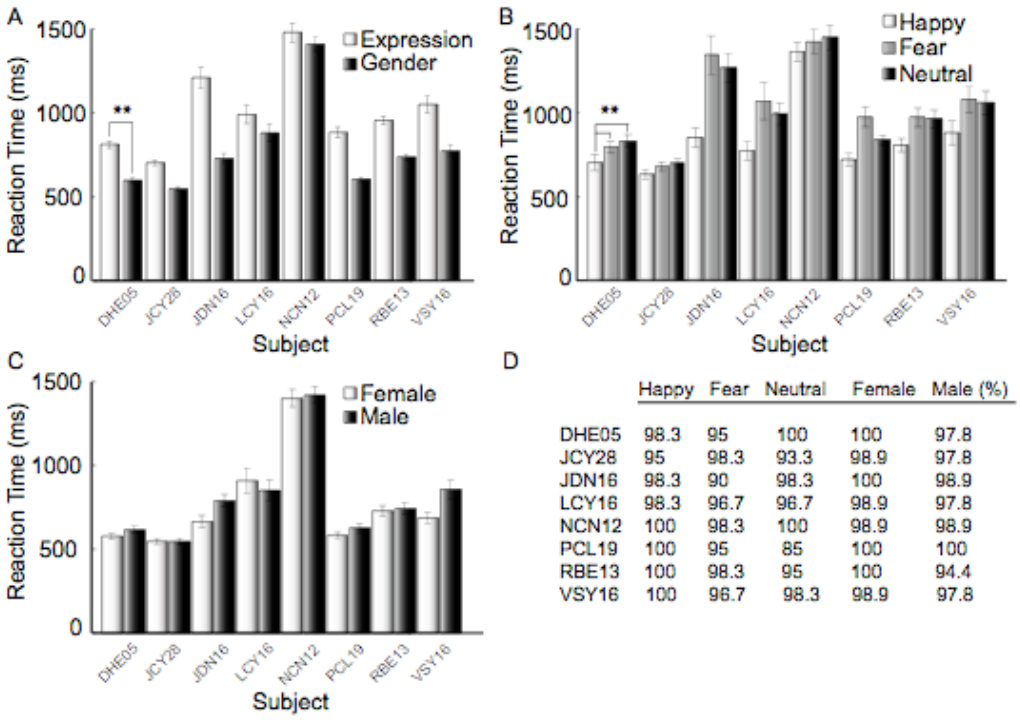
General Linear Model Deconvolution We used a GLM deconvolution approach (20 predictors per condition) to estimate BOLD response amplitudes to happy and fearful faces in "mouth" and "eye" ROIs, during gender and expression tasks. In a fixed effects analysis, contrasts of happy versus fear were tested for significance for each individual time point between 3-9s after onset. In a second level statistical analysis, we collapsed beta weights (parameter estimates in the GLM analysis) across time points 3-9s and performed, in a random effects analysis of all 9 subjects, a three-way repeated measures 2x2x2 ANOVA with expression (happy/fear), task (gender/expression) and region ("mouth"/"eyes") as independent variables. Finally, as we found differences at different time points, we also ran a four-way ANOVA analysis with expression, task, region and time (2x2x2x7). The

constraint of time was added by taking the beta weights at individual time points over the peak of the BOLD signal, i.e., between 3-9s (rather than averaged across times points 3-9s as was performed in the three-way ANOVA).

4.3. Results

4.3.1. Behaviour

Reaction Time We tested whether task modulated reaction time by means of one-way repeated measures ANOVAs (correct trials only). Subjects were faster to respond during the 2AFC (alternative forced-choice) gender task (mean 750ms, n=5) than during the 3AFC expression task (mean 1018ms) ($F(1, 14) = 23.6$, $p = 0.001$, Figure 4.2.A). Within tasks, subjects were significantly faster to respond to happy faces (mean 787ms) than to fearful (mean 926ms) and neutral faces (mean 1024ms) ($F(2, 21) = 14.8$, $p = 0.0004$, (Figure 4.2.B) and equally fast to categorize female (mean 698ms) and male faces (mean 734ms) ($F(1, 14) = 2.9$, $p = 0.12$, (Figure 4.2.C).



	Happy	Fear	Neutral	Female	Male (%)
DHE05	98.3	95	100	100	97.8
JCY28	95	98.3	93.3	98.9	97.8
JDN16	98.3	90	98.3	100	98.9
LCY16	98.3	96.7	96.7	98.9	97.8
NCN12	100	98.3	100	98.9	98.9
PCL19	100	95	85	100	100
RBE13	100	98.3	95	100	94.4
VSY16	100	96.7	98.3	98.9	97.8

Figure 4.2.A. Average reaction times during expression and gender tasks. B. Average reaction times to happy, fearful and neutral faces during the expression task. C. Average reaction times to female and male faces during the gender task. D. Categorization accuracy for happy, fearful, neutral, male and female judgements.

Accuracy Subjects completed a learning phase in which they categorized the expression and gender of the face stimuli to a 95% correct criterion. During fMRI scans, accuracy was slightly better on the gender task than the expression task (not significant, one-way repeated measures ANOVA, $F(1, 14) = 4.122$, $p = 0.08$). Mean accuracy across subjects was 98.7%, 96.0% and 95.8% for "happy", "fear" and "neutral" respectively in the expression task, and 99.5% and 97.9% for female and male respectively in the gender task (Figure 4.2.D).

4.3.2. "MOUTH" AND "EYE" REGIONS OF INTEREST

Identification of ROIs Contrasts of mouth and eye checkerboard mapping conditions were used to define five non-overlapping ROIs in each hemisphere in individual subjects: "mouth" regions in dorsal V1/V2 and dorsal V3/V3a, and "eye" regions in ventral V1, V2 and V3/V4 (Figure 4.1.B. and Figure 4.3.). "Mouth" regions in dorsal V1 and V2 were not separable, as early visual areas border each other with a mirrored representation of the visual field at the horizontal and vertical meridians, and the mouth checkerboard crosses the vertical meridian. Therefore, only two "mouth" regions were identified. Thresholds were kept above $F>3.2$ but were slightly adjusted individually in order to get the most optimal separation of "feature" regions within each visual area. [DHE05, $t(3002) > \pm 3.70$; JCY28, $t(3002) > \pm 3.82$; JDN16, $t(3002) > \pm 3.61$; NCN12, $t(3002) > \pm 3.62$; RBE13, $t(3002) > \pm 3.78$; SJH25, $t(3002) > \pm 3.78$; VSY16, $t(3002) > \pm 3.29$; all $p< 0.0003$ correcting for multiple comparisons using a false discovery rate (FDR) correction of 0.01. However for two subjects thresholds had to be lowered to $t(3002) > \pm 2.27$ (LCY16) and $t(3002) > \pm 2.07$ (PCL19) in order to obtain comparable regions of interest (Figure 4.3.).

Task-dependent activation of ROIs Once "mouth" and "eye" regions were defined, we investigated with an independent set of data how these areas of cortex participated in the processing of happy and fearful faces, during gender and expression tasks. Collapsing across subjects and hemispheres, from these ROIs we extracted the average deconvolved BOLD responses to visualize activation patterns to face stimuli (stimuli were identical across tasks). A comparison of individual time points (3-9s after onset) revealed differential effects of expression in the "mouth" ROI when judging gender and in the "eyes" ROI when judging expression, ($p<0.05$, Figure 4.4. for V1). Specifically, we observed significantly higher activation to "happy" over "fear" in the cortical representation of the mouth, when gender was judged. In contrast we observed significantly higher activation to "happy" over "fear" in the cortical representation of the eyes, when expression was judged. This was replicated in ROI analysis of V3/V3A ("mouth"), and V2 and V3/V4 ("eyes", Figures 4.5. and 4.6.). The three-way ANOVA of expression, task and ROI revealed the existence of significant two-way interactions between expression and region ($F(7,64) = 10.2$, $p < 0.01$), and region and task ($F(7,64) = 11.4$, $p < 0.01$), supporting that the cortical representation of face features in early visual areas respond differentially according to task. Generally, significant differences in V1, V2 and V3/V4 (ventral "eye" regions) occurred with a slightly slower latency than in V1/V2 and V3/V3a (dorsal "mouth" regions). The temporal difference might reflect the slightly longer reaction times during the expression task than the gender task. In order to take this difference into account, we performed a four-way ANOVA and added the constraint of time, to reveal a significant interaction between the expression of the face, task, ROI and time ($F(55, 448), = 13.52$, $p = 0.03$). To visualize the interaction of ROI and task we present the difference between "happy" and "fear" over all time points of the BOLD signal (Figure 4.6), and the average maximum difference in

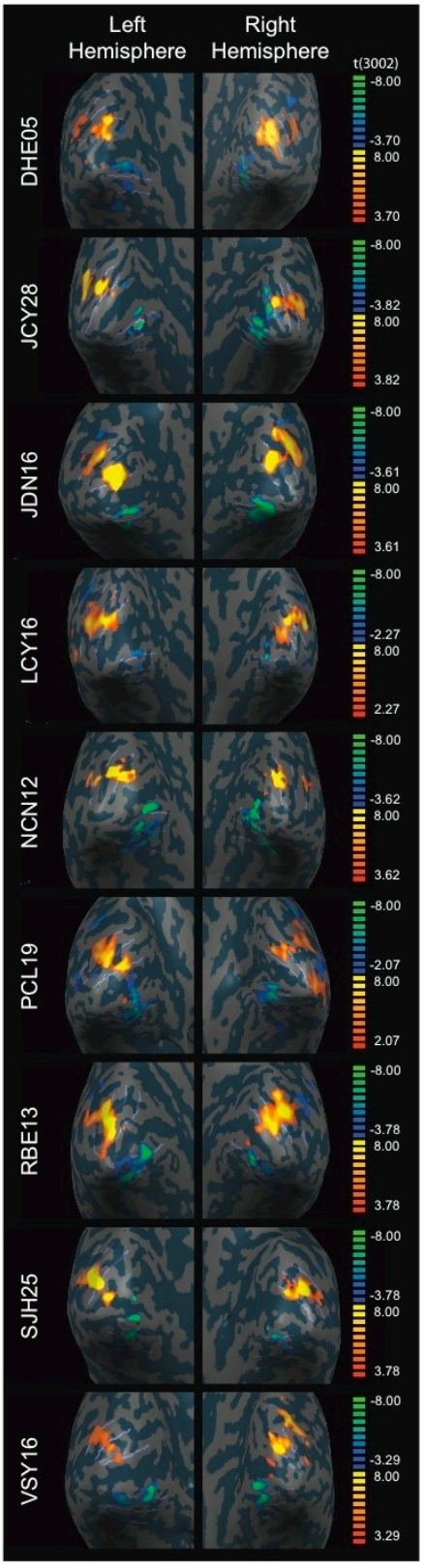


Figure 4.3. Cortical representation of mouth and eyes in left and right hemispheres for all subjects.

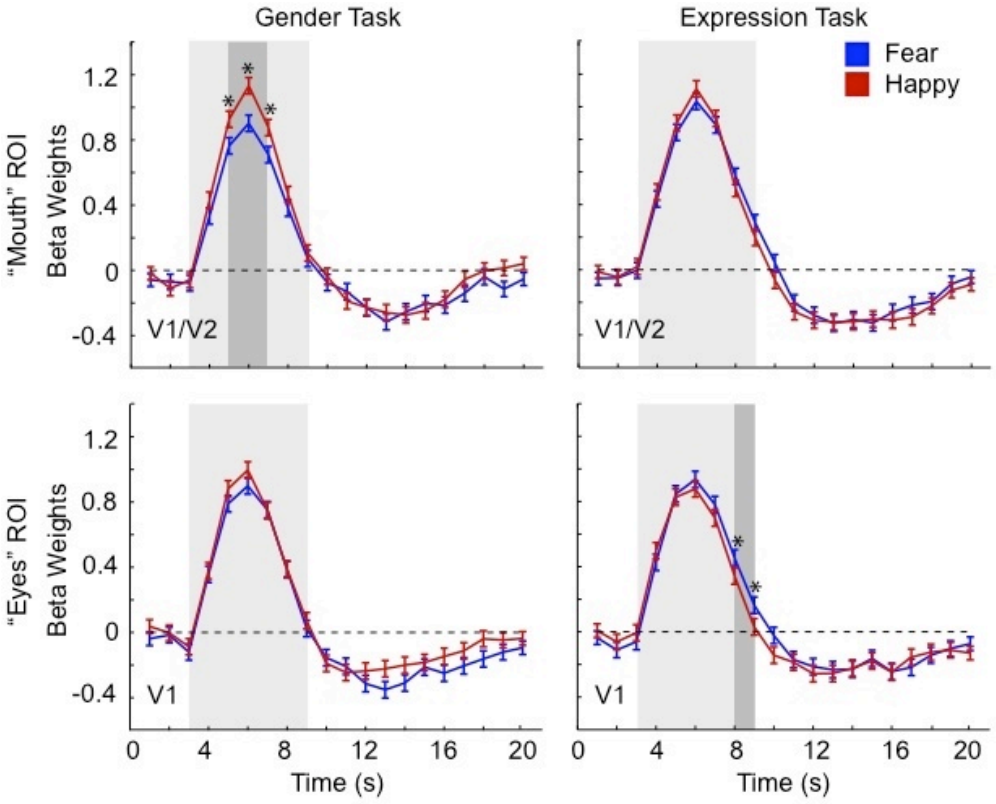


Figure 4.4. Deconvolved BOLD signal time courses to happy and fearful faces in V1 across subjects, presented by task (gender and expression) and region (mouth, V1/V2 and eyes, V1). Contrasts between happy and fearful faces were tested for significance at individual time points between 3-9s after onset (pale grey shading). Significant differences are marked with black asterisks (p<0.05, and dark grey shading). Error bars report standard errors between subjects.

the ROIs (Figure 4.6.). Negative values plotted in Figure 4.6. indicate "fear" activation is greater than "happy"; this occurred in the "eye" ROI but only when judging expression. Conversely, positive values indicate increased activation to "happy" over "fear", and were observed in the "mouth" ROI but only when judging gender. Generally, significant differences in V1, V2 and V3/V4 (i.e. ventral "eye" regions) occurred with a slightly slower latency than in V1/V2 and V3/V3a (dorsal "mouth" regions, see timing of orange line sections in Figure 4.6.). In other words, the latency of the differential processing in the cortical representation of the eyes (expression task) tended to be slightly later than in the mouth (gender task).

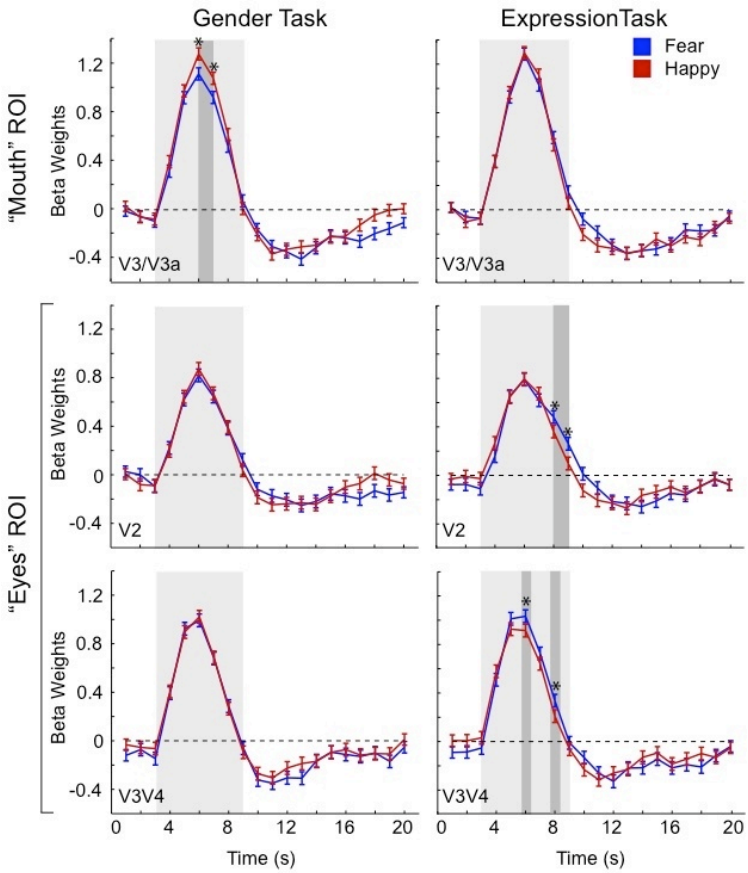


Figure 4.5. Deconvolved BOLD signal time courses to happy and fearful faces in V2 and V3/V4 ("eye" ROIs) and V3/V3A ("mouth" ROI), across subjects.

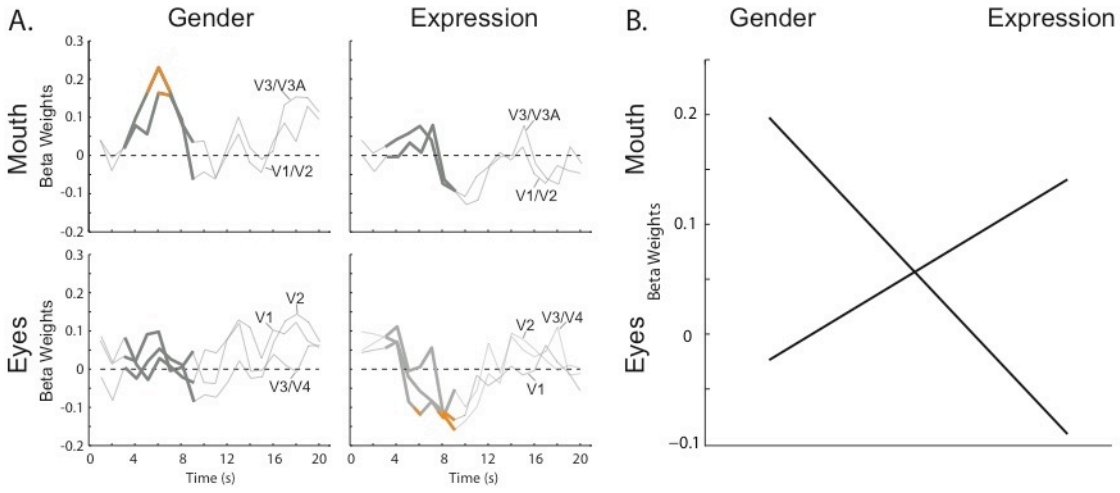


Figure 4.6. Difference between "happy" and "fear" time courses in the "mouth" and "eyes" during gender and expression tasks in all early visual areas (tested for significance, thick grey lines; significantly different, orange lines). Negative values mean "fear" activation was greater than "happy". B. Absolute maximum values of "happy"-"fear" time courses

between 3-9s after onset during gender and expression tasks, averaged across "mouth" ROIs and "eye" ROIs.

4.4. INFORMATION SENSITIVITY IN EARLY VISUAL AAREAS

Humans are experts at extracting diagnostic features, and this information modulates signals in higher visual areas. Our data reveal early retinotopic cortex also engages task-dependently during face processing. Although the stimuli are presented are identical, the type of classification task the subjects are performing determines modulation of primary sensory cortex. We discuss two factors that might contribute to our findings, firstly how recurrent interactions of face-processing areas with early visual areas might be used to recruit detailed diagnostic information. We also suggest how attentional enhancement of early visual processing might target spatially-specifically regions of cortex corresponding to diagnostic features.

4.4.1. TOP-DOWN PROCESSING IN THE CORTICAL FACE NETWORK

Face processing is associated with a circumscribed network of higher visual areas (Haxby et al., 2000; Ishai, 2008), which does not incorporate a role of early visual areas. Illusory face detection (Zhang et al., 2008) and face imagery tasks (O'Craven et al., 2000; Ishai et al., 2000) reveal this network of higher visual areas to be engaged. Projections from frontal areas (Mechelli et al., 2004) may be crucial for the integration of task-relevant face features in specialised higher visual areas (Sigala and Logothetis, 2002, Schyns et al., 2007, 2009, Smith et al., 2008; Smith et al, 2009), and may reflect predictive coding of forthcoming face perception dependent on behavioural state (Summerfield et al., 2006). Whilst it has been suggested that feedback connections from temporal areas guide face-selective occipital areas to extract fine-grained features required for face processing (Gauthier et al. 2000; Rossion et al. 2003), thus far there is little motivation to suggest this reaches V1. What might the role of early visual areas be? If top-down signals tune neurons in temporal

areas to diagnostic features, feature-selective signals from here could extend back to earlier stages of processing. In this framework, V1, providing high-resolution representations of features, could be sensitized to features integrated in higher areas. Indeed, recent evidence suggests there is a direct pathway from early visual areas to the FFA (Kim et al., 2006; Rossion, 2008), and this is quite possibly bidirectional. Although direct evidence for this in humans is lacking at present, tracing studies in non-human primates reveal weak afferent connections from visually sensitive temporal areas (TEO, TE) to V1 (Barone et al., 2000; Felleman & Van Essen, 1991; Perkel, et al., 1986; Rockland, 1994). Additional evidence that features extracted in higher, more specialised areas are projected back to V1 is provided by work on apparent motion processing (Muckli et al., 2005; Ahmed et al., 2008; Wibral et al., 2009) or motion integration (Harrison et al., 2007).

4.4.2. ATTENTIONAL MODULATION OF EARLY VISUAL AREAS

Our results are most likely associated with spatial attention shifts in response to the task switch. Subjects were instructed to keep central fixation and therefore no explicit instruction was given to shift the spatial focus of attention. However, subjects were engaged in a classification task (gender/expression), which triggers specific and intrinsic strategies to recruit information from certain spatial frequencies (Martinez et al 2001, Schyns et al., 2007, 2009, Smith & Schyns 2009) from certain visual field coordinates (Roelfsema et al., 2007). Attentional influences thought to arise from the frontal eye fields (FEF) and intraparietal sulcus (IPS, Bressler et al., 2008) could target retinotopic primary visual cortex (Kanwisher and Wojciulik 2000) during face processing, with higher areas conveying global information to the local computations performed in V1 to get more detailed information.

Attention-related BOLD signals are stronger than is expected from the mild change in fire rate observed in cell level electrophysiology (Luck et al. 1997; Roelfsema et al.,

2007). This is taken as an indication that attentional changes are related to incoming projections and other measures of neuronal activity that affect membrane potential fluctuations and the associated energy consumption (Logothetis et al. 2001; Viswanathan and Freeman 2008; Thiele et al., 2009). Visual attention decreases low frequency baseline correlation of neurons (Fries et al., 2008; Cohen and Maunsell, 2009; Mitchell et al., 2009) and increases gamma band synchronisation (Fries et al., 2008; Womelsdorf et al., 2006; Rodriguez et al., 2009; Taylor et al., 2005) all of which might have an increase effect on the BOLD signal (Goense and Logothetis 2008; Niessing et al., 2005). One could argue for signal differences in the diagnostic ROI but also equalized signal in this location, the former reflecting enhanced processing of the relevant feature (e.g. "happy" over "fear" in the mouth, "fear" over "happy" in the eyes, Schyns et al., 2009) and the latter ceiling effects (e.g. due to attention being primed on the eyes in the gender task and mouth in the expression task, Gosselin and Schyns, 2001). The temporal attribute we observe in the "eyes" ROI during the expression task could even be related to dynamics of attention shifting. These hypotheses stand in parallel and cannot be excluded from the current data. That task-relevant information is extracted differentially from spatial locations as shown in the response patterns of retinotopic visual areas responding to eye and mouth locations, suggests V1 can be used to track covert shifts of attention (identifiable in the BOLD response in early visual areas, Li et al, 2008), analogous to psychophysically tested shifts (Schyns et al., 2007). Super et al., (2004) and Super & Lamme (2007) demonstrated in the monkey increased firing rate of V1 neurons whose receptive fields corresponded to the target location for the forthcoming saccade, and Geng et al., (2009) a similar result in human retinotopic cortex.

Recent evidence suggests top-down influences descending the visual hierarchy targeting V1 play a functional role in visual processing. This is the first demonstration of

task-specific information extraction in retinotopically-mapped face features in V1 (to V3). Further experiments are crucial to *i)* examine if activity is predictive of behavioural performance (here performance reached ceiling levels and subjects were informed of the task), *ii)* correlate with subject-specific diagnostic information use (reverse correlation), *iii)* characterize effective connectivity/causal influence with higher visual areas, *iv)* investigate priming of the cortical representation of features according to spatial frequency content of diagnostic information.

CHAPTER FIVE

VISUAL SENSITIVITY TO DIAGNOSTIC INFORMATION DURING FACIAL EXPRESSION CATEGORIZATION IN HUMANS

5.1. DIAGNOSTIC INFORMATION TO INVESTIGATE BRAIN MECHANISMS OF EXPRESSION CATEGORIZATION

Facial expression processing elicits activation within specific brain areas, with visual, frontal and limbic areas tuned to extract emotional content from faces during social interaction. Recently the importance of effective and functional connectivity within this network to understand functional regulation between areas was documented (Fairhall & Ishai, 2007; Summerfield et al., 2006, see also Friston 1994), and studies applying classification images techniques to face categorization tasks show how cognitive theories (e.g. attention or top-down influences) can be related to brain processing (e.g. modulation of a brain signal by specific visual stimulus characteristics, see Schyns et al., 2003; Smith et al., 2004; Schyns et al., 2007; Smith et al., 2008; Schyns et al., 2009; Smith et al., 2009; van Rijsbergen & Schyns, 2009). In this thesis, diagnostic features have been used to a) characterize a significant brain event (N170) during processing in this network by using brain-imaging signals to reveal a sequential order during the processing of face features in occipitotemporal areas, and b) implicate early visual areas in addition to this network by localizing regions of early visual cortex that respond task-dependently during face processing. Both of these experiments suggest a role of top-down modulation of visual cortex during facial expression categorization, which is also discussed in the context of eye movements.

5.2. THE VISUAL SYSTEM SELECTS DIAGNOSTIC INFORMATION

The control of gaze during visual scanning is thought to rely on both automatic and controlled mechanisms (Schneider & Shiffrin, 1977). Given the salience of faces, an automatic scanning of faces seems likely to some extent. Indeed, stereotyped scanpaths falling on specific regions round the eyes, nose and mouth support this (Yarbus, 1967; Mertens et al; 1993). However, this automaticity cannot account for an active drive to acquire diagnostic features of which the distribution in the face differs between expressions, and which accumulates over fixations as shown in Chapter 2. That saccadic eye movements are aimed to fixate diagnostic features during free-viewing conditions when categorizing the basic expressions suggests the oculomotor system is tuned to extract high-resolution information specifically relevant to the identification of each expression, rather than stereotypically processing each in the same way. In other words, these results confirm facilitation by cognitive mechanisms to guide saccades to diagnostic inputs (Malcolm et al., 2008), channelling high-resolution task-relevant features from stimulus (Castelhano et al., 2009) to cortical regions for efficient expression discriminations.

Cortical control of eye movements

Current models of saccadic control assume an integral cognitive model (Findlay & Gilchrist, 2001; Henderson, 2003; Chen & Zelinsky, 2006; Zelinsky et al., 2006; Henderson, 2007), whereby attention, task, planning and working memory play a critical role (Hollingworth et al., 2008; Hollingworth & Luck, 2009). Indeed, a significant input to saccadic control centres is of cortical origin (Schiller & Tehovnik, 2005), where such cognitive functioning occurs. In Chapters 3 and 4, the cortical sensitivity to diagnostic features was presented, at later and earlier stages of processing respectively, but prior to when saccades are executed. Therefore, although a mechanistic basis cannot be inferred from the current data, as the brain has represented the diagnostic information for the task

possibly preceding the initiation of eye movements, we can tentatively discuss how the top-down modulation of sensory cortex during face processing and the top-down control of eye-movements could engage common mechanisms.

A saccade is a rapid, ballistic movement of the eye, in order to bring regions of importance into the focus of highest visual acuity, the fovea. Substantial progress has been made in understanding how the oculomotor system serves saccadic mechanisms. The *amplitude* of a saccade is encoded by the duration of activity in motor neurons within three oculomotor nuclei. The activation of the six extraocular muscles (driven by activity in premotor neurons within two gaze centres in the brainstem) controls the *direction* of a saccade. The question then becomes how top-down task demands, such as diagnostic information extraction, drive the control of these gaze centres. As yet this remains unclear, however anatomical considerations provide some interesting clues.

Neurons in the reticular formation of the brain stem form saccade-related gaze centres that directly innervate oculomotor neurons (Luschei & Fuchs 1972; Keller 1974), connected in a feedback loop to control horizontal and vertical eye movements. Importantly, these gaze centres receive direct input from the superior colliculus and frontal eye fields (and indirectly from the frontal eye fields via the superior colliculus). The superior colliculus projects to both horizontal and vertical gaze centres, providing motor commands to move the eye to an intended location in order to bring visual information into foveation. The superior colliculus is modified by inputs from the frontal eye fields, the posterior parietal cortex and the substantia nigra pars reticulata. Activation of the frontal eye fields relates to the selection of the visual information to be targeted, and is involved in suppressing reflexive saccades and generating voluntary saccades. The posterior parietal cortex is implicated in the visual guidance of saccades by shaping attentional demands (Thompson et al., 1996) of which we expect to play a role in an active expression judgment

task, suggesting visual neurons here are selectively activated by stimuli features that are behaviourally relevant. Furthermore, the substantia nigra pars reticulata funnels input from the frontal cortex, operating as a gating mechanism for the voluntary control of saccades, and modulating the activity of the superior colliculus. In Chapter 1, the role of the frontal cortex in cognitive aspects of expression categorization was introduced, and was expanded in Chapter 3 where we suggested the top-down modulation of temporal regions drives the sensitivity to specific features. Moreover, this modulation had occurred within 170ms, possibly prior to when saccades occur, suggesting frontal regions represent a good candidate for at least some role in controlling the extraction of diagnostic information during expression categorization via saccadic eye movements. The ventral visual cortical pathway involved in face and object recognition has been implicated previously in the neural circuitry controlling rapid eye movements (see Kirchner & Thorpe, 2006).

Guidance of fixation location

The combination of bottom-up and top-down factors in guiding eye movements is central to understanding efficient visual search. A vast body of work tells us that mechanisms of categorization modulate the use of available visual information (e.g. Schyns & Oliva, 1994, 1999; Schyns et al., 2002; Schyns & Gosselin, 2003). Our measure of fixation diagnosticity confirms that eye movements are strongly constrained by the top-down requirement to encode diagnostic, task-dependent information (albeit with some possible contribution from bottom-up factors). This seems especially likely given that observers know they are extracting information from a face, and unlike other objects and scenes, faces have a consistent composition (e.g. two eyes, a nose and a mouth).

That fixations are tuned for diagnosticity supports the idea of context in combining both bottom-up and top-down control mechanisms (e.g. Torralba et al., 2006), in contrast to the view that the saliency of bottom-up factors modulates fixation locations (e.g. Itti &

Koch, 2000). We suggest that diagnostic features are fixated prior to categorical decisions, and that this must be under top-down control. Furthermore, regions where fixation is directed to might reflect the spatial frequency composition of diagnostic features, which are detailed by Smith & Schyns (2009). This would provide paramount evidence that visual categorization demands drive the control of eye movements. Generally, the features that diagnose facial expressions (with the notable exception of the broad smiling mouth in "happy") are represented at a fine scale (e.g. the wrinkly frown in sadness, the white of the eyes in "fear") implying foveation is required to extract HSF information. Aside from stimulus-driven characteristics and task-driven factors of eye movement control, it is also of interest how the visual system stores and maps each input against what is and what is not diagnostic, and in turn how this modulates further top-down control. How the execution of eye movements and the time of visual processing (Kirchner & Thorpe, 2006; Bacon-Macé et al., 2007) are linked to categorization processes (e.g. reaction time and accuracy of judgements) also relates to this. Eye movements are an appropriate measure of processing speed because they can be initiated rapidly (Bussettini et al., 1997; Masson et al., 2000).

The evidence presented in Chapter 2 of a top-down determination of fixations reported here raises further questions. For example, this is an important platform from which more exhaustive investigations can be launched, i.e. by combining eye movement techniques with Bubbles allows investigation of the precise facial features underlying behavioural parameters associated with aspects of eye movement behaviour. We agree that this study is a first step towards dissecting how subjects saccade to and from features that modulate behaviour, and that a gaze contingent paradigm modelling retinal filtering in combination with Bubbles sampling would prove useful. What we have performed here is a step in that direction; subjects were allowed to fixate freely within a complete (unsampled) stimulus, but revealed that they do indeed fixate the features we define as "diagnostic". The

advantage of faces over other stimuli to address such issues of eye movements towards features that underlie behaviour is that the spatial location of features is stable, enabling the system to use this knowledge to guide information extraction. For these reasons, this is a useful platform to investigate the cortical networks supporting the extraction, encoding and integration of diagnostic information.

Neural processing during fixations

The duration of fixations (how long the eye remains stable on a region of importance during visual search) may also be indicative of cognitive processing similar to fixation locations (revealing attention). Although fixation durations are now more frequently incorporated into computational models of eye movement control (e.g. Engbert et al., 2005), this has been studied primarily in the context of reading. Interestingly, we observed no effect of fixation duration and so how this reflects cognitive and perceptual factors during expression categorizaton requires further exploration. Furthermore, how saccade programming differs between a fixation on a diagnostic versus a non-diagnostic region, and how this modulates the subsequent fixation location/duration is also of great interest (see Nuthmann et al., 2010 for a computational model of fixation duration that accounts for saccade programming). Indeed, it could be that fixation duration differences would be observed as a function of task.

Summary

We used diagnostic information extraction to demonstrate cognitive processing during the processing of facial expressions. Although the neural control of eye movements as a function of cognitive architecture is still an active area of research, we know that face processing engages the ventral visual pathway. Thus saccade planning and execution to extract diagnostic features is likely dependent on links between temporal and frontoparietal cortical pathways. These mechanisms, in turn, will inform means of attention and working

memory, and how they modulate fixation duration and location during facial expression categorization.

5.3. THE N170 INTEGRATES DIAGNOSTIC INFORMATION

To resolve the computational underpinnings of cognitive processes such as facial expression categorization requires techniques such as those described in Chapter 3. As revealed by optical imaging, neurons responding to related facial features are arranged in clusters of approximately 1mm in size, and this spatial arrangement of cells means the activity of such assemblies is capable of producing a measurable electrophysiological signal (Wang et al., 1996). Here, we described how the face-sensitive N170 event-related potential is linked to the dynamics of visual categorization of facial expressions. By applying classification image techniques to behavioural and EEG data we show that this brain event reflects the systematic integration of information, such that the eyes are processed first and information lower in the face later. This integration stops at the region of the face in which the diagnostic information is located. By exploring spatial frequency use, we demonstrate that the classification image technique can quantitatively determine which features of complex visual stimuli are used during facial expression categorization. Furthermore, for the first time, we estimated the facial features that modulated brain activity during the N170. The finding that informative features for recognition are not processed simultaneously but in an orderly progression over early stages of face processing, and that integration stops when information for behavioural judgements has been processed, is instructive for understanding the processes involved in visual categorization, and in particular the integration of bottom-up and top-down processes.

The coding of diagnostic features in the visual cortex

The question of how visual facial information is transformed into conscious percepts of expression has occupied the field of cognitive neuroscience for some time.

Central to this is the activation of the ventral visual pathway from V1 to inferior temporal cortex. Our results reveal that neurons in occipitotemporal regions show selectivity for the diagnostic facial features that underlie behavioural judgments, suggesting a degree of top-down cognitive control aimed at temporal "recognition" modules of the ventral visual pathway. This could be achieved via interactions between occipital and temporal regions with the prefrontal cortex (Bar at al., 2006). Frontal (and limbic) regions are known to contribute to cognitive mechanisms, providing a conceptual representation of facial expressions, although this interaction between frontal and occipitotemporal regions is not completely understood. Attention has also been demonstrated to enhance activation to preferred stimuli in object-selective cortex (Wojciulik et al., 1998; O'Craven et al., 1999; Murray & Wojciulik 2004). Although precisely how selective visual attention manifests in the representations that lead to categorization is unknown, i.e. how it modulates neuronal representation in temporal cortex, that observers are engaged by diagnostic features suggests this is possible.

Schyns et al., (2009) demonstrate that attention to spatial frequency content in occipitotemporal areas drives the bilateral extraction of combinations of features for behaviour, initially encoding local information in high spatial frequency bands around the eyes, before zooming out to process the face at lower spatial frequencies and finally zooming back in to locate the diagnostic features at high local resolution. This suggests both a fixed (local to global to local) and flexible (diagnostically-driven) pattern of spatial frequency use during facial expression categorization in occipitotemporal areas over 140-200ms of processing. van Rijsbergen & Schyns (2009) expanded on this by demonstrating that over the first 400ms of expression processing, feature sensitivity spreads bilaterally across both occipitotemporal regions to converge in central parietal regions, and that this shifts from a sensitivity to information across all spatial frequencies to a fine representation

of diagnostic features. This suggests the P300 ERP may reflect sensitivity to very fine details diagnostic of face categorizations. A complex representation of feature combinations dynamically shifting over time and space, suggesting functional phases of activity during face processing was also shown by Smith et al., (2009). The authors traced the processing of three features specifically in time but also throughout the cortex to reveal that features are initially processed in isolation in occipital areas, prior to which task demands drive the sensitivity to combinations of features in occipitotemporal regions. The dynamic sensitivity of the cortical face network to diagnostic features is becoming increasingly well defined. With regard to how non-human primate studies can contribute to this, for example, a specifically interconnected hierarchical network dedicated to face processing has been revealed in the temporal lobe of the macaque monkey (Moeller et al., 2008). Stimulation of individual patches in this network leads to activation in a subset of other patches whilst stimulation outside these patches does not. Further studies such as this will help to gain insight into the circuitry of temporal "face" areas.

Recent evidence that the modulation of the FFA by expression occurs in the same voxels in the cortex as the modulation produced by selective attention to faces, suggests that temporal areas (FFA) are under top-down influences not only of frontoparietal networks but also by the regions recruited in expression processing. However, the extent to which cognitive and emotional sources of attention interact in higher regions, such as prefrontal cortex, remains unclear, as does the putative involvement of the amygdala in triggering indirect attentional effects and direct feedback effects on temporal cortex. In the macaque, prefrontal face patches are thought to represent dedicated modules for face processing and could underpin the visual processing of faces by working in combination with temporal areas (Tsao et al., 2008). These frontal areas could receive dense input from temporal areas and/or attentional control centers, and then project back to temporal regions

to modulate visual sensitivity to faces.

Summary

The correct categorization of expressive faces relies on the processing of specific facial features. Behavioural and EEG classification image techniques are used to infer the dynamics of feature extraction during the recognition of the basic facial expressions in Chapter 3. The results reveal a process that integrates visual information over approximately 50 milliseconds prior to the face-sensitive N170 event-related potential, starting at the eye region, and proceeding gradually towards lower regions. The finding that informative features for recognition are not processed simultaneously but rather in an orderly progression over a short time period is instructive for understanding the processes involved in visual recognition, and in particular the integration of bottom-up and top-down processes. This implies some degree of automatic (as integration begins in the eyes) and goal-directed (as integration stops at behavioural information) control during visual processing of expressive faces over a brain event (N170) thought to be a specific face-marker.

5.4. EARLY VISUAL AREAS ARE SENSITIVE TO DIAGNOSTIC FEATURES

Increased activation in sensory cortex to expressive (e.g. fearful) faces has been observed in the earliest stage of the cortical visual pathway, V1 (Morris et al. 1998; Vuilleumier et al. 2001; Pessoa et al. 2002). We extend these findings in Chapter 4 by showing retinotopically-mapped regions of early visual cortex responding to diagnostic features do so as a function of top-down task expectations. Although impossible to conclude from the current data, the amygdala has been shown to both feed back as far as V1 and also exhibit sensitivity to fearful eyes, so may, in some way, modulate the effects we observed in early visual areas. As measured with fMRI, the timing of this is conceivable. Early visual cortices are positioned to participate in high-level recognition via

feedback connections from anterior temporal cortex as well as the amygdala and frontal cortex.

Traditionally, V1 is conceptualized as a cortical processing stage at which contrast, spatial frequency and orientation are extracted at a given retinal position (Carandini et al. 2005). Functional brain imaging experiments have contributed to the notion that V1, however, is also exposed to considerable feedback activation and is consistently involved in various cognitive tasks including visual spatial attention (Kanwisher & Wojciulik, 2000; Ress & Heeger, 2003), mental tracking (Kaas et al., 2009), mental imagery (Slotnick et al., 2005), visual expectation (Kastner et al., 1999) and visual working memory (Harrison & Tong 2009). To investigate the involvement of V1 in this task-dependent information extraction we mapped the representation of "eye" and "mouth" positions in retinotopic visual areas (V1-V3) and examined univariate activity changes within these regions-of-interest as a function of task. Our strategy revealed that the cortical representation of diagnostic features (eyes and mouth) is differentially recruited depending on the categorization task in early visual areas V1-V3. This activity is typically a property of ventral temporal regions.

A role of V1 in face processing?

Previous brain imaging research has found that retinotopic visual areas do not only respond to strictly retinotopic space coordinates but also to illusory distortions of perceived space (Murray et al., 2006). Another example shows V1 activation along non-stimulated retinotopic coordinates when these regions are exposed to a visual motion illusion (Muckli et al., 2005; Sterzer 2006). These findings suggest an activation profile in V1 involving cortical feedback and lateral interaction. Indeed, recent evidence from our group shows that non-stimulated regions of V1 can discriminate between natural visual scenes displayed in the surrounding visual field (Smith & Muckli, 2009). These experiments were performed

using multivariate pattern classifier analysis (MVPC), which has emerged as a powerful tool to detect subtle influences in the fMRI BOLD signal of V1 (e.g. Kamitani & Tong, 2005; Haynes & Rees, 2005; Kamitani & Tong, 2006; Walther et al., 2009). These findings provide a strong motivation to consider the face classification data from Chapter 4, in which we found V1 to be involved in the processing of face features in an additional analysis. There are two hypotheses that would be interesting to compare: (1) V1 contributes to the task by retinotopically-specific mechanisms that facilitate the processing of diagnostic information at the respective location, or (2) V1 is informed by spatially extended feedback mechanisms of the more global context of the facial expression extracted, for example, from higher visual areas back-projected to larger parts of V1. The second mechanism could be used to enhance categorization mechanisms, change global filter properties (i.e. spatial frequency) or provide contextual information in general (i.e. for predictive coding, Bar, 2004, 2007). These hypotheses could be tested by training a linear pattern classifier to differentiate the emotional content of the presented faces (happy or fear) using single trial response estimates from each of the diagnostic information patches (eyes and mouth), and comparing this to the performance of a classifier trained on the response estimates of the remaining part of V1 that processes non-diagnostic information (face shape, nose, ears, etc but not eyes or mouth). Local processing of hypothesis 1 would predict that diagnostic vertices would favourably cluster around the retinotopic coordinates of the diagnostic feature position (eyes and mouth). Hypothesis 2 would predict a wide distribution of informative vertices even at places where the presented faces provide minimal diagnostic information for the perceptual decision.

Processing of face information serves various cognitive tasks and social functions including the identification and recognition of familiar people, the classification of facial expressions and recognition of emotional state, the discrimination of gender, the

engagement of empathy, or the evaluation of attractiveness (Haxby et al., 2000; Bruce & Young, 1986). Distributed cortical and sub-cortical networks are involved in this cognitive processing (Haxby et al., 2000; Ishai et al., 2008), and many of theses areas have direct connections to area V1. In general, almost the entire information on which higher areas perform face-related processing is fed forward from area V1. Thus, a modulatory involvement of early visual areas could be beneficial for the processing of complex features at higher processing stages. For example top-down tuning to relevant image features could help drive more efficient filtering at a relatively early processing stage (see Ahissar & Hochstein, 2002). Our data show that V1 is involved in the extraction of complex face features in a dynamic, task-dependent way. (It is important to note that the actual images are identical across the two tasks). Since we know that many other areas are important in expression recognition (e.g. Adolphs, 2002), they might be the regions that drive feedback to V1 in the context of the task. Our effects could also reflect a shifting in spatial attention. The cholinergic system is associated with attentional mechanisms to enhance the processing of sensory stimuli (Everitt & Robbins, 1997; Yu & Dayan, 2002; Hasselmo & McGaughy, 2004; Sarter et al., 2005), and is recruited through both bottom-up, stimulus driven mechanisms and by top-down, goal-directed mechanisms, suggesting it's involvement in stimulus processing reflects the combined influence of both bottom-up and top-down attentional processes (Sarter et al, 2005). Using fMRI, Furey et al., (2008) revealed enhanced cholinergic activity selectively increased neural activation to stimuli relevant to the task whilst reducing neural responses to task-irrelevant information.

Summary

Smith et al., (2008) and Chapter 3 show that diagnostic features modulate the spatial extent and temporal dynamics respectively, of brain signals in higher temporal visual areas specialised for face processing. However in the context of top-down signals

active in the visual system, the degree to which these higher visual areas engage earlier cortical stages (V1/V2/V3) in the processing of diagnostic features remains to be elucidated. We have identified the cortical representation of the eyes and mouth using retinotopic mapping. We contrasted activation in these regions of interest to happy and fearful faces, during gender and expression tasks. We reveal for the first time that task-dependent activation exists within the earliest cortical representation (V1 to V3) of diagnostic features. This strategic encoding of face images is beyond typical V1 properties and suggests top-down influences extending to early retinotopic stages of processing.

5.5. DIAGNOSTIC INFORMATION AT DIIFFERENT STAGES OF VISUAL PROCESSING: A COGNITIVE PROCESS

The importance of the face is widely regarded in anthropology, as is that of facial expression signaling in social intelligence. This thesis has reviewed how evidence for the latter comes from a number of fields in psychology, revealing a vast amount of literature aimed at developing a comprehensive theoretical framework detailing the spatial and temporal resolution of expression recognition. Furthermore, this thesis describes thee experiments to show how the nature of specific stimulus information – the diagnostic features - can provide a window into how the facial expression perception system functions.

We have used diagnostic features to report three things: 1) Inputs to the visual system reflect a need to extract task-relevant information to guide behaviour. This could rely on complex cortical and subcortical control of saccadic eye movements. 2) Previous experiments have successfully correlated electroencephalographic signals to features that are diagnostic for a given face categorization (see Schyns et al., 2003; Smith et al., 2004) but never had this been applied to the biologically relevant task of categorizing the basic expressions. We have inferred the feature processing content of the N170 over

occipitotemporal regions and related this to behavioral judgments, and suggest a role of attention in this processing. 3) The representation of diagnostic features in the brain had also never been explored at the earliest cortical stage of visual processing, V1. We identified regions of cortex activated by specific facial features using retinotopic mapping and modulated the task conditions under which these cortical areas respond. An interaction of task and region suggests that top-down processing in the cortical face network extends all the way to early retinotopic stages, possibly to refine the sensitivity of higher-order areas to stimulus features, to aid the optimal and rapid extraction of emotional content of faces by the human brain.

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