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From individual to crowd perception

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From Individual to Crowd Perception

How Motions and Emotions Influence
the Perception of Identity,
Social Interactions,
and Bodily Muscle Activations

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**From Individual to Crowd Perception:
How Motions and Emotions Influence the
Perception of Identity, Social Interactions, and
Bodily Muscle Activations**

Proefschrift

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door

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Imagine: you are going to a game of your favourite soccer team with some of your friends. When you arrive at the stadium, there is a large crowd of people and you look around to find your friends. Without effort, you pick out one of them and you walk towards him. He sees you, and smiles. You greet the others, introduce yourself to someone you haven't met before, and together you enter the stadium.

In passing, someone stomps you on the shoulder with his left hand and swipes at your face with the right. At first you duck to avoid a blow, but then you realize it is an acquaintance you haven't seen in a while. You jokingly lean back to cover your face in defence and cower for the fake onslaught. Nobody around you even blinks an eye in response to your mock fight. The match begins, people cheer and the atmosphere is one of joy and happiness.

However, after the match, the mood suddenly changes. Members of opposite teams start to behave threateningly towards each other; other people around them are scared. Within seconds, a panic spreads.

In this scenario, several neurocognitive processes occur rapidly and with minimal conscious effort. First of all, humans look alike. We all have a round face, two ears, two eyes above a nose and a mouth. How do we pick out the people we know among so many others? How do we immediately see that there is a new person in your otherwise stable group of friends? This process of face identification is an important topic of the first part of this dissertation, in which we also turn to those for who the story above seems like a fairy tale: people with face blindness, or prosopagnosia.

Secondly, we are very quickly able to determine whether someone is acting threateningly. When we see an angry person, how do we respond? What happens to our own body postures? Or if we see a scared person, what do we do ourselves? Sometimes it feels like our body takes over. Additionally, we are very sensitive to the things that happen with, or to, other people around us: people might not even spare a second glance for a mock fight, but a real altercation grabs our attention immediately. When we see a cheerful crowd, we feel happy. But when the situation turns dangerous, when we see people who are collectively scared, our brain quickly responds. What happens in our own body when we interact with angry or fearful individuals and what happens in the brain when we perceive emotional crowds will be discussed in part II of this dissertation.

1 |

Introduction

Part I: The recognition of identity and emotion in the face

The face provides us with a wealth of information about a person (Bruce & Young, 1986), first and foremost the identity, but also other major facial attributes like gender, age and facial expression. Information from these different channels is normally processed automatically and effortlessly. There are notorious exceptions to this ability, perhaps the most striking one a deficit in recognizing a person by the face, which is called prosopagnosia. In extreme cases, people with prosopagnosia cannot recognize the face of their own spouse or children. The face specificity of this person recognition deficit is underscored by the fact that identity can still be gleaned from other features such as the individual's voice, gait, or clothing.

Before we go deeper into prosopagnosia specifically, it is necessary to look into a normal, healthy way of the brain to process faces. The question of how we are able to correctly and quickly recognize so many faces has captured the interest of researchers for quite a while. It is generally accepted that humans are experts at recognizing faces (Carey, 1992; Diamond & Carey, 1977; Farah, Wilson, Drain, & Tanaka, 1998). One important finding that strongly supports this view of a specialization for faces regards the configural way in which we seem to process faces. Configural processing generally refers to the ability of apprehending the whole configuration of the face in a single sweep. The test of configuration ability that still occupies central place in the assessment of intact face perception is the inversion effect. Yin (1969) reported the remarkable observation that recognition for faces drops quite dramatically, more so than any other type of object that is normally perceived in a typical or canonical orientation. Apparently, even though inverted faces are visually the same, they engage other processes, or the same processes to a lesser extent, than upright faces.

Further evidence for face specialization can be found in the brain itself. Neuroimaging studies have identified several regions that respond more strongly to faces than any other kind of object. In addition to face selectivity as found in the superior temporal sulcus (STS) (Hoffman & Haxby, 2000; Ishai, Ungerleider, Martin, & Haxby, 2000; Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011a; Puce, Allison, Bentin, Gore, & McCarthy, 1998), one of the first such identified regions is the fusiform face area (FFA), located in the fusiform gyrus (or occipitotemporal gyrus), on the ventral surface of the temporal lobe (Kanwisher, McDermott, & Chun, 1997; Kanwisher & Yovel, 2006; Puce, Allison, Gore, & McCarthy, 1995; Sergent, Ohta, & MacDonald, 1992). The FFA not only shows preferential activation for faces, it is released from adaptation when face identity changes, indicating that the FFA is specifically sensitive for face identity (Andrews & Ewbank, 2004; Gauthier et al., 2000; Haxby et al., 1999; Ishai et al., 2000; Kanwisher et al., 1997; McCarthy, Puce, Gore, & Allison, 1997;

Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Winston, Henson, Fine-Goulden, & Dolan, 2004). Another face selective region can be found in the lateral inferior occipital gyrus and is known as the occipital face area (OFA) (Gauthier et al., 2000; Haxby, Hoffman, & Gobbini, 2000; Ishai et al., 2000; Pitcher, Walsh, & Duchaine, 2011b; Rotshtein et al., 2005; Weiner & Grill-Spector, 2010). These regions together are now seen as a distributed face processing network (Calder & Young, 2005; Haxby et al., 2000).

With this short summary of normal face processing in mind, we can turn to the question of what might be at fault in prosopagnosia.

Acquired prosopagnosia

Prosopagnosia was initially identified as a face identity recognition deficit resulting from brain damage in adulthood (acquired prosopagnosia), and quite a few cases have been reported over the last hundred years (Farah, 1990). With a few exceptions, almost all reports concern single cases. The lesion sites that cause these severe face recognition problems seem to be quite widely distributed among cases, but often appearing around the occipitotemporal sites, or the fusiform gyrus (Meadows, 1974) and the occipital face area (Bouvier & Engel, 2006). However, also damage to the anterior temporal lobes is an often occurring cause for prosopagnosia (Kriegeskorte, Formisano, Sorger, & Goebel, 2007; Lee, Scahill, & Graham, 2008), which indicates yet again that face recognition is dependent on a large network in the brain (Haxby et al., 2000).

An important issue in prosopagnosia research is the question of whether these deficits are face specific, or if the face recognition impairments are also accompanied by lower level visual processing deficits or object recognition. One can only speak of ‘pure’ prosopagnosia when the impairments selectively entail face processing. Otherwise, the face recognition problems could merely be a result of lower level impairments, which have their influence on all sorts of higher level visual representations. In other words, to what extent is face and object processing dissociable? Or is a face just a more complicated kind of object? Even though many cases of AP reported in the literature also have object recognition deficits (Farah, 1990), there are also pure cases of AP (Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010). See Table 1 for an overview of the reported cases in the literature. Similarly, there are also cases of ‘object agnosia’ (Moscovitch, Winocur, & Behrmann, 1997) with spared facial recognition abilities, again indicating that face and object processing can be dissociated.

As previously discussed, faces are normally processed in a configural way, which is another reason to suspect that faces are a unique stimulus category warranting its own specific processing route at least for a large part. Early on, it was suggested that acquired prosopagnosia might follow deficits in this ability (Levine & Calvanio, 1989) and indeed, it was often found that the ability to process faces configurally is impaired in prosopagnosia. It was found that patients with prosopagnosia were more than normally sensitive to inversion and that their inversion sensitivity went in the opposite direction to that of controls (Barton, Zhao, & Keenan, 2003; de Gelder & Rouw, 2000a; Farah, Wilson, Drain, & Tanaka, 1995a). This phenomenon was variously labelled inverted face inversion effect (Farah et al., 1995a), inversion superiority (de Gelder, Bachoud-Levi, & Degos, 1998), and the “paradoxical inversion” effect by de Gelder and collaborators (de Gelder & Rouw, 2000a, 2000b). However, the occurrence of a paradoxical inversion effect went against the then dominant notion that loss of configuration processing and its replacement by feature processing is at the core of acquired prosopagnosia (Levine & Calvanio, 1989; Sergent & Signoret, 1992). If the ability to process the configuration would simply have been wiped out by the brain lesion, stimuli that normally trigger configuration-processing routines (e.g., upright faces) and stimuli that do not depend crucially on orientation-sensitive processes (like inverted faces and a host of other non-orientation-specific objects) would be treated similarly and recognized equally well or equally poorly. However, when detailed results began to show that upright and inverted faces are not processed similarly, it became difficult to conclude that the core of the deficit in prosopagnosia is a loss of configuration perception and its replacement by feature processing. To understand this pattern of a conflict between processing routines, the notion was developed that faces are processed by two different routes, one that was called the face detection system, the other the face recognition system that contains both whole-based and part-based processes (de Gelder & Rouw, 2001).

Table 1 gives an overview of APs in the literature, their lesion locations and whether they are impaired at object recognition, configural processing, part-based processing, face memory and emotion recognition. Cases in which configural processing is normal are quite rare, with almost all APs in which configural processing was tested one way or another were found to show abnormal patterns or impaired configural processing.

Name AP	Lesion Site	Abnormal Face Inversion Effect or Impaired Configural Processing	Whole-Part Processing or Part Processing Ability	Face Memory Impairment	Emotion Recognition Impairment	References
AP cases with impaired object matching ability						
Sandy	R Occip L	Normal		Yes	Yes	- Susilo, Yovel, Barton, and Duchaine (2013)
Grace	R inf Temp L R mFusiform G L mFusiform G	Normal		Yes		- Dalrymple et al. (2011) - Susilo et al. (2013)
SM	Inf Temp L R Ant Temp R R Post Temp R Basal Ganglia		Global advantage in global/local task		No	- Behrmann and Kimchi (2003) - Gauthier, Behrmann, and Tarr (1999) - Marotta, Genovese, and Behrmann (2001) - Humphreys, Avidan, and Behrmann (2007)
RG	B Post Occip Temp L	Abnormal - Normal Face Inversion	Impaired by whole in part matching		No	- de Gelder, Frissen, Barton, and Hadjikhani (2003b)
DF	B LOC B Occip Temp R B mOccip Pariet R L Parietal Occip S B OFA			Yes	Yes	- Steeves et al. (2006) - Steeves et al. (2009)
FW	B Occip L					- Whiteley and Warrington (1977)
QL	R Occip L					- Whiteley and Warrington (1977)
FM	B Occip Temp C Fusiform G Inf Temp C L Thalamus				Yes	-(Moro, Berlucchi, Lerch, Tomaiuolo, & Aglioti, 2008); Moro et al. (2012)
CR	R Temp L R mOccip L					- Gauthier et al. (1999) Marotta, McKeef, and Behrmann (2002)
AR	R Temp L L Inf Temp R		Impaired			- Saumier, Arguin, and Lassonde (2001)
RN	B Pariet Temp C B Occip Temp L	Abnormal	Local advantage in global/local task		No	- Behrmann and Kimchi (2003) - Marotta et al. (2002) - Humphreys et al. (2007)
S005 S006 S012	R mOccip Temp C	Abnormal				- Barton (2008)
SC	L Ant Temp L R Occip L	Impaired	No whole advantage			- Stephan, Breen, and Caine (2006)
P008 S013	B Ant Temp L L Ant Temp L	Abnormal	Normal			- Barton (2008)
S004 S010	B Pos Occip L	Abnormal	Impaired eye processing			- Barton (2008)
S007	R Occip Temp L L Occip Temp R Ant Temp L	Abnormal	Impaired eye processing			- Barton (2008)
Patient 1 GA	B Ant Temp L	Impaired	Impaired by presence of whole in part matching		No	- de Gelder et al. (2003) - Barton, Cherkasova, and O'Connor (2001) - Barton, Press, Keenan, and O'Connor (2002)
MD Patient 7 Patient 2	B Post Occip Temp L R FFA	Impaired	Normal		No	- de Gelder et al. (2003) - Barton et al. (2001) - Barton et al. (2002)
AD	B Inf Occip L B Inf Temp G B m Occip G	No face inversion			Yes	- de Gelder, Pourtois, Vroomen, and Bachoud-Levi (2000) - de Gelder et al. (1998)
NS	B Occip-Temp J	No face inversion	No part-to-whole advantage			- Delvenne, Seron, Coyette, and Rossion (2004)
HJA	B Occipital C B Ant Temp C B Lingual G B fusiform G	No face inversion	- Impaired at Thatcherized faces - Normal part matching - Impaired by whole in part processing		Yes	- Boutsen and Humphreys (2002) - Humphreys, Donnelly, and Riddoch (1993) - Riddoch and Humphreys (1987) - Young, Humphreys, Riddoch, Hellawell, and Dehaan (1994)
RB	L Occip Temp L	Paradoxical Face Inversion	Impaired by whole in part matching		No	- de Gelder et al. (2003)
LH S011	B Occip Temp L R Frontal Temp L R Ant Temp L	Paradoxical Face Inversion	- Impaired eye processing - Impaired by whole in part processing			- Barton (2008) - de Gelder and Rouw (2000b) - de Gelder and Rouw (2000c) - Farah, Levinson, and Klein (1995b) - Farah, McMullen, and Meyer (1991) - Levine and Calvanio (1989) - Levine, Warach, and Farah (1995) - Farah et al. (1995a)

Name AP	Lesion Site	Abnormal Face Inversion Effect or Impaired Configural Processing	Whole- Part Processing or Part Processing Ability	Face Memory Impairment	Emotion Recognition Impairment	References
AP cases with unknown object matching ability						
VH	R Ant Temp L					- Evans, Hegg, Antoun, and Hodges (1995)
W	Occip L					- Bruyer et al. (1983)
BM	Right hemispherectomized	Impaired			No	- Sergent and Villemure (1989)
Patient 3	R mOccipTemp C R FFA R Inf Parietal Lobule R Ventromed Front L L Insula L Parahippocamp G L Ventromed Front L	Impaired				- Barton et al. (2001) - Barton et al. (2002)
Patient 5	R m Occip L R Fusiform G R Lingual G	Impaired				- Barton et al. (2001) - Barton et al. (2002)
AP cases with intact object matching ability						
Patient 1	R Inf Occip R R Fusiform G	Normal				- Wada and Yamamoto (2001)
Herschel	Suppression of: R Occip Temp G R Occip G R Lingual G	Normal		Yes	Yes	- Rezlescu, Pitcher, and Duchaine (2012)
B-AT1	B Ant Temp L B mTemp L B Inf Temp L			Yes	No	- Fox, Hanif, Iana, Duchaine, and Barton (2011)
LR	R mTemp G R Ant Temp L R Inf Temp L R Amyg		- Impaired eye, not mouth, processing	Yes		- Bukach, Bub, Gauthier, and Tarr (2006)
Anna	B Sec Visual C R Post Cingulate G R Sup Parietal L R Premotor Area R Motor Area			Yes	No	- De Renzi and di Pellegrino (1998)
OR	R Temp L R Sup Temp G R Angular G R Pariet L R Primary Visual C					- De Renzi, Perani, Carlesimo, Silveri, and Fazio (1994)
WA	R Occip L					- Whiteley and Warrington (1977)
Case 3	R Temp Occip L R Fusiform R Lingual G			No		- Takahashi, Kawamura, Hirayama, Shiota, and Isono (1995)
DN	R Occip R L Occip Temp G				No	- Mattson, Levin, and Grafman (2000)
Case 1	B Inf Occip Temp C				No	- Clarke, Lindemann, Maeder, Borruat, and Assal (1997)
Case 2	B m Temp L B Inf Temp L B Fusiform G				No	- Clarke et al. (1997)
MT	R Temp Pariet L			Yes	No	- Henke, Schweinberger, Grigo, Klos, and Sommer (1998) - Schweinberger, Klos, and Sommer (1995)
WF	B Temp Basal Cont Enlarged ventricles			Yes	No	- Henke et al. (1998)
S009	R mOccip Temp C	Abnormal				- Barton (2008) - de Gelder et al. (2003)
DC	B mOccip L R Fusiform G B Lingual Gyrus B BA 18/19	Impaired	Impaired			- Rivest, Moscovitch, and Black (2009)
PS	R Inf Occip C R mTemp G R Post Cereb L Fusiform G L FFA R OFA	No face inversion	- Uses mouths rather than eyes - No whole-part advantage	Yes	No	- Busigny et al. 2010 - Busigny et al., 2010 - Caldara et al., 2005 - Ramon et al., 2010 - Rossion et al., 2003 - Schiltz et al., 2006 - Sorger et al., 2007 - Steeves et al. (2009)
Galen	R Temp L R m Occip L R Parahip G R Fusiform G R FFA R OFA	No face inversion		Yes		- Susilo et al. (2013)

Name AP	Lesion Site	Abnormal Face Inversion Effect or Impaired Configural Processing	Whole-Part Processing or Part Processing Ability	Face Memory Impairment	Emotion Recognition Impairment	References
AP cases with intact object matching ability						
Florence R-AT1	R Ant Temp L Hippocampus Amygdala	No face inversion		Yes	No	- Fox et al. (2011) - Susilo et al. (2013)
GG	R Occip L R Fusiform G R Parahip G R Occip-Temp C	No face inversion	- Impaired eye, not mouth, processing - No part-to-whole advantage	Yes		- Van Belle et al. (2011) - Busigny et al. (2010)
FB	R Fusiform G R Inf Temp G R mTemp G R Inf Occip G	No face inversion		Yes	No	- Riddoch, Johnston, Bracewell, Boutsen, and Humphreys (2008)
RC	R Temp L R STS R Ant Inf Front G R (Pre)motor A	No face inversion	Impaired by whole in part processing	Yes		- Wilkinson et al. (2009)
RP	Close head injury. No discernable lesion visible	Paradoxical Face Inversion	Impaired by whole in part matching			- de Gelder and Rouw (2000a) - Rouw and de Gelder (2002)
KC Patient 5 Patient 4	R mOccip Temp L R FFA	Paradoxical Face Inversion	Impaired by whole in part matching		No	- de Gelder et al. (2003) - Barton et al. (2001) - Barton et al. (2002)
MK	R Vent Occip Temp C R Fusiform Gyrus	Paradoxical Face Inversion	Impaired by whole in part matching		No	- de Gelder et al. (2003)

Table 1. Acquired prosopagnosia cases, lesion locations and summary of configural processing, whole-to-part or featural processing, face memory and emotion recognition ability, sorted by object recognition and configural processing ability.

In this dissertation, results are presented on (emotional) face memory, face and object recognition ability and configural processing in a new case of acquired prosopagnosia due to bilateral loss of the fusiform gyrus, but with normal activity in the right OFA and STS. Also, we assess the APs facial expression recognition abilities. As the expression of facial emotion is inextricably linked to the face, there has been a debate on whether the mechanisms for the recognition of facial identity and facial expression are separate (Bruce & Young, 1986; Haxby et al., 2000) or if this is too simple a representation (Calder & Young, 2005). In addition, we tested whether the AP is normally able to recognize bodily expression and integrate facial and bodily expressions.

Developmental prosopagnosia

In contrast with prosopagnosia caused by acquired brain damage or congenital brain abnormalities, there is increasing evidence for the occurrence of face recognition disorders without clear evidence of brain damage. The term developmental prosopagnosia (DP) was coined in order to stress that this disorder is most likely a result of a failure to acquire normal face recognition skills in the course of otherwise normal cognitive development and for reasons still very poorly understood.

Firstly, on the issue of face specificity, again the literature reveals that some DP individuals exhibit deficits in within-class object recognition (Behrmann, Avidan, Marotta, & Kimchi, 2005; Duchaine, Germine, & Nakayama, 2007a; Duchaine & Nakayama, 2005; Garrido, Duchaine, & Nakayama, 2008), whereas others do not (Duchaine, 2006; Duchaine, Dingle, Butterworth, & Nakayama, 2004; Lee, Duchaine, Wilson, & Nakayama, 2010; Nunn, Postma, & Pearson, 2001; Palermo et al., 2011; Yovel & Duchaine, 2006). Secondly, again similarly to the AP literature, a major focus to date is whether there is a deficit in configural perception in DP and whether this is associated with or compensated for by more than average skill at feature processing. Impaired configural processing has often been found in DP (Avidan, Tanzer, & Behrmann, 2011; Behrmann et al., 2005; Daini, Comparetti, & Ricciardelli, 2014; Duchaine, Yovel, Butterworth, & Nakayama, 2006; Duchaine, Yovel, & Nakayama, 2007b; Huis in 't Veld, van den Stock, & de Gelder, 2012; Palermo et al., 2011; Righart & de Gelder, 2007; Rivolta, Schmalzl, Coltheart, & Palermo, 2010; Rouw & de Gelder, 2002), but not always (de Gelder & Rouw, 2000a; Susilo et al., 2010).

The absence of lesions makes the DP group a bit more difficult to study. In recent years, brain imaging has been a powerful research tool for face perception researchers, but functional magnetic resonance imaging (fMRI) investigations have not yet yielded a clear picture on how the areas and networks normally related to face processing function in people with developmental prosopagnosia. Some studies find normal face-specific activations (Avidan, Hasson, Malach, & Behrmann, 2005; Avidan et al., 2014; Hasson, Avidan, Deouell, Bentin, & Malach, 2003; Marotta et al., 2001; Williams, Berberovic, & Mattingley, 2007; Zhang, Liu, & Xu, 2015) or normal activity within the putative face recognition network but abnormal activation in the extended networks (Avidan & Behrmann, 2009; Avidan et al., 2014). However, many studies find reduced activation or an absence of face specificity or adaptation in the FFA (Avidan & Behrmann, 2009; Bentin, Degutis, D'Esposito, & Robertson, 2007; DeGutis, Bentin, Robertson, & D'Esposito, 2007; Dinkelacker et al., 2011; Furl, Garrido, Dolan, Driver, & Duchaine, 2011, 2011b; Hadjikhani & de Gelder, 2002; Minnebusch, Suchan, Koster, & Daum, 2009; Williams et al., 2007). In addition, other possible neurological explanations have been suggested. For example, diminished cortical grey matter volume (Dinkelacker et al., 2011; Garrido et al., 2009), disrupted connectivity (Thomas et al., 2009) or cerebellar hypoplasia (van den Stock, Vandenbulcke, Zhu, Hadjikhani, & de Gelder, 2012) may be held accountable. Furthermore, research on hereditary disorders and (neuro)genetics may give rise to further explanations on how this developmental process may go astray (Grueter et al., 2007; Johnen et al., 2014; Kennerknecht, Kischka, Stemper, Elze, & Stollhoff, 2011).

To take matters a step further, can research provide evidence for dissociation between face identity and emotion recognition by studying prosopagnosia? And if not,

to what extent does the processing of facial identity and emotional expression overlap, and can emotional expression as a context be beneficial for face identity recognition in prosopagnosia? Of particular interest is the finding of van den Stock, van de Riet, Righart, and de Gelder (2008), who found more FFA activity in controls than DPs for neutral faces, but similar activity levels between the groups for happy and fearful faces. Also, there is accumulating evidence indicating that face recognition is sensitive to contextual influences such as facial and bodily expressions (de Gelder et al., 2006; de Gelder & van den Stock, 2011b). Some of the questions addressed in this dissertation regard the ability of both individuals with acquired and developmental to recognize emotion, and whether emotional expressions in faces and bodies can benefit their face identity processing.

But first, let us turn to the question of what happens in our own bodies when we perceive fear or anger in others.

Part II: The perception of natural, emotional social interactions.

Faces, bodies and voices are the major sources of social and emotional information and as such have dominated research. Recently, it has been argued that social interactions should be studied more predominantly in neuroscience (Schilbach et al., 2013). Faces especially have always been one of the main focuses in neuropsychological research. This is not just limited to facial identity recognition studies or to which brain networks are responsible for processing the perception of emotional facial expressions; there is a vast amount of research on how humans perceive and express facial expressions. Some of this work resulted in the creation of The Facial Action Coding System (FACS) which extensively describes which facial muscles are recruited for expressing emotion (Ekman & Friesen, 1978). The creation of the FACS has proved to be a valuable tool for a wide range of research applications. Using the FACS and electromyography recordings (EMG), many studies have examined conscious and unconscious facial responses to emotional faces (Dimberg, 1990, see Hess and Fischer, 2013 for a review).

Interestingly, using the FACS, it was found that muscles used for expressing a certain emotion also respond to the perception of that same emotion. For example, a smile recruits the zygomaticus major in the cheek and a frown the corrugator supercilii in the brow, and these muscles are also activated by the perception of the same emotion that they help express, an automatic process that can be measured using electromyography (Dimberg & Thunberg, 1998). Even though this finding suggests that we imitate what we see, this process also occurs when stimuli are processed

without visual awareness, and in response to non-face stimuli such as bodily expressions or vocalizations (Bradley & Lang, 2000; Dimberg, Thunberg, & Elmehed, 2000; Grezes et al., 2013; Hietanen, Surakka, & Linnankoski, 1998; Kret, Stekelenburg, Roelofs, & de Gelder, 2013; Magnee, Stekelenburg, Kemner, & de Gelder, 2007b; Tamietto et al., 2009) and thus probably reflects more than just motor mimicry of the seen behavior. In addition, a few neuroimaging studies assessed the overlapping neural mechanisms of perceiving and imitating facial expressions or the correlations between facial muscle activity and BOLD responses. Imitating facial expressions activates the somatosensory and premotor cortices, but this activity also extends to emotion-processing regions, suggesting that imitating an expression does not merely reflect motor behavior (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Lee, Josephs, Dolan, & Critchley, 2006; Leslie, Johnson-Frey, & Grafton, 2004). More specifically, the neural correlates of automatic facial muscle responses differ per emotion, where reactions of the zygomaticus major have been found to correlate with activity in the inferior frontal gyrus, the supplementary motor area and the cerebellum, whereas corrugator supercilii activation was correlated with activity of the hippocampus, insula and superior temporal sulcus (Likowski et al., 2012).

As mentioned before, again we see that most of the literature to date has focused on the face. However, in the last decade it has become increasingly clear that bodily expressions are an equally valid means of communicating emotional information (de Gelder, 2009; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004). Bodily expressions, more so than facial expressions, quickly activate cortical networks involved in action preparation, action understanding and biological motion (Kret, Pichon, Grezes, & de Gelder, 2011), possibly more so for emotions that are negative or threatening (de Gelder et al., 2004). For example, the perception of an angry or fearful person activates networks in the brain that facilitates the perception and execution of action, such as the (pre)motor areas and the cerebellum (Grezes, Pichon, & de Gelder, 2007; Pichon, de Gelder, & Grezes, 2008, 2009, 2012).

This corroborates the idea that in daily life, expressing emotion with the body is an automatic, reflex-like behavior that is often triggered as soon as a response is required to something in the environment (Rossion, Hanseeuw, & Dricot, 2012). This is also very easy to imagine if we take social interactions again one step further, from face to body perception, to crowd perception. In day-to-day situations, one often sees a few individuals at the same time, acting either as individuals or as a group. In situations that are potentially critical it becomes very important to quickly perceive the mood of a crowd, for example when panic breaks out (Helbing, Farkas, & Vicsek, 2000). Unfortunately, research on these types of situations is scarce.

In short, as the body and social interactions have been neglected in these lines of research, another important aim of my research has been the creation of a Body Action Coding System and the assessment of how the behavior and movements of individuals in a large group emotional people are processed by the brain, which can be found in part II of this thesis.

Outline of the thesis

In this thesis, we consider the neurological underpinnings of the processes relating to face identity and emotion recognition and social interactions, as described in the starting scenario.

Starting with the recognition of facial identity, in **chapter 2**, the experiments and results of the FEAST (Facial Expression and Action Stimulus Test) are described and normative data on these tests from a relatively large and diverse group of healthy control subjects is presented. The FEAST is a behavioral test battery developed in the lab to assess face memory, face and object processing both of wholes and parts, configural processing, and facial expression recognition in prosopagnosia. In **chapter 3 and 4**, the FEAST is used to assess face recognition processes in two groups of people suffering from longstanding face recognition deficits that to the best of our knowledge are not related to any known neurological condition: developmental prosopagnosia. Secondly, the effects of emotional context, such as facial and bodily expression, on face recognition and memory in these groups are reported. In **chapter 3** we specifically assess the effect of emotion on face memory and of emotional body language on face identity processing. In **chapter 4**, we also look at emotional face memory, but additionally explore the facial expression recognition of human and canine facial expressions in DP. Finally, in **chapter 5**, the FEAST is used to assess these processes in a new case of acquired prosopagnosia due to bilateral loss of the fusiform face area. In addition, bodily expression recognition and face and body expression integration in this case is explored.

Then we make a jump to the next step in social interaction after which the effect of whole bodily expressions and movement on the perceiver in multiple person interaction is studied. In **chapters 6 and 7**, we present the novel Body Action Coding System, which not only explores which bodily muscles are used in bodily expressions, but also the bodily muscle responses of the neck, shoulders, arms, back and legs when perceivers are confronted with angry and fearful body language. Finally, in **chapter 8**, we take a look at the cortical networks that are specifically sensitive to the motion and social interaction in large crowds, and whether this dynamic movement information is

differentially processed depending on the emotion of the crowd. See Table 2 for an overview.

	Participants	Method	Experiments	Emotion
2	Sample from general population	Behavioral testing FEAST	Neutral face memory Emotional face memory Face/Object matching Face/Object parts Facial expressions	All
3	Developmental prosopagnosia Matched controls	Behavioral testing FEAST	Neutral face memory Emotional face memory Face/Object matching Face/Object parts Face/Body compounds	All
4	Developmental prosopagnosia Matched controls	Behavioral testing FEAST	Neutral face memory Emotional face memory Face/Object whole matching Face/Object parts Facial expression	All
5	Acquired prosopagnosia 'EP' Matched controls	Behavioral testing FEAST fMRI face/body localizer	Neutral face memory Emotional face memory Face/Object matching Face/Object parts Facial expressions Bodily expressions Face/body compounds	All
6	Students	EMG	Passive viewing and active imitation of videos of bodily expressions of emotion	Fear Anger
7	Students	EMG	Passive viewing and active imitation of videos of bodily expressions of emotion	Neutral Happy Fear
8	Students	fMRI	Passive viewing of interactive of individually behaving emotional crowds	Neutral Happy Fear

Table 2. Overview of the participant samples, techniques and experiments in the dissertation.

Hypotheses

1. Subjects with acquired and developmental prosopagnosia are impaired at face, but not object processing.
2. Subjects with developmental and acquired prosopagnosia have impaired face memory as compared to a control group.
3. Configural processing is impaired in acquired and developmental prosopagnosia. More specifically, whereas healthy controls are expected to show a face inversion effect (higher accuracy on upright face recognition than inverted face recognition), subjects with acquired and developmental prosopagnosia will not be sensitive to face inversion or show a paradoxical face inversion effect.
4. Subjects with developmental and acquired prosopagnosia will be more impaired at human facial expression recognition than controls, but are not expected to have general emotion recognition problems. Therefore it is hypothesized that subjects with developmental prosopagnosia perform equally well as controls on canine expression recognition, and the acquired prosopagnosia subject is expected to perform normally on bodily expression recognition.
5. The presence of emotional context is expected to benefit face identity recognition and memory in developmental prosopagnosia
6. It is hypothesized that it is possible to measure automatic and covert bodily muscle responses caused by the perception of emotional bodily expressions in others with electromyography.
7. It is expected that the brain is sensitive to the behavior between individuals in a crowd. A group of dynamically interacting individuals will enhance activity in action perception and action preparation networks as compared to a group of individually behaving persons.
8. More specifically, we hypothesize that there will be an emotion by behavior interaction, such that action perception and execution, body motion and emotion perception networks will be specifically responsive to the more salient interactively fearful crowds than individually behaving fearful crowds and both individually/interactively happy crowds.

Part 1:

Perception of identity and emotion

**FROM INDIVIDUAL TO
CROWD PERCEPTION:
how motions and
emotions INFLUENCE
THE PERCEPTION OF
identity, social
INTERACTIONS, and
bodily MUSCLE
ACTIVATIONS.**

2 |

The Facial Expression Action Stimulus Test. A test battery for the assessment of face memory, face and object perception, configuration processing and facial expression recognition

There are many ways to assess face perception skills. In this study, we describe a novel task battery FEAST (Facial Expression Action Stimulus Test) developed to test recognition of identity and expressions of human faces as well as stimulus control categories. The FEAST consists of a neutral and emotional face memory task, a face and object identity matching task, a face and house part-to-whole matching task, and a human and animal facial expression matching task. The identity and part-to-whole matching tasks contain both upright and inverted conditions. The results provide reference data of a healthy sample of controls in two age groups for future users of the FEAST.

Adapted from:

de Gelder, B., **Huis in 't Veld**, E.M.J., & van den Stock, J. (in press). *Frontiers in Psychology: Emotion Science*.

Introduction

An important issue in prosopagnosia research is how to establish whether an individual with poor face recognition skills specifically suffers from prosopagnosia. The question of how we are able to correctly and quickly recognize so many faces has captured the interest of researchers for some time. In view of the rich information carried by the face, an assessment of specific face processing skills is crucial. Two questions are central. One, what specific dimension of facial information are we focusing on, and two, is its loss specific for faces. To date, there is no consensus or golden standard regarding the best tool and performance level that allows diagnosing individuals with face recognition complaints as having prosopagnosia. Several tests and tasks have been developed, such as the Cambridge Face Memory Test (Duchaine & Nakayama, 2006), the Benton Facial Recognition Test (Benton, Sivan, Hamsher, Varney, & Spreen, 1983), the Cambridge Face Perception Task (Dingle, Duchaine, & Nakayama, 2005), the Warrington Recognition Memory Test (Warrington, 1984) and various tests using famous faces (such as adaptations of the Bielefelder famous faces test (Fast, Fujiwara, & Markowitsch, 2008)). These each provide a measure or a set of measures relating to particular face processing abilities, e.g. matching facial identities or rely on memory for facial identities which is exactly what is problematic in people with face recognition disorders. More generally, beyond the difference between perception and memory, there is not yet a clear understanding of how the different aspects of normal face perception are related, so testing of face skills should cast the net rather wide.

A test battery suitable for the assessment of prosopagnosia should take some additional important factors into account. Firstly, to assess the face specificity of the complaints, the test battery should include not only tasks with faces, but also an equally demanding and object control condition with control stimuli that are visually complex, that are also seen from multiple viewpoints. Secondly, an important finding classically advanced to argue for a specialization for faces regards the configural way in which we seem to process faces, so the task should enable the measurement of configural processing of faces and objects. The matter of configuration perception also has been tackled in several different ways, such as with the composite face task (Young, Hellawell, & Hay, 1987), the whole-part face superiority effect (Tanaka & Farah, 1993) or more recently, using gaze-contingency (van Belle et al., 2011). We choose to focus on the classical face inversion effect (Farah, Wilson, Drain, & Tanaka, 1995; Yin, 1969), whose simple method is well suited to study object inversion effects. Besides using the inversion effect, configuration- versus feature-based processing can also be investigated more directly by part-to-whole matching tasks (de Gelder, Frissen, Barton, & Hadjikhani, 2003). Furthermore, previous studies have found

positive relationships between the ability to process faces configurally and better face memory (DeGutis, Wilmer, Mercado, & Cohan, 2013; Huis in 't Veld, van den Stock, & de Gelder, 2012; Richler, Cheung, & Gauthier, 2011; Wang, Li, Fang, Tian, & Liu, 2012) indicating that configural processing might facilitate memory for faces.

Additionally, there is accumulating evidence in support of an interaction between face identity and face emotion processing (Chen, Lander, & Liu, 2011; van den Stock & de Gelder, 2012, 2014; van den Stock et al., 2008) and there is increasing evidence that configuration processing is positively related to emotion recognition ability (Bartlett & Searcy, 1993; Calder & Jansen, 2005; Calder, Young, Keane, & Dean, 2000; Calvo & Beltran, 2014; Durand, Gallay, Seigneuric, Robichon, & Baudouin, 2007; Mckelvie, 1995; Palermo et al., 2011; Tanaka, Kaiser, Butler, & Le Grand, 2012; White, 2000). We therefore extended our test battery with tasks targeting emotion recognition and emotion effects on face memory, by adding an emotional face memory task and a facial expression matching task. To stay with the rationale of our test that each skill tested with faces must also be tested with a selected category of control objects, we used canine face expressions.

Taking all these aspects into account, we constructed a face perception test battery named the Facial Expression Action Stimulus Test (FEAST). The FEAST is designed to provide a detailed assessment of multiple aspects of face recognition ability. Most of the subtests have been extensively described and validated on the occasion of prosopagnosia case reports and small group studies (de Gelder, Bachoud-Levi, & Degos, 1998; de Gelder et al., 2003; de Gelder, Pourtois, Vroomen, & Bachoud-Levi, 2000; de Gelder & Rouw, 2000a, 2000b, 2000c, 2001; de Gelder & Stekelenburg, 2005; Hadjikhani & de Gelder, 2002; Huis in 't Veld et al., 2012; Righart & de Gelder, 2007; van den Stock, de Gelder, de Winter, van Laere, & Vandenbulcke, 2012; 2013; van den Stock et al., 2008). So far the test battery was not presented systematically as it had not been tested on a large sample of participants receiving the full list of subtests. Here, we report a new set of normative data for the finalized version of the FEAST, analyse the underlying relationships of the tasks, and freely provide the data and stimulus set to the research community for scientific purposes.

Method

Subjects

The participants were recruited between 2012 and 2015 from acquaintances of lab members and research students. Participation was voluntarily and no monetary

reward was offered. The following inclusion criteria were applied: right-handed, minimally 18 years old, normal or corrected-to-normal vision and normal basic visual functions as assessed by the Birmingham Object Recognition Battery (line length, size, orientation, gap, minimal feature match, foreshortened view and object decision) (Riddoch & Humphreys, 1992). A history of psychiatric or neurological problems, as well as any other medical condition or medication use which would impair participation or the results, or history of a concussion, were exclusion criteria. This study was carried out in accordance with the recommendations and guidelines of the Maastricht University ethics committee, the 'Ethische Commissie Psychologie' (ECP). The protocol was approved by the Maastricht University ethics committee (ECP-number: ECP-128 12_05_2013).

In total, 61 people participated in the study. Three subjects were 80, 81 and 82 years old. Even though they adhered to every inclusion criteria, they were also excluded from the analyses due to being outliers on age (more than 2 standard deviations from the mean). The sample thus consisted of 58 participants, between 18 and 62 years old ($M = 38$, $SD = 15$). Of those, 26 are male, between 19 and 60 years old ($M = 38$, $SD = 15$) and 32 women between 18 and 62 years old ($M = 39$, $SD = 16$). There are no differences in age between the genders ($t(1,56) = -0.474$, $p = .638$).

However, an age distribution plot (see Figure 1) reveals a gap, where there are only 6 participants between 35 and 49. Therefore, the sample is split in two: one "young adult" group, younger than 42 and a "middle aged" group of participants between 47 and 62 years old. The young adult age group consisted of 15 men between 19 and 37 years old, ($M = 26$, $SD = 6$) and 17 women between 18 and 41 years old ($M = 26$, $SD = 8$). The middle aged group consisted of 11 men between 47 and 60 years old ($M = 53$, $SD = 4$) and 15 women between 50 and 62 years old ($M = 55$, $SD = 3$).

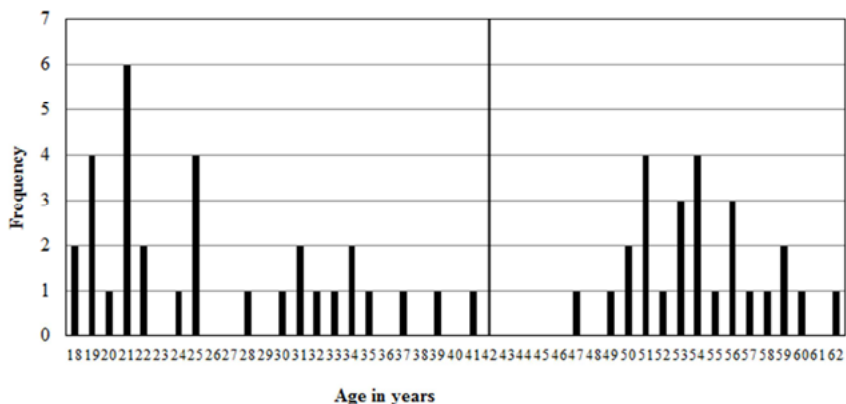


Figure 1. Age distribution of the sample with the young adult group between 18 and 41 years old, and a middle aged group between 47 and 62 years old.

Experimental stimuli and design

The face and shoe identity matching task, face and house part-to-whole matching task, Neutral and Emotion Face Memory task (FaMe-N and FaMe-E) have been previously described including figures of trial examples (Huis in 't Veld et al., 2012).

Face and shoe identity matching task and the inversion effect

The face and shoe identity-matching task (de Gelder et al., 1998; de Gelder & Bertelson, 2009) was used to assess identity recognition and the inversion effect for faces and objects. The test contained 4 conditions with a 2 category (faces and shoes) x 2 orientation (upright and inverted) factorial design. The materials consisted of greyscale photographs of shoes (8 unique shoes) and faces (4 male, 4 female; neutral facial expression) with frontal view and $\frac{3}{4}$ profile view. A stimulus contained three pictures: one frontal view picture on top and two $\frac{3}{4}$ profile view pictures underneath. One of the two bottom pictures (target) was of the same identity as the one on top (sample) and the other was a distracter. The target and distracter pictures of the faces were matched for gender and hairstyle. Each stimulus was presented for 750 ms and participants were instructed to indicate by a button press which of the two bottom pictures represented the same exemplar as the one on top. Participants were instructed to answer as quickly but also as accurately as possible, and responses during stimulus presentation were possible. Following the response, a black screen with a fixation cross was shown for a variable duration (800-1300 ms). The experiment consisted of four blocks (one block per condition). In each block, 16 stimuli were presented 4 times in a randomized order, adding up to a total of 64 trials per block. Each block was preceded by 4 practice trials, during which the participants received feedback about their response. See Figure 2.

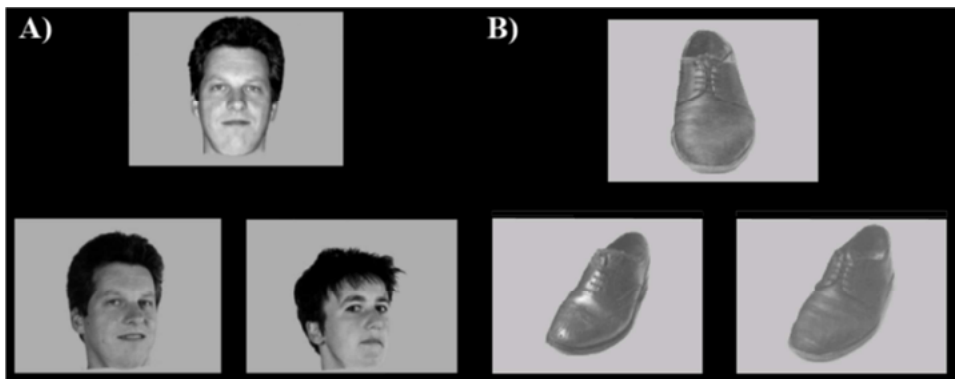


Figure 2. Stimulus examples of A) upright faces and B) upright shoes trial in the face and shoe identity matching task.

Face and house part-to-whole matching task

This task is developed to assess holistic processing. The test also consisted of 4 conditions, with a 2 category (faces and houses) x 2 orientation (upright and inverted) factorial design. Materials consisted of greyscale pictures of eight faces (four male; neutral facial expression, photographed in front view and with direct gaze) and eight houses. From each face, part-stimuli were constructed by extracting the rectangle containing the eyes and the rectangle containing the mouth. House-part stimuli were created using a similar procedure, but the parts consisted of the door or window. The trial procedure was similar to the faces and object matching task, where a whole face or house was presented on top (sample), with a target part-picture and a distractor part-picture presented underneath. Each trial was presented for 750 ms and participants were instructed to indicate by a button press which of the two bottom pictures represented the same exemplar as the one on top. Participants were instructed to answer as quickly but also as accurately as possible, and responses during stimulus presentation were possible. Following the response, a black screen with a fixation cross was shown for a variable duration (800-1300 ms). The experiment consisted of eight blocks (two blocks per condition). In each block, 16 stimuli were presented 2 times in a randomized order, adding up to a total of 32 trials per block and 64 trials per condition. Within blocks, the presentation of the two parts (eyes or mouth, window or door) was randomized in order to prevent participants to pay attention only to one specific feature. The first block of each condition was preceded by 4 practice trials, during which the participants received feedback about their response. See Figure 3.

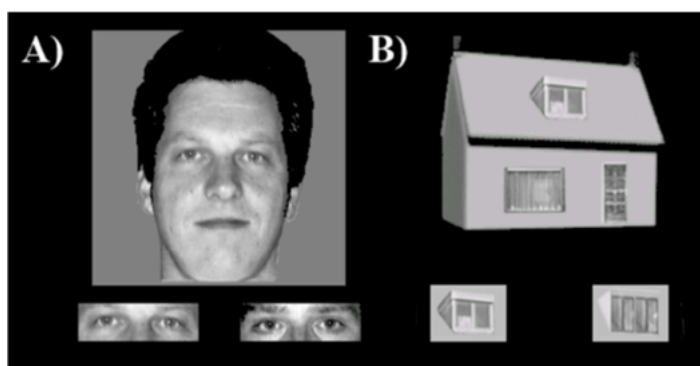


Figure 3. Stimulus examples of an A) upright face and eyes and B) upright house and windows trial in the face and house part-to-whole matching task.

Facial Expression Matching Task (FEM-H and FEM-C)

The FEM is a match-to-sample task used to measure emotion recognition ability in both human and canine faces. The experiment was divided into two parts. The first part consisted of human facial expressions (anger, fear, happy, sad, surprise, disgust). The materials consisted of greyscale photographs of facial expressions of 34 female identities and 35 male identities taken from the Karolinska Directed Emotional Faces (KDEF) (Lundqvist, Flykt, & Öhman, 1998). A trial consisted of three pictures: one picture on top (sample) and two pictures underneath. One of the two bottom pictures showed a face expressing the same emotion as the sample, the other was a distracter. The target and distracter pictures of the faces were matched for gender for the human stimuli. Each trial was presented until a response was given, but participants were instructed to answer as quickly and accurately as possible. Following the response, a black screen with a fixation cross was shown for a variable duration (800-1300 ms). Each emotional condition contained 10 trials (5 male) in which the target emotion was paired with a distracter from each of the other emotions once per gender, resulting in 60 trials in total. The first part was preceded by 4 practice trials, during which the participants received feedback about their response.

The second part consisted of canine facial expressions. In total, 114 pictures of dogs which could be perceived as angry (17), fearful (27), happy (17), neutral (29) and sad (24) were taken from the internet by EH. These pictures were validated in a pilot study using 28 students of Tilburg University in exchange for course credit. The participants indicated of each photo whether they thought the dog was expressing anger, fear, happiness, sadness or no emotion in particular (neutral). Twelve angry, 12 fearful and 12 happy canine expressions were accurately recognized by more than 80% of the participants and used in the experiment. The canine part consisted of 72 trials in total, 24 per emotion condition, in which each target emotion was paired with each of the distracter emotion 12 times. The experiment was preceded by 2 practice trials, during which the participants received feedback about their response. See Figure 4.

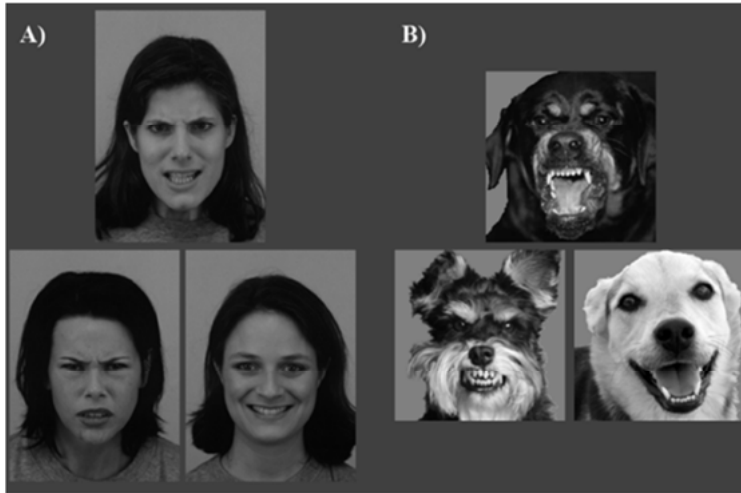


Figure 4. Example stimulus of the Facial Expression Matching Task with an angry target and happy distracter stimulus trial for the A) human and B) canine experiment.

Neutral Face Memory task (FaMe-N)

Based on the Recognition Memory Test (Warrington, 1984), the FaMe-N consists of an encoding and a recognition phase. The stimuli consist of 100 grayscale Caucasian faces (50 male) with a neutral facial expression, in front view, with frontal eye gaze. The stimuli were taken from a database created at Tilburg University. Trials in the encoding phase consisted of the presentation of a single stimulus for 3000 ms, followed by a black screen with a white fixation cross with a duration of 1000 ms. Participants were instructed to encode each face carefully and told that their memory for the faces would be tested afterwards. The encoding block consisted of 50 trials.

The recognition phase immediately followed upon the encoding phase. A trial in the recognition phase consisted of the simultaneous presentation of two adjacent faces. One was the target face and was also presented in the encoding phase. The other face was not previously presented in the encoding phase and served as distracter. Fifty trials were randomly presented and target and distracter presentation side were evenly distributed. Participants were instructed to indicate as quickly and also as accurately as possible which face they had seen in the encoding phase. The stimulus pairs were matched for gender and hairstyle.

Emotional Face Memory task (FaMe-E)

This task was designed by adapting the FaMe-N task by using stimuli containing emotional instead of neutral faces. Images were taken from the NimStim database (Tottenham et al., 2009) and stimuli created at Tilburg University. The stimuli

consisted of 96 photographs (53 female) with direct eye gaze and frontal view. The individuals in the stimuli express fear, sadness, or happiness. There was no overlap in identities with the FaMe-N. The procedure was similar to the FaMe-N, but with 48 trials (16 per emotion) in both phases. The pictures making a stimulus pair were matched for emotion and hairstyle and in most trials also gender. See Figure 5.

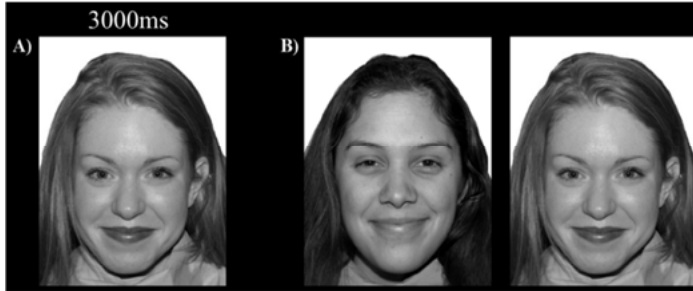


Figure 5. Example stimulus of a happy face presentation in the encoding phase (A) and a happy distractor (left) and happy target (right) in the recollection phase.

Analyses

Accuracies were calculated as the total proportion of correct responses for both the total score of each task and for each condition separately. Average response times from stimulus onset were calculated from the correct responses only. For all tasks, reaction times faster than 150 ms were excluded from analyses. In addition, for the identity matching task and part-to-whole matching task, reaction times longer than 3000 ms were excluded from analyses. For the other tasks, reaction times longer than 5000 ms were excluded from analyses. The number of outliers is reported in the results. One control subject did not complete the face and house part to whole matching task.

In addition, the internal consistency of the trials in the tasks are assessed with the Kuder Richardson coefficient of reliability (KR 20), reported as ρ_{KR20} , which is analogous to Cronbach's alpha but suitable for dichotomous measures (Kuder & Richardson, 1937).

The results were analysed using repeated measures GLMs, with the experimental factors as within subject variables and age group and gender as between subject variables. Interaction effects were further explored using post-hoc paired samples t-tests. The assumption of equality of error variances was checked with a Levene's test. The assumption of normality was not formally tested; as the sample is larger than 30 and repeated measures GLMs are quite robust against violations of normality.

Inversion scores were calculated by subtracting the accuracy and reaction time scores on the inverted face condition from the upright condition. A positive score indicates that accuracy was higher, or the reaction time was longer, on the upright condition. A negative score indicates higher accuracy or reaction times for the inverted condition. To assess whether a stronger configuration processing as measured by a higher accuracy inversion effect is related to improved face memory and emotion recognition, multiple linear regression analyses were performed with accuracy scores on the FaMe-N, FaMe-E and both FEM tasks as dependent variable and age, gender, and four inversion scores (face identity, shoe identity, face-part and house-part) as predictors. In addition, correlations between all tasks were calculated.

Lastly, percentile ranks of all tasks and correlations between all tasks were calculated and reported for both the accuracy scores and reaction times (see Tables 8 to 11).

Results

Face and shoe identity matching task

The task has a good internal consistency of $\rho_{KR20} = 0.912$. The following number of outliers were discarded; upright faces: a total of 0.86% outliers across ten participants ($M = 3.2$ trials, $SD = 2.7$, $min = 1$, $max = 8$); inverted faces: 0.7% across ten participants ($M = 2.6$ trials, $SD = 2.7$, $min = 1$, $max = 10$); upright shoes: 0.9% across 15 participants ($M = 2.1$ trials, $SD = 2$, $min = 1$, $max = 7$) and inverted shoes: 0.5% across four participants ($M = 4.8$ trials, $SD = 5.7$, $min = 1$, $max = 13$).

A repeated measures GLM on accuracy scores with category (faces, shoes) and orientation (upright, inverted) as within-subject factors and gender and age group as between-subject factors revealed a category by orientation interaction effect ($F(1,54) = 16.955$, $p < .001$, $\eta^2_p = .24$). Paired samples t-tests show that upright faces are recognized more accurately than inverted faces ($t(57) = 3.464$, $p = .001$) and inverted shoes are recognized better than upright shoes ($t(57) = -2.254$, $p = .028$). Also, the middle aged group is less accurate overall ($F(1,54) = 4.342$, $p = .042$, $\eta^2_p = .07$).

A repeated measures GLM with a similar design on reaction times showed that faces are matched slower than shoes ($F(1,54) = 16.063$, $p < .001$, $\eta^2_p = .23$), upright faces and shoes are matched slower than inverted ones ($F(1,54) = 7.560$, $p = .008$, $\eta^2_p = .12$) and the middle aged group responded slower ($F(1,54) = 15.174$, $p < .001$, $\eta^2_p = .22$). See Figure 7 and Table 1.

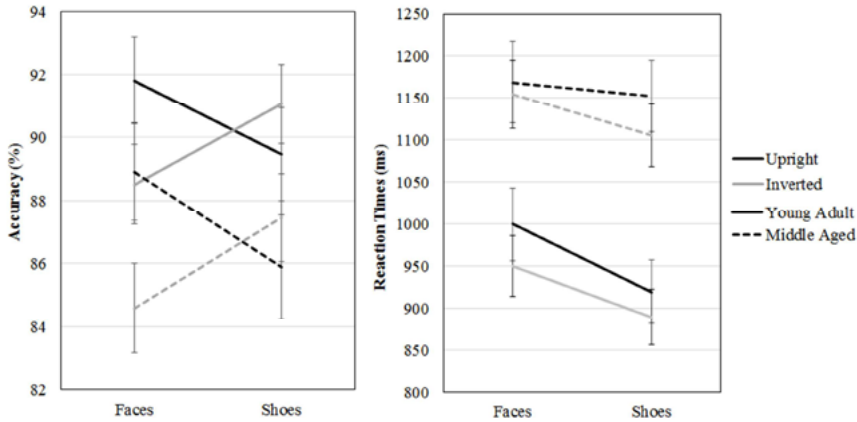


Figure 7. Means and standard errors of the mean of the accuracy and reaction times on the face and shoe matching task, split by age group.

		Young Adult		Middle Aged	
Accuracy		M (%)	SD	M (%)	SD
Faces	Upright	92	7	89	9
	Inverted	89	8	85	8
Shoes	Upright	89	7	86	7
	Inverted	91	7	88	8
Reaction Times (ms)		M	SD	M	SD
Faces	Upright	999	202	1162	280
	Inverted	951	202	1146	225
Shoes	Upright	920	175	1147	231
	Inverted	891	177	1100	201

Table 1. Means and standard deviations on the face and shoe matching task by age group.

Face and house part-to-whole matching task

The task has a good internal consistency of $\rho_{KR20} = .865$. The following number of outliers were discarded; upright face parts: a total of 1.02% outliers across 38 participants ($M = 2.7$ trials, $SD = 2.2$, $min = 1$, $max = 8$); inverted face parts: 1.1% across 41 participants ($M = 3.2$ trials, $SD = 3.2$, $min = 1$, $max = 13$); upright house parts: 1.5% across 54 participants ($M = 2.5$ trials, $SD = 2.8$, $min = 1$, $max = 12$) and inverted house parts: 0.9% across 33 participants ($M = 2.2$ trials, $SD = 1.6$, $min = 1$, $max = 6$).

A repeated measures GLM on accuracy scores with category (faces, houses) and orientation (upright, inverted) as within-subject factors and gender and age group as between-subject factors revealed a three way age group by category by orientation interaction effect ($F(1,53) = 5.413, p = .024, \eta^2_p = .09$). Overall, both age groups are better at part to whole matching of houses ($F(1,53) = 153.660, p < .001, \eta^2_p = .75$). However, the young adult group is more accurately able to part to whole match upright than inverted faces ($t(31) = 5.369, p < .001$), whereas the middle aged group is not ($t(24) = 0.952, p = .351$), but no such group differences are found for house inversion (young adult group: $t(31) = -0.958, p = .345$, middle aged group: $t(24) = -0.490, p = .628$).

The same repeated measures GLM on reaction times revealed a three way gender by age group by category interaction effect ($F(1,53) = 5.539, p = .022, \eta^2_p = .10$). To assess this effect, the repeated measures GLM with category (faces, houses) and orientation (upright, inverted) as within-subject factors and age group as between-subject factors was run for males and females separately. For the female group, a category by age group interaction effect is found ($F(1,29) = 7.022, p = .013, \eta^2_p = .20$), whereas no significant effects were found for men. See Figure 8 and Table 2.

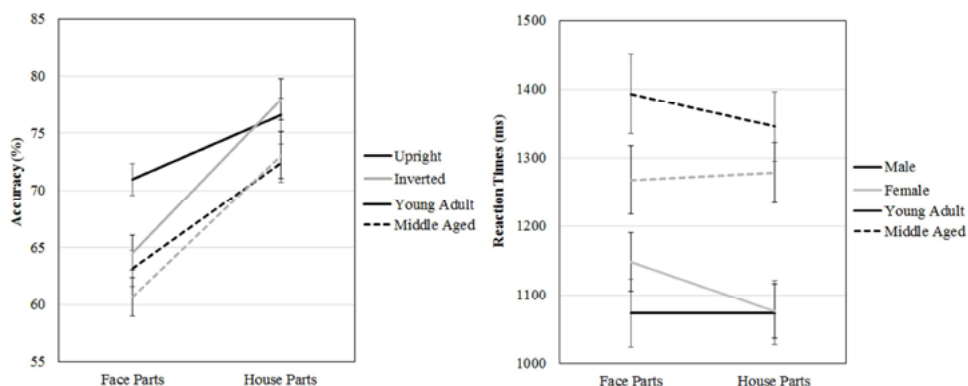


Figure 8. Means and standard errors of the mean of the accuracy and reaction times on the face and house part-to-whole matching task split by age group.

		<u>Young Adult</u>		<u>Middle Aged</u>	
Accuracy		M (%)	SD	M (%)	SD
Face Parts	Upright	71	8	63	7
	Inverted	65	9	61	7
House Parts	Upright	77	8	72	9
	Inverted	78	11	73	9
Reaction Times (ms)		M	SD	M	SD
Face Parts	Upright	1127	186	1346	218
	Inverted	1099	222	1299	215
House Parts	Upright	1104	172	1307	163
	Inverted	1046	166	1309	178

Table 2. Means and standard deviations on the face and house part-to-whole matching task by age group.

Facial Expression Matching Task

Human facial expressions (FEM-H).

The task has a reasonably good internal consistency of $\rho_{KR20} = 0.769$. The following number of outliers were discarded from 47 participants; 14% in total (Anger: 2.5%, disgust: 1.8%, fear: 3.4%, happy: 0.7%, sad: 3.5%, surprise: 2.2%, $M = 10.4$ trials, $SD = 6.6$, $min = 1$, $max = 27$).

A repeated measures GLM on the accuracy scores with emotion (fear, sadness, anger, disgust, surprise and happy) as within subject variables and gender and age group as between subject variables showed a main effect of emotion ($F(5,50) = 88.169$, $p < .001$, $\eta^2_p = .90$). Post-hoc contrasts reveal that fear is recognized least accurate, worse than sadness ($F(1,54) = 15.998$, $p < .001$, $\eta^2_p = .23$), on which accuracy rates are in turn lower than anger ($F(1,54) = 63.817$, $p < .001$, $\eta^2_p = .54$). Also, happy is recognized the best with higher accuracy scores than surprise ($F(1,54) = 49.157$, $p < .001$, $\eta^2_p = .48$).

The same repeated measures GLM revealed a main effect of emotion ($F(5,50) = 15.055$, $p < .001$, $\eta^2_p = .60$). Happy was also recognized the fastest (as compared to surprise ($F(1,54) = 7.873$, $p = .007$, $\eta^2_p = .13$) and disgust was recognized slower than anger ($F(1,54) = 7.776$, $p = .007$, $\eta^2_p = .13$). Also, the middle aged age group is slower overall ($F(1,54) = 15.280$, $p < .001$, $\eta^2_p = .22$). See Figure 9 and Table 3.

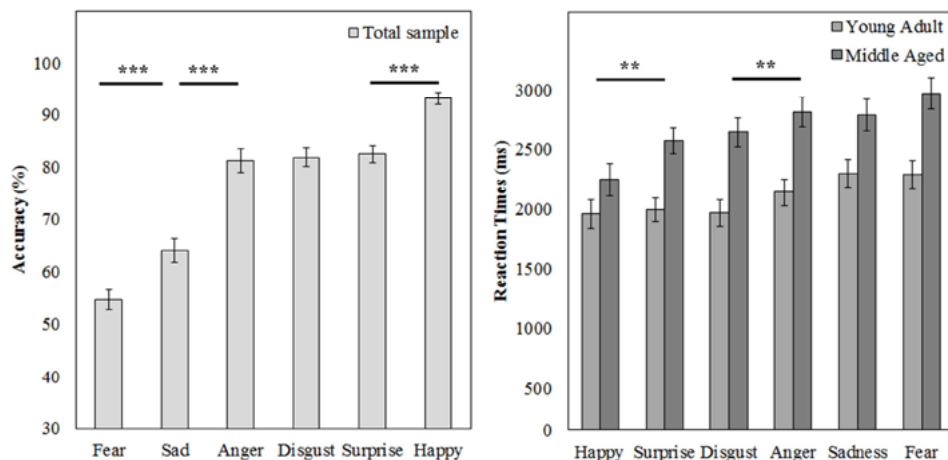


Figure 9. Means and standard errors of the mean of the accuracy of the whole group and reaction times on the FEM-H split by age group. *** $p < .001$, ** $p < .05$.

	Young Adult		Middle Aged	
	M (%)	SD	M (%)	SD
Accuracy				
Total	79	9	74	10
Anger	85	16	77	18
Fear	57	14	53	15
Happy	94	8	92	10
Disgust	82	13	82	12
Sad	69	17	59	15
Surprise	86	11	79	14
Reaction Times (ms)	M	SD	M	SD
Total	2064	583	2628	493
Anger	2122	707	2819	541
Fear	2279	674	2976	662
Happy	1941	727	2253	647
Disgust	1951	627	2635	604
Sad	2276	733	2776	586
Surprise	1976	551	2574	598

Table 3. Means and standard deviations on the FEM-H by age group.

Canine facial expressions (FEM-C).

The task has a good internal consistency of $\rho_{KR20} = 0.847$. From 35 participants, 5.3% of the trials were discarded (Anger: 1.1%, fear: 2.8%, happy: 1.4%, $M = 6.3$ trials, $SD = 4.9$, $min = 1$, $max = 22$).

A repeated measures GLM on the accuracy scores with emotion (fear, anger and happy) as within subject variables and gender and age group as between subject variables revealed a main effect of emotion ($F(2,53) = 37.049, p < .001, \eta^2_p = .58$). Fear was recognized least accurately (as compared to happy, $F(1,54) = 65.310, p < .001, \eta^2_p = .55$). Also, the middle aged group was less accurate at this task than the young adult group ($F(1,54) = 8.045, p = .006, \eta^2_p = .13$).

Similarly, for reaction times a main effect of emotion ($F(2,53) = 66.335, p < .001, \eta^2_p = .72$); anger is recognized quicker than happy ($F(1,54) = 74.880, p < .001, \eta^2_p = .58$), which is in turn recognized a faster than fear ($F(1,54) = 17.588, p < .001, \eta^2_p = .25$). Additionally, again the middle aged group is slower overall ($F(1,54) = 19.817, p < .001, \eta^2_p = .27$). See Figure 10 and Table 4.

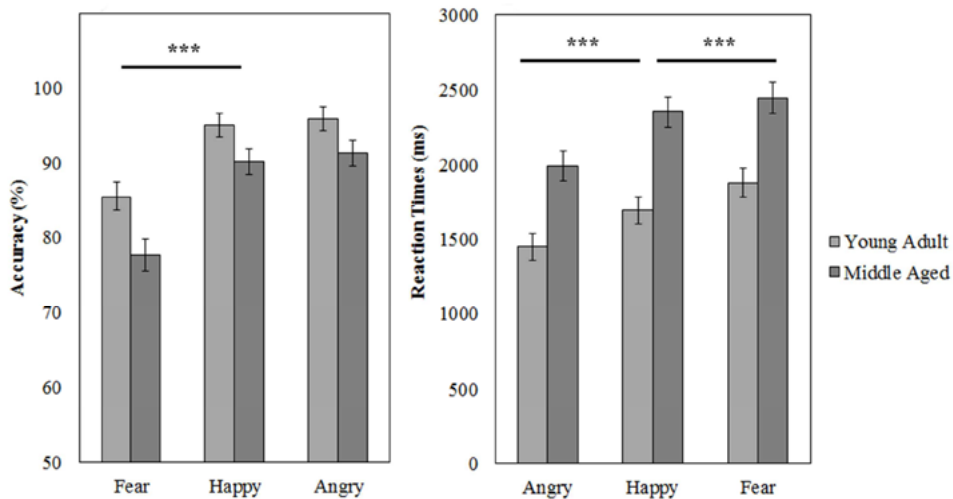


Figure 10. Means and standard errors of the mean of the accuracy and reaction times on the FEM-Canine split by age group. *** $p < .001$.

	Young Adult		Middle Aged	
Accuracy	M (%)	SD	M (%)	SD
Total	92	8	86	7
Anger	96	8	91	9
Happy	86	11	77	11
Fear	95	9	90	9
Reaction Times (ms)	M	SD	M	SD
Total	2064	583	2628	493
Anger	1446	532	1998	440
Happy	1874	613	2455	392
Fear	1683	571	2351	465

Table 4. Means and standard deviations on the FEM-C by age group.

Neutral Face Memory task (FaMe-N)

The task has a good internal consistency of $\rho_{KR20} = 0.808$. In total 232 trials (8%) were outliers across 50 participants ($M = 4.6$, $SD = 4.5$, $min = 1$, $max = 24$).

The participants scored on average 78% correct ($SD = 12\%$) on the FaMe-N. No differences in accuracy scores on the FaMe-N are found for gender ($F(1,54) = 0.238$, $p = .628$, $\eta^2_p = .004$) or age group ($F(1,54) = 0.469$, $p = .496$, $\eta^2_p = .009$), nor is there any interaction effect.

Also, the average reaction time was 2121 ms ($SD = 501$) no difference in reaction times were found for gender ($F(1,54) = 0.211$, $p = .648$, $\eta^2_p = .004$) but the effect of age group was near significance ($F(1,54) = 3.768$, $p = .057$, $\eta^2_p = .065$). See Figure 11 and Table 5.

Emotional Face Memory task (FaMe-E)

The task has a good internal consistency of $\rho_{KR20} = 0.799$. In total 125 trials (4,5%) were outliers across 34 participants ($M = 3.7$, $SD = 3.5$, $min = 1$, $max = 19$).

Repeated measures GLM on accuracy scores and reaction times scores with emotion (fear, happy, sad) as within-subject factors and gender and age group as between subject variables revealed no significant effects.

However, a gender by age group by emotion three-way interaction effect was found for reaction times, ($F(2,53) = 3.197$, $p = .049$, $\eta^2_p = .11$). Figure 11 shows that the pattern of results between men and women is reversed when the age groups are compared. It looks like young adult women seem quicker to recognize sadness than middle aged women: indeed, if the repeated measures is run for men and women separately, with emotion as within subject variables and age group as between, no effects of emotion or age group are found for men. However, for women, a trending emotion by age group interaction is found ($F(2,29) = 2.987$, $p = .066$, $\eta^2_p = .17$). See Figure 11 and Table 5.

In addition, we directly compared the FaMe-N and FaMe-E using a repeated measures GLM on accuracy scores and reaction times scores on the neutral, fearful, happy and sad conditions as within-subject factors and gender and age group as between subject variables, but no significant effects were found.

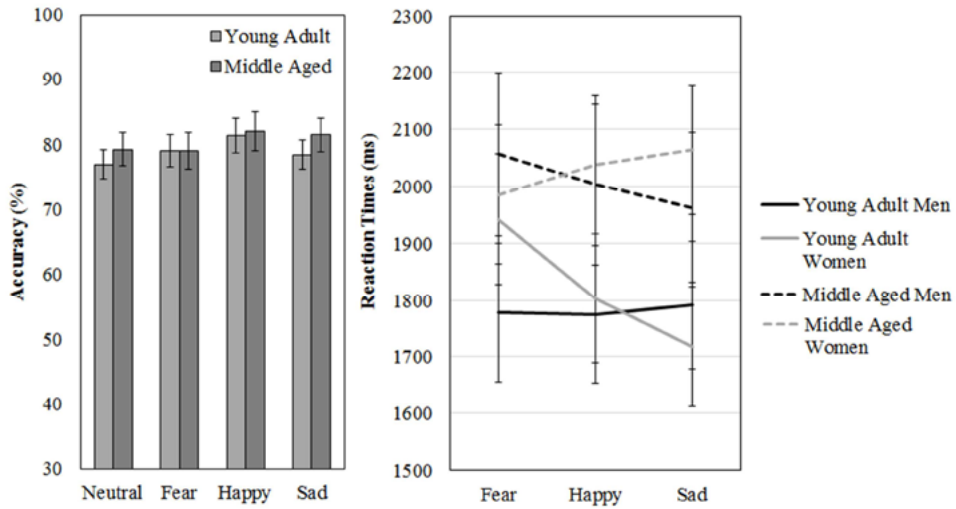


Figure 11. Means and standard errors of the mean of the A) accuracy and B) reaction times on the FaMe-N and FaMe-E. *** $p < .001$.

		Male				Female			
		Young Adult		Middle Aged		Young Adult		Middle Aged	
Accuracy (%)		M	SD	M	SD	M	SD	M	SD
FaMe-Neutral	Total	77	16	81	11	77	13	78	10
FaMe-Emotion	Total	78	14	84	7	81	11	78	15
	Fear	78	13	82	7	80	16	76	17
	Happy	80	19	86	10	83	11	78	17
	Sad	77	15	83	7	80	12	80	13
Reaction Times		M	SD	M	SD	M	SD	M	SD
FaMe-Neutral	Total	1920	532	2285	540	2090	483	2236	429
FaMe-Emotion	Total	1785	525	2007	246	1821	416	2025	430
	Fear	1778	544	2056	320	1942	540	1986	402
	Happy	1775	564	2003	275	1803	399	2038	540
	Sad	1791	514	1962	258	1718	414	2063	479

Table 5. Means and standard deviations on the FaMe-N and the FaMe-E by gender and age group.

Relationships between tasks

In the current sample, no significant predictive relationship between configuration processing as measured by the inversion effect and face memory scores were found. See Table 6.

Step 1	FaMe-N			FaMe-E		
	B	Se B	β	B	Se B	β
Constant	0.730	0.047		0.754	0.043	
Gender	-0.010	0.032	-0.039	0.003	0.029	0.013
Age	0.002	0.001	0.186	0.001	0.001	0.183
R ²	0.036			0.034		
Step 2	B	Se B	β	B	Se B	β
Constant	0.728	0.059		0.778	0.052	
Gender	-0.010	0.036	-0.040	-0.008	0.032	-0.037
Age	0.001	0.001	0.182	0.001	0.001	0.150
Face Inversion	0.001	0.003	0.034	-0.001	0.003	-0.066
Shoe Inversion	-0.001	0.005	-0.027	-0.0004	0.004	-0.014
Face Part Inversion	0.000	0.003	-0.001	-0.003	0.003	-0.142
House Part Inversion	-0.001	0.003	-0.053	-0.003	0.003	-0.153
R ² change	0.004			0.044		

Table 6. Regression coefficients of the inversion scores on the tasks for configural and feature-based processing on the total scores of the Face Memory–Neutral and the Face Memory–Emotion task.

Similarly, no significant relationship between configuration processing and emotion recognition scores were found, aside from a negative effect of age on accuracy on the FEM-H and FEM-C, see Table 7. In addition, see Tables 8 and 9 for correlations between the all the tasks and subtasks of the FEAST.

Step 1	FEM-H			FEM-C		
	B	Se B	β	B	Se B	β
Constant	0.831	0.034		0.955	0.028	
Gender	-0.003	0.023	-0.014	-0.011	0.020	-0.076
Age	-0.002	0.001	-0.264 *	-0.001	0.001	-0.261
R ²	0.07			0.034		
Step 2	B	Se B	β	B	Se B	β
Constant	0.829	0.041		0.965	0.035	
Gender	-0.003	0.026	-0.019	-0.019	0.021	-0.127
Age	-0.002	0.001	-0.255	-0.002	0.001	-0.319 *
Face Inversion	0.000	0.002	-0.024	0.001	0.002	0.091
Shoe Inversion	0.000	0.003	0.017	-0.004	0.003	-0.181
Face Part Inversion	0.000	0.002	-0.021	-0.001	0.002	-0.092
House Part Inversion	-0.004	0.002	-0.227	0.000	0.002	-0.033
R ² change	0.054			0.044		

Table 7. Regression coefficients of the inversion scores on the tasks for configural and feature-based processing on the total scores of the Facial Expression Matching- Human and Canine task.

* = $p < .05$

Furthermore, percentile ranks for accuracy scores as percentage correct and the reaction times are reported in Tables 8 and 9, and the correlations between all tasks are reported in Tables 10 and 11.

Percentile ranks young adult group									
		<u>2</u>	<u>5</u>	<u>10</u>	<u>25</u>	<u>50</u>	<u>75</u>	<u>90</u>	<u>95</u>
FaMe-N		36	43	61	72	78	86	94	99
FaMe-E		48	55	65	71	79	91	96	98
Faces	Upr	72	76	80	89	93	98	98	98
	Inv	69	69	73	85	91	95	98	99
Shoes	Upr	64	71	83	86	91	94	97	98
	Inv	73	78	81	88	92	97	98	100
Face Parts	Upr	50	54	60	66	71	78	81	86
	Inv	48	50	52	58	65	71	78	81
House Parts	Upr	59	60	65	72	78	81	88	91
	Inv	41	54	65	72	78	84	91	93
FEM-H		53	60	65	74	82	85	90	90
FEM-C		57	75	85	88	94	97	98	99
Percentile ranks middle aged group									
		<u>2</u>	<u>5</u>	<u>10</u>	<u>25</u>	<u>50</u>	<u>75</u>	<u>90</u>	<u>95</u>
FaMe-N		56	57	64	72	81	88	93	94
FaMe-E		42	47	65	77	82	90	94	96
Faces	Upr	69	70	75	82	91	95	98	99
	Inv	63	65	72	81	86	89	93	97
Shoes	Upr	69	70	75	81	88	91	94	96
	Inv	67	68	75	86	89	93	96	99
Face Parts	Upr	48	49	53	57	64	67	73	75
	Inv	44	44	50	57	61	68	70	73
House Parts	Upr	53	53	58	67	75	78	83	89
	Inv	55	57	62	66	72	79	87	90
FEM-H		50	54	63	67	73	83	87	91
FEM-C		67	70	75	83	88	92	94	97

Table 8. Percentile ranks corresponding to accuracy scores (as percentage correct) split by age group for all tasks and subtasks.

Percentile ranks young adult group									
		<u>2</u>	<u>5</u>	<u>10</u>	<u>25</u>	<u>50</u>	<u>75</u>	<u>90</u>	<u>95</u>
FaMe-N		1220	1248	1329	1621	1996	2329	2589	3210
FaMe-E		869	978	1097	1462	1842	2145	2505	2582
Faces	Upr	671	693	733	832	974	1112	1293	1472
	Inv	670	673	708	782	908	1068	1235	1407
Shoes	Upr	591	663	707	777	922	1049	1204	1263
	Inv	605	617	666	741	879	1010	1177	1227
Face Parts	Upr	591	718	910	1025	1130	1259	1281	1484
	Inv	481	544	909	997	1084	1230	1393	1499
House Parts	Upr	688	774	882	1001	1073	1228	1332	1445
	Inv	577	710	921	954	1023	1161	1252	1361
FEM-H		1080	1090	1169	1659	2032	2482	2769	3267
FEM-C		798	887	1123	1256	1458	2048	2581	2911
Percentile ranks middle aged group									
		<u>2</u>	<u>5</u>	<u>10</u>	<u>25</u>	<u>50</u>	<u>75</u>	<u>90</u>	<u>95</u>
FaMe-N		1380	1389	1623	1948	2142	2631	2932	3194
FaMe-E		1359	1389	1466	1803	2025	2231	2510	2787
Faces	Upr	680	735	851	985	1114	1286	1560	1903
	Inv	683	713	846	988	1116	1328	1484	1503
Shoes	Upr	667	709	822	975	1134	1310	1483	1614
	Inv	722	746	815	935	1085	1280	1378	1391
Face Parts	Upr	807	854	1026	1236	1353	1492	1648	1722
	Inv	720	783	980	1207	1319	1452	1621	1627
House Parts	Upr	985	1011	1078	1190	1355	1401	1531	1599
	Inv	1017	1018	1074	1173	1274	1469	1555	1658
FEM-H		1885	1887	1915	2212	2642	3004	3264	3640
FEM-C		1687	1688	1699	1905	2245	2603	2738	2987

Table 9. Percentile ranks corresponding to reaction times split by age group for all tasks and subtasks.

		FaMe-N	FaMe-E	Faces		Shoes		Face Parts		House Parts		FEM-H
				Upr	Inv	Upr	Inv	Upr	Inv	Upr	Inv	
FaMe-E		0.67	-									
Faces	Upr	0.24	0.41	-	-	-	-	-	-	-	-	-
	Inv	0.15	0.36	0.51	-	-	-	-	-	-	-	-
Shoes	Upr	0.20	0.23	0.60	0.61	-	-	-	-	-	-	-
	Inv	0.27	0.34	0.60	0.63	0.69	-	-	-	-	-	-
Face Parts	Upr	0.09	0.07	0.27	0.44	0.46	0.40	-	-	-	-	-
	Inv	0.15	0.25	0.46	0.47	0.48	0.56	0.50	-	-	-	-
House Parts	Upr	0.03	0.06	0.44	0.49	0.44	0.44	0.50	0.47	-	-	-
	Inv	0.06	0.17	0.48	0.60	0.52	0.50	0.65	0.63	0.64	-	-
FEM-H		0.18	0.44	0.39	0.37	0.28	0.30	0.23	0.16	0.18	0.35	-
FEM-C		0.49	0.54	0.52	0.36	0.34	0.49	0.31	0.32	0.24	0.23	0.46

Table 10. Correlation matrix between the accuracy scores on all tasks. White; $p < .01$, light grey; $p < .05$, dark grey; ns.

		FaMe-N	FaMe-E	Faces		Shoes		Face Parts		House Parts		FEM-H
				Upr	Inv	Upr	Inv	Upr	Inv	Upr	Inv	
FaMe-E		0.60	-	-	-	-	-	-	-	-	-	-
Faces	Upr	0.53	0.60	-	-	-	-	-	-	-	-	-
	Inv	0.50	0.57	0.86	-	-	-	-	-	-	-	-
Shoes	Upr	0.53	0.51	0.84	0.89	-	-	-	-	-	-	-
	Inv	0.46	0.54	0.77	0.91	0.89	-	-	-	-	-	-
Face Parts	Upr	0.39	0.50	0.63	0.71	0.70	0.76	-	-	-	-	-
	Inv	0.45	0.44	0.52	0.63	0.61	0.66	0.78	-	-	-	-
House Parts	Upr	0.42	0.54	0.68	0.74	0.74	0.77	0.85	0.74	-	-	-
	Inv	0.41	0.46	0.57	0.68	0.68	0.71	0.83	0.80	0.89	-	-
FEM-H		0.40	0.54	0.43	0.47	0.53	0.53	0.35	0.36	0.53	0.48	-
FEM-C		0.59	0.57	0.52	0.54	0.61	0.58	0.45	0.44	0.58	0.48	0.81

Table 11. Correlation matrix between the reaction times on all tasks. All correlations are significant at the $p < .01$ level.

Discussion

In this study, we provide normative data of a large group of healthy controls on several face and object recognition tasks, face memory tasks and emotion recognition tasks. The effects of gender and age were also reported, and normative data is provided. All tasks have a good internal consistency and an acceptable number of outliers.

Firstly, face and object processing and configuration processing was assessed. As expected, upright face recognition is more accurate than inverted face recognition, in line with the face inversion effect literature (Farah et al, 1995; Yin, 1969). Interestingly, even though the middle aged group was less accurate than the young

adults group, their response patterns regarding face and object inversion were comparable. As configurational processing measured by upright-inverted inversion scores was not influenced by gender or age, this is a stable effect in normal subjects. The absence of any interaction effects with age group or gender indicates that category specific configuration effects are stable across gender and between young adulthood and middle age. This implies it is a suitable index to evaluate in prosopagnosia assessment. Secondly, the face and house part to whole matching task seems to be a harder task than the whole face and shoe matching task, as indicated by overall lower accuracies. Young adults are more sensitive to inversion in this task.

Thirdly, we found that fear and sadness recognition on our FEM-H task was quite poor, but that anger, disgust, surprise and happiness were recognized above 80% accuracy. Similarly, canine emotions were recognized very well, although fear was also the worst recognized canine emotion and the older age group scored slightly worse and slower on this task, confirming that this subtest provides a good control.

Lastly, no effects of gender or age were found on neutral face memory, and participants scored quite well on the task, with an average of almost 80% correct. Similarly, no clear effects of age, gender or emotion were found on face memory as measured with the FaMe-E, except that it seems that middle aged women are slower to recognize previously seen identities when they expressed sadness. Interestingly, this is in line with the “age-related positivity effect” (Reed & Carstensen, 2012; Samanez-Larkin & Carstensen, 2011). In general, the results corroborate those from other studies on the effect of emotion on memory (Johansson, Mecklinger, & Treese, 2004), but a wide variety of results has been reported in the literature (Bate et al., 2010; D'Argembeau & van der Linden, 2011; Dobel et al., 2008; Langeslag, Morgan, Jackson, Linden, & van Strien, 2009; Liu, Chen, & Ward, 2014; Righi et al., 2012). In addition, we did not find any relationships between configuration perception and face memory. This can be due to the fact that unlike in samples with DPs and controls, there is less variability in inversion scores and memory scores (i.e. most participants will not have any configuration processing deficits similar to DPs and in contrast to DPs, most controls are not severely limited on face memory).

The results indicate that age is most likely a modulating factor when studying face and object processing, as the responses of the middle aged group is often slower. One explanation besides a general cognitive decline with age can be found in the literature on the effect of age on facial recognition, where an ‘own-age bias’ is often found (Firestone, Turk-Browne, & Ryan, 2007; He, Ebner, & Johnson, 2011; Lamont, Stewart-Williams, & Podd, 2005; Wiese, 2012). The ‘own-age bias’ in face recognition refers to the notion that individuals are more accurate at recognizing faces from individuals belonging to the age category of the observer. For instance, children are better at

recognizing child faces and adults are better at recognizing adult faces. Future researchers wishing to use the FEAST should compare the results of their participants with the appropriate age group, or should control for the effects of age or ideally, test age-matched controls. Gender on the other hand does not seem so influential, but this article provides guidelines and data for both gender and age groups regardless.

Some limitations of the FEAST should be noted. One is the lack of a non-face memory control condition using stimuli with comparable complexity. However, a recent study with a group of 16 DPs showed that only memory for faces, in contrast to hands, butterflies and chairs was impaired (Shah, Gaule, Gaigg, Bird, & Cook, 2014), so for this group this control condition might not be necessary. Also, the specific effects of all emotions, valence and arousal may be taken into account in future research. The face memory test could be complemented with the use of target and distractor images that show the face in the test phase from a different angle than in the training phase, as is done in the matching tests. In addition, the low performance on fear recognition should be assessed. In short, the FEAST provides researchers with an extensive battery for neutral and emotional face memory, whole and part-to-whole face and object matching, configural processing and emotion recognition abilities.

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Configuration perception, face memory and face context effects in developmental prosopagnosia

This study addresses two central and controversial issues in developmental prosopagnosia (DP), configuration- versus feature-based face processing and the influence of affective information from either facial or bodily expressions on face recognition. A sample of 10 DPs and 10 controls were tested with a previously developed face and object recognition and memory battery (Facial Expressive Action Stimulus Test, FEAST), a task measuring the influence of emotional faces and bodies on face identity matching (Face–Body Compound task), and an emotionally expressive face memory task (Emotional Face Memory task, FaMe-E). We show that DPs were impaired in upright, but not inverted, face matching but they performed at the level of controls on part-to-whole matching. Second, DPs showed impaired memory for both neutral and emotional faces and scored within the normal range on the Face–Body Compound task. Third, configural perception but not feature-based processing was significantly associated with memory performance. Taken together the results indicate that DPs have a deficit in configural processing at the perception stage that may underlie the memory impairment.

Adapted from:

Huis in 't Veld, E.M.J., van den Stock, J., & de Gelder, B. (2012). *Cognitive Neuropsychology*, 29, 464-481.

Introduction

As previously explained in the introduction of this dissertation, an important area of research regarding face processing in healthy people and prosopagnosia subjects revolved around the question whether we process faces as a whole and whether people can acquire prosopagnosia due to a loss of configural perception. In contrast to acquired prosopagnosia, face blindness can occur without any apparent brain damage, otherwise known as developmental prosopagnosia (DP). Also in this group, it has been quite consistently found that a configural processing ability was not only lost, but that a remnant or faulty system even impaired the use of a feature processing route (see chapter 1).

In addition, the question remains how facial and bodily expressions influence in the facial recognition and memory abilities in this group without apparent lesions. There is increasing evidence that there is no complete dissociation between processes related to perceiving facial identity and facial expression (see Calder & Young, 2005, for a review), but little is known about the role that facial and bodily expressions play in facial identity recognition. For example, the amygdala, orbitofrontal cortex, parahippocampal cortex, and lateral temporal regions may play an important role during the retrieval of faces previously seen with an emotional expression (Satterthwaite et al., 2009; Sergerie, Lepage, & Armony, 2005, 2006; Sterpenich et al., 2006). As there is accumulating evidence indicating that face recognition is sensitive to contextual influences such as facial and bodily expressions (de Gelder et al., 2006; de Gelder & van den Stock, 2011b), it is expected that the presence of an emotional expression benefits facial identity processes in DP.

Against this background, the aim of the current study is three-fold. First, data on the FEAST from a relatively large and diverse group of people suffering from longstanding face recognition deficits is presented. Secondly, the effects of emotional context (facial and bodily expressions) on face recognition and memory are assessed. Finally, the association between face recognition mechanisms at the perceptual stage with subsequent performance at the memory stage is assessed.

Method

Participants

Developmental Prosopagnosia (DP) Group

Participants were recruited between 2008 and 2012 via an announcement on our website (<http://www.tilburguniversity.edu/gezichtsblindheid>). Participants applied for participation through email or by telephone. An initial invitation letter was sent out in which the procedure and purpose of the study were explained. An appointment at Tilburg University was made when the participants consented to participate. Participants signed for informed consent. Participation was rewarded with reimbursement of travel costs and payment of €10 an hour. The total testing time was about 3 hours, divided in two or three sessions, according to the preference of the participant. Afterwards, the participants received a short written overview of the purpose of each test and their scores. The study was approved by an ethical committee. The sample used in this study consisted of 10 DPs who met the following inclusion criteria: complaints of longstanding difficulties with face recognition, normal or corrected-to-normal vision, and normal basic visual functions as assessed by the Birmingham Object Recognition Battery (line length, size, orientation, gap, minimal feature match, foreshortened view, and object decision; Ridloch & Humphreys, 1992). A history of psychiatric or neurological problems was an exclusion criterion.

This resulted in the inclusion of 9 women and 1 man between the ages of 22 and 65 years ($M = 43.3$, $SD = 15.4$). All DPs reported problems with face recognition since childhood, such as recognizing friends and family. The DPs also indicated that they had problems with watching movies due to not being able to recognize the characters. Also, they complained about frictions in personal relationships that were caused by failing to recognize familiar people and reported that they had been described as arrogant or aloof due to these problems with recognition. All DPs reported that they tried to recognize others by actively focusing on non-facial identity features, such as attributes, haircuts, the voice, mannerisms, or body posture. As a first exploration and in order to establish continuity with the literature, we assessed face recognition using the Benton Facial Recognition Test (BFRT; Benton et al., 1983). The DPs scored significantly lower on the BFRT than did the controls, $t(18) = 3.38$, $p < .01$.

Control group

The control group was recruited among the acquaintances of the lab members. The control group (not part of the sample reported in chapter 2) consisted of 4 women and 6 men between the ages of 21 and 59 years ($M = 36.4$, $SD = 13.0$) with matched

backgrounds and education levels. Participation was voluntarily, and the controls were not given a monetary reward. The control group did not differ from the DPs with regard to age, $t(18) = -1.08$.

Experimental stimuli and design

FEAST

The tasks as described in chapter 2, with exception of the FEM-H and FEM-C, were used.

Face-Body Compounds Identity matching task (FBC-i)

Pictures of facial expressions were taken from the AKDEF (Lundqvist & Litton, 1998) and from our own database. In a pilot study, the faces were randomly presented one by one on a screen and participants ($N=20$) were instructed to categorize the emotion expressed in the face in a seven alternative forced choice paradigm (anger, disgust, fear, happiness, neutral, surprise or sadness). On the basis of this pilot study, 80 fearful (40 female) and 80 neutral (40 female) facial expressions were selected, all recognized correctly by at least 75% of the participants. All the faces were photographed in front view and with direct gaze. Stimuli of whole body expressions were taken from the BEAST database and selected on the basis of a similar pilot study (de Gelder & van den Stock, 2011a). The selected stimuli displayed fearful body postures and neutral body postures. An instrumental action (pouring water in a glass) was used as neutral (not fearful) body postures, because like the fearful expressions, instrumental actions elicit movement and action representation and we wanted to control for these variables. Forty fearful (20 female) and 40 instrumental (20 female) body expressions were selected. Face-body compounds were created by carefully resizing and combining both the facial and bodily expressions. A total of 80 compound stimuli were created following a 2 face (fearful and neutral) \times 2 body (fearful and neutral) factorial procedure, resulting in 20 stimuli (10 male) per condition. Face and body were always of the same gender, but in only half of the compound stimuli the face and body expressed the same emotion. A trial consisted of one compound stimulus presented on top, and two faces presented left and right underneath. The target stimulus was the same as the face of the compound stimulus and the other a distracter matched on emotional expression as well as main visual features, such as hair colour and gender. Participants were instructed to indicate which of the two bottom faces matched the one of the compound stimulus. The stimuli were presented for 750 ms and inter stimulus interval was 2000 ms. The experiment started with two practice trials, during which the subject received feedback. See Figure 1.



Figure 1. Example of a trial of each of the four conditions of the Face-Body Compounds (FBC) matching task. A) Face fearful, Body fearful, B) Face neutral, Body fearful, C) Face fearful, Body neutral, D) Face neutral, Body neutral.

Results

See Table 1 for an overview of the Z-scores per DP, calculated with the mean and standard deviations of the control group, of the accuracy and RTs on the FEAST and the experimental tasks.

		L.F.	A.R.	P.V.	M.G.	B.B.	M.B.	B.G.	I.S.	S.T.	M.R.
		Z	Z	Z	Z	Z	Z	Z	Z	Z	Z
ACC											
	BFRT	-2.19	0.09	-0.69	-2.19	-0.99	-2.19	-1.59	-1.29	-1.29	-0.69
	FaMe-N	-1.54	-2.37	-2.37	-0.99	-1.54	-2.10	-1.54	-0.72	-0.17	-0.72
	Face matching Upr	-2.25	-5.21	-5.21	-6.06	-5.64	-1.82	-1.40	-3.94	-1.40	-5.64
	Inv	0.18	-1.62	-2.22	-2.51	-0.72	-1.62	-0.42	-2.22	-0.12	-4.31
	Shoe matching Upr	-0.06	0.77	-1.99	-1.16	0.77	-0.33	-0.61	-0.89	0.22	-0.89
	Inv	0.64	0.44	-1.37	1.05	1.25	0.44	0.04	-1.57	0.44	-0.16
	Face-PM Upr	1.53	-1.51	0.12	0.12	-0.21	-0.64	-0.86	-2.16	-0.96	-0.21
	Inv	2.40	-0.40	-0.75	0.07	-0.51	-0.40	-0.40	-0.63	-0.28	0.42
	House-PM Upr	1.14	-1.42	-0.61	-2.01	0.09	0.68	-0.02	-0.61	-0.96	-0.02
	Inv	0.95	-1.08	-0.76	-0.12	0.42	0.31	0.10	-0.65	-0.87	0.52
	FaMe-E	-1.60	-2.43	-0.77	-1.88	-3.26	-3.26	-1.33	-1.33	-0.22	0.06
	FBC-i	—	-0.49	-1.72	-1.72	0.39	-0.49	-1.72	-1.89	0.04	-0.67
		L.F.	A.R.	P.V.	M.G.	B.B.	M.B.	B.G.	I.S.	S.T.	M.R.
Reaction Times		Z	Z	Z	Z	Z	Z	Z	Z	Z	Z
	BFRT	-2.19	0.09	-0.69	-2.19	-0.99	-2.19	-1.59	-1.29	-1.29	-0.69
	FaMe-N	-1.62	1.39	-0.93	2.62	1.06	-0.03	-0.25	1.88	1.05	0.15
	Face matching Upr	1.54	3.08	-0.19	3.01	7.47	0.52	0.73	-0.86	4.14	1.44
	Inv	0.89	2.07	0.20	2.48	6.04	0.14	0.39	-0.99	4.30	0.89
	Shoe matching Upr	1.32	-0.17	1.72	0.44	1.51	0.41	0.98	2.84	5.63	1.54
	Inv	0.89	-0.32	-0.44	0.21	-0.28	-0.51	-0.09	-0.24	3.38	0.39
	Face-PM Upr	6.82	1.53	-0.60	-0.01	3.00	-0.28	-1.13	-0.78	3.49	0.97
	Inv	6.30	0.52	-0.66	0.22	1.05	-0.74	0.06	-1.49	2.70	-0.03
	House-PM Upr	3.33	0.69	-1.04	0.85	0.40	-0.27	-0.16	-0.59	1.88	-0.06
	Inv	4.01	0.49	0.29	1.04	0.20	-0.22	-0.32	-0.59	1.85	-0.28
	FaMe-E	0.25	1.23	-0.84	0.41	1.15	-1.19	-1.26	-0.09	0.78	0.14
	FBC-i	—	1.19	-0.60	1.71	1.84	0.15	-0.02	-0.76	1.94	0.99

Table 1. Z-scores of accuracy and reaction times as a function of group. Light grey: $p < .05$, Dark grey: $p < .01$.

Basic test battery (FEAST)

Neutral Face Memory task (FaMe-N)

The accuracy of the DP's was significantly lower than controls ($t(18) = 3.56, p < .01$) but there were no differences in RTs ($t(18) = -1.03, p > .05$). See Figure 2.

Emotional Face Memory task (FaMe-E)

Mean accuracies (proportion correct responses) and response times were calculated for every condition. The results are shown in Figure 2. Repeated measures ANOVA with emotion (fear, happy, sad) as within-subject factor and group (DP and control) as between-subject factor was carried out on the accuracy and response time data. This revealed for the accuracy data a main effect of group; controls had higher accuracy scores than DPs ($F(1,18) = 12.76, p < .01$). Furthermore, a main effect of emotion ($F(2,36) = 8.10, p < .001$) was found. Bonferonni corrected pair wise comparisons revealed that accuracy was significantly lower in the fear condition than the happy condition for both groups.

Repeated measures ANOVA on the RTs resulted in a trend for a group x emotion interaction effect ($F(2,17) = 3.19, p = .06$). Controls were slower than DPs in the fear condition, but faster than DPs in the happy and sad conditions. See Figure 2.

Comparing results on the FaMe-N and the FaMe-E

Additionally, separately conducted paired samples t-tests comparing RTs on the FaMe-N with the total FaMe-E revealed the DPs were slower on the FaMe-N than the total FaMe-E ($t(9) = 2.65, p < .05$), but this was not the case for the control group ($t(9) = 1.34, p > .05$).

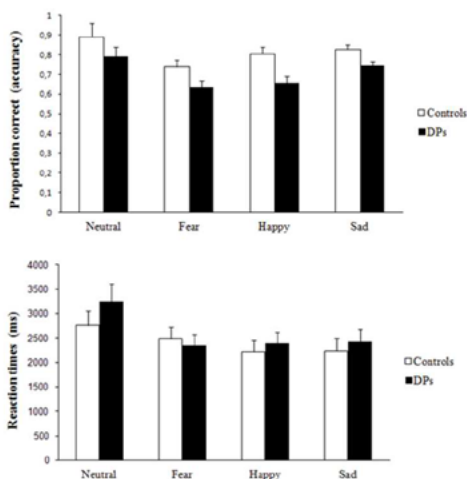


Figure 2. Accuracies and RTs on the FaMe-N and FaMe-E as a function of group and emotion.

Faces and objects matching task

Repeated measures ANOVA with category (faces and shoes) and orientation (upright and inverted) as within-subject factors and group (DP and control) as between-subject factor was carried out on the accuracy and response time data. For accuracy there was an interaction effect of group \times category ($F(1,18) = 17.68, p < .001$) and group \times orientation ($F(1,18) = 5.92, p < .05$). Post-hoc test show that the group \times category interaction was a result of a higher accuracy of controls on (upright and inverted) faces than DPs, while controls and DPs scored similarly on the (upright and inverted) shoes condition. A similar pattern explains the group \times orientation interaction; controls have higher accuracy ratings in the upright (faces and shoes) condition than DPs, however, controls and DPs scored similarly in the inverted (faces and shoes) condition.

The same repeated measures ANOVA on the RT data resulted in a group \times orientation ($F(1,18) = 25.40, p < .001$) interaction. DPs are significantly slower than controls and this lag is more pronounced when the stimuli are presented upright.

Additionally, to explicitly test the face inversion effect for faces and shoes, t-tests comparing the inversion effect (calculated by subtracting results on the inverted condition from the upright condition) were performed. DPs showed face inversion superiority ($M = -2.0, SD = 3.74$) and controls show the normal face inversion effect ($M = 1.9, SD = 1.72$), $t(18) = 2.99, p < .05$. However, no significant differences between DPs and controls were found for shoe inversion scores (DP: $M = -1.7, SD = 3.56$, Controls: $M = .40, SD = 4.06$; $t(18) = 1.23, p > .05$).

Face and house part-to-whole matching task

Repeated measures ANOVA with category (faces and houses) and orientation (upright and inverted) as within-subject factors and group (DP and control) as between-subject factor was carried out on the accuracy and response time data. This revealed for the accuracy data a category \times orientation interaction effect ($F(1,18) = 6.82, p < .05$). Accuracy scores on house-part matching were on average higher than the accuracy scores on face-part matching. However, accuracy on house-part matching was the same regardless of orientation. In contrast, accuracy decreased on inverted face-part matching compared to upright face-part matching. No significant differences were found between controls or DPs.

Repeated measures ANOVA on the RTs resulted in a main effect of category ($F(1,18) = 8.86, p < .001$); RTs were higher for face-part matching than house-part matching. T-tests comparing the inversion effects were performed, but yielded no significant results.

Face-Body Compounds (FBC) matching task

Mean accuracies (proportion correct responses) and response times from stimulus onset for the correct trials only were calculated for every condition. The results are shown in Figure 3. A repeated measures ANOVA with facial expression (fearful and neutral) and bodily expression (fearful and neutral) as within-subject factors and group (DP and control) as between-subject factor was carried out on the accuracy and response time data. This revealed for the accuracy data a main effect of group ($F(1,17) = 5.58, p < .05$); controls had higher accuracy scores than DPs overall. Also, a main effect of bodily expression ($F(1,17) = 11.46, p < .05$) was found. Accuracy was lower on conditions with a fearful body, compared to a neutral body. Further explorations comparing the scores of controls and DPs on each condition separately using t-tests show that controls had higher accuracy scores than DPs only when both the body and the face are neutral ($t(17) = 2.66, p < .05$).

For the RTs, a group \times facial expression ($F(1,17) = 7.66, p = .01$) and a trend for a facial expression \times bodily expression ($F(1,17) = 4.22, p = .056$) interaction effect were found. The group \times facial expression interaction is a result of higher RTs when the facial expression is fearful compared to neutral for the DPs, while in contrast, the RTs were the same for both conditions for the controls. The facial expression \times bodily expression effect was caused by higher RTs when both the face and bodily expression express fear.

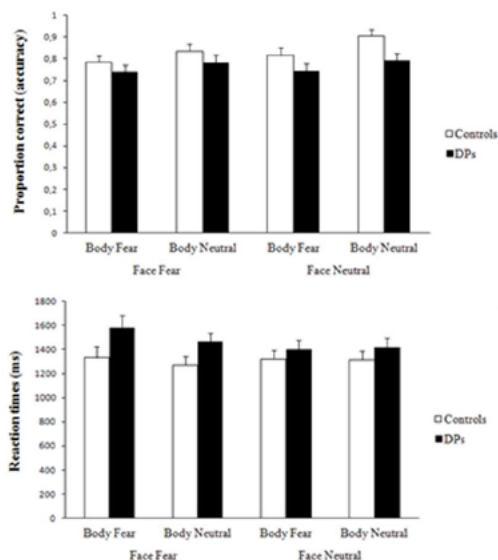


Figure 3. Accuracies and RTs on the FBC task as a function of group, facial emotion and body emotion.

The different subtests and experiments measure different aspects of face recognition. The relation between them is not yet clearly understood and calculating the relations between performances in the two groups provides useful insights in this question.

Effect of configural and feature based processing on memory task performance

In order to evaluate whether mechanisms measured at the perception stage (i.e. configural processing and feature-based processing) are predictive of memory performance, total scores on upright and inverted whole face and whole shoe matching (as measured by the faces and objects matching task) and total scores on upright and inverted face and house part-to-whole matching (as measured with the face and house part-to-whole matching task) were entered simultaneously in a regression analysis, to assess which of these predictors is significantly related to the total accuracy score on the FaMe-N. The same procedure was followed to assess the strength of association with the FaMe-E separately (see Table 2).

We observed that only the ability to match upright whole faces significantly and positively predicted face memory and this for neutral faces as well as for faces with an emotional expression.

		Face Memory–Neutral			Face Memory–Emotional		
		<i>B</i>	<i>SE B</i>	β	<i>B</i>	<i>SE B</i>	β
Face matching	Upr	0.651	0.270	0.937*	0.823	0.308	1.007*
	Inv	−0.406	0.379	−0.468	−0.849	0.433	−0.834
Shoe matching	Upr	0.616	0.373	0.514	0.532	0.426	0.377
	Inv	−0.235	0.306	−0.270	−0.401	0.350	−0.393
Face–PM	Upr	−0.052	0.157	−0.119	0.370	0.179	0.719
	Inv	0.193	0.109	0.380	0.003	0.124	0.005
House–PM	Upr	−0.189	0.124	−0.496	−0.104	0.142	−0.233
	Inv	0.067	0.198	0.129	−0.269	0.226	−0.441
		$R^2 = .58; F(8, 19) = 1.92$			$R^2 = .61; F(8, 19) = 2.11$		

Table 2. Regression coefficients of the total accuracy scores on the task conditions for configural and feature-based processing on the total accuracy scores of the FaMe-N and FaMe-E. * $p < .05$.

Relationship between the inversion effect and face memory

To further explore the relationship between the (paradoxical) inversion effect and memory performance, a score for the strength of the inversion effect for each stimulus category in both the faces and objects matching task and the face and house part-to-whole matching task was calculated by subtracting the total accuracy on the inverted condition from the upright condition. Entering these predictors simultaneously in a

linear regression model to predict the total accuracy scores on the FaMe-N and the FaMe-E separately revealed that the strength of the face inversion effect significantly predicted accuracy scores on the FaMe-E (see Table 3).

		Face Memory–Neutral			Face Memory–Emotional		
		<i>B</i>	<i>SE B</i>	β	<i>B</i>	<i>SE B</i>	β
Face matching	Upr – Inv	0.519	0.285	0.442	0.794	0.307	0.576*
Shoe matching	Upr – Inv	0.192	0.289	0.182	0.196	0.311	0.159
Face–PM	Upr – Inv	–0.091	0.096	–0.213	0.074	0.104	0.148
House–PM	Upr – Inv	–0.082	0.127	–0.164	–0.042	0.137	–0.072
		$R^2 = .30, F(4, 19) = 1.622$			$R^2 = .41, F(4, 19) = 2.64$		

Table 3. Regression coefficients of the inversion scores on the tasks for configural and feature-based processing on the total scores of the FaMe-N and FaMe-E. * $p < .05$.

Discussion

The aim of the current study was to investigate face-processing deficits of a relatively large group of DPs and to focus specifically on the relation between configural and feature-based processes tested in separate tasks of faces and objects recognition. In addition, the role of these two processes for face memory of unfamiliar faces was considered. We also took into account the possible role of affective information for face memory and studied neutral faces and facial expressions separately. Finally, the role of realistic facial and bodily expressions contexts on face recognition was assessed. In support of the notion of face specificity, we established that the DP group showed impaired ability on matching upright faces, but not objects. Most importantly, the controls showed the expected inversion effect for faces, but the DPs did not. These findings are in line with other studies showing that DPs are impaired in configural processing specifically for faces (Avidan et al., 2011; Behrmann et al., 2005), (de Gelder & Rouw, 2000a; Duchaine, 2006; Duchaine et al., 2007b; Farah et al., 1995a; Palermo et al., 2011). Furthermore, six DPs even had higher accuracy ratings on inverted faces than upright faces, a surprising pattern known as the paradoxical inversion superiority effect.

In contrast, it is worth noting that DPs are equally able as controls to match parts in the context of a whole stimulus, whether a whole face or a whole house, and this indicates a normal feature-processing ability. This latter result taken together with the inversion effect result indicates that DP is not simply a matter of a loss of configuration perception combined with an intact processing of features (de Gelder & Rouw, 2001). If that were the case, DPs would be able to apply their normal feature

perception skills to match whole faces, and their performance would be the same whether the stimulus is upright or inverted. Note that there is no difference in feature-processing ability between stimulus categories in the sense that DPs are not better than controls at feature matching, which might have been evidence for a compensation strategy for impaired configuration matching. Based on these results, we conclude that the DP group shows evidence of a specific deficit on configuration-sensitive face tasks. However, this deficit is not to be viewed as a complete loss or insensitivity to the face configuration.

The next question concerns the role of affective information in the face and the context of the body. Interestingly, when a forced-choice face-matching task is conducted, similar to that in the faces and objects matching test but with additional expressive faces and bodies, the differences in accuracy between controls and DPs are clearly less pronounced. Controls still score better at this task overall, but this is mainly due to a better performance of controls on the specific condition in which both the facial and bodily expression of the stimuli are neutral. This thus confirms the previous result of a deficit with neutral faces. But when the face or body expresses a fearful emotion, DPs perform at the level of controls, and this is even the case when the task is one of face identity matching. These findings are in line with previous reports showing that emotional information reduces the face perception impairments in both acquired and developmental prosopagnosia (de Gelder et al., 2003; van den Stock et al., 2008a). The results also indicate that controls and DPs are equally influenced in their ability to match identity when a fearful body is present. This is in line with the results from previous studies that find normal body processing in DPs (Duchaine et al., 2006; van den Stock et al., 2008), but see (Moro et al., 2012) for a report of body agnosia in a case of acquired prosopagnosia.

Finally, our assessment of memory for faces shows that DPs are significantly impaired when they are asked to remember neutral faces compared to controls, and this is in line with the results from previous studies (Duchaine et al., 2007a; Duchaine & Nakayama, 2006b; Righart & de Gelder, 2007; Stollhoff, Jost, Elze, & Kennerknecht, 2011; van den Stock et al., 2008). The DPs also score significantly worse than the controls on the emotional memory test. Furthermore, memory for faces is impaired more strongly when the face expresses emotion, especially fear. Previous studies assessing the effect of emotion on memory for faces have yielded inconsistent results. (Johansson et al., 2004) found that the discrimination between previously seen or new faces was unaffected by emotional expression and argued that valence differentially affected processes underlying recognition by familiarity and recollection. Other studies find increased accuracy for retrieving faces seen with a fearful expression (Righi et al., 2012; Sergerie et al., 2005). The pattern of responses on the RTs, however, is interesting: Emotional expression does not influence RTs for the DPs. This

contrasts with the performance of controls, who are slower than DPs when the face expresses fear, but faster when the expression is sad or happy. Additionally, DPs but not controls are overall faster in the emotional face memory task than in the neutral task. A possible explanation can be found in a neuroimaging study van den Stock (2008) showing that fusiform face area (FFA) activation in DPs was lower for neutral faces, but comparable to that in controls for emotional faces. We suggested that this increase of activation in response to emotion may result from a boost of the emotion-processing system but not specifically the face-processing system. The results of the current experiments seem to partly support this claim, as emotional expression decreased response times for DPs. However this boost of emotional expression is not associated with an increased recognition of facial identity in a memory task.

The final question concerns possible relations between the different tasks and the abilities they measure. The results indicate a positive relationship between the (in)ability to remember faces and the ability to match upright faces as measured with the face-matching task. Only accuracy scores on the upright faces condition in the faces and shoes task significantly predicted scores on the neutral and emotional memory tasks, and the strength of the (paradoxical) face inversion effect predicted performance on the emotional face memory task. We tentatively conclude that impaired configural processing may play an important role in consolidation of a face in memory and/or memory retrieval. These results are in line with accumulating evidence that the ability to process faces configurally is positively related to face recognition ability (Wang, Li, Fang, Tian, & Liu, 2012), also in DPs (Richler, Cheung, & Gauthier, 2011), as measured with the composite face task, and in “super-recognizers” (Russell, Duchaine, & Nakayama, 2009). More research is needed to further explore these results with additional measures of holistic (face) processing, such as the composite face task or a global/local task (Navon, 1977). Also, the precise processes and underlying neurological correlates of this effect need further exploration.

In conclusion, the current study shows that the face-processing impairment in DP is specifically related to configural processes but does not affect feature processing in either a positive or a negative direction, and that identity recognition deficit is reduced when the face conveys emotional information. Furthermore, configural processing at the perception stage is predictive of face recognition at the memory stage. Lastly, the comparative approach at the basis of FEAST makes it a useful tool in prosopagnosia research and clinical practice.

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Facial identity and emotional expression recognition in developmental prosopagnosia

In this study, we assessed face memory, face and object recognition, and configural processing ability in a large group of DPs. In addition, we aim to extent on the literature on emotion recognition ability in DP. A sample of 21 DPs was tested with the FEAST, a battery including neutral and emotional face memory tasks, an upright and inverted faces and object matching task, an upright and inverted face and object part matching task and a human and canine facial expression matching task. It was found that DPs were impaired in configurational processing, but not part-to-whole matching. Also, DPs showed impaired memory for both neutral and emotional faces and furthermore, configural processing slightly predicted face memory scores. Also, DPs are impaired at emotion recognition as compared to controls, but only for human and not canine facial expressions. Taken together the results indicate that facial expression and facial identity processing are not dissociable processes.

Adapted from:

Huis in 't Veld, E. M. J., & de Gelder, B. (submitted).

Introduction

As reviewed in the introduction of this dissertation, research on prosopagnosia has focused on face specificity, configuration perception and fMRI research to find abnormalities in face processing networks. Individuals who suffer from developmental prosopagnosia (DP) provide us with a unique opportunity to assess these processes in the absence of any overt brain damage or other deficits (Behrmann & Avidan, 2005). However, when it comes to research into the emotion recognition abilities of DPs, contradictory results have been reported. In line with the model as proposed by Bruce & Young (1986) and Haxby et al. (2000), there have been reports of DPs who were able to recognize or match facial expressions normally (Dinkelacker et al., 2011; Duchaine, Parker, & Nakayama, 2003; Humphreys et al., 2007; Lee et al., 2010; Nunn et al., 2001; Palermo et al., 2011).

However, other findings report contradictory results, which may indicate that facial identity and facial expression recognition may not be governed by completely separate mechanisms (in line with the model presented by Calder & Young, 2005). For example, some DPs in a family were found to be impaired on emotion recognition, while others scored normally (Schmalzl, Palermo, & Coltheart, 2008). In another study, a DP showed a similar ability to match expression as a control group, albeit with slower response latencies, and also slightly benefited from same facial identity in an emotion matching task (Bentin et al., 2007). Similarly, one DP in de Gelder (2003) was better at recognizing emotions than identities and furthermore, emotional expressions improved his configural processing. In a study testing six DPs and controls, even though no average group differences in emotion recognition were reported, four DPs scored between 80% and 93% accuracy whereas the lowest scoring control participant performed at 93% correct and the other 5 performed at a perfect 100% accuracy (Dobel, Boelte, Aicher, & Schweinberger, 2007). Additionally, two out of four DPs scored abnormally on four different emotion recognition tasks (Minnebusch, Suchan, Ramon, & Daum, 2007) and lastly, an 8 year old boy scored above chance when asked to judge emotional expressions, but worse than controls (Brunsdon, Coltheart, Nickels, & Joy, 2006).

In addition to these studies where the findings are not clearly indicating a deficit nor normal emotion recognition abilities, there are also cases of DPs whose emotion recognition was more convincingly found to be impaired. One of the first reported cases of DP was a then 12 year old girl, A.B., who showed problems with emotion recognition in a follow up study 15 years later (de Haan & Campbell, 1991; McConachie & Helen, 1976). Another DP performed worse than controls on an emotion labelling task, an emotion categorization and emotionally morphed faces task

and an Eyes Test (Duchaine et al., 2006). In addition, the DP known as LG scored abnormally low on the recognition of disgusted, angry and sad facial expressions and on sad bodily expressions, but was almost perfectly able to recognize disgusted, fearful and angry bodies. Furthermore, unlike controls, LG's facial expression recognition was not affected by the presence of a conflicting bodily expression. (Ariel & Sadeh, 1996; Aviezer, Hassin, & Bentin, 2012). Overall, there seems to be evidence that DPs are more likely to score worse on tasks of facial emotion recognition than controls.

Besides the already discussed importance of holistic processing for face identity recognition, there is evidence that holistic processing is also important for emotion recognition (Bartlett & Searcy, 1993; Calder & Jansen, 2005; Calder, Young, Keane, & Dean, 2000; Calvo & Beltran, 2014; Durand, Gallay, Seigneure, Robichon, & Baudouin, 2007; Mckelvie, 1995; Palermo et al., 2011; Tanaka, Kaiser, Butler, & Le Grand, 2012; White, 2000). The question arises whether the deficits in holistic processing of identity may be related to any emotion recognition problems in DP. Palermo et al. (2011) found weaker holistic coding for emotional expression in DPs than controls and Calder et al. (2000) found evidence of independency, as the performance on either an emotional expression or identity composite task was not influenced by congruency of the other. Also, the strength of configural processing as measure with the face inversion effect significantly predicted emotional face memory scores (Huis in 't Veld et al., 2012).

To assess these issues, a group of subjects with developmental prosopagnosia and controls were tested on neutral and emotional face memory ability, configural processing and emotion recognition. Based on these studies, we tested two hypotheses. The first hypothesis was that the DP group will have impaired emotion recognition compared to controls. Secondly, we tested whether configural processing ability will predict emotion recognition ability.

Method

Participants

Recruitment procedure and inclusion.

The developmental prosopagnosia (DP) group was recruited between 2010 and 2014 via an announcement on our website (<http://www.tilburguniversity.edu/gezichtsblindheid>) and through a newspaper article on prosopagnosia printed in several newspapers in the Netherlands (Als je bekenden niet

herkent. (2012, July 18). Wegener Dagbladen). Participants applied for participation through email or by telephone. An initial invitation letter and preliminary screening questionnaire was sent out in which the procedure and purpose of the study was explained. An appointment at Tilburg University was made if the participants consented to participate.

The control participants were recruited from acquaintances of lab members and by Tilburg University master thesis students, who recruited from their own acquaintances and family members. Participation was voluntarily and the controls were not given a monetary reward.

The study was approved by the Maastricht University ethics committee and adhered to the declaration of Helsinki. Written informed consent was provided by all participants. The following inclusion criteria were applied: normal or corrected-to-normal vision and normal basic visual functions as assessed by the Birmingham Object Recognition Battery (line length, size, orientation, gap, minimal feature match, foreshortened view and object decision) (Riddoch & Humphreys, 1992). The face recognition problems had to be longstanding (since childhood) and not a result of any possible event such as an accident, operation or other health issue. A history of psychiatric or neurological problems, as well as any other medical condition or medication use which would impair participation or the results, or the occurrence of a concussion at any time in life, were exclusion criteria's. All DPs were in good health. One female DP withdrew from the experiment, because she indicated the tasks were too tiring and difficult for her.

Developmental Prosopagnosia (DP) Group.

The sample consisted of 21 DPs, 11 women between 29 and 66 years old ($M = 48.2$, $SD = 11.34$) and 10 men between 42 and 72 years old ($M = 60.7$, $SD = 11.8$). Two DPs were left-handed. All DPs reported problems with face recognition since childhood and complain about frictions in personal relationships that were caused by failing to recognize familiar people and report they have been described as arrogant or aloof due to these problems with recognition. Also, they indicate that recognition is especially problematic when the person is outside the normal context and that they have problems with watching movies due to not being able to recognize the characters from scene to scene. All DPs reported they try to recognize others by actively focusing on non-facial identity features, such as attributes, haircuts, the voice, mannerisms or body posture. As a first exploration and in order to establish continuity with the literature we assessed face recognition using the Benton Facial Recognition Test (BFRT; Benton, et al., 1983). The DPs scored significantly lower on the BFRT ($M = 41.7$, $SD = 4.2$) than the controls ($M = 45.6$, $SD = 4.2$), $F(1, 52) = 11.399$, $p = .001$. Three

DP's scored slightly lower than normal on the length match task of the BORB with scores of 23 (WH) and 24 (SG and AB).

Control group.

The control group consisted of 33 participants, 18 women aged between 22 and 62 ($M = 49.7$, $SD = 10.68$) and 15 men between the ages of 24 and 60 ($M = 46.1$, $SD = 12.9$) with matched backgrounds and education levels. Two controls were left-handed. The control group did not differ significantly from the DPs with regard to age ($t(52) = -1.862$, $p = .068$).

Procedure

The session started with reading and signing an informed consent form, followed by a structured interview (including an additional screening questionnaire) to get a complete overview of the face recognition problems during the lifespan. The experimental phase started with completing the BORB, followed by the computerized tasks and ended with the BENTON. The participants completed the tasks with their dominant hand. Participation of the DPs was rewarded with reimbursement of travel costs and payment of €10, - an hour. The total testing time was about 2 hours with possible breaks after the completion of one task, dependent on the needs of the participant. Afterwards, the participants received a short written overview of the purpose of each test and their scores.

Basic test battery (FEAST)

The FEAST as described in chapter 2 (de Gelder, Huis in 't Veld, & van den Stock, in press) including the Neutral Face Memory task (FaMe-N), the Emotional Face Memory task (FaMe-E), the Faces and objects matching task, the Face and house part-to-whole matching task and the human and canine Facial Expression Matching Task (FEM-H and FEM-C) was used to test all participants.

Data analyses

Accuracies were calculated as the total proportion of correct responses for both the total score of each task and for each condition separately. Average response times from stimulus onset were calculated from the correct responses only. For all tasks, reaction times faster than 150 ms were rejected and in addition, for the faces and objects matching task and face and house part-to-whole matching task, reaction times longer than 3000 ms and on the other tasks, reaction times longer than 5000 ms were rejected. To compare the scores from the DP's with the control group, Crawford and Howell's (Crawford & Howell, 1998) t-test scores were calculated with the mean and

standard deviations of the control group. This t-test is an improved version of the Z-score transformation in order to better compare an individual's scores with a control group and can be interpreted using the t-distribution with (n-1) degrees of freedom (Crawford, Garthwaite, & Howell, 2009). Only one of the two blocks of the house part matching upright condition of the faces and house part-to-whole matching task were properly recorded for participants AA and GZ, and thus no t-scores were calculated. The results of the Neutral Face Memory task were analysed using an independent samples t-test. The results of the remaining tasks were analysed using repeated measures GLMs with the design of the task as within-subject variables and group (DP or control) as between subject variables. Main effects were further explored using post hoc contrasts and interaction effects with paired samples t-tests.

Additionally, face, face part, shoe and house part inversion scores were calculated by subtracting the accuracy and reaction time scores on the inverted face condition from the upright condition. A positive score indicates that accuracy was higher, or the reaction time was longer, on the upright condition. A negative score indicates higher accuracy or reaction times for the inverted condition. To test whether the strength of configural processing defined as the inversion scores predicted face memory and emotion recognition ability, multiple linear regressions were run with accuracy scores on the FaMe-N, FaMe-E and both FEM task as dependent variable and age, gender, face and shoe inversion scores and facepart and housepart accuracy inversion scores as predictors.

Results

See Table 1 and 2 for the z-scores of accuracy and reaction times for each DP as compared to the control group.

	Face Memory		Faces and Objects Matching task				Faces and Objects Part Matching task				Emotion Matching Task	
	Neutral	Emotion	Faces Upr	Faces Inv	Shoes Upr	Shoes Inv	Faces Upr	Faces Inv	Houses Upr	Houses Inv	Human	Canine
1	-0.45	-0.87	-2.87	-2.45	-2.89	-2.12	-0.58	-0.59	-	-1.55	0.09	-0.25
2	-4.83	-5.04	-1.91	-1.33	0.35	-0.89	1.07	0.98	-	1.29	-1.94	-0.04
3	-3.22	0.52	-1.91	-3.01	-1.07	-0.89	-0.21	-0.98	0.70	0.10	-2.67	-5.02
4	2.52	-0.48	0.42	-1.15	0.96	0.83	1.26	0.20	-0.77	0.39	-0.83	1.00
5	-0.91	0.72	-0.36	0.89	1.16	1.08	1.99	0.20	1.07	0.10	-3.96	-10.62
6	-1.37	0.12	0.42	0.15	-0.46	0.59	1.07	-0.78	0.15	0.39	-0.46	-1.49
7	-1.83	-1.87	-0.16	-0.03	-0.06	0.34	1.44	0.78	1.26	1.29	0.09	-1.70
8	-4.60	-0.08	-2.10	-0.59	0.15	-0.15	-1.13	-1.95	-0.95	-1.10	-4.51	-2.74
9	-0.22	0.12	0.61	1.08	0.76	0.83	1.26	1.37	1.44	1.14	-1.02	0.79
10	-1.14	-1.67	-2.87	-0.03	-1.47	-0.64	0.16	-1.37	-0.03	-0.20	-1.38	-0.45
11	-5.75	-1.27	-6.16	-0.59	-0.26	0.34	-0.95	0.39	-0.40	-0.80	-3.04	-0.45
12	-3.91	-2.46	-5.58	-3.38	0.76	-0.39	0.89	1.37	1.81	1.74	-1.75	-5.43
13	-2.98	-1.87	-3.84	-2.45	-0.87	-2.12	1.44	1.95	-0.03	-2.90	0.64	-0.04
14	-2.06	-1.27	-2.29	-0.96	-1.27	-1.62	0.52	0.59	0.70	0.99	-1.38	-1.70
15	-2.52	0.32	-3.45	-1.71	-1.88	-1.62	0.89	-1.76	-0.59	-0.95	0.83	0.17
16	-0.68	-1.67	-0.55	0.71	1.36	1.08	2.73	0.20	2.18	2.19	1.38	1.00
17	-4.83	-0.28	-3.45	-1.15	-1.07	-0.89	-1.50	-1.56	-1.14	-1.40	-2.67	-1.49
18	-6.91	-0.67	-1.91	-2.08	-1.47	-2.61	-1.13	-0.39	-0.22	-1.70	0.27	-0.25
19	-6.91	-2.26	-2.87	-2.63	-1.88	-1.13	-1.13	-1.56	-1.14	-1.25	0.09	0.17
20	-3.68	0.72	-2.10	-0.03	-2.08	-2.85	-0.58	0.00	0.89	0.99	-1.02	0.59
21	-3.22	-2.46	-0.36	-0.59	0.76	-0.39	1.63	0.20	0.33	1.44	-1.20	-0.04

Table 1. T-values of the accuracy scores of the DPs compared to the control group. Light grey; $p < .05$ and dark grey; $p < .01$ (one-tailed).

	Face Memory		Faces and objects Matching task				Faces and objects Part Matching task				Emotion Matching Task	
	Neutral	Emotion	Faces Upr	Faces Inv	Shoes Upr	Shoes Inv	Faces Upr	Faces Inv	Houses Upr	Houses Inv	Human	Canine
1	-0.20	-2.02	-1.09	-0.71	-1.04	-0.76	-1.72	-1.70	-1.40	-1.04	-2.68	-1.13
2	3.30	4.41	1.26	1.26	1.17	0.48	0.76	1.41	0.23	0.48	1.19	0.22
3	1.44	0.17	0.73	1.45	0.62	0.48	1.49	0.98	0.98	0.89	2.26	2.49
4	1.17	-0.90	0.24	0.93	0.63	0.18	-0.15	-0.15	0.26	0.41	1.45	0.60
5	1.23	1.02	-0.48	0.39	-0.32	0.22	0.74	0.99	0.13	0.41	1.79	4.14
6	0.75	0.07	0.67	0.51	0.05	0.29	0.65	0.93	1.08	0.36	1.51	0.47
7	-0.56	-1.50	0.34	-0.07	0.35	0.64	0.28	0.29	-0.55	-0.63	0.49	1.23
8	2.04	1.53	1.27	0.31	0.29	0.03	1.41	2.49	1.21	1.32	2.28	2.70
9	1.70	1.91	0.85	0.97	0.86	0.41	-0.04	0.21	-0.04	0.11	1.42	1.20
10	1.18	-0.37	0.57	-0.21	-0.14	-0.04	0.49	0.59	-0.01	0.78	0.64	1.07
11	2.26	2.32	-0.90	-0.07	-0.32	-0.46	-1.64	0.01	0.37	0.50	1.65	0.56
12	2.08	2.16	2.08	2.98	0.66	0.46	0.55	0.96	0.53	0.51	0.44	2.79
13	1.22	1.19	0.53	0.58	0.42	0.57	0.28	0.47	-0.22	-0.12	-0.65	-0.14
14	-0.91	0.29	0.68	-0.11	-1.25	0.09	-0.07	-0.02	0.47	-0.02	1.07	1.28
15	2.69	1.72	0.53	0.45	0.75	0.54	0.72	0.47	0.61	0.15	0.25	0.49
16	1.51	-0.33	0.22	0.57	0.36	0.27	-0.05	0.15	-0.08	-0.35	-0.20	-1.12
17	3.39	2.62	0.65	2.26	0.94	1.59	2.30	2.92	1.67	1.78	2.68	1.57
18	3.75	1.47	1.10	-1.35	-1.45	-1.44	-1.02	-0.57	-1.08	-0.44	-0.52	0.62
19	3.17	-1.49	-1.17	-0.28	-0.82	-0.36	-0.27	0.89	1.12	1.23	-1.30	-0.47
20	2.44	0.94	2.18	1.11	1.90	1.53	1.01	0.90	0.24	0.25	0.98	0.13
21	1.24	0.70	0.71	1.09	1.09	0.89	0.71	0.89	0.76	0.28	0.79	1.61

Table 2. T-values of the reaction times of the DPs compared to the control group. Light grey; $p < .05$ and dark grey; $p < .01$ (one-tailed).

Neutral Face Memory task (FaMe-N).

The DPs scored significantly less accurately ($t(1, 52) = 7.390, p < .001$) and slower than the controls ($t(1, 52) = -5.432, p < .001$). See Figure 1.

Emotional Face Memory task (FaMe-E).

A repeated measures with emotion (fear, happy, sad) as within-subject variable and group as between subject variable was run on accuracy and reaction time scores. Controls scored more accurately than DPs, regardless of emotion ($F(1, 52) = 9.579, p = .003, \eta^2_p = .16$). No effect of emotion on face memory was found ($F(2, 51) = 0.682, p = .510, \eta^2_p = .03$). The same was found for reaction speed; DPs responded slower than controls ($F(1, 52) = 4.754, p = .034, \eta^2_p = .08$) but no effect of emotion was found ($F(2, 51) = 0.637, p = .533, \eta^2_p = .02$). See Figure 1.

Comparing results on the FaMe-N and the FaMe-E.

Repeated measures GLM's with task (FaMe-N, FaMe-E) as within-subject variable and group as between subject variable were run for accuracy and reaction time separately. For accuracy scores, a group by task interaction effect was found ($F(1, 52) = 19.719, p < .001, \eta^2_p = .28$). Paired samples t-tests show that controls do not benefit from emotion on the face ($t(1, 32) = -1.427, p = .163$) whereas DPs are better able to remember emotional faces than neutral faces ($t(1, 20) = -4.663, p < .001$). This interaction effect was also found for reaction times ($F(1, 52) = 14.682, p < .001, \eta^2_p = .22$). Both controls ($t(1, 32) = 3.769, p = .001$) and DPs ($t(1, 20) = 6.590, p < .001$) are quicker on the FaMe-E than the FaMe-N, but this difference is more distinct for DPs.

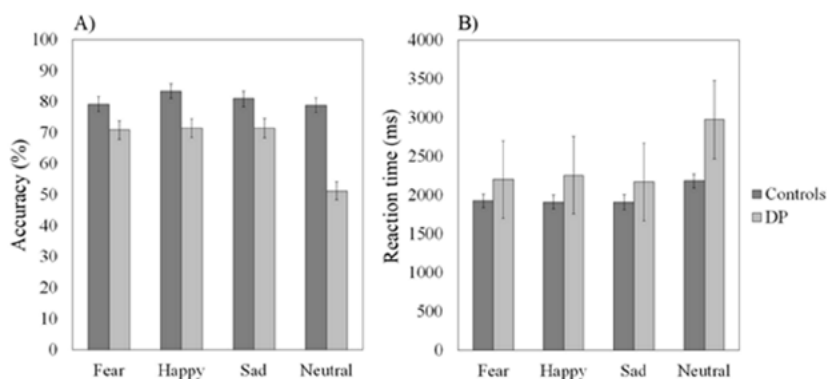


Figure 1. Means and standard errors of the A) accuracy scores and B) reaction times on the neutral and emotional face memory task.

Faces and objects matching task.

A repeated measures GLM with condition (faces, shoes), orientation (upright, inverted) as within subject variables and group as between subject variable was run on accuracy and reaction time scores separately. For accuracy, a three-way group by condition by orientation interaction was found ($F(1, 52) = 7.078, p = .01, \eta^2_p = .12$). This is due to the different pattern of results the DPs show as compared to the controls. Whereas controls have higher scores on upright faces than inverted faces ($t(1, 31) = 4.173, p < .001$) and on inverted shoes than upright shoes ($t(1, 31) = -2.096, p = .044$), the DPs are equally accurate at recognizing upright versus inverted faces ($t(1, 20) = -0.873, p = .393$) and shoes ($t(1, 20) = -1.612, p = .123$). Also, DPs are significantly worse at face recognition than the controls, but perform at the same level for shoe recognition (condition by group interaction; $F(1, 52) = 16.067, p < .001, \eta^2_p = .24$). For reaction times, a group by condition interaction effect was found ($F(1, 52) = 7.248, p = .01, \eta^2_p = .12$); DPs are slower at recognizing faces than controls, whereas reaction times are similar in the shoe condition. Furthermore, a main effect of orientation was found ($F(1, 52) = 7.368, p = .009, \eta^2_p = .12$); both DPs and controls are slower in recognizing upright stimuli. See Figure 2.

Furthermore, t-tests on the face and shoe inversion accuracy scores further indicate that the controls show on average a face inversion effect ($M = 0.06, SD = 0.08$), whereas the DPs show a paradoxical face inversion effect ($M = -0.02, SD = 0.12, t(1,52) = 2.93, p = .005$). This was not found for the shoe inversion accuracy scores ($t(1,52) = -0.10, p > .05$).

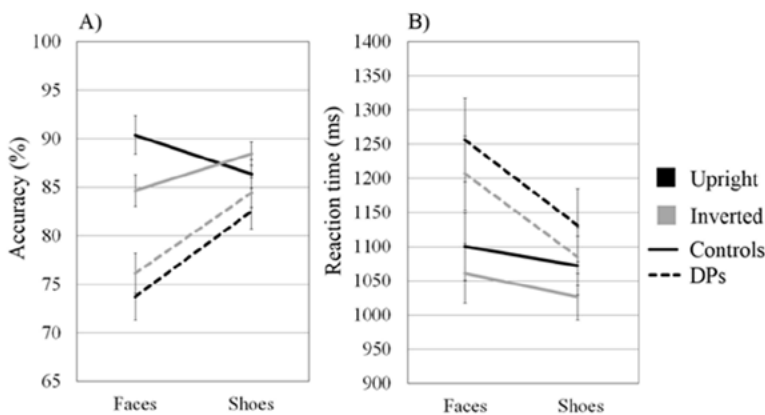


Figure 2. Means and standard errors of the A) accuracy scores and B) reaction times on the faces and objects matching task.

Face and house part-to-whole matching task.

A repeated measures GLM with a 2 condition (face parts, house parts) and 2 orientation (upright, inverted) design and group as between subject variable was run on accuracy and reaction time scores separately. For accuracy, a condition by orientation interaction effect was found ($F(1, 52) = 6.415, p = .014, \eta^2_p = .11$); upright face parts are recognized more accurately than inverted face parts ($t(1, 53) = 3.940, p < .001$), whereas inversion for house stimuli did not decrease accuracy scores ($t(1, 53) = 0.409, p = .68$). However, a marginal orientation by group interaction effect was also found ($F(1, 52) = 4.189, p = .046, \eta^2_p = .08$); indicating that DPs are slightly better at recognizing upright stimuli, but not inverted stimuli. Only a main effect of condition was found for reaction times ($F(1, 52) = 6.297, p = .015, \eta^2_p = .11$). Both DPs and controls are quicker at recognizing house parts than face parts. See Figure 3.

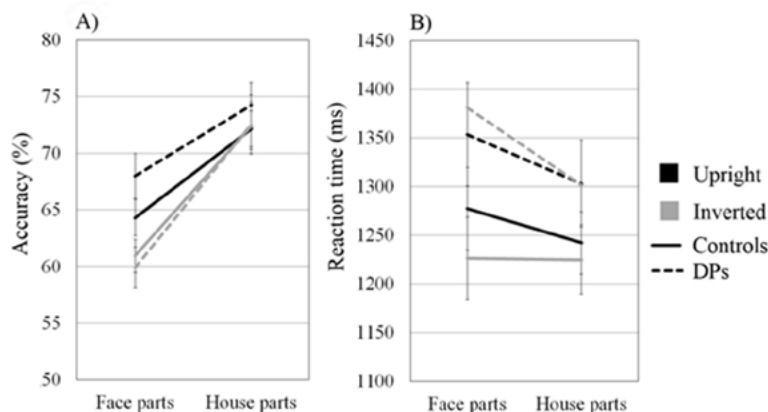


Figure 3. Means and standard errors of the A) accuracy scores and B) reaction times on the face and house part-to-whole objects matching task.

Facial Expression Matching Task.

Human emotional expressions. A repeated measures GLM with human emotions (fear, happy, sad, disgust, anger, surprise) as within-subjects variables and group as between subject variable was run on the accuracy and reaction time data. The controls score higher on emotion recognition than the DPs ($F(1, 52) = 11.266, p = .001, \eta^2_p = .18$). Also, a main effect of emotion was found ($F(5, 48) = 59.389, p < .001, \eta^2_p = .86$). Fear was recognized least accurate, followed by sadness ($F(1, 52) = 21.493, p < .001$) and anger ($F(1, 52) = 28.288, p < .001$). Happiness was recognized the best (compared to disgust, $F(1, 52) = 47.600, p < .001$). The same pattern was found for reaction times. The controls are faster than the DPs ($F(1, 52) = 5.073, p = .029, \eta^2_p = .09$) and there

was a main effect of emotion ($F(5, 48) = 23.384, p < .001, \eta_p^2 = .71$). Surprise is recognized quicker than fear, sad or anger ($F(1, 52) = 12.640, p = .001$) and happy is recognized the fastest ($F(1, 52) = 34.425, p < .001$). See Figure 4.

Canine emotional expressions. A repeated measures GLM with the canine emotions (happy, angry, fearful) as within-subjects variables and group as between subject variable on the accuracy and reaction time data. Three DPs scored extremely low on this task (lower than 3SD below the mean, also see Table 1). Only a main effect of emotion was found ($F(2, 48) = 39.053, p < .001, \eta_p^2 = .62$), but there were no differences between DPs and controls ($F(1, 49) = 1.691, p = .199, \eta_p^2 = .03$). Angry and happy were recognized better than fear ($F(1, 49) = 72.515, p < .001, \eta_p^2 = .60$). However, the controls were slightly quicker in recognizing the canine emotions ($F(1, 49) = 4.567, p = .038, \eta_p^2 = .09$) and again, a main effect of emotion was found ($F(2, 48) = 59.904, p < .001, \eta_p^2 = .71$). Anger was recognized quicker than happy ($F(1, 49) = 63.163, p < .001, \eta_p^2 = .56$), which in turn was recognized quicker than fear ($F(1, 49) = 8.589, p = .005, \eta_p^2 = .15$). See Figure 4.

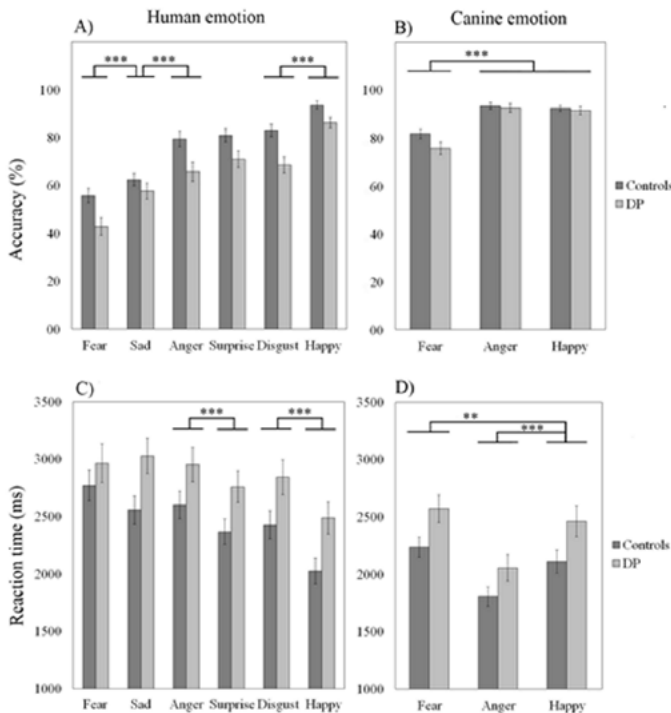


Figure 4. Means and standard errors of the accuracy scores on the A) human and B) canine FEM task, and reaction times C) human and D) canine FEM task. *** $p < .001$.

Relationship between configural processing, face memory and emotion recognition.

Only small, positive predictive effects of face inversion scores were found on neutral, but not emotional, face memory scores. Higher face inversion scores (positive scores indicate a higher accuracy on upright face recognition as compared to inverted face recognition) are indicative of higher neutral face memory scores. See Table 3 and Figure 5A.

Step 1	FaMe-N			FaMe-E		
	B	Se B	β	B	Se B	β
Constant	0.733	0.121		0.723	0.079	
Gender	-0.001	0.002	-.093	0.036	0.034	.036
Age	0.040	0.052	.108	0.001	0.001	.058
R ²	0.023			0.023		
Step 2	B	Se B	β	B	Se B	β
Constant	0.654	0.126		0.712	0.086	
Gender	0.000	0.002	-.015	0.030	0.037	.120
Age	0.040	0.054	.107	0.001	0.002	.077
Face Inversion	0.555	0.244	.311 *	0.206	0.168	.177
Shoe Inversion	-0.138	0.467	-.041	-0.194	0.321	-.088
Face Part Inversion	0.021	0.275	.011	-0.078	0.189	-.061
House Part Inversion	-0.397	0.291	-.187	-0.064	0.200	-.046
R ² change	0.137			0.042		

Table 3. Regression coefficients of the inversion scores on the tasks for configural and feature-based processing on the total scores of the Face Memory–Neutral and the Face Memory–Emotional task. * = $p < .05$.

Similarly, a small positive predictive effect of face inversion scores was found for human facial expression recognition ability, but not for canine emotion recognition. Additionally, age was negatively related to the recognition of canine facial expressions. See Table 4 and Figure 5B.

FEM-H				FEM-C		
Step 1	B	Se B	β	B	Se B	β
Constant	0.801	0.078		1.048	0.080	
Gender	-0.002	0.001	-.149	-0.017	0.035	-.066
Age	-0.012	0.034	-.051	-0.004	0.001	-.329 *
R ²	0.023			0.107		
Step 2	B	Se B	β	B	Se B	β
Constant	0.773	0.084		1.061	0.087	
Gender	-0.001	0.001	-.103	-0.034	0.037	-.132
Age	-0.018	0.036	-.073	-0.004	0.002	-.335 *
Face Inversion	0.326	0.162	.281 *	0.139	0.169	.112
Shoe Inversion	-0.165	0.311	-.075	-0.342	0.324	-.145
Face Part Inversion	-0.074	0.183	-.058	-0.199	0.191	-.147
House Part Inversion	-0.124	0.194	-.090	-0.150	0.202	-.102
R ² change	0.092			0.056		

Table 4. Regression coefficients of the inversion scores on the tasks for configural and feature-based processing on the total scores of the Facial Expression Matching- Human and Canine task.

* = $p < .05$

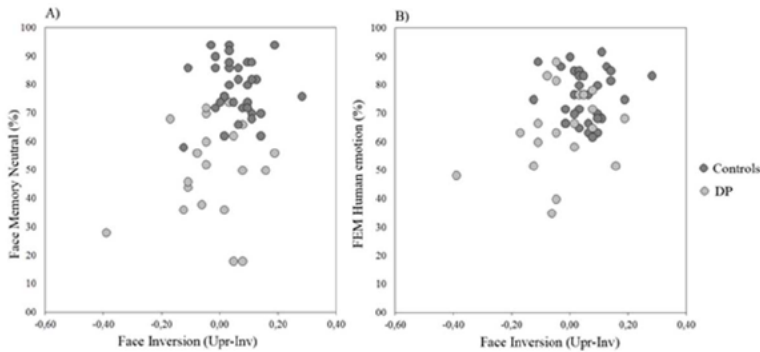


Figure 5. Scatter plot of the proportion correct face inversion accuracy scores with the A) FaMe-N and the B) FEM human emotion task accuracy scores.

Lastly, total accuracy scores on the FEM-H and FEM-C were regressed on the total accuracy scores on the FaMe-E, controlled for age and gender, to assess whether emotion recognition ability predicted scores on emotional face memory, but this was not the case (FEM-H: $\beta = .223$, $t(53) = 1.27$, $p > .05$, FEM-C: $\beta = -.061$, $t(53) = -.33$, $p > .05$).

Discussion

The aim of the current study was to assess the extent to which facial identity recognition and emotion recognition processing are separate processes, by testing a group of DPs and controls using a battery with neutral and emotional face memory tasks, whole and part based face and object recognition tasks and emotion recognition task. Firstly, it was hypothesized that emotion recognition would be impaired in the DP group. Secondly, it was hypothesized that deficits in configural processing are related to deficits in emotion recognition.

The results of the current study support the first hypothesis, as the DP group scored less accurate on the recognition of all emotional expressions in the emotional sample-to-match task. Also, no group differences were found on the canine version of the task, which indicates these emotion recognition problems are fairly specific for human facial expressions. This is in line with studies reporting that DPs are impaired in facial expression recognition, but not for example in the recognition of emotion conveyed through the body (Aviezer et al., 2012; van den Stock et al., 2008). As already discussed in the introduction, there are many conflicting reports in the literature regarding the emotion recognition abilities of DPs. Figure 5 may shed some light on why these conflicting results are found, as it shows that there is quite some variability in the accuracy scores in the DP group. This is in line with reports of both normal and abnormal emotion recognition in DPs (Minnebusch et al., 2007), even in one family (Schmalzl et al., 2008). Thus, single cases or small sample studies can easily provide distorted results of what seems to be a heterogeneous group (Le Grand et al., 2006).

In contrast, there seems to be a consensus on the issue of configural processing in DP. In line with the results found earlier on the same face and object matching task and face and house part-to-whole matching task (Huis in 't Veld et al., 2012), it was found that DPs are impaired on face, but not object or part-based matching and that they show a paradoxical face inversion effect, indicative of impaired holistic processing. We hypothesized that the extent to which configural processing was impaired, operationalized by the face inversion effect, would be positively related to emotion recognition ability. We found tentative evidence to support this hypothesis, as a small positive relationship was found between the inversion effect and emotion recognition ability, in line with previous reports (Bartlett & Searcy, 1993; Calder & Jansen, 2005; Calder et al., 2000; Calvo & Beltran, 2014; Durand et al., 2007; Mckelvie, 1995; Palermo et al., 2011; Tanaka et al., 2012; White, 2000) which could be an explanation of the relative impairment in emotion recognition in DP.

Also, in line with results consistently reported in the literature, it was found that the DP group was less able to remember faces than controls (Avidan et al., 2011; Aviezer

et al., 2012; Bentin et al., 2007; Dinkelacker et al., 2011; Duchaine et al., 2003; Duchaine et al., 2006; Duchaine et al., 2007; Hadjikhani & de Gelder, 2002; Huis in 't Veld et al., 2012; Lee et al., 2010; Minnebusch et al., 2007; Righart & de Gelder, 2007; Shah et al., 2014; Susilo et al., 2010; Tanzer, Freud, Ganel, & Avidan, 2013; van den Stock et al., 2008). Additionally, we found a small positive predictive effect of configural processing on neutral face memory. These results taken together with similar findings reported previously (J. DeGutis, Wilmer, Mercado, & Cohan, 2013; Huis in 't Veld et al., 2012; Richler, Cheung, & Gauthier, 2011; Wang, Li, Fang, Tian, & Liu, 2012) indicate that configural processing at least facilitates memory for faces.

Similarly as controls and as previously mentioned in chapter 2, we found no differential effect of emotion (happy, sad or fearful) on face memory scores. Also, we find a beneficial effect of emotional expression on face identity memory for DPs, but not the controls. To date, there hasn't been an extensive investigation into the effects of emotion on face memory in DP. The current results are both in line with and contrasting those found by (Dinkelacker et al., 2011), where the DPs scored equally well as controls on the recollection of negative (angry and fearful) faces and worse on neutral, but also on positive faces. Looking at the pattern of results, this is probably due to a decrease in recognition accuracy of negative faces for the controls, as opposed to an increased accuracy for emotional faces in DPs as found in the current study. Similarly, in our previous study using the same tasks but a smaller sample of DPs, we found that DPs performed worse on both memory tasks than controls, but also that DPs and controls were less accurately able to remember fearful faces (Huis in 't Veld et al., 2012). However, in that same study we also found that the presence of emotional bodies improved face identity recognition, which again indicates that the presence of emotion can improve face processing.

Even though the results in the literature are conflicting, what mechanisms could explain the current results? It is known that remembering neutral faces activates different cortical areas than remembering emotional faces (Fischer, Sandblom, Nyberg, Herlitz, & Backman, 2007). Interestingly, van den Stock et al. (2008) found normal FFA activation in a DP group when emotional, but lower than usual activation when neutral faces were shown. Similarly, normal amygdala and superior temporal sulcus activation was found for emotional faces in acquired prosopagnosia (de Gelder et al., 2003), who then argued for a dual route of face perception, where DPs may benefit more from the effect of emotion through subcortical networks activations. In addition, these activations in areas such as the amygdala and insula may also facilitate memory encoding through, for example, connections to the prefrontal cortex and hippocampus (Armony & Sergerie, 2007; Dinkelacker et al., 2011; Muscatell, Addis, & Kensinger, 2010; Phelps, 2004; Roder, Mohr, & Linden, 2011; Sergerie, Lepage, & Armony, 2005) and FFA (Vuilleumier & Pourtois, 2007). This also fits with the model

of Gobbini and Haxby (2007), who postulate that the emotional response to a person is a crucial part of successful face recognition. In short, the effect of emotion on face memory is still under debate, and is not exhaustively studied in DP. The current test battery does not contain a non-face control condition, but a recent study with a group of 16 DPs showed that only memory for faces, in contrast to hands, butterflies and chairs was impaired (Shah et al., 2014). Especially, the specific effects of all emotions, valence and arousal should be taken into account in future research, as we only studied fearful, sad and happy faces whereas (Dinkelacker et al., 2011) only made a positive (happy) versus negative (fearful and angry) faces.

Overall, both the finding that configural processing is related to face memory and that emotional expression can enhance face memory may have implications for the development of training applications to remediate face recognition disorders. Consistent with the idea that there is configural processing in DP, it strengthens the notion that configural processing would be a good starting point if one aims to improve face recognition, as reported recently (DeGutis, Cohan, & Nakayama, 2014).

Recognition and integration of facial and bodily expressions in acquired prosopagnosia

The current study presents a new case of acquired prosopagnosia, with damage to the bilateral occipitotemporal/fusiform gyrus but with an intact right occipital face area. His face and object processing was assessed using the FEAST. In addition, face and body selective brain regions were localized using fMRI. In addition to his facial expression recognition, his bodily expression recognition and the integration of faces and bodies were assessed with a bodily expression matching task and congruent and incongruent face-body compounds. His low level visual processing was intact, but his face memory was severely impaired as well as his upright face recognition. Also in this AP, we found evidence of impaired configural processing. His facial expression recognition was selectively impaired, but he was normally able to recognize bodily expressions. Furthermore, he was influenced by emotional bodies during facial expression recognition, but not the other way around.

Adapted from:

Huis in 't Veld, E. M. J., Zhan, M., & de Gelder, B. (submitted).

Introduction

In chapter 1, a short review in the literature on (configural) face processing in subjects with prosopagnosia with brain damage can be found. In chapters 3 and 4, we explored holistic processing, face memory, emotion recognition and the effect of emotion on face recognition in developmental prosopagnosia. In this group, we found that emotional body language influenced face identity perception and emotion had a beneficial effect on face even in the presence of impaired emotion recognition as compared to controls.

Configural processing as the explanation for failure of facial identity recognition is seen as the main culprit and has the focus of prosopagnosia studies. By comparison, there has not been much attention to the emotion recognition abilities in AP and the existing reports are conflicting. Some studies report APs cases who were normal in emotion perception (Tranel, Damasio, & Damasio, 1988), with lesions in the secondary visual cortex and occipital lobes (De Renzi & di Pellegrino, 1998), the right anterior temporal lobes (Evans, Heggs, Antoun, & Hodges, 1995), the bilateral occipital lobes (Bruyer et al., 1983), the right fusiform, inferior and middle temporal and inferior occipital gyri (Riddoch et al., 2008) and a right hemispherectomized patient (Sergent & Villemure, 1989). Other patients show mild impairments, such as DN, with left sided damage to the left occipito-temporal gyrus (Mattson et al., 2000). The patients HJA (with damage in the occipital lobes) and GK (with damaged parietal lobes) (Humphreys, Donnelly, & Riddoch, 1993) did not score so well on facial expression recognition. Interestingly, whereas HJA was impaired for static but not dynamic expressions, GK showed the exact opposite pattern.

In many studies, the results are also not so clear cut. For example, a patient suffering from damage to the left anterior temporal lobes and right occipital lobes was quite successful at recognizing happiness, in contrast to a borderline impairment on surprise, and a very low success rate for fear, sadness, disgust and anger (Stephan, Breen, & Caine, 2006). Two APs, one with bilateral parietotemporal damage and density inhomogeneities in occipitotemporal cortex and the other with right anterior and posterior temporal cortex damage were tested using an unambiguous expression recognition task and scored significantly impaired and slow on the recognition of anger, disgust, sadness and fear. They were able to, recognize happy and surprise, albeit with higher response latencies (Humphreys, Avidan, & Behrmann, 2007).

Again, the issue of the dissociability of emotion and identity recognition issue was investigated in this group in several ways with different results. For example, two APs (B-AT1 with bilateral temporal lobe damage and R-AT1 with right temporal lobe and amygdala damage) were normally able to recognize emotion, but not identity, using a

morphed face discrimination tasks with varying identities and emotions, regardless of the varying identities or emotions (Fox et al., 2011). This in contrast to other studies where emotion was found to influence face recognition processes, such as in well studied AP case 'PS' who not only benefited from emotional facial expressions in an identity visual search task, but emotional cues influenced her scores stronger than those of controls. Similarly, when asked to detect changes in faces or houses, she was better able to detect changes in fearful rather than neutral faces (Peelen, Lucas, Mayer, & Vuilleumier, 2009). In line with this, AP patient AD was found to be impaired in overt static and dynamic facial expression recognition, but voice expressions were influenced by facial expressions, suggesting that covert emotional expression recognition was still present (de Gelder, Pourtois, Vroomen, & Bachoud-Levi, 2000). In addition, emotion recognition abilities of five APs with occipitotemporal lesions were tested by de Gelder et al. (2003b). They were better able to match faces based on emotion than on identity and more importantly, the paradoxical face inversion effect (better behavioral performance with inverted than with upright faces) often seen found in AP was abolished and the pattern returned to a normal inversion effect if the faces expressed emotion. In addition, emotional expressions caused activation in related networks in the brain, such as the fusiform gyrus, superior temporal sulcus, orbitofrontal gyrus and amygdala.

One way to test the specificity of the emotion recognition problems in AP is to test other categories than faces. Bodily expressions are valid carriers of emotional information (de Gelder et al., 2010) and similarly as for face processing, there are specialized areas for body processing, such as the fusiform body area (FBA), adjacent to the FFA (Peelen & Downing, 2005) and the extrastriate body area (EBA) (Downing, Jiang, Shuman, & Kanwisher, 2001). Also, it has been suggested that both faces and bodies are processed similarly and configurally, as shown by the finding of the 'body inversion effect' (Meeren, Hadjikhani, Ahlfors, Hamalainen, & de Gelder, 2008; Reed, Stone, Bozova, & Tanaka, 2003; Robbins & Coltheart, 2012; Yovel, Pelc, & Lubetzky, 2010) and the finding that inversion of both kind of stimuli both increased and delayed the N170 (Minnebusch, Suchan, & Daum, 2009; Righart & de Gelder, 2007b; Stekelenburg & de Gelder, 2004). To date, bodily emotion expression recognition is barely studied in prosopagnosia. In patient PS, it was found that the right fusiform gyrus, including the FFA and FBA, are intact and respond strongly to emotional bodily expressions. Not surprisingly, PS does not report any problems in body recognition (Peelen et al., 2009). Additionally, Susilo et al. (2013) tested four AP subjects, with bilateral fusiform face area, occipital face area and STS damage (AP1), occipital lobe damage (AP2), right temporal lobe damage, extending to the middle fusiform and inferior temporal lobe (AP3) and damaged right FFA and OFA (AP4). All four APs were normally able to discriminate bodies and three APs also showed a normal body

inversion effect. Recently, Susilo, Yang, Potter, Robbins, and Duchaine (2015) tested AP 'Galen', with damage in the right temporal, middle occipital, parahippocampal and fusiform gyrus (including the FFA and OFA) and the right FBA, on eight body detection, posture, identity and expression recognition tasks. Similar to previous studies, Galen scored normally on all these tasks.

In contrast, Moro et al. (2012) tested the face, body and object discrimination ability of a 35 year old male AP (FM) with damage in the temporo-occipito-parietal cortex, including the fusiform area and the thalamus. FM was impaired in both face part (f.e. eyes, noses, lips) and body part (upper limbs, f.e. hands, arms, and forearms) discrimination. In addition, FM completed a delayed sample-to-match task, in which he had to match the identity or the emotion of neutral or fearful bodies and faces, friendly or growling dogs and harmless or dangerous knives. FM was able to match both the emotion and identity of dogs and knives above chance. In contrast, FM performed poorly in matching the identity of faces and bodies, but scored above chance at emotion matching, especially when the to-be-matched sample, shown first, was fearful.

In the current study, we test the neutral and emotional face memory, face and object recognition, and facial expression recognition ability of an AP subject 'EP' with bilateral inferior occipito-temporal damage. It is expected that he is impaired in face memory and face identity recognition, but not in object recognition, and that he will show the paradoxical face inversion effect. In view of the conflicting reports on emotional expression recognition in the literature, we expect at least some impairment. Additionally, as faces and bodies are rarely seen in isolation, we explore to what extent EP is influenced by incongruence in facial and bodily expressions using face body compounds. This task assesses not only isolated facial and bodily expression recognition, but (a lack of) incongruency effects on either task might shed light on how EP processes facial and bodily expressions.

Method

Acquired prosopagnosia (AP) patient

The acquired prosopagnosia patient EP (male, right handed, born in 1966) suffered two successive cerebrovascular incidents in October 2012 that damaged large areas of the occipitotemporal gyrus bilaterally, with the most extensive damage in the right hemisphere, resulting in face recognition loss. As it was immediately apparent that he

was unable to recognize his immediate family, his wife contacted us through email after finding our website.

Lesion locations

EP was scanned at Maastricht University in November 2012, using a 3T whole-body scanner (Magnetom Trio, Siemens, Erlangen, Germany) equipped with a 20-element head-neck coil. A T1-weighted anatomical image (1x1x1 mm³ isotropic) was acquired with an MPRAGE sequence, TR = 2250 ms, TE = 2.17 ms. In the right hemisphere, damage was located along the middle-posterior part of the collateral sulcus, and extends superiorly into the white matter including the ventral part of the optic radiation. A large part of the anterior 4th occipital gyrus (anterior O4, middle-posterior part of the fusiform gyrus) is involved. The inferior lingual gyrus is also involved (TAL coordinate: x=17, y=-66, z=-10) (See Figure 1A). However, the temporal part of the fusiform gyrus and a small part of the posterior O4 are spared (see Figure 1B). The posterior boundary of the lesion is along the posterior transverse collateral sulcus. In the left hemisphere, the lesion also occurred along the middle-posterior part of the collateral sulcus, involving less the white matter than in the right hemisphere. The white matter involved appears to be in two locations, in the fusiform gyrus and O4. See Figure 1C. Also, see Table 1 for location coordinates in Talairach space.

	X		Y		Z		Size
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	
Right	27.6 (6.3)	13 to 49	-64.9 (7.2)	-80 to -43	-15.1 (4.0)	-7 to -26	2573
Left	-33.7 (5.2)	-44 to -22	-64.3 (10.4)	-79 to -42	-16.5 (3.4)	-9 to -24	536

Table 1. Centre of gravity Table of the lesions on the left and right hemisphere in Talairach coordinates Size in 1x1x1mm³ voxels.

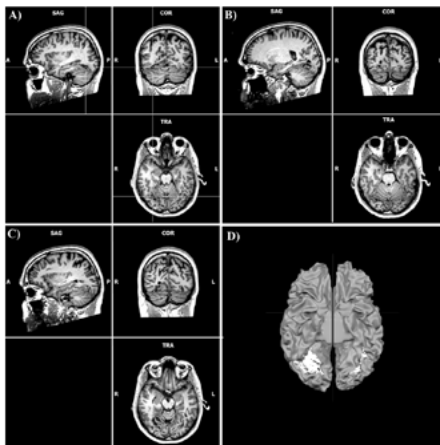


Figure 1. A) Lesion in the right hemisphere. Cursor: x=32, y=-65, z=-18. B) Lesion in the right hemisphere, showing large part of the T4 and posterior part of O4 are spared. C) Left hemisphere lesion in T4 and O4. D) Inferior view of the lesion location with damaged area in white.

Visual field mapping

EP's visual field was tested using a computerized visual field mapping task. A high-resolution visual perimetry was administered the same day of fMRI testing with stimuli consisting of small white circles (1° ; stimulus luminance 95 cd/m^2) presented against a dark background (2 cd/m^2) on a 27-inch computer monitor. The stimuli were presented one at a time for 300 ms at each of 64 different positions (16 stimuli for each visual quadrant) with onset and offset signalled by two different sounds. The inter-stimulus interval was 3 sec. The patient was required to fixate and report verbally the detection of any stimulus on the screen and its location. This procedure enabled us to map the patient's visual field within an ideal grid spanning 25° of horizontal and 20° of vertical eccentricity. A visual perimetry was also performed with flickering, instead of static, stimuli. The same procedure as before was used, with the only exception that white circles were presented for 300 ms with a flickering rate of 20 Hz. In agreement with the lesion location, EP showed a scotoma in the upper left visual quadrant spanning approximately 15° horizontally from the center and 10° vertically.

fMRI localizer

EP and 4 age-matched control participants (between 41 to 52 years old, $M = 45.75$, of which 2 were male) also underwent a functional localizer scan in order to locate face and body processing areas. The stimuli were grey-scaled pictures of faces, bodies, tools, and houses, each spanning within a visual angle of 6.92 degrees. Stimuli of the same category were presented in blocks of 12 seconds. Within one block, each stimulus was presented for 450 ms, followed by an interval of 580 ms. The inter-block interval was also 12 seconds. Each category block was presented 5 times in the localizer run. The total length of the localizer run was 540 seconds. Stimuli were back-projected onto a screen behind the participants' head. The participants viewed the screen through a mirror attached to the head coil, with a viewing distance of $\sim 75 \text{ cm}$.

There are two versions (A and B) for the localizer run, which only differed in the order of the blocks. EP was scanned with both A and B, 3 of the controls were scanned with A, the 4th one was scanned with B. The localizer was scanned with a T2-weighted gradient echo EPI sequence with 29 slices without gaps, covering the occipital and temporal lobes ($2 \times 2 \times 2 \text{ mm}^3$ resolution, $\text{TR} = 2000 \text{ ms}$, $\text{TE} = 30 \text{ ms}$, flip angle = 90° , matrix size = 128×128). The functional MRI data were analysed in BrainVoyager (Brain Innovation, Maastricht, the Netherlands). The data underwent standard preprocessing steps, including slice scan time correction, 3D motion correction, spatial smoothing ($\text{FWHM} = 4 \text{ mm}$), and temporal filtering (GLM-Fourier filtering of 2

cycles). The datasets were aligned to individual anatomical images and were transformed into Talairach space.

A standard GLM was fitted to the data, with the 4 stimulus categories entered as the main predictors, and the z-normalized motion parameters as confounds. The face and body categories were contrasted against the baseline (faces > baseline, bodies > baseline), and against the other 3 categories (faces > bodies, houses, tools, bodies > faces, houses, tools), respectively. All the results were corrected for multiple comparisons (False Detection Rate < .05).

Controls

Twenty controls were selected from the larger control group who were tested on the FEAST as described in chapter 2). The sample consisted of 9 men (between 47 and 56 years old, $M = 51.9$, $SD = 3.1$) and 11 women (between 50 and 56 years old, $M = 53.0$, $SD = 1.8$). There were no significant age differences between the male and female controls ($F(1,19) = 0.992$, $p = .332$). Unfortunately, as EP's age is on the low end of the age distribution of the middle aged adult (see chapter 2, Figure 1), EP was significantly younger than the average of this control group ($Z = -2.56$, $p < .01$).

Separately, the scores on the Body Emotion Action Stimulus Task (BEAST) were compared to a control group of family and acquaintances of the lab members, without history of psychiatric or neurological problems. In total, six men (between 25 and 37 years old, $M = 31.0$, $SD = 3.8$) and seven women (between 25 and 58 years old, $M = 36.4$, $SD = 10.8$) participated.

Lastly, the scores on the FBC-emotion (FBC-e) task (described below) were compared to a control group of Tilburg University students, without history of psychiatric or neurological problems, who participated for course credit. This sample consisted of 36 students between 18 and 28 years old ($M = 20.8$, $SD = 2.9$). Of those, 23 were female (between 18 and 25 years old, $M = 19.5$, $SD = 2.0$) and 13 were male (between 18 and 28 years old, $M = 22.9$, $SD = 3.1$).

Behavioral testing

EP was tested behaviorally in November 2012 in two separate sessions. He ranked as severely impaired on the BFRT (Benton, Sivan, Hamsher, Varney, & Spreen, 1983) with a score of 10 out of 27. He scored normal on the line length, size, orientation, minimal feature and orientation tasks of the Birmingham Object Recognition Battery tasks (Riddoch & Humphreys, 1992), but abnormally on the object decision task (on which he indicated all animals and tools existed).

Experimental stimuli and design

Facial Expression Action Stimulus Test (FEAST)

EP completed the FEAST as described in chapter 2. He felt the face and house part-to-whole matching task was too difficult for him and was unable to perform the task in a normal manner. Consequently, the experiment was aborted. Also, the canine version of the Facial Expression Matching task was not yet developed at the time.

Body Emotion Action Stimulus Test (BEAST) matching task.

Stimuli. Whole body angry, fearful, happy and sad expressions were taken from the BEAST stimulus database (144 in total, 72 males) (de Gelder & van den Stock, 2011a).

Experiment. Each trial consisted of a stimulus presented on top with two other stimuli underneath (see Figure 2). Trial presentation was unlimited and the participants indicated with a button press whether the left or right stimulus expressed the same emotion as the stimulus on top. The sample-to-match experiment consisted of 48 trials, 12 per emotion condition (half male) with each other emotion appearing as a distracter three times.



Figure 2. Example of the BEAST matching task trial with an angry stimulus on top and an angry target (left) and fearful distractor (right).

Face Body Compound emotion matching task (FBC-e)

Stimuli. The stimuli consisted of 120 face body compounds, of which half were male. The stimulus could be a congruent face body compound (both the face and the body are angry, happy, or fearful), an incongruent face body compound (angry face + happy body, happy face + angry body, fearful face + happy body, happy face + fearful body) or a control stimulus (in which the face or the body was replaced by a grey square). Each condition contained 10 unique identities. See Figure 3 for stimulus examples.

Experiment. The FBC-e consisted of two parts (facial versus bodily expression recognition) with two experimental blocks each (angry versus happy and fearful versus happy). Participants were instructed to indicate the emotion expression of either the face or the body, while ignoring the other part of the stimulus. Half of the participants started with the facial expression task, and the order of the blocks was counterbalanced. Participants responded with the index finger of the right and the left hand, using the P and Q buttons. Each block consisted of 60 randomly presented trials, with an 800 ms stimulus duration and an inter-trial interval of 750-1250 ms. The location of the response alternatives (left versus right) was also counterbalanced across participants.

Facial Expression task. In this part, the participants are asked to indicate the facial expression of the stimuli and contained two blocks. The task had a 2 facial expressions (angry, happy or fearful, happy) versus 3 bodily expressions (angry, happy, condition or fearful, happy, condition) design. Each of the 6 conditions contained 20 trials.

Bodily Expression task. In this part, the participants viewed the same stimuli and the blocks had the same design as the facial expression task, but participants indicated whether the body was fearful or angry.

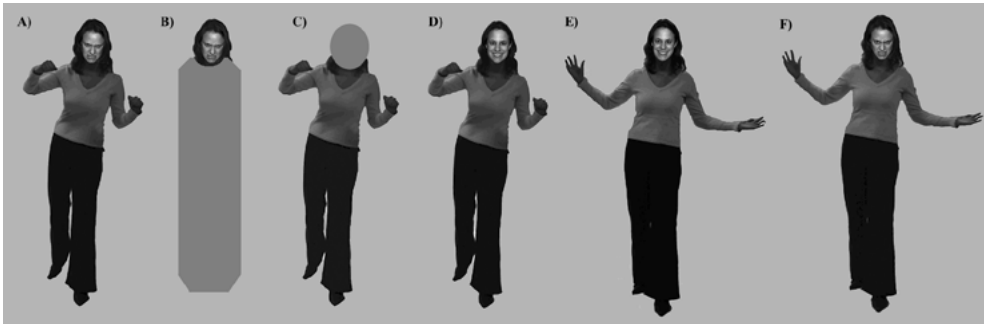


Figure 3. Example face-body compound stimuli of the FBC-e task. A) Congruent stimulus with an angry face and an angry body, B) Angry face control stimulus, C) Angry body control stimulus, D) Incongruent stimulus with a happy face and an angry body, E) congruent stimulus with a happy face and happy body and F) incongruent stimulus with an angry face and happy body.

Analyses

Accuracies were calculated as the total proportion of correct responses for both the total score of each task and for each condition separately. Average response times from stimulus onset were calculated from the correct responses only. For all tasks, reaction times faster than 150 ms were excluded from analyses. In addition, for the face and object matching task, part-to-whole matching task, BEAST and FBC tasks

reaction times longer than 3000 ms were excluded from analyses. For the other tasks, reaction times longer than 5000 ms were excluded from analyses.

The results were analysed using repeated measures GLMs, using the experiment design as within subject variables and age group and gender as between subject variables. Interaction effects were further explored using post-hoc paired samples t-tests. The assumption of equality of error variances was checked with a Levene's test.

To test face and object inversion effects, inversion scores of the faces and objects matching task were calculated by subtracting the accuracy and reaction time scores on the inverted face condition from the upright condition. A positive score indicates that accuracy was higher, or the reaction time was longer, on the upright condition. A negative score indicates higher accuracy or reaction times for the inverted condition.

For the FBC task, difference scores were computed by subtracting the appropriate control condition (faces with a grey body scare or bodies with a grey face) from the variables of interest for each participant. For example, [happy face/happy body]-[happy face/control body]. This way, six conditions are condensed to a 2 face (angry/happy or fear/happy) by 2 body (angry/happy or fear/happy) design controlled for baseline. Positive scores indicate higher accuracy or and reaction times than the control condition, negative scores indicate lower accuracy and lower reaction times than the control condition. Repeated measures GLMs with face (anger, happy/fear, happy) and body (anger, happy/ fear, happy) as within subject variables were run.

To compare the scores from EP with the control group, Crawford and Howell's (1998) t-test scores were calculated with the mean and standard deviations of the control group and interpreted using the t-distribution with $n-1$ degrees of freedom.

Results

Face activation

EP showed preferential face activation (faces > houses, bodies, tools) in the right posterior parahippocampal gyrus, in the posterior part of the inferior occipital sulcus, corresponding to the location of OFA, and a small cluster at the point where the right superior temporal sulcus rises. See Table 2.

Subject	Cluster	Peak voxel			Cluster size (mm ³)
		x	y	z	
EP	R pSTS	55	-41	9	25
	R OFA	35	-76	-11	39
	R Posterior Parahippocampal gyrus	30	-39	-20	97
Controls					
HJ	R pFFA	40	-57	-17	3
	L OFA	-36	-86	-17	2
RP	R aFFA	42	-43	-17	416
	L aFFA	-42	-46	-18	561
	R pFFA	41	-60	-17	948
	R OFA	37	-83	-11	792
	L OFA to pFFA	-42	-84	-10	2191
	R STS	40	-34	8	213
	R Middle Temporal Gyrus	55	-64	15	13
CV	R aFFA	37	-46	-13	86
	L FFA	-38	-35	-13	186
	L Fusiform gyrus	-42	-54	-12	15
	R pFFA	43	-62	-15	53
	L pFFA	-45	-63	-15	221
	R Middle Temporal Gyrus	44	-61	13	10
	R Middle Temporal Gyrus	44	-61	13	10
TW	R aFFA	41	-48	-21	196
	L aFFA	-40	-49	-22	276
	R OFA	38	-71	-14	817
	L OFA	-41	-76	-19	72

Table 2. Clusters locations in Talairach coordinates and cluster sizes that respond more strongly to faces than bodies, tools or houses, FDR < .05 corrected.

Body activation

EP showed normal activation in response to bodies, bilaterally in the EBA and the right FBA. Also, two small clusters in the right STS were found. See Table 3.

		Peak voxel			Cluster size
Subject	Cluster	X	Y	Z	(mm3)
EP	R EBA 1	54	-57	-2	44
	R EBA 2	47	-73	3	150
	R EBA 3	43	-69	-10	76
	L EBA	-55	-69	0	815
	R STS	56	-27	1	34
	R pSTS	46	-39	9	11
	R FBA	37	-40	-21	28
Controls					
HJ	R EBA	37	-64	2	27
RP	R EBA	42	-74	10	1518
	L EBA	-45	-79	10	530
	R FBA	47	-51	-12	252
CV	R EBA	44	-68	16	2305
	L EBA	-46	-67	3	2188
	R FBA	37	-57	-8	120
	L FBA	-43	-43	-12	438
TW	R EBA	44	-64	0	552
	L EBA	-55	-68	1	45

Table 3. Clusters locations in Talairach coordinates and cluster sizes that respond more strongly to bodies than faces, tools or houses, FDR < .05 corrected.

Behavioral testing

Neutral and Emotional Face Memory task (FaMe-N and FaMe-E)

For the control group, no effects of emotion (neutral, fear, happy, sad) were found on accuracy ($F(3,17) = 0.420, p = .741, \eta^2_p = .069$). The AP was significantly impaired on neutral face memory and emotional face memory, with an accuracy of respectively 54% ($Z = -2.79, p < .01$) and 48% (total: $Z = -3.52, p < .005$; Fear: $Z = -2.33, p < .05$, Happy: $Z = -2.79, p < .05$, Sad: $Z = -4.19, p < .001$). Interestingly, he seems to benefit slightly from fearful expression in recollection, as compared to happy or sad, but his performance is still around chance level.

No specific effects of emotion (fear, happy, sad) were found on reaction times, but controls were quicker to recognize emotional rather than neutral faces ($F(3,17) = 4.251, p = .021, \eta^2_p = .429$). In contrast, EP was not significantly slower on any of the tasks (FaMe-N: $Z = 0.04$, FaMe-E: $Z = 0.72$, Fear: $Z = 0.77$, Happy: $Z = 1.39$, Sad: $Z = -0.58$). See Figure 4.

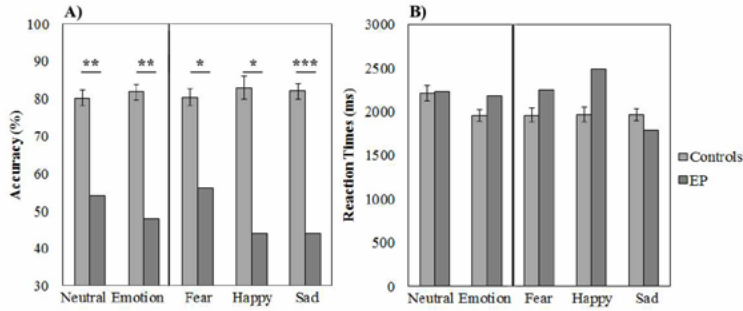


Figure 4. Means and standard error of the means of the A) accuracy and B) reaction times of controls and the AP on the FaMe-N and FaMe-E, * $p < .05$, ** $p < .01$, *** $p < .001$ as calculated with Z-scores.

Faces and objects matching task

The control group showed the expected condition by orientation interaction ($F(1,19) = 13.734$, $p = .001$, $\eta^2_p = .420$), where upright faces are recognized more accurately than inverted faces. EP was significantly impaired in upright face recognition ($Z = 2.90$, $p < .01$), upright shoe matching ($Z = 4.15$, $p < .001$) and inverted shoe matching ($Z = 2.79$, $p < .001$) but not in inverted face matching ($Z = 1.09$). Whereas the controls show a face inversion effect, EP shows a significantly different and paradoxical inversion effect ($Z = 1.81$, $p > .05$), but no difference in object inversion scores were found ($Z = 1.46$).

In contrast, no effects of condition or orientation were found on reaction times in the control group, and EP was equally fast on all conditions (upright faces ($Z = 0.12$), inverted faces $Z = (0.72)$, upright shoes ($Z = 0.40$) or inverted shoes ($Z = 0.23$)). Also, no differences in face ($Z = 1.08$) or shoe ($Z = -0.62$) inversion scores were found. See Figure 5.

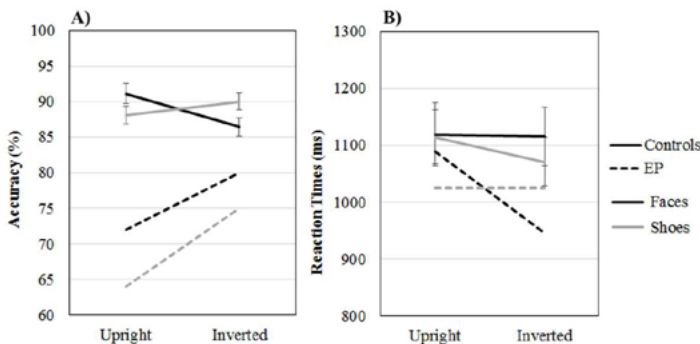


Figure 5. Means and standard error of the means of the A) accuracy and B) reaction times of controls and the AP on the faces and objects matching task.

Facial Expression Matching Task

On the facial expression matching task, EP's overall score was fairly normal ($Z = -1.45$), however, there were large differences depending on the specific emotions. EP was normally able to recognize fear ($Z = 0.42$), sadness ($Z = 0.03$), scored quite low but not significantly different from controls on anger ($Z = -1.45$) and surprise ($Z = -1.45$). In contrast, EP was severely impaired at recognizing happy facial expression recognition ($Z = -8.69, p < .001$) but scored a 100% correct on disgust ($Z = 1.82, p < .05$), which suggests that he confused happy with disgust.

Again, EP was not significantly slower on the task (overall: $Z = 0.36$, anger: $Z = -0.88$, fear: $Z = -1.08$, happy: $Z = 0.78$, disgust: $Z = -0.20$, sadness: $Z = 0.68$) except on surprise matching $Z = 1.79, p < .05$). See Figure 6.

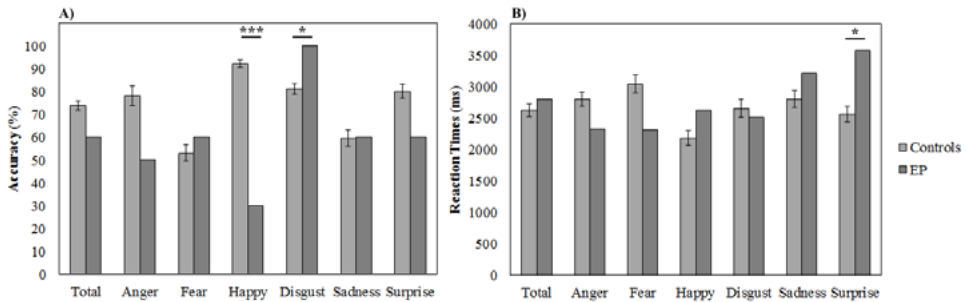


Figure 6. Means and standard error of the means of the A) accuracy and B) reaction times of controls and the AP on the FEM-H. * $p < .05$, *** $p < .001$) as calculated with Z-scores

BEAST matching task

On the BEAST matching task, a main effect of emotion was found for accuracy ($F(3,10) = 13.196, p < .001, \eta^2_p = .80$). Post-hoc contrasts show that fear was recognized the worst (less accurately than anger, $F(1,12) = 8.084, p = .015, \eta^2_p = .40$). See Figure 9. EP was normally able to recognize all emotions (Anger: $Z = -0.68$, Fear: $Z = -0.04$, Happy: $Z = 0.68$, Sad: $Z = 0.70$).

For reaction times, a near significant main effect of emotion was found ($F(3,10) = 3.482, p = .058, \eta^2_p = .51$), probably due to the almost significant lower reaction times on sad as compared to happy ($F(1,12) = 3.474, p = .087, \eta^2_p = .23$). Also, EP was not slower than the controls on this task (Anger: $Z = 0.04$, Fear: $Z = 0.85$, Happy: $Z = 0.03$, Sad: $Z = -0.04$). See Figure 7.

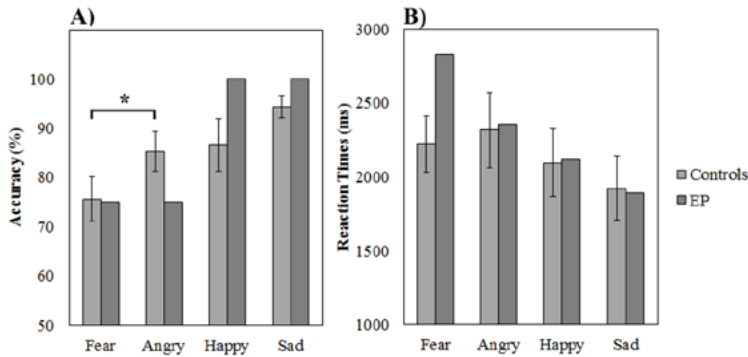


Figure 7. Means and standard error of the means of the A) accuracy and B) reaction times of controls and the AP on the BEAST.

Face Body Compound emotion matching task (FBC-e)

Is the face angry or happy?

A repeated measures GLM with face (angry, happy) and body (angry, happy) as within subject factors was run on the baseline corrected control accuracy data. This resulted in a face by body interaction effect ($F(1,35) = 5.645, p = .023, \eta^2_p = .14$). Paired samples t-test show that when the face is angry, accuracy is the same whether the body is angry or happy ($t(35) = 1.357, p = .183$). In contrast, when the face is happy and the body is angry, accuracy is lower than when the body is also happy ($t(35) = 2.129, p = .040$). No effects were found for reaction times. See Figure 8 and 9 and see Table 4 for the Z scores of EP on all conditions.

Is the face fearful or happy?

A repeated measures GLM with face (fearful, happy) and body (fearful, happy) as within subject factors was run on the baseline corrected control accuracy data. No significant effects were found. See Figure 8 and 9 and see Table 4 for the Z scores of EP on all conditions.

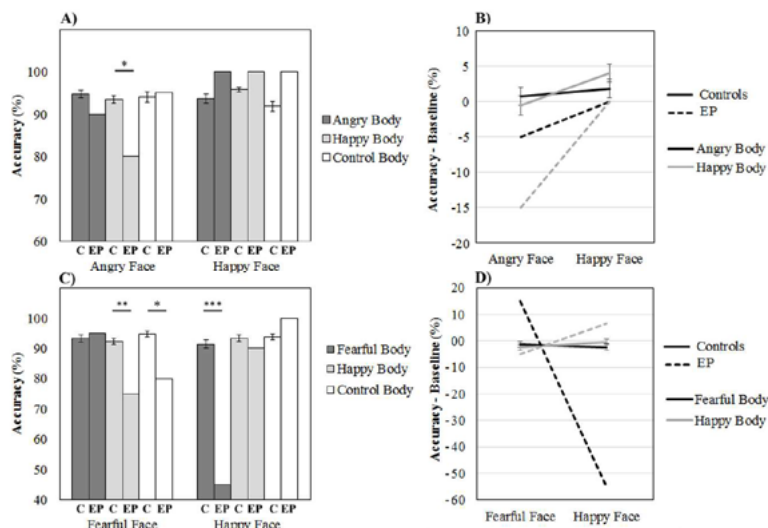


Figure 8. Means and standard errors of accuracy scores of the controls and EP on A) all conditions and B) condition – baseline difference scores on the angry versus happy facial expression task and C) all conditions and D) condition – baseline difference scores on the fearful versus happy facial expression task of the FBC-e. A score of zero in graphs B and D indicate that the score is the same as in the control condition. C = controls. * $p < .05$, ** $p < .01$, *** $p < .001$ as calculated by Z-scores.

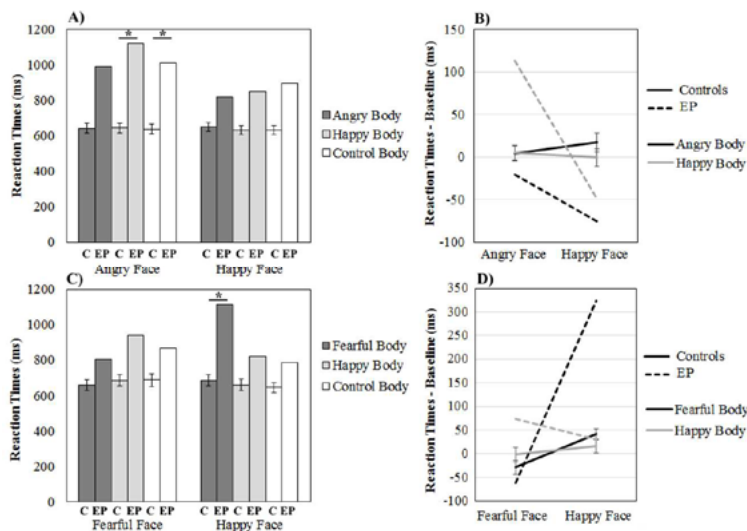


Figure 9. Means and standard errors of reaction times of the controls and EP on A) all conditions and B) condition – baseline difference scores on the angry versus happy facial expression task and C) all conditions and D) condition – baseline difference scores on the fearful versus happy facial expression task of the FBC-e. A score of zero in graphs B and D indicate that the score is the same as in the control condition. C = controls. * $p < .05$, as calculated by Z-scores.

ACC				RT		
Body				Body		
Face	Angry	Happy	Control	Angry	Happy	Control
Angry	-0.92	-2.50	0.13	1.949	2.707	2.308
Happy	0.95	1.26	1.12	1.087	1.410	1.735
Face	Fearful	Happy	Control	Fearful	Happy	Control
Fearful	0.232	-2.817	-2.482	0.842	1.350	0.801
Happy	-5.934	-0.502	1.115	2.189	0.781	0.851

Table 4. Z-Scores of EP on the FBC-e facial expression task. Light grey; $p < .05$. Grey; $p < .01$, Dark grey; $p < .001$).

Is the body angry or happy?

A repeated measures GLM with face (angry, happy) and body (angry, happy) as within subject factors was run on the baseline corrected control accuracy data. This resulted in a face by body interaction effect ($F(1,35) = 12.615, p = .001, \eta^2_p = .27$). Paired samples t-test show two expected congruency effects: accuracy is higher when the body and the face are both angry, as compared to when the face is happy ($t(35) = 3.964, p < .001$). Similarly, accuracy is higher when both the body and the face are happy, as compared to a happy body with an angry face ($t(35) = -2.978, p = .005$). EP shows the same pattern of results. See Figure 10 and 11 and Table 5 for the Z scores of EP on all conditions.

Is the body fearful or happy?

A repeated measures GLM with face (fearful, happy) and body (fearful, happy) as within subject factors was run on the baseline corrected control accuracy data. This resulted in a face by body interaction effect ($F(1,35) = 17.831, p < .001, \eta^2_p = .34$). Again, the paired samples t-test show the same two congruency effects with higher accuracy when the face is congruent with the body in both conditions (fearful body and fearful face versus happy face; ($t(35) = 3.177, p = .003$), happy body and happy face versus fearful face; ($t(35) = -4.789, p < .001$). EP shows the same pattern of results. See Figure 10 and 11 and Table 5

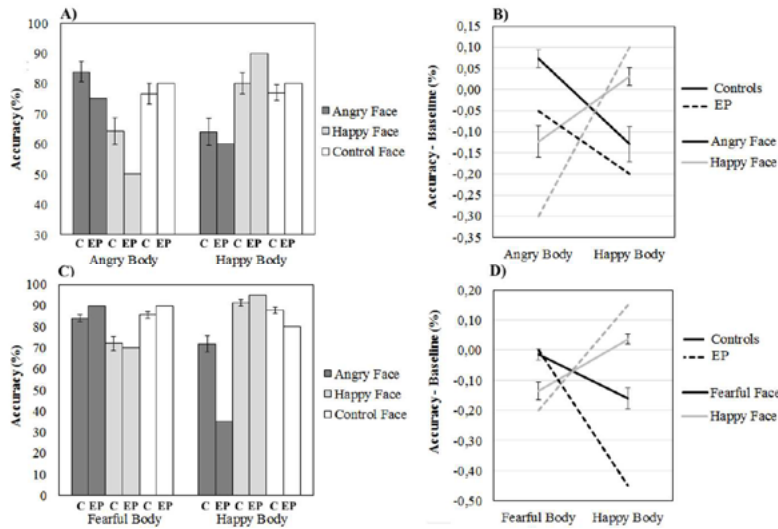


Figure 10. Means and standard errors of accuracy scores of the controls and EP on A) all conditions and B) condition – baseline difference scores on the angry versus happy bodily expression task and C) all conditions and D) condition – baseline difference scores on the fearful versus happy bodily expression task of the FBC-e. A score of zero in graphs B and D indicate that the score is the same as in the control condition. C = controls.

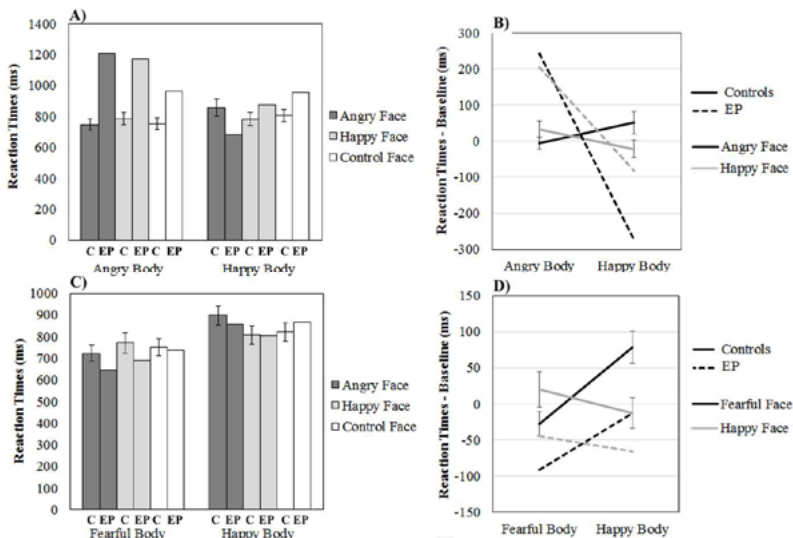


Figure 11. Means and standard errors of reaction times of the controls and EP on A) all conditions and B) condition – baseline difference scores on the angry versus happy bodily expression task and C) all conditions and D) condition – baseline difference scores on the fearful versus happy bodily expression task of the FBC-e. A score of zero in graphs B and D indicate that the score is the same as in the control condition. C = controls.

<u>ACC</u>				<u>RT</u>		
Face				Face		
Body	Angry	Happy	Control	Angry	Happy	Control
Angry	-0,45	-0,53	0,16	1,921	0,767	-0,564
Happy	-0,15	0,48	0,19	0,439	0,198	1,617
Body	Fearful	Happy	Control	Fearful	Happy	Control
Fearful	0,643	-0,100	0,478	0,149	-0,376	-0,094
Happy	-1,518	0,451	-0,870	-0,263	-0,049	-0,165

Table 5. Z-Scores of EP on the FBC-e bodily expression task.

Discussion

In the current study, we report a new case of acquired prosopagnosia on a large set of behavioral tasks testing neutral and emotional face and body recognition. EP has damage to the right anterior occipital gyrus, the middle and posterior fusiform gyrus, inferior lingual gyrus and the left temporal and occipital lobes. Consequently, EP lacks an FFA bilaterally, but parts of the right temporal fusiform gyrus and right posterior occipital gyrus are spared and he shows face specific activation in the right OFA, right STS and right parahippocampal gyrus.

Firstly, we aimed to assess basic face recognition and object recognition abilities of EP and the extent to which he still has intact configural processing. His score on the BFRT was severely impaired. Similar to many other APs described in the literature, EP was very impaired at upright but not at inverted face recognition, in a simultaneous sample-to-match task. As expected, this pattern indicates that his configural processing is disrupted, which often has been associated with damage to the fusiform gyrus, especially the FFA or fusiform gyrus (Barton, 2008; Barton et al., 2001; Barton et al., 2002; Busigny & Rossion, 2010; Caldara et al., 2005; de Gelder et al., 2003b; Fox et al., 2011; Ramon et al., 2010; Riddoch et al., 2008; Rivest et al., 2009; Rossion et al., 2003; Schiltz & Rossion, 2006; Steeves et al., 2006; Susilo et al., 2013; van Belle et al., 2011). Also, this case underlines the importance of a complete face processing network and supports the hypothesis that the presence of an intact right occipital face area is not sufficient for successful face recognition for EP (Pitcher, Walsh, & Duchaine, 2011; Steeves et al., 2006).

A continuing debate in the prosopagnosia literature concerns the specificity of the deficit and whether individuals with prosopagnosia also lost the ability to recognize objects. AP scored normally on all tasks of the BORB, with the exception of the object decision task, in which participants have to indicate whether animals and object are

real (which was also the case with patient FM (Moro et al., 2012) and SM and RN (Behrmann & Kimchi, 2003). However, on the shoe part of the faces and objects recognition task, his scores were well below those of controls. Even though his low level visual processing and object matching as measured with the BORB seem normal, it is hard to say conclusively whether his object recognition is completely normal.

Furthermore, on both the neutral and emotional face memory tasks, his accuracy was severely impaired. This result was quite expected, as almost all cases of APs in the literature are reported to have impaired memory for faces. However, not much is known about the effect of emotion on face memory in AP. EPs pattern of results might suggest that he is slightly better able to remember fearful faces, rather than happy or sad faces, even though his performance is still very much impaired. It has been previously established that emotion, especially fear, can influence identity processing (Peelen et al., 2009) but the literature on emotional modulation on memory is inconsistent. Both the finding that emotional expression does not influence memory for controls (Johansson, Mecklinger, & Treese, 2004) and that EP benefits slightly from fearful expressions, are in line with some studies. Fearful expressions very quickly influence visual processing (Righi et al., 2012) and dorsolateral prefrontal cortex (Sergeyev, Lepage, & Armony, 2005) which might lead to enhanced memory for fearful faces in EP.

Another possible confounding factor regarding his results on the emotional face memory task entails his ability to recognize facial expressions in the first place. His total performance on the task in total was comparable to that of controls. In contrast, the pattern of results on happy and disgust recognition seem to indicate that he often confuses happy for disgust whereas his performance on fear and sadness recognition is similar to controls. Spared emotion recognition ability or mild impairments are often found in those APs with damage to the occipital lobes or occipitotemporal/fusiform regions (Bruyer et al., 1983; De Renzi & di Pellegrino, 1998; Fox et al., 2011; Mattson et al., 2000; Riddoch et al., 2008), comparable to EP (but not always, HJA (Humphreys et al., 1993)). On the other hand, anterior temporal lobe or parietal lobe damage (Humphreys et al., 1993; Humphreys et al., 2007; Stephan et al., 2006), or damage to the OFA (Steeves et al., 2006) seems to cause more problems in emotion recognition (but not always, R-AT1, Fox et al., 2011). In short, even though the FFA is modulated by emotion (de Gelder et al., 2003b; Fox, Moon, Iaria, & Barton, 2009; Harry, Williams, Davis, & Kim, 2013; Kawasaki et al., 2012; van den Stock, van de Riet, Righart, & de Gelder, 2008; Xu & Biederman, 2010), these results tentatively point to the conclusion that the fusiform gyrus is not necessary for facial expression recognition. As EP has an intact amygdala, hippocampal gyrus and normal STS and OFA activity, activity in these areas might modulate and facilitate his facial expression recognition and memory for faces (de Gelder et al., 2003b; Garrido,

Barnes, Sahani, & Dolan, 2012; Phelps, 2004; Vuilleumier, Armony, Driver, & Dolan, 2001). It was previously established that emotion can influence configural processing (de Gelder et al., 2003b). APs were better able to match faces based on emotion than on identity and more importantly, the normal paradoxical face inversion effect as found in prosopagnosia was abolished if the faces expressed emotion.

However, in the current study, we cannot pinpoint a reason why EP is impaired at happy recognition and instead tends to interpret expressions as disgust. A similar problem in happy and disgust recognition was reported in AP 'DF' (Steeves et al., 2006). One explanation could be that emotion is also often configurally processed (Calder, Young, Keane, & Dean, 2000; Durand, Gallay, Seigneuric, Robichon, & Baudouin, 2007; Tanaka, Kaiser, Butler, & Le Grand, 2012). Having a configural face processing impairment, he might turn to feature based processing to compare and recognize the emotional expressions instead. Unfortunately, we could not reliably test whole-to-part eye and mouth recognition in EP, but there is quite some evidence that APs are impaired at eye processing and tend to look at the mouth region (Barton, 2008; Bukach, Bub, Gauthier, & Tarr, 2006; de Gelder & Rouw, 2000a, 2000c; Farah, Wilson, Drain, & Tanaka, 1995; Farah, Levinson, & Klein, 1995; Levine & Calvanio, 1989; van Belle et al., 2011), which is also true for patient PS. Contradictorily, happy expressions were found to be the only emotion that can be reliably recognized by the mouth only (Calvo, Fernandez-Martin, & Nummenmaa, 2014), however, Du, Tao, and Martinez (2014) found that it is quite possible to express "happy disgust", in which a smile incorporates action units around the nose, mouth and cheeks usually reserved for disgusted faces. Also, disgust is often expressed with an open mouth in which the teeth are visible, which could be misconstrued for a smile by EP. It is important in future research, or at least in follow up studies with EP, that another task than our own face and house part matching task is used to assess feature processing.

Lastly, we assessed bodily expression recognition and more importantly, the integration of faces and bodies in AP. In healthy participants, facial expression recognition is influenced by bodily expressions. For example, when an angry face is paired with a fearful body or a fearful face with an angry body, the accuracy of recognition decreases and the reaction times increase and this incongruency effect is visible very early during psychophysiological recordings (Meeren, van Heijnsbergen, & de Gelder, 2005). Similarly, if faces are morphed between fearful and happy in several steps, and paired with a happy or fearful body, the facial expression is more likely to be rated as happy when it is paired with a happy body and vice versa, especially when the face is at its most ambiguous (van den Stock, Righart, & de Gelder, 2007). When EP has to choose whether a face is angry or happy without any bodily information (i.e. a grey square), his scores are comparable to those of controls, although he is slower at recognizing angry faces. When the face expresses anger, the

controls are not influenced by the presence of neither a happy nor an angry body. In short, an angry face seems to be a very strong stimulus. However, EP is led by the happy body and is more likely to say that the angry face is happy when it is paired with a happy body and in addition, he is slower than controls in this condition. In contrast, controls are better at recognizing a happy face when it is accompanied by a happy body, but EP is not, even though his scores in all conditions are comparable to controls.

When the face can be either happy or fearful, the results are slightly different. EP is worse on fearful, but not happy face recognition in the control condition.

Furthermore, whereas controls are not influenced by either congruent or incongruent bodily information, EP is again influenced strongly by the presence of a happy body when the face is fearful. Even more striking is the fact that his ability to recognize a happy face drops to below chance, when it is paired with a fearful body, and his reaction time also increases dramatically. When it comes to his ability to recognize bodily expressions, while ignoring the adjacent face, another picture emerges.

Controls show a normal congruency effect of higher accuracy when the facial expression matches the expression of the body, regardless of the emotion. EP's scores are not only comparable in accuracy and reaction times, but the pattern of results is also the same. In short, EP performs normal in all aspects in the body expression recognition task, regardless of facial expression information.

A puzzling finding is that EP is quite impaired at happy recognition in the FEM task, but not the FBC task. Again, it seems that EP tends to confuse happy only with disgust, but not with anger or fear. The task is quite easy in that regard, as the face can be either happy or angry, or happy or fearful.

Lastly, the results are partly in line with those found in developmental prosopagnosia research, where normal body recognition (Duchaine, Yovel, Butterworth, & Nakayama, 2006), normal FBA and EBA activity in response to bodies (van den Stock et al., 2008). Even though configural processing for bodies seems impaired in DP, upright bodies still cause a N170 in response (Righart & de Gelder, 2007b).

Interestingly, DP 'LG' was impaired at facial expression recognition, normally able to recognize emotional bodily expressions without faces, but he didn't show a normal congruency effect or face-body integration when he was asked to recognize facial expressions paired with bodies (Aviezer, Hassin, & Bentin, 2012).

In conclusion, firstly, EP is normally able to recognize happy, fearful and angry bodily expressions. As the fMRI data indicate that he has normal FBA, EBA and STS activation in response to bodies, this is an expected result. It is also in line with the finding that most APs are normally able to process bodies and bodily expressions, with exception

of the one tested by Moro et al. (2012) who had damage to the left EBA and right FBA and close to the right EBA. Secondly, EP is strongly influenced by bodily expressions when he is asked to indicate the emotion of a face. This result is not surprising in light of his facial recognition difficulties but normal body processing. Especially the fact that a fearful body strongly influenced his perception of a happy face seems logical, combined with his apparent problems in happy facial recognition difficulties. Thirdly, it also points to the fact that AP normally integrates facial and bodily information, that he processes a face and a body as a whole.

This initial exploration of a new AP case study has a few limitations. For example, we did not conduct a very exhaustive clinical examination of EP's function, such as his performance in general on neuropsychological tests or fMRI data. However, EP's health and cognitive functioning was very thoroughly assessed over time by his own physician and neurologist. Also, we lacked proper age-matched controls on the behavioral tasks, especially as a student aged sample serves as a control group on the FBC-e task. In chapter 2 we reported that age influences the results on many tasks, however, considering that EP scored normally both in accuracy and reaction times on many (control or non-face) conditions of the tasks, it is not expected that age influences the conclusions to a large extent in this specific case. However, efforts should be made to find more appropriate controls in the future, which is part of the ongoing FEAST project as described in chapter 2. Furthermore, as in chapters 2, 3, 4, we have conducted many different experiments and statistical analyses, on small samples. The results should therefore be carefully interpreted, and the robustness of the findings should be examined by for example testing the explored underlying mechanisms with different tasks. Related to this issue, in the discussion part of this thesis it will be discussed also how single case studies can provide conflicting reports, and therefore it is also important to realise that this is a first, extensive evaluation of a case, the results of which should be carefully interpreted in relation to the current literature. This also applies to fMRI results regarding the functional localiser. Even though this approach is specifically aimed at locating face and body selective areas in a person, the results of EP and the age matched controls show that there is a large variability both in the number of located areas, their location and their size. These issues should be assessed more carefully in the future with more fine-grained fMRI techniques and analyses.

Part 2:
Emotional social interactions
between two or more people

**FROM INDIVIDUAL TO
CROWD PERCEPTION:
how motions and
emotions INFLUENCE
THE PERCEPTION OF
identity, social
INTERACTIONS, and
BODILY MUSCLE
ACTIVATIONS.**

6 |

The Body Action Coding System I. Muscle activations during the perception and expression of emotion

Body postures provide clear signals about emotional expressions, but so far it is not clear what muscle patterns are associated with specific emotions. This study lays the groundwork for a Body Action Coding System by investigating what combinations of muscles are used for emotional bodily expressions and assessing whether these muscles also automatically respond to the perception of emotional behavior. Surface electromyography of muscles in the arms (biceps and triceps) and shoulders (upper trapezius and deltoids) were measured during both active expression and passive viewing of fearful and angry bodily expressions. The biceps, deltoids, and triceps are recruited strongly for the expression of anger and fear expression predominantly depends on the biceps and the deltoids. During passive viewing, all muscles automatically activate during the passive viewing of anger. During fear perception, a clear activation can be seen in the trapezius, deltoid, and triceps muscles, whereas the biceps shows inhibition. In conclusion, this study provides more insight into the perception and expression of emotions in the body.

Adapted from:

Huis in 't Veld, E. M. J., van Boxtel, G. J. M., & de Gelder, B. (2014). *Social Neuroscience*, 9, 249-264.

Introduction

When it comes to emotional responses in the body, Darwin (1872) already suggested a functional link between emotional reactivity and postural responses as a way to react appropriately to the environment. It has already been found in many studies that established that the body responds to emotional stimuli, or that our response to emotion stimuli is influenced by the body or vice versa. For example, the body moves away from or freezes upon the perception of aversive and arousing stimuli (Azevedo et al., 2005; Eerland, Guadalupe, Franken, & Zwaan, 2012; Facchinetti, Imbiriba, Azevedo, Vargas, & Volchan, 2006; Hillman, Rosengren, & Smith, 2004; Horslen & Carpenter, 2011; Lelard et al., 2013; Roelofs, Hagenaaars, & Stins, 2010; Stins et al., 2011). Also, it is easier to move or push towards appetitive stimuli than to aversive stimuli (Chen & Bargh, 1999; Marsh, Ambady, & Kleck, 2005), which is also done with more muscle force (Coombes, Cauraugh, & Janelle, 2006), although this may only be the case if attention is directed towards the affective content of the target (Rotteveel & Phaf, 2004). In addition, flexing or extending the arm has differential effects on picture ratings (Cacioppo, Priester, & Berntson, 1993) or the startle response (Thibodeau, 2011).

Furthermore, studies using transcranial magnetic stimulation (TMS) of the motor cortex showed that action observation is related to motor facilitation of muscles that are used in the execution of the observed movement (Fadiga, Craighero, & Olivier, 2005; Hardwick, McAllister, Holmes, & Edwards, 2012; Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006). This facilitation effect is enhanced by emotion (Baumgartner, Willi, & Jancke, 2007; Coelho, Lipp, Marinovic, Wallis, & Riek, 2010; Coombes et al., 2009; Enticott et al., 2012; Hajcak et al., 2007; Oliveri et al., 2003; van Loon, van den Wildenberg, van Stegeren, Hajcak, & Ridderinkhof, 2010). Interestingly, listening to unpleasant sounds or music (Giovannelli et al., 2013; Komeilipoor, Pizzolato, Daffertshofer, & Cesari, 2013), observing negative scenes (Borgomaneri, Gazzola, & Avenanti, 2013), fearful faces (Schutter, Hofman, & van Honk, 2008) or emotional bodily expressions (Borgomaneri, Gazzola, & Avenanti, 2012) also increase action preparation measured as motor-evoked potentials of muscles in the hands. Finally, there is increasing evidence that affective processing influences activity at the level of the spinal cord. For example, the amplitude of the tendon reflex is increased after watching aversive or sexually arousing stimuli (Bonnet, Bradley, Lang, & Requin, 1995; Both, van Boxtel, Stekelenburg, Everaerd, & Laan, 2005) and two spinal cord fMRI studies showed that negative emotional stimuli result in activity in those parts of the cervical spinal cord that are related to control of the upper limbs (McIver, Kornelsen, & Smith, 2013; Smith & Kornelsen, 2011).

To sum up, it seems likely that there is a link between observing emotion and responses of muscles in the body, not just in the face. However, to assess whether bodily muscles also respond to the perception of emotions and if so, whether they show the same pattern of activation as during the expression of the emotion, it needs to be explored which muscles are used for which emotional expressions. Thus, the aim of the current study is twofold. The first aim is to lay the groundwork for a Body Action Coding System (BACS), describing which muscles are used in the expression of emotion. To make a beginning with this, we focused on four muscles in the shoulders and arms (the upper trapezius descendens, the anterior deltoid, the biceps brachii, and the long head of the triceps brachii) and assessed their involvement in fearful and angry bodily expressions. These muscles were chosen because their function in moving the shoulders (i.e., shrugging) and arms (i.e., raising the arms and bending them) makes them likely candidates for executing angry and fearful body expressions. Also, these muscles have been found to activate during cognitively stressful tasks (Roman-Liu, Grabarek, Bartuzi, & Choromanski, 2013; Willmann & Bolmont, 2012). Therefore, it was hypothesized that these muscles would also activate in response to the perception of emotional bodily expressions.

Method

Participants

Forty-four undergraduates of Tilburg University participated in exchange for course credit. Participants read and signed an ethical consent form according to the Declaration of Helsinki and were screened to assess physical, psychological, and neurological health. Nine students were excluded from the analysis; one subject suffered from muscular dystrophy, one had recently suffered a severe concussion, three did not follow instructions, one was an outlier on age (48 years), and three were left-handed. The recording sessions of five other participants were aborted by the researcher, because the participants indicated they felt unwell. The sample therefore consisted of 30 healthy individuals (two males) between 18 and 26 years old ($M = 20.1$, $SD = 2.2$) with normal or corrected- to-normal vision.

Stimulus Materials and Procedure

The experiments consisted of two emotion conditions: fear and anger. Twenty-four videos of 3000 ms were used, in which an actor opens a door followed by a fearful (12 videos) or angry (12 videos) reaction. These stimuli are well recognized and controlled for movement and emotional intensity (Grezes et al., 2007; Pichon et al.,

2008, 2009, 2012). The face of the actor was blurred. The videos were projected life size on the wall with a projector, in front of the participant who was standing upright. In total, there were 72 randomly presented trials: 36 for the anger condition and 36 for the fear condition with an inter-trial interval (ITI) between 9 and 11 s, during which a black screen with a white fixation cross on the chest height of the stimulus was shown. The experiment was divided in two blocks of 36 trials with a break in between. This procedure was used in both experiments.

Experiment 1: Passive viewing

The participants were instructed to view all the videos while maintaining an upright posture, the head facing forward, feet positioned 20–30 cm apart, squared but relaxed shoulders, and arms hanging loosely next to the body. The participants were asked to stand as still as possible while keeping a relaxed stance and to minimize unnecessary movements, such as moving the head, shifting stance, or tugging at hair or clothing. The participants were told that they would see the same videos as in experiment 1 and instructed to mimic the emotional reaction of the actor. Participants were urged to do this as convincingly as possible using their whole body. The subjects first viewed the whole video adopting the same stance as in experiment 1, and after the offset of each movie imitated the emotional movement of the actor, before returning to their starting position and posture. This was first practiced with the experimenter to assure the subjects understood the procedure. See Figure 1.

Experiment 2: Imitation

Experiment 2 always followed after experiment 1. The order of the experiments was not counterbalanced, to prevent habituation to the videos and to keep the participants naïve to the purpose of the study during the passive viewing experiment.

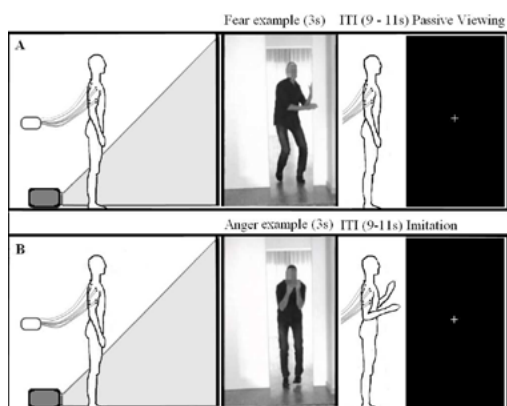


Figure 1. Schematic overview of the experimental setup and trials for experiment 1 (A) and 2 (B).

Electrophysiological recording and analyses

The recordings took place in a dimly lit and electrically shielded room. Bipolar EMG recordings were made from the upper trapezius descendens, the anterior deltoid, the biceps brachii, and the long head of the triceps brachii bilaterally. The location of each electrode was carefully established according to the SENIAM recommendations (Hermens & Freriks, 1997) and cleaned with alcohol. Flat-type active electrodes (2 mm diameter), filled with conductive gel, were placed on each muscle with an inter-electrode distance of 20 mm. Two electrodes placed on the C7 vertebrae of the participant served as reference (common mode sense) and ground (driven right leg) electrodes. EMG data were digitized at a rate of 2048 Hz (BioSemi ActiveTwo, Amsterdam, the Netherlands).

To reduce subject awareness of the aim of the study, the participants were told that the electrodes measured heart rate and skin conductance. The researcher could see and hear the participant through a camera and an intercom. The data were processed offline using BrainVision Analyzer 2.0 (Brain Products). Eight channels were created, one for each recorded muscle bilaterally, by subtracting electrode pairs. These channels were filtered using a band-pass filter (20–500 Hz, 48 dB/octave) and a notch filter (50 Hz, 48 dB/octave). The data were then rectified, smoothed with a lowpass filter of 50 Hz (48 dB/octave) and segmented into 9 1-s epochs including a 1-s pre-stimulus baseline. The epochs were visually inspected and outlier trials were manually removed per channel per condition. There exists a large variance in the baseline or “resting” EMG activity across participants but also across muscles. Thus, outliers were not based on a cut-off criterion. Trials with movement or artifacts in the pre-stimulus baseline and trials with overt movement during the projection of the stimulus were rejected and removed. The remaining trials of each channel were averaged, filtered with 9 Hz, down sampled to 20 Hz and exported.

Statistical analyses

Only channels with at least 30 valid trials per emotion condition were kept for analysis. To examine the development of the EMG signal across time, average EMG amplitude of 500 millisecond bins were calculated and divided by the average EMG amplitude of the first second before baseline presentation. This way, EMG magnitude of 16 time points (8 s), of which the first six time points are during stimulus presentation, was expressed as a proportion compared to pre-stimulus baseline, or in other words, change compared to baseline where 1 is no change, a positive number indicates an increase in EMG amplitude, and a negative number indicates a decrease.

The analyses consisted of fitting linear mixed effects growth models. This technique allows the estimation of individual differences in time course patterns by modeling variances of slopes and intercepts. Also, it is better equipped to handle missing data (such as outliers) or heterogeneous correlations between time points, and it models patterns of activity more flexibly and efficiently than standard ANOVA or repeated-measures ANOVA. In addition, several assumptions for more standard statistic approaches are usually not met by the data, such as homogeneity of regression slopes and case independence, however, this does not pose a problem for multilevel models. To illustrate, the time course of activity of one muscle can be linear, while the other muscle may display a quadratic time course. Also, the outliers per time point per condition can differ. These are problems badly handled by standard ANOVAs, and consequently, multilevel models have been suggested as the standard analysis for psychophysiology studies (Bagiella, Sloan, & Heitjan, 2000). In order to assess whether the EMG signal of a specific muscle changes over time in response to a specific emotion, growth models were fitted to the data after the removal of outliers per time point, starting with a simple model allowing a fixed intercept and a fixed linear effect of time. The model was then extended step by step to include random intercepts, quadratic and cubic effects of time, and random slopes of time. This results in an increasingly complex model with one extra degree of freedom with each step. To assess the model fit, $-2 \log$ likelihood was compared and tested with the chi square distribution. A heterogeneous autoregressive covariance structure (ARH1) was used, which allows for higher correlations between adjacent time points than between time points that are further apart. In this way, the model that best explains the time course of the EMG amplitude of a muscle in response to a specific emotion was determined. Fixed effects represent the overall equation of how EMG activity changes over time, while random effects allow the estimation of an equation for each subject separately. For the passive viewing experiment, all 16 time points were modelled, including the six time points during stimulus presentation. For the imitation condition, only the time period after which the participants started moving was modelled.

Results

The first hypothesis pertains to the question of which muscles we use in the active expression of fearful and angry emotion, thus the results from experiment 2 will be presented first.

Expression of anger

EMG amplitude for angry expressions of the right trapezius muscle showed significant variability across intercepts (Wald $Z = 3.096$, $p = .002$), and a model with a fixed cubic effect of time fits the data well ($F(1, 269.33) = 16.155$, $p < .001$). The EMG time courses of the right deltoid also varied across intercepts (Wald $Z = 2.785$, $p = .005$), and a fixed quadratic effect of time was found ($F(1, 284.70) = 183.681$, $p < .001$). The same was found for the right biceps (Wald $Z = 2.422$, $p = .015$; $F(1, 285.64) = 221.45$, $p < .001$) and the right triceps (Wald $Z = 2.655$, $p = .008$; $F(1, 293.18) = 182.260$, $p < .001$). See Table 1A and Figure 2A.

Unlike the findings of the right trapezius, a model with random intercepts (Wald $Z = 3.005$, $p = .003$) and a fixed quadratic effect of time ($F(1, 267.40) = 124.023$, $p < .001$) was established in the left trapezius. The same model fits well for the left deltoid (Wald $Z = 2.802$, $p = .005$; $F(1, 291.92) = 212.260$, $p < .001$), the left biceps (Wald $Z = 2.317$, $p = .021$; $F(1, 288.83) = 215.778$, $p < .001$), and the left triceps (Wald $Z = 2.650$, $p = .008$; $F(1, 292.79) = 171.51$, $p < .001$). See Table 1B and Figure 2C.

Expression of fear

The EMG time course of the right trapezius during the active expression of fear was best fitted by a model with random intercepts (Wald $Z = 3.351$, $p = .001$) and a fixed cubic effect of time ($F(1, 266.31) = 37.702$, $p < .001$), and the same was found for the right deltoid (Wald $Z = 3.381$, $p = .001$; $F(1, 288.96) = 15.73$, $p < .001$), the right biceps (Wald $Z = 3.408$, $p = .001$; $F(1, 293.75) = 50.496$, $p < .001$), and the right triceps (Wald $Z = 3.254$, $p = .001$; $F(1, 286.68) = 22.160$, $p < .001$). See Table 2A and Figure 2B.

Also on the left side, the EMG activation of the trapezius during fearful emotional expressions shows significant variation in intercepts (Wald $Z = 3.329$, $p = .001$) and a fixed cubic effect of time ($F(1, 264.58) = 22.721$, $p < .001$). This model also fits the time courses for the left deltoid (Wald $Z = 3.235$, $p = .001$; $F(1, 288.30) = 8.149$, $p = .005$), the left biceps (Wald $Z = 3.230$, $p = .001$; $F(1, 290.38) = 52.256$, $p < .001$), and the left triceps (Wald $Z = 2.710$, $p = .007$; $F(1, 284.636) = 40.598$, $p < .001$). See Table 2B and Figure 2D.

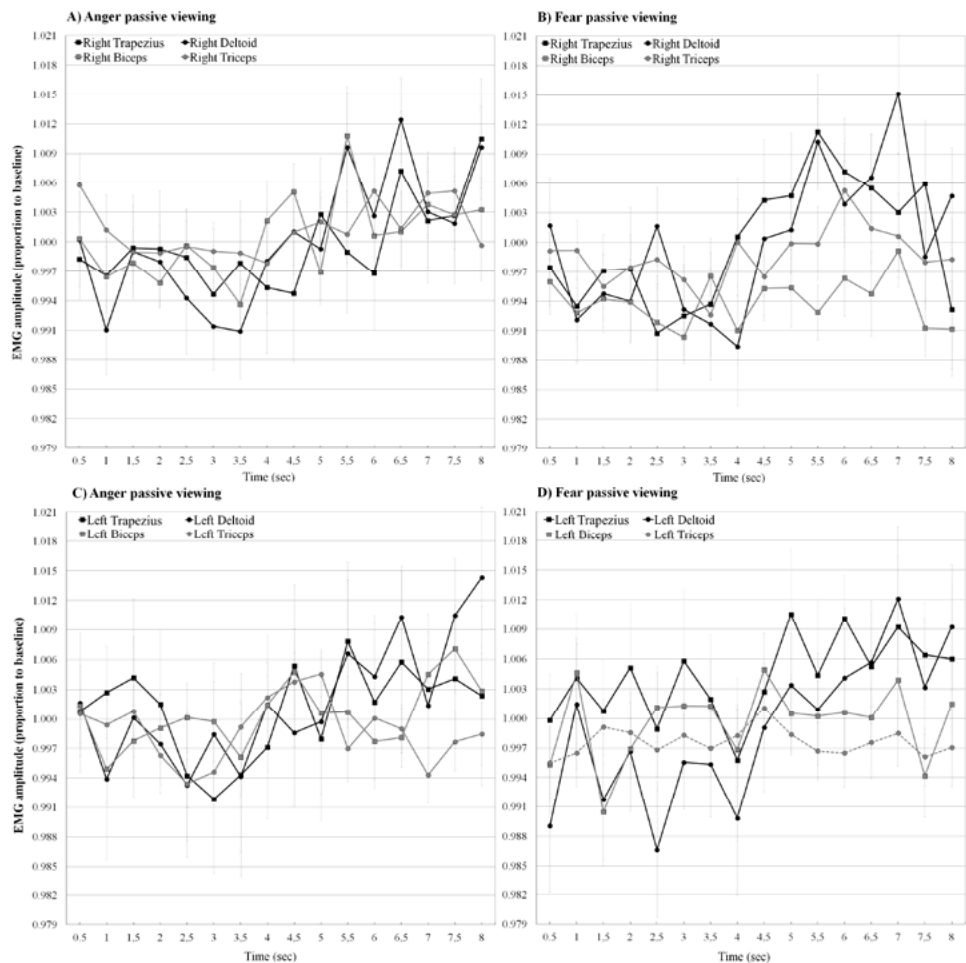


Figure 2. Muscle activations as EMG amplitudes (proportion to baseline) and standard errors of the mean during experiment 1 of active imitation of A) anger and B) fear on the right side of the body and C) anger and D) fear on the left side of the body. The first three seconds represent EMG activity during stimulus presentation.

A) Parameter estimates of effects in the anger imitation condition of muscles on the right.						
	Fixed parameter			Random parameter		
N	B	SE B	95% CI (L)	95% CI (U)	Variance	SE Var
Trapezius 28	Intercept	-16.816632	2.653917	-22.041599	-11.591665	0.423723
	Linear	4.847297	0.791117	3.289732	6.404862	***
	Quadratic	-0.379447	0.074934	-0.526978	-0.231917	***
Deltoid 30	Cubic	0.009108	0.002266	0.004646	0.013569	***
	Intercept	-36.559576	3.231923	-42.920121	-30.199032	4.535052
	Linear	8.187642	0.609520	6.987904	9.387380	***
Biceps 30	Quadratic	-0.370303	0.027323	-0.424083	-0.316523	***
	Intercept	-53.078026	4.298910	-61.538455	-44.617597	5.982452
	Linear	11.960488	0.815990	10.354370	13.566605	***
Triceps 30	Quadratic	-0.545642	0.036666	-0.617812	-0.473472	***
	Intercept	-27.821614	2.394145	-32.532763	-23.110465	2.535705
	Linear	6.233984	0.456561	5.335430	7.132539	***
B) Parameter estimates of effects in the anger imitation condition of muscles on the left.	Quadratic	-0.278014	0.020593	-0.318543	-0.237485	***
	Fixed parameter			Random parameter		
N	B	SE B	95% CI (L)	95% CI (U)	Variance	SE Var
Trapezius 28	Intercept	-7.368409	0.884879	-9.110204	-5.626614	0.584604
	Linear	1.862532	0.168547	1.530683	2.194381	***
	Quadratic	-0.084915	0.007625	-0.099927	-0.069902	***
Deltoid 30	Intercept	-29.107268	2.431887	-33.892811	-24.321724	2.638577
	Linear	6.653852	0.462438	5.743717	7.563987	***
	Quadratic	-0.303527	0.020834	-0.344529	-0.262524	***
Biceps 30	Intercept	-51.124373	4.181579	-59.353725	-42.895020	4.635856
	Linear	11.582544	0.798220	10.011475	13.153614	***
	Quadratic	-0.528522	0.035980	-0.599338	-0.457706	***
Triceps 30	Intercept	-26.770849	2.419585	-31.532155	-22.009543	2.302925
	Linear	6.044664	0.460794	5.137775	6.951552	***
	Quadratic	-0.271910	0.020762	-0.312773	-0.231048	***

Table 1. Parameter estimates, 95% confidence intervals and significance levels of the best fitting model for each muscle on the A) right and B) left in the anger imitation condition. *** $p < .001$.

A) Parameter estimates of effects in the fear imitation condition of muscles on the right.									
		Fixed parameter				Random parameter			
	N	B	SE B	95% CI (L)	95% CI (U)	Variance	SE Var		
Trapezius	28	Intercept	-13.586930	1.774283	-17.080182	-10.0936778	0.363596	0.108490	
		Linear	4.195433	0.527254	3.157318	5.2335472	***		
		Quadratic	-0.352304	0.049878	-0.450508	-0.2541011	***		
		Cubic	0.009260	0.001508	0.006291	0.0122294	***		
Deltoid	30	Intercept	-49.658602	7.469411	-64.359535	-34.9576697	5.257285	1.555001	
		Linear	13.789454	2.23715	9.412720	18.1661876	***		
		Quadratic	-1.066311	0.210437	-1.480495	-0.6521270	***		
		Cubic	0.025229	0.006361	0.012710	0.0377472	***		
Biceps	30	Intercept	-67.983222	7.040261	-81.838563	-54.1278800	4.579910	1.343974	
		Linear	19.675100	2.085134	15.571407	23.7787940	***		
		Quadratic	-1.631923	0.196593	-2.018833	-1.2450140	***		
		Cubic	0.042115	0.005927	0.030451	0.0537792	***		
Triceps	30	Intercept	-26.628178	3.749136	-34.007319	-19.2490374	1.097177	0.337149	
		Linear	7.641949	1.111734	5.453752	9.8301456	***		
		Quadratic	-0.606756	0.104850	-0.813129	-0.4003827	***		
		Cubic	0.014878	0.003161	0.008657	0.0210983	***		
B) Parameter estimates of the effects in the fear imitation condition of muscles on the left.									
		Fixed parameter				Random parameter			
	N	B	SE B	95% CI (L)	95% CI (U)	Variance	SE Var		
Trapezius	28	Intercept	-15.131948	2.489351	-20.0331945	-10.2307014	0.595624	0.178911	
		Linear	4.613153	0.738491	3.159094	6.0672112	***		
		Quadratic	-0.384508	0.069690	-0.521726	-0.2472903	***		
		Cubic	0.010022	0.002102	0.005882	0.0141613	***		
Deltoid	30	Intercept	-38.688450	7.647443	-53.740065	-23.6369339	3.542957	1.095133	
		Linear	10.600930	2.260819	6.151131	15.0507285	***		
		Quadratic	-0.799096	0.212823	-1.217980	-0.3802126	***		
		Cubic	0.018294	0.006409	0.005681	0.0309079	***		
Biceps	30	Intercept	-61.428651	6.126881	-73.487130	-49.3701721	2.388762	0.739662	
		Linear	17.776169	1.824166	14.185906	21.3664322	***		
		Quadratic	-1.467461	0.172590	-1.807147	-1.1277750	***		
		Cubic	0.037710	0.005217	0.027443	0.0479776	***		
Triceps	30	Intercept	-28.473937	3.266751	-34.903845	-22.0440284	0.436227	0.160963	
		Linear	8.332419	0.969981	6.423178	10.2416600	***		
		Quadratic	-0.685778	0.091566	-0.866009	-0.5055462	***		
		Cubic	0.017607	0.002763	0.012168	0.0230459	***		

Table 2. Parameter estimates, 95% confidence intervals and significance levels of the best fitting model for each muscle on the A) right and B) left in the fear imitation condition. *** $p < .001$.

Secondly, it was hypothesized that the muscles involved in the active expression of emotion also show activation during the passive viewing of these emotions. The results of experiment 1 are shown below.

Passive viewing of angry expressions

The EMG time courses of the right trapezius showed significant variance in intercepts across participants (Wald $Z = 2.778$, $p = .005$), and a model with fixed quadratic effect of time ($F(1, 376.87) = 4.317$, $p = .038$) where the effect of time was allowed to vary across

participants (Wald $Z = 2.726$, $p = .006$) fits the data best. The EMG activity of the right deltoids was best explained by a fixed cubic effect of time ($F(1, 434) = 4.651$, $p = .032$) where the intercepts across participants are also allowed to vary (Wald $Z = 3.483$, $p < .001$). For the right biceps, a fixed linear effect of time ($F(1, 420) = 9.691$, $p = .002$) with only varying intercepts was found (Wald $Z = 3.070$, $p = .002$). Last, the EMG amplitudes of the right triceps were found to be cubic ($F(1, 405.05) = 9.164$, $p = .003$) with varying intercepts (Wald $Z = 2.684$, $p = .007$) and time (Wald $Z = 2.654$, $p = .008$). See Table 3A and Figure 3A.

The EMG time course of the left trapezius muscle could be described only by a linear trend in amplitude over time ($F(1, 415.90) = 3.493$, $p = .062$), but the intercepts across participants varied significantly (Wald $Z = 3.585$, $p < .001$). The same model was found to fit the time course of the left deltoid activity (random intercepts; Wald $Z = 3.488$, $p < .001$, linear effect of time; $F(1, 450) = 10.632$, $p = .001$) and left biceps activity (Wald $Z = 3.362$, $p < .001$; $F(1, 447.10) = 4.851$, $p = .028$). No significant model was found for the left triceps. See Table 3B and Figure 3C.

Passive viewing of fearful expressions

EMG activity of the right trapezius was best explained by a fixed cubic effect of time ($F(1, 390) = 12.289$, $p = .001$) with varying intercepts (Wald $Z = 3.219$, $p = .001$). EMG activity of the right deltoid changed linearly ($F(1, 445.80) = 18.48$, $p < .001$) over time also with significant variance across intercepts (Wald $Z = 3.397$, $p = .001$). The EMG time course of the right biceps was best explained by a fixed cubic effect of time ($F(1, 406) = 3.866$, $p = .05$) where the intercepts (Wald $Z = 2.617$, $p = .009$) and slopes of the linear effect of time (Wald $Z = 2.047$, $p = .041$) are allowed to vary across participants. The same was found for the right triceps (random intercepts; Wald $Z = 2.279$, $p = .023$, slope; Wald $Z = 2.363$, $p = .018$, fixed cubic effect of time; $F(1, 420) = 5.460$, $p = .02$). See Table 4A and Figure 3B.

On the left side of the body, EMG amplitudes of the trapezius showed a trend for a fixed linear effect of time ($F(1, 416.98) = 3.249$, $p = .07$) with varying intercepts across participants (Wald $Z = 3.448$, $p = .001$). The same model was found to fit the time courses of the left deltoid (Wald $Z = 3.442$, $p = .001$; $F(1, 450) = 17.801$, $p < .001$). No model could be fitted on the EMG amplitudes of the biceps or triceps. See Table 4B and Figure 3D.

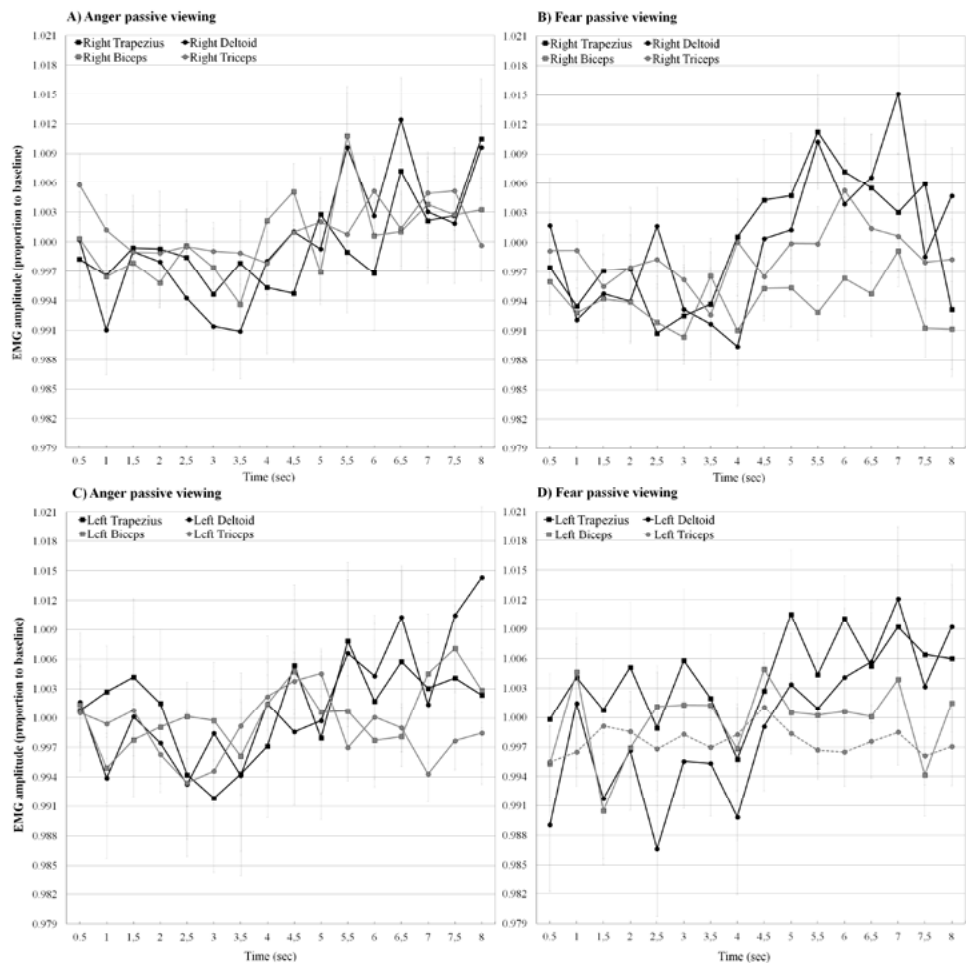


Figure 3. Muscle activations as EMG amplitudes (proportion to baseline) and standard errors of the mean during experiment 2 of passive viewing of A) anger and B) fear on the right side of the body and C) anger and D) fear on the left side of the body. The first three seconds represent EMG activity during stimulus presentation. Activity below one indicates deactivation as compared to baseline.

A) Parameter estimates of effects in the anger condition of muscles on the right.							
		Fixed parameter				Random parameter	
N	B	SE B	95% CI (L)	95% CI (U)		Variance	SE Var
Trapezius 27	Intercept	1.00026	0.004919	0.990394	1.010130	0.000353	0.000127
	Linear	-0.00123	0.000973	-0.003142	0.000685	*	0.000004
	Quadratic	0.00011	0.000052	0.000006	0.000209	*	
Deltoid 29	Intercept	1.00388	0.005832	0.992387	1.015372	0.000285	0.000082
	Linear	-0.00518	0.002429	-0.009955	-0.000406	*	
	Quadratic	0.00077	0.000327	0.000126	0.001411	*	
Biceps 28	Cubic	-0.00003	0.000013	-0.000052	-0.000002	*	
	Intercept	0.99641	0.002123	0.992179	1.000647	0.000065	0.000021
	Linear	0.00048	0.000154	0.000176	0.000780	**	
Triceps 29	Intercept	1.00967	0.003569	1.002623	1.016726	0.000106	0.000039
	Linear	-0.00505	0.001504	-0.008011	-0.002097	***	0.000001
	Quadratic	0.00066	0.000201	0.000265	0.001054	***	
	Cubic	-0.00002	0.000008	-0.000039	-0.000008	**	
B) Parameter estimates of effects in the anger condition of muscles on the left.							
		Fixed parameter				Random parameter	
N	B	SE B	95% CI (L)	95% CI (U)		Variance	SE Var
Trapezius 28	Intercept	0.99884	0.006495	0.985667	1.012014	a	0.000999
	Linear	0.00049	0.000263	-0.000026	0.001009		0.000279
Deltoid 30	Intercept	0.99330	0.005088	0.983091	1.003500	0.000523	0.000150
	Linear	0.00098	0.000301	0.000389	0.001571	***	
Biceps 30	Intercept	0.99725	0.002661	0.991931	1.002570	0.000128	0.000038
	Linear	0.00038	0.000174	0.000041	0.000725	*	

Table 3. Parameter estimates, 95% confidence intervals and significance levels of the best fitting model for each muscle on the A) right and B) left in the anger passive viewing condition. * $p < .05$, ** $p < .01$, *** $p < .001$. ^a $p = .062$.

A) Parameter estimates of the effects in the fear condition of muscles on the right.									
N		Fixed parameter				Random parameter			
		B	SE B	95% CI (L)	95% CI (U)	Variance	SE Var		
Trapezius	26	Intercept	1.005194	0.006722	-0.013098	-0.001707	0.000281	0.000087	
		Linear	-0.007402	0.002897	0.000504	0.002037	**		
		Quadratic	0.001271	0.000390	-0.000083	-0.000023	**		
		Cubic	-0.000051	0.000015	-0.013098	-0.001707			
Deltoid	30	Intercept	0.992060	0.003511	0.985030	0.999090	0.000234	0.000069	
		Linear	0.000949	0.000221	0.000515	0.001383	***		
Biceps	29	Intercept	0.998577	0.004067	0.990547	1.006607	0.000129	0.000049	
		Linear	-0.003026	0.001725	-0.006417	0.000365	0.000001	0.0000004	
		Quadratic	0.000443	0.000231	-0.000011	0.000898			
		Cubic	-0.000018	0.000009	-0.000035	0.000000	*		
Triceps	30	Intercept	1.003527	0.003957	0.995726	1.011327	0.000091	0.000040	
		Linear	-0.003778	0.001766	-0.007248	-0.000307	*	0.000001	0.000001
		Quadratic	0.000556	0.000236	0.000091	0.001020	*		
		Cubic	-0.000021	0.000009	-0.000039	-0.000003	*		
B) Parameter estimates of the effects in the fear condition of muscles on the left.									
N		Fixed parameter				Random parameter			
		B	SE B	95% CI (L)	95% CI (U)	Variance	SE Var		
Trapezius	28	Intercept	0.999970	0.004896	0.990106	1.009834	0.000489	0.000142	
		Linear	0.000474	0.000263	-0.000043	0.000991	a		
Deltoid	30	Intercept	0.988826	0.004600	0.979611	0.998040	0.000410	0.000119	
		Linear	0.001195	0.000283	0.000638	0.001751	***		

Table 4. Parameter estimates, 95% confidence intervals and significance levels of the best fitting model for each muscle on the A) right and B) left in the fear passive viewing condition. * $p < .05$, ** $p < .01$, *** $p < .001$, ^a $p = .07$.

Discussion

The first aim of the current study was to start building a BACS and to assess the involvement of four muscles in the execution of fearful and angry body movement. The results show that the four measured muscles in the shoulders and arms are used in both angry and fearful bodily expressions. However, the extent to which the muscles are recruited show a slightly different pattern. Whereas the biceps, deltoids, and triceps are used strongly for the expression of anger, the expression of fear predominantly depends on the biceps and the deltoids. To create a BACS that specifies in a more discriminate manner what combination of action units uniquely describes specific bodily expressions, we need to extend this research in the future to include more muscles and emotions. However, this combination of the recruited muscle patterns together with the intensity of the muscle response already provides a fairly unique description of the two emotional expressions.

Second, we hypothesized that muscles in the body would also respond automatically to the observation of emotional bodily expressions. The results show that it is indeed possible to detect small but significant activations in bodily muscles. The activation patterns found in the passive viewing experiment overlap, but do not exactly match, the found activation patterns in the imitation experiment. The imitation of anger involves all four muscles to some degree, and all four muscles on the right automatically activate significantly during passive viewing of anger. During fear perception, a clear activation can be seen in the trapezius, deltoid, and triceps muscles, whereas the biceps muscle shows deactivation (Figure 3B). The triceps and biceps may thus play an important role when it comes to discriminating between the expression and observation of anger and fear.

Even though the trapezius does not play a major role in the expression of emotion as compared to the other muscles, this muscle does clearly respond to the perception of emotion, especially fear. This may be related to the function of the upper trapezius in posture stability, whereas it only plays a supporting role in moving the shoulders (Johnson, Bogduk, Nowitzke, & House, 1994). Also, trapezius activity is related sympathetic arousal (Krantz, Forsman, & Lundberg, 2004) and is sensitive to cognitive stressors (Lundberg et al., 2002; Wijsman, Grundlehner, Penders, & Hermens, 2013). Furthermore, muscles in the neck are stimulated by areas related to gaze shifts and orienting such as the caudate nucleus (Akaike, Ohno, & Tsubokawa, 1989) and superior colliculus (Corneil, Olivier, & Munoz, 2002), which are areas also involved in the perception of emotional body language (de Gelder, 2006).

It is interesting to note that all muscles are inhibited during stimulus presentation and activate only after stimulus offset. This may be a result of the interactive nature of the videos. An appropriate response to the person in the video can only be formulated at the offset of the video, because only then the whole emotional action of the other person is

seen. Muscle activity inhibitions have been previously related to orienting responses, anticipation to events, or sound discrimination (Stekelenburg & van Boxtel, 2001, 2002; van Boxtel, Damen, & Brunia, 1996) but may also depend on the specific innervation of the muscle. The muscles in our study are differently innervated from facial muscles and from each other; the trapezius by the spinal accessory nerve (Walker, 1990), the anterior deltoid and triceps by the axillary nerve (de Seze et al., 2004) and the biceps brachii by the musculocutaneous nerve (Schünke, Schulte, Schumacher, Ross, & Lamperti, 2006). Inhibitory responses can be very specific to the situation and vary per muscle within the same person, for example, perceiving pain in another person's hand causes corticospinal inhibition in the corresponding own hand, but excitability in the opposite hand (Avenanti, Minio-Paluello, Sforza, & Aglioti, 2009).

The second aim of the study was to assess whether it is possible to detect small changes in muscle activity without any overt movement. However, without the foundation of a BACS, it is difficult to infer solid conclusions from the results, such as whether the activations found in the passive viewing experiment are the result of processes related to mimicry of the seen movements or whether the same results will be found when participants are subjected to faces, audio, or other non-body-related emotional stimuli such as animals or scenes. Based on previous work related to facial EMG, it can be expected that these activations do not merely reflect a motor mapping of the observed movements and that bodily muscles will also activate in response to these situations (Bradley & Lang, 2000; Dimberg et al., 2000; Grezes et al., 2013; Hietanen et al., 1998; Kret et al., 2013; Magnee et al., 2007b; Tamietto et al., 2009).

The first and most important aim of the current study was to create a BACS that describes what action units are used for expressing emotional expressions. This article is only the first exploration in this direction, and it was decided to start with only fearful and angry expressions.

The Body Action Coding System II.

Muscle activations during the perception and expression of emotion

Research into the expression and perception of emotions has mostly focused on facial expressions. Recently, body postures have become increasingly important in research, but knowledge on muscle activity during the perception or expression of emotion is lacking. The current study continues the development of a Body Action Coding System (BACS), which was initiated in a previous study, and described the involvement of muscles in the neck, shoulders and arms during expression of fear and anger. The current study expands the BACS by assessing the activity patterns of three additional muscles. Surface electromyography of muscles in the neck (upper trapezius descendens), forearms (extensor carpi ulnaris), lower back (erector spinae longissimus) and calves (peroneus longus) were measured during active expression and passive viewing of fearful and angry body expressions. The muscles in the forearm were strongly active for anger expression and to a lesser extent for fear expression. In contrast, muscles in the calves were recruited slightly more for fearful expressions. It was also found that muscles automatically responded to the perception of emotion, without any overt movement. The observer's forearms responded to the perception of fear, while the muscles used for leaning backwards were activated when faced with an angry adversary. Lastly, the calf responded immediately when a fearful person was seen, but responded slower to anger. There is increasing interest in developing systems that are able to create or recognize emotional body language for the development of avatars, robots, and online environments. To that end, multiple coding systems have been developed that can either interpret or create bodily expressions based on static postures, motion capture data or videos. However, the BACS is the first coding system based on muscle activity.

Adapted from:

Huis in 't Veld, E. M. J., van Boxtel, G. J. M., & de Gelder, B. (2014). *Frontiers in Behavioral Neuroscience*, 8, 330

Introduction

To extend the work on the Body Action Coding System, we will turn to the muscles in the forearms, lower back and legs. We chose these muscles based on studies in a more clinical setting have found that psychological factors, such as fear of pain, influence the activation patterns of muscles in the back in chronic lower back pain patients (Geisser, Haig, Wallbom, & Wiggert, 2004; Watson, Booker, & Main, 1997). In addition, Coombes et al. (2006); Coombes et al. (2009) found increased force production and motor evoked potentials of finger and wrist extensors following a negative stimulus. Additionally, muscles in the legs have a different muscle tone if one imagines the self in a painful situation (Lelard et al., 2013).

The current study continues the work on the Body Action Coding System by firstly assessing the role of muscles in the lower back, forearms and calves involved in the expression of fear and anger, and secondly, determine whether it is possible to measure covert responses in these muscles during the passive viewing of emotion.

Method

The stimuli described below, the experimental procedure, EMG data acquisition, processing procedures and statistical analyses are similar to what is reported in the previously mentioned BACS I article (Huis in 't Veld, van Boxtel, & de Gelder, 2014).

Participants

Forty-eight undergraduates of Tilburg University participated in exchange for course credit. Participants read and signed an informed ethical consent form and completed a screening form to assess physical, psychological, and neurological health. The study was approved by the Maastricht University ethical committee. The following participants were excluded from analysis: one subject suffered from hypermobility, one from fibromyalgia, four used medication, three were left-handed, and one did not adhere to the instructions. The data for three participants was of overall low quality and sessions for five participants were aborted by the researcher; two felt uncomfortable standing still (which made them dizzy), two felt uncomfortable in the electrically shielded room (indicating it was oppressive), and one felt unwell. Three participants failed to adhere to the dress code which prevented the measurements of the calf muscles, but all other muscles were measured. The sample therefore consisted of 30 healthy right-handed individuals between 18 and 24 year old, 12 males ($M = 21.2$, $SD = 2.2$) and 18 females ($M = 19.5$, $SD = 2.2$) with normal or corrected-to-normal vision.

Stimulus materials and procedure

The experiments consisted of two emotion conditions, Fear and Anger. Twenty-four videos of 3000 ms were used, in which an actor opens a door followed by a fearful (12 videos) or angry (12 videos) reaction (see Figure 1)). These stimuli have been used in other studies (Grezes et al., 2007; Pichon et al., 2008, 2009, 2012) and are well-recognized and controlled for movement and emotional intensity. The face of the actor was blurred. The videos were projected life-size on the wall, in front of the participant who was standing upright. In total there were 72 randomly presented trials, 36 for the Anger condition and 36 for the Fear condition, with an inter-trial interval (ITI) between 9 and 11 s. During the ITI a black screen with a white fixation cross at chest height of the stimulus was shown. The experiment was divided into 2 blocks of 36 trials with a break in between. The same procedure was used in both experiments.



Figure 1. Stimulus examples. Still frames from an angry (upper) and fearful (lower) stimulus video.

Experiment 1: Passive viewing

The participants were instructed to view all the videos while maintaining an upright posture with the head facing forward, feet positioned 20–30 cm apart, squared but relaxed shoulders and arms hanging loosely next to the body. They were asked to stand as still as possible while keeping a relaxed stance, and to minimize unnecessary movements, such as moving the head, shifting stance, or tugging at hair or clothing.

Experiment 2: Imitation

The participants were told that they would see the same videos as in experiment 1 and instructed to mimic the emotional reaction of the actor. They were urged to do this as convincingly as possible using their whole body. The subjects first viewed the whole video adopting the same stance as in experiment 1, and after the offset of each

movie, imitated the emotional movement of the actor and then returned to their starting position and posture. This was first practiced with the experimenter to ensure the subjects understood the procedure. (see Figure 2). Experiment 2 always followed experiment 1. The order of the experiments was not counterbalanced, in order to prevent habituation to the videos and to keep the participants naïve as to the purpose of the study during the passive viewing experiment.

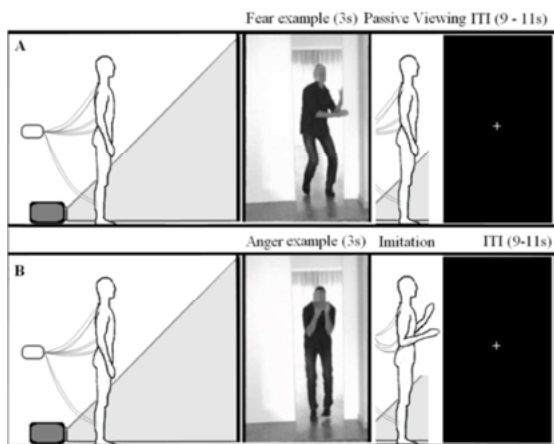


Figure 2 Experimental setup. Schematic overview of the experimental setup for experiment 1 (A) and 2 (B).

Electrophysiological recordings and analyses

The recordings took place in a dimly lit and electrically shielded room. Bipolar EMG recordings were made from the upper trapezius descendens (neck), the extensor carpi ulnaris (the wrist extensors in the dorsal posterior forearm), the erector spinae longissimus (lower back), and the peroneus longus (calf). The erector spinae longissimus in the lower back extends the trunk and is activated by backwards leaning or returning to an upright position after flexion. The peroneus longus in the calves is used in eversion of the foot and planar flexion of the ankle, or pushing off the foot. The location of each electrode pair was carefully established according to the SENIAM recommendations for the trapezius, erector spinae longissimus and the peroneus longus (Hermens and Freriks, 1997). To measure the extensor carpi ulnaris activity, the electrodes were placed on a line between the olecranon process of the ulna and the wrist, on the bulky mass of the muscle, approximately 6 cm from the olecranon process. A schematic overview of muscle and electrode locations can be found in **Figures 5 and 6**, but see the SENIAM recommendations for exact electrode placements (Hermens and Freriks, 1997). The electrode sites were cleaned with alcohol and flat-type active electrodes (2 mm diameter), filled with conductive gel,

were placed on each muscle with an inter-electrode distance of 20 mm. Two electrodes placed on the C7 vertebrae of the participant served as reference (Common Mode Sense) and ground (Driven Right Leg) electrodes. EMG data was digitized at a rate of 2048 Hz (BioSemi ActiveTwo, Amsterdam, Netherlands). To reduce subject awareness of the aim of the study, the participants were told that the electrodes measured heart rate and skin conductance. The researcher could see and hear the participant through a camera and an intercom.

The data were processed offline using BrainVision Analyzer 2.0 (Brain Products). Eight channels were created, one for each recorded muscle bilaterally, by subtracting electrode pairs. These channels were filtered using a band-pass filter (20–500 Hz, 48 dB/octave) and a notch filter (50 Hz, 48 dB/octave). The signal can be contaminated by the ECG signal. If this ECG contamination is stronger in one electrode of a pair, the ECG noise is not removed by subtraction. This is usually the case in the lower back recordings, as one electrode is closer to the heart than the other. In these cases, an independent component analysis was performed, which produces a sets of independent components present in the data, after which the EMG signal was rebuilt without the ECG component (Mak, Hu, & Luk, 2010; Taelman, Mijovic, van Huffel, Devuyt, & Dutoit, 2011). The data was then rectified, smoothed with a low-pass filter of 50 Hz (48 dB/octave) and segmented into 10 one-second epochs including a 1 s pre-stimulus baseline. The epochs were visually inspected and outlier trials were manually removed per channel per condition. Trials with movement or artifacts in the pre-stimulus baseline and trials with overt movement during the projection of the stimulus were rejected and removed. The remaining trials of each channel were averaged, filtered with 9 Hz, down sampled to 20 Hz and exported.

Statistical analyses

Only channels with at least 30 valid trials per emotion condition were kept for analysis. To allow for comparison between participants, the data was normalized by expressing the EMG activity as a proportion to baseline for every muscle and emotion. This proportion was calculated by dividing the average activity of 500 ms bins by the average activity of the 1000 ms pre-stimulus baseline, during which the participant stood in a relaxed stance without any stimulus presentation. A value of one signifies no change, whereas values below one signify deactivation and those above one, activation. This resulted in normalized EMG magnitudes of 16 time points (8 s) in the passive viewing condition and 18 time points (9 s) in the active imitation condition, of which the first six time points are during stimulus presentation. To assess the shape and significance of these EMG time courses for each muscle response to each emotion, multilevel growth models were fitted. These models were built step-by-step, starting with a simple linear model with a fixed intercept and slope, to which quadratic and

cubic effects of time and random intercepts and slopes are added. Every step is tested by comparing the -2 Log Likelihood with a chi-square distribution. For a more detailed explanation and justification for this method, see Bagiella et al. (2000); Huis in 't Veld et al. (2014). For the passive viewing experiment, all 16 time points were modelled, including the six time points during stimulus presentation. For the imitation condition, only the time period after the participants started moving was modelled.

Results

The first hypothesis pertains to the question of which muscles are used in the active expression of fearful and angry emotion and thus, the results from experiment 2 will be presented first.

Expression of anger

All models of time courses of EMG activity in the active anger condition for the muscles on the right benefited from the inclusion of random intercepts, even though the parameters themselves were not always significant (trapezius; Wald $Z = 2.93$, $p = .003$, forearm; Wald $Z = 1.56$, $p > .05$, lower back; Wald $Z = 1.42$, $p > .05$, calf; Wald $Z = 1.38$, $p > .05$). The EMG time courses of the right trapezius, the right forearm and the right calf were best described by a model with a fixed quadratic effect of time (trapezius; $F(1, 255) = 72.78$, $p < .001$, forearm; $F(1, 252) = 205.23$, $p < .001$, calf; $F(1, 237) = 116.22$, $p < .001$), with an additional random effect of time for the forearm (Wald $Z = 1.86$, $p = .06$) and the calf (Wald $Z = 2.59$, $p = .01$). A model with a fixed cubic effect of time ($F(1, 252) = 4.51$, $p = .035$) and a random effect of time (Wald $Z = 2.04$, $p = .04$) best fitted the EMG time course of the right lower back. See Table 1A and Figure 3A.

On the left, the random intercepts did not reach significance but inclusion did improve the models (trapezius; Wald $Z = 1.38$, $p > .05$, forearm; Wald $Z = 1.65$, $p > .05$, lower back; Wald $Z = 1.45$, $p > .05$, calf; Wald $Z = 1.45$, $p > .05$). Trapezius, forearm, lower back and calf EMG time courses were best described by models with a fixed quadratic effect of time (trapezius; $F(1, 249) = 111.69$, $p < .001$, forearm; $F(1, 271) = 194.97$, $p < .001$, lower back; $F(1, 245) = 216.19$, $p < .001$; calf; $F(1, 237) = 108.40$, $p < .001$) and with an additional random effect of time (trapezius; Wald $Z = 2.48$, $p = .013$, lower back; Wald $Z = 1.99$, $p = .047$, calf; Wald $Z = 2.23$, $p = .025$). See Table 1B and Figure 4A.

Expression of fear

Random intercepts were also included in all models on the right (trapezius; Wald $Z = 2.93$, $p = .003$, forearm; Wald $Z = 2.38$, $p = .017$, lower back; Wald $Z = 1.24$, $p > .05$, calf; Wald $Z = 3.01$, $p = .003$). EMG activity of the right trapezius, forearm and calf were found to follow a fixed cubic trend, unlike the quadratic trends found for anger expression (trapezius; $F(1, 253) = 22.01$, $p < .001$, forearm; $F(1, 265) = 29.63$, $p < .001$, calf; $F(1, 246) = 22.69$, $p < .001$). Activity in the lower back also followed a fixed cubic effect of time ($F(1, 248) = 14.50$, $p < .001$) where the slopes vary across participants (Wald $Z = 1.86$, $p = .06$), which was also found for anger expression. See Table 2A and Figure 3B.

On the left, the intercepts varied across participants in all models (trapezius; Wald $Z = 2.77$, $p = .006$, forearm; Wald $Z = 2.51$, $p = .012$, lower back; Wald $Z = 2.65$, $p = .008$, calf; Wald $Z = 3.10$, $p = .002$). Furthermore, the time courses were similar as those on the right side, with cubic effects of time (trapezius; $F(1, 262) = 15.60$, $p < .001$, forearm; $F(1, 239) = 25.61$, $p < .001$, lower back; $F(1, 253) = 4.44$, $p = .036$, calf; $F(1, 269) = 13.41$, $p < .001$). See Table 2B and Figure 4B.

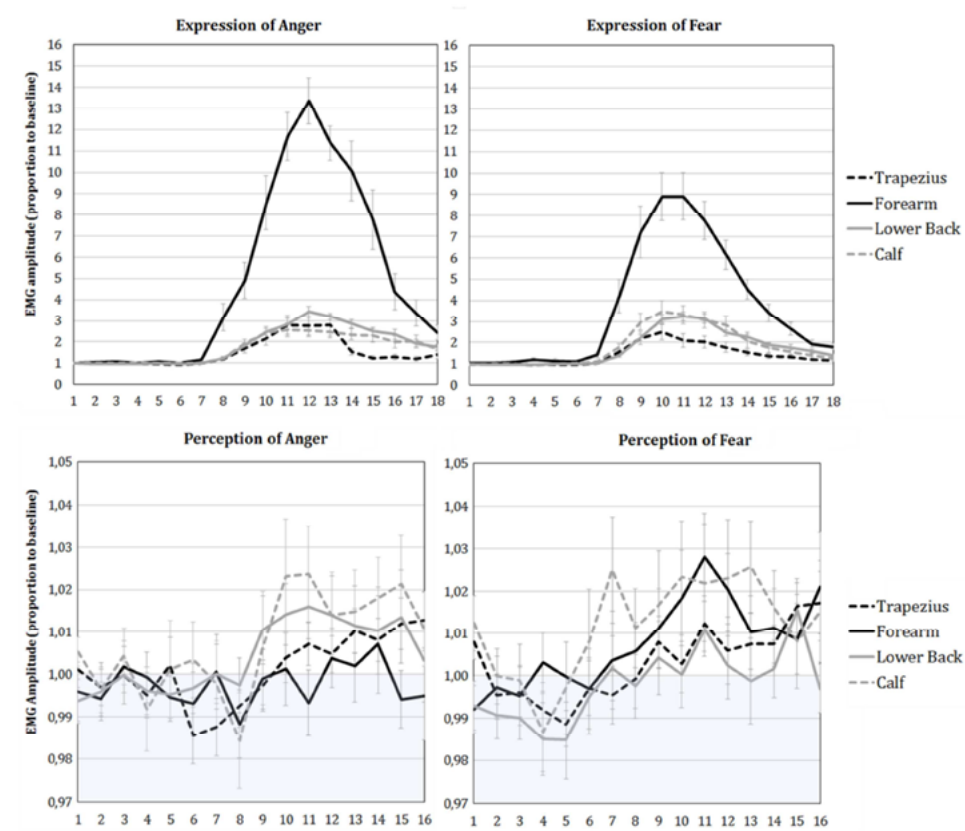


Figure 3. Muscle activations in experiment 1 and 2 on the right side of the body. EMG amplitudes and standard errors of the mean of muscles on the right during active imitation of anger (A) and fear (B) and during passive viewing of anger (C) and fear (D). The first six time points represent EMG activity during stimulus presentation. Activity below one (in grey area) indicates deactivation as compared to baseline.

A) Parameter estimates of the effects in the anger imitation condition of muscles on the right.									
		Fixed parameter				Random parameter			
	N	B	SE B	(L)	(U)		Variance	SE Var	
Trapezius	23	Intercept	-3.988	0.697	-5.360	-2.615	***	0.670	0.229
		Linear	1.039	0.120	0.802	1.275	***		
		Quadratic	-0.042	0.005	-0.052	-0.0326	***		
Forearm	24	Intercept	-34.598	2.938	-40.382	-28.814	16.199	10.370	
		Linear	7.319	0.506	6.323	8.315	***	0.153	0.082
		Quadratic	-0.296	0.021	-0.337	-0.255	***		
Lower Back	23	Intercept	-2.462	1.571	-5.557	0.632	0.332	0.233	
		Linear	0.424	0.433	-0.430	1.279		0.004	0.002
		Quadratic	0.028	0.038	-0.046	0.103			
Calf	22	Intercept	-3.381	0.448	-4.263	-2.499	0.304	0.221	
		Linear	0.896	0.080	0.739	1.053	***	0.010	0.004
		Quadratic	-0.034	0.003	-0.041	-0.028	***		
B) Parameter estimates of the effects in the anger imitation condition of muscles on the left.									
Trapezius	24	Intercept	-2.691	0.388	-3.454	-1.928	0.218	0.158	
		Linear	0.750	0.068	0.615	0.884	***	0.006	0.002
		Quadratic	-0.029	0.003	-0.034	-0.024	***		
Forearm	23	Intercept	-30.766	2.580	-35.844	-25.688	1.258	0.766	
		Linear	6.515	0.456	5.618	7.412	***		
		Quadratic	-0.263	0.019	-0.300	-0.226	***		
Lower Back	23	Intercept	-5.505	0.483	-6.456	-4.555	0.374	0.258	
		Linear	1.302	0.084	1.137	1.468	***	0.005	0.002
		Quadratic	-0.050	0.003	-0.057	-0.044	***		
Calf	22	Intercept	-2.946	0.424	-3.781	-2.111	0.266	0.184	
		Linear	0.802	0.074	0.656	0.948	***	0.005	0.002
		Quadratic	-0.031	0.003	-0.037	-0.025	***		

Table 1. Expression of anger. Parameter estimates, 95% confidence intervals and significance levels of the best fitting model for each muscle on the A) right and B) left in the anger imitation condition. * $p < .05$, *** $p < .001$.

A) Parameter estimates of the effects in the fear imitation condition of muscles on the right.									
N		Fixed parameter			95% CI		Random parameter		
		B	SE B	(L)	(U)		Variance	SE Var	
Trapezius	22	Intercept	-9.720	1.674	-13.017	-6.422	0.345	0.118	
		Linear	2.873	0.464	1.959	3.787	***		
		Quadratic	-0.221	0.041	-0.301	-0.141	***		
Forearm		Cubic	0.005	.001	0.003	0.007	***		
	24	Intercept	-52.953	6.826	-66.392	-39.514	3.882	1.631	
		Linear	14.341	1.881	10.637	18.045	***		
Lower Back		Quadratic	-1.071	0.164	-1.393	-0.749	***		
		Cubic	0.025	0.005	0.016	0.034	***		
Calf	23	Intercept	-10.410	1.491	-13.3463	-7.474	0.238	0.192	
		Linear	2.820	0.413	2.006	3.634	***	0.003	0.002
		Quadratic	-0.189	0.036	-0.260	-0.118	***		
		Cubic	0.004	0.001	0.002	0.006	***		
	21	Intercept	-15.298	2.205	-19.640	-10.955	0.911	0.328	
		Linear	4.256	0.610	3.054	5.458	***		
		Quadratic	-0.312	0.053	-0.417	-0.207	***		
		Cubic	0.007	0.001	0.004	0.010	***		
B) Parameter estimates of the effects in the fear imitation condition of muscles on the left.									
Trapezius	23	Intercept	-9.405	1.804	-12.957	-5.853	0.336	0.121	
		Linear	2.747	0.501	1.762	3.733	***		
		Quadratic	-0.206	0.044	-0.292	-0.120	***		
Forearm		Cubic	0.005	0.001	0.002	0.007	***		
	21	Intercept	-57.413	7.357	-71.905	-42.921	4.546	1.814	
		Linear	15.304	2.029	11.307	19.301	***		
Lower Back		Quadratic	-1.113	0.177	-1.461	-0.765	***		
		Cubic	0.025	0.005	0.015	0.034	***		
	22	Intercept	-9.072	1.922	-12.856	-5.288	0.229	0.087	
		Linear	2.415	0.533	1.366	3.464	***		
		Quadratic	-0.151	0.047	-0.243	-0.059	***		
		Cubic	0.003	0.001	0.0001	0.005	*		
Calf	23	Intercept	-13.382	2.358	-18.025	-8.740	1.058	0.341	
		Linear	3.690	0.651	2.409	4.971	***		
		Quadratic	-0.263	0.057	-0.374	-0.151	***		
		Cubic	0.006	0.002	0.003	0.009	***		

Table 2. Expression of fear. Parameter estimates, 95% confidence intervals and significance levels of the best fitting model for each muscle on the A) right and B) left in the fear imitation condition. * $p < .05$, *** $p < .001$.

It was hypothesized that the muscles involved in the active expression of emotion also show activation during passive viewing of these emotions. The results of experiment 1 are shown below.

Passive viewing of angry expressions

The intercepts of all time courses of muscles on the right in response to anger showed significant variance across participants (trapezius; Wald $Z = 2.72$, $p = .007$, forearm;

Wald $Z = 2.60$, $p = .009$, lower back; Wald $Z = 2.22$, $p = .026$, calf; Wald $Z = 2.72$, $p = .007$). Furthermore, the EMG time course of the right trapezius was best described by a model with a fixed quadratic effect of time ($F(1, 307) = 16.62$, $p < .001$) where the effect of time was also allowed to vary (Wald $Z = 2.43$, $p = .015$). Even though there was a significant variance in intercepts for the EMG time courses of the muscle in the forearm, no significant effects of time could be found. The activity of the lower back followed a cubic trend ($F(1, 336) = 7.23$, $p = .008$) and the best fitting model also allowed the effect of time to vary (Wald $Z = 2.81$, $p = .005$). Finally, a fixed cubic effect of time ($F(1, 253) = 6.09$, $p = .014$) was found for the time course of the calf muscle. See Table 3A and Figure 3C.

Also on the left side, the intercepts of most time courses, with the exception of the calf, showed significant variance across participants (trapezius; Wald $Z = 2.63$, $p = .009$, forearm; Wald $Z = 2.50$, $p = .013$, lower back; Wald $Z = 2.74$, $p = .006$). The same model as found in the right trapezius was also found to fit best, with a fixed quadratic effect of time ($F(1, 308) = 18.80$, $p < .001$) and a random effect of time (Wald $Z = 2.49$, $p = .013$). In contrast to the lack of activity in the right, the left wrist extensors slightly, but significantly, responded to the perception of anger (fixed cubic effect of time; $F(1, 254) = 5.18$, $p = .024$). In the left lower back, a more complicated model was found, with only a significant random, but not fixed, effect of time (Wald $Z = 2.45$, $p = .014$) and a significant covariance between intercepts and slopes (-0.80 , Wald $Z = -8.60$, $p < .001$), signalling that slopes decrease as intercepts increase. Also, a fixed quadratic effect of time ($F(1, 182) = 7.77$, $p = .006$) where the effect of time is also allowed to vary (Wald $Z = 2.23$, $p = .026$) fit the data of the calf best. See Table 3B and Figure 4C.

Passive viewing of fearful expressions

In response to fear, the intercepts of all time courses of muscles on the right also significantly varied across participants (trapezius; Wald $Z = 2.65$, $p = .008$, forearm; Wald $Z = 2.37$, $p = .018$, lower back; Wald $Z = 3.01$, $p = .003$, calf; Wald $Z = 2.34$, $p = .02$). A different model was found for the right trapezius in response to fear than to anger; the best fitting model included a fixed cubic effect of time ($F(1, 294) = 6.94$, $p = .009$) where the effect of time was also allowed to vary (Wald $Z = 1.78$, $p = .07$). The right forearm did respond significantly to the perception of fear, in contrast to the lack of response to anger, with a fixed linear effect of time ($F(1, 208) = 19.96$, $p < .001$). The time course of the right lower back indicates a slight response to fear with a simple fixed linear effect of time ($F(1, 340) = 16.27$, $p < .001$). Similar to the response to anger, a model with a fixed cubic effect of time ($F(1, 252) = 11.99$, $p = .001$) but with an additional random effect of time (Wald $Z = 2.12$, $p = .034$) fit the time course of the calf. See Table 4A and Figure 3D.

On the left side of the body, the intercepts of all models also varied significantly (trapezius; Wald $Z = 2.56, p = .011$, forearm; Wald $Z = 2.36, p = .018$, lower back; Wald $Z = 2.20, p = .028$, calf; Wald $Z = 2.29, p = .022$). EMG amplitudes of the left trapezius followed the same pattern as on the right, with a fixed cubic effect of time ($F(1, 308) = 5.90, p = .016$) with varying slopes across participants (Wald $Z = 2.65, p = .008$). The left forearm also significantly responded to fear, with a fixed cubic effect of time ($F(1, 183) = 14.17, p < .001$) but this model only fit 12 participants. One participant was removed from the analyses on the time courses of the left lower back in response to fear, due to a severely deviant time course. The resulting model included a cubic fixed effect ($F(1, 301) = 9.4, p = .002$) and a random effect of time (Wald $Z = 2.42, p = .016$). Finally, the same model as found in the right calf was found in the left calf in response to fear, with a fixed cubic effect of time ($F(1, 202) = 5.83, p = .017$) but with an additional random effect of time (Wald $Z = 2.31, p = .021$). See Table 4B and Figure 4D.

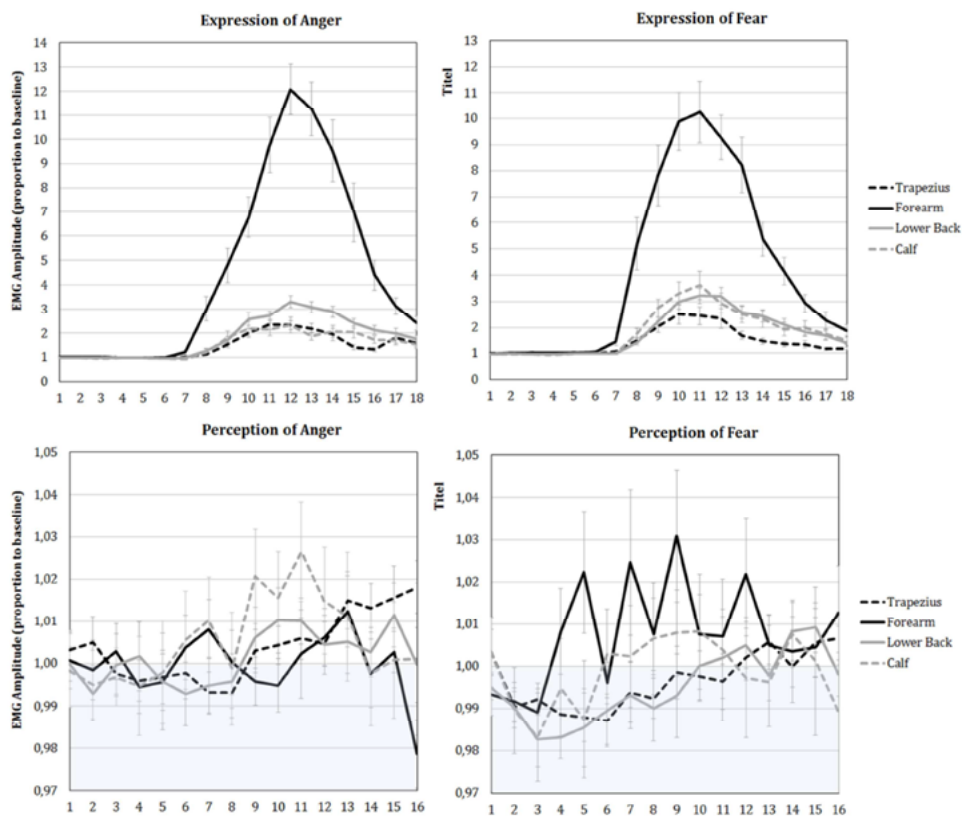


Figure 4. Muscle activations in experiment 1 and 2 on the left side of the body. EMG amplitudes and standard errors of the mean of muscles on the right during active imitation of anger (A) and fear (B) and during passive viewing of anger (C) and fear (D). The first six time points represent

EMG activity during stimulus presentation. Activity below one (in light grey area) indicates deactivation as compared to baseline.

A) Parameter estimates of the effects in the anger passive viewing condition of muscles on the right.								
		Fixed parameter			95% CI		Random parameter	
	N	B	SE B	(L)	(U)	Variance	SE Var	
Trapezius	22	Intercept	1.002	0.005	0.991	1.013	0.0004	0.0001
		Linear	-0.002	0.001	-0.004	-0.0005	*	2.619e-6
		Quadratic	5.070e-5	5.070e-5	0.0001	0.0003	***	
Forearm	16	Intercept	0.996	0.006	0.984	1.008	0.0004	0.0002
		Linear	1.001	0.008	0.986	1.016	0.0003	0.0001
		Quadratic	-0.005	0.003	-0.012	0.001	7.948e-6	2.826e-6
Lower Back	24	Intercept	1.001	0.008	0.986	1.016	0.0003	0.0001
		Linear	-0.005	0.003	-0.012	0.001	7.948e-6	2.826e-6
		Quadratic	0.001	0.0004	0.0002	0.002	*	
Calf	17	Intercept	-4.55e-5	1.69e-5	-7.873e-5	-1.220e-5	***	
		Linear	1.014	0.012	0.991	1.038	0.0008	0.0003
		Quadratic	0.002	0.0006	0.0004	0.003	*	
Calf	17	Intercept	-0.010	0.005	-0.019	-0.001	*	
		Linear	0.002	0.0006	0.0004	0.003	*	
		Quadratic	-6.022e-5	2.441e-5	-0.0001	-1.215e-5	*	
B) Parameter estimates of the effects in the anger passive viewing condition of muscles on the left.								
Trapezius	22	Intercept	1.005	0.005	0.994	1.016	0.0004	2.916e-5
		Linear	-0.003	0.001	-0.005	-0.001	**	3.224e-6
		Quadratic	0.0002	5.370e-5	0.0001	0.0003	***	
Forearm	17	Intercept	1.008	0.009	0.991	1.025	0.0001	0.0005
		Linear	-0.006	0.004	-0.014	0.002		
		Quadratic	0.001	0.0005	3.478e-6	0.002	*	
Lower Back	23	Intercept	-4.620e-5	2.03e-5	-8.609e-5	-6.208e-6	*	
		Linear	0.994	0.007	0.980	1.009	0.001	0.0003
		Quadratic	0.0009	0.0006	-0.0004	0.002	6.629e-6	2.708e-6
Calf	13	Intercept	0.984	0.009	0.966	1.001		
		Linear	0.006	0.002	0.001	0.010	**	1.669e-5
		Quadratic	-0.0003	0.0001	-0.0005	-8.501e-5	**	7.481e-6

Table 3. Passive viewing of angry expressions. Parameter estimates, 95% confidence intervals and significance levels of the best fitting model for each muscle on the A) right and B) left in the anger passive viewing condition. * $p < .05$, ** $p < .01$, *** $p < .001$.

A) Parameter estimates of the effects in the fear passive viewing condition of muscles on the right.									
N		Fixed parameter			95% CI			Random parameter	
		B	SE B	(L)	(U)	Variance	SE Var		
Trapezius	21	Intercept	1.011	0.007	0.997	1.024	0.0004	0.0002	
		Linear	-0.008	0.003	-0.013	-0.003	***	1.258e-6	7.065e-7
		Quadratic	0.001	0.0003	0.0004	0.002	***		
		Cubic	-3.545e-5	1.346e-5	-6.194e-5	-8.956e-6	***		
Forearm	14	Intercept	0.993	0.006	0.980	1.006	0.0004	0.0002	
		Linear	0.002	0.0004	0.001	0.002	***		
Lower Back	23	Intercept	0.986	0.006	0.975	0.997	0.0005	0.0002	
		Linear	0.001	0.0003	0.001	0.002	**		
Calf	18	Intercept	1.014	0.010	0.993	1.035	0.001	0.0003	
		Linear	-0.009	0.004	-0.017	-0.001	*	5.390e-6	2.538e-6
		Quadratic	0.002	0.001	0.001	0.003	***		
		Cubic	-7.415e-5	2.141e-5	-0.0001	-3.198e-5	***		
B) Parameter estimates of the effects in the fear passive viewing condition of muscles on the left.									
Trapezius	22	Intercept	1.007	0.007	0.993	1.021	0.0004	0.0001	
		Linear	-0.008	0.003	-0.013	-0.002	***	4.823e-6	1.820e-6
		Quadratic	0.001	0.0004	0.0003	0.002	***		
		Cubic	-3.480e-5	1.432e-5	-6.299e-5	-6.615e-6	**		
Forearm	12	Intercept	0.985	0.010	0.964	1.005	0.001	0.0003	
		Linear	0.007	0.002	0.004	0.011	***		
		Quadratic	-0.0004	9.819e-5	-0.001	-0.0002	***		
Lower Back	22	Intercept	0.999	0.007	0.985	1.013	0.0004	0.0001	
		Linear	-0.008	0.0035	-0.014	-0.002	**	6.322e-6	2.614e-6
		Quadratic	0.001	0.0004	0.0004	0.002	***		
		Cubic	-4.864e-5	1.586e-5	-7.986e-5	-1.742e-5	***		
Calf	15	Intercept	1.000	0.012	0.976	1.025	0.001	0.0004	
		Linear	-0.006	0.005	-0.015	0.003	1.298e-5	5.628e-6	
		Quadratic	0.001	0.0006	2.343e-5	0.002	*		
		Cubic	-5.645e-5	2.337e-5	-0.0001	-1.037e-5	**		

Table 4. Passive viewing of fearful expressions. Parameter estimates, 95% confidence intervals and significance levels of the best fitting model for each muscle on the A) right and B) left in the fear passive viewing condition. * $p < .05$, ** $p < .01$, *** $p < .001$.

Discussion

The objective of this study was to extend the BACS by assessing the involvement of muscles in the forearms, the lower back and the calves in expressing angry and fearful bodily expressions and additionally, to determine whether these muscles also respond to the observers' passive perception of emotion. It was found that the wrist extensors in the forearm (extensor carpi ulnaris) are very strongly involved in angry and, to a lesser extent, fearful movements. Muscles in the lower back (erector spinae longissimus) were activated equally during the expression of both fear and anger, while the muscles in the calf (peroneus longus) were recruited slightly more for the expression of fear. For the muscles in the neck (upper trapezius descendens), the results from BACS I were replicated, with almost overlapping time courses for fear expression and a similar, but slightly delayed, activation pattern for anger expression. When these results are combined with those of BACS I, it is possible to extract unique patterns of muscle activity for angry versus fearful movements. The biceps were found to be the most important muscle for anger expression, followed secondly by forearm, then by shoulder and lastly by triceps activation. In contrast, a fearful expression was marked by forearm activity, followed by an equally strong involvement of shoulders and biceps, while activity of the triceps is quite low (see Figure 5). Considering the function of the muscles, these findings are in line with previous descriptions of angry and fearful movements, such as raising the forearms to the trunk or stretching the arms downward with palms held up (anger) and lifting the arms with the hands held up protectively with the palms outward (fear) (Coulson, 2004; Dael, Mortillaro, & Scherer, 2012b; Demeijer, 1989; Kessous, Castellano, & Caridakis, 2010; Kleinsmith, De Silva, & Bianchi-Berthouze, 2006; Sawada, Suda, & Ishii, 2003; Wallbott, 1998). See Figure 1 for examples of these movements in the stimuli. Furthermore, similar postures were found to correspond to higher arousal ratings (Kleinsmith, Bianchi-Berthouze, & Steed, 2011).

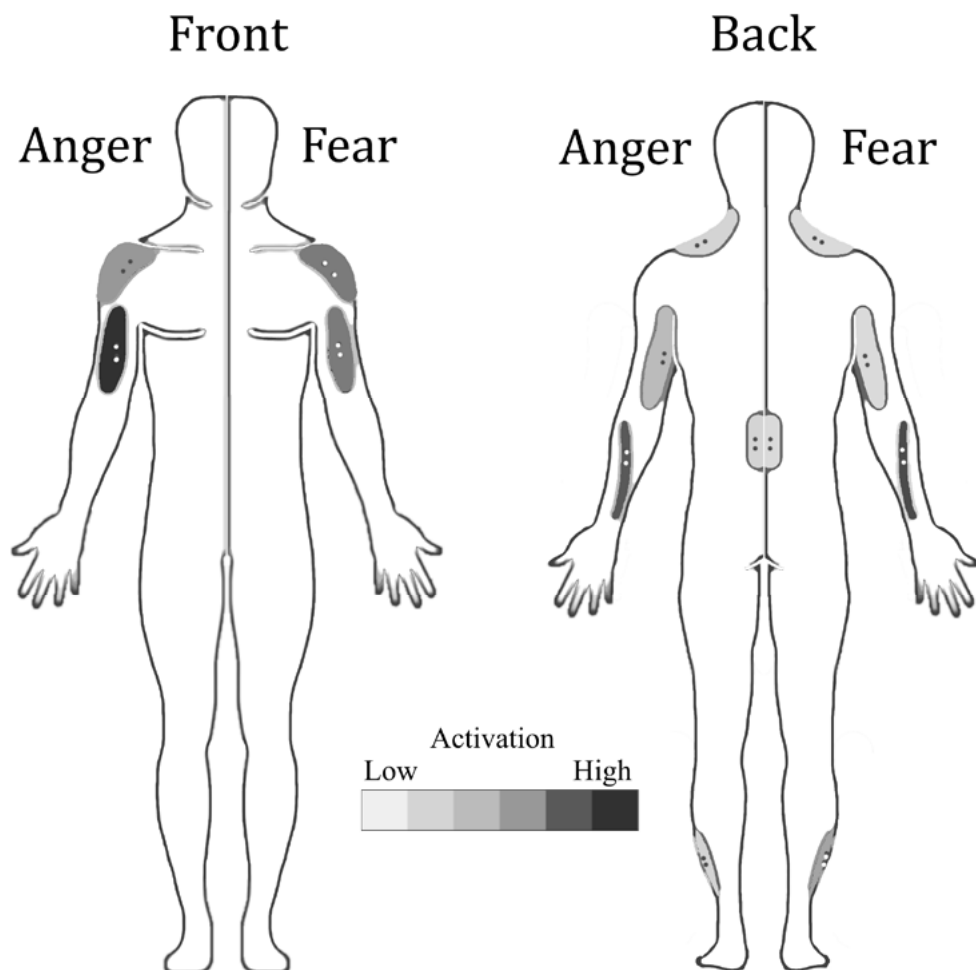


Figure 5 BACS of emotional expression. Schematic overview of the muscles involved in overt fearful and angry emotional expression. Muscles involved in the expression of anger are plotted on the left; those involved in fear expression are plotted on the right. Darker colours indicate a greater involvement. Electrode locations are shown with dots.

The second aim of the study was to assess automatic muscle activations in response to the perception of emotion in others, without any overt movement. The trapezius showed a very similar response both in time (with a quadratic time course for anger and a cubic effect of time for fear) and amplitude as found previously (Huis in 't Veld et al., 2014). The wrist extensors, the most active muscles during fear expression, quite strongly respond only to the perception of fear in others. In contrast, the perception of an angry expression caused a sudden activation of a muscle in the lower back, normally used for leaning backwards. The muscles in the calf strongly activated

in response to both fear and anger, but with very different time patterns. Whereas the response of the calf to an angry person only occurs after the angry movement is directed at the observer (i.e., after stimulus presentation), there is an immediate response when a fearful person is seen (during stimulus presentation). The peroneus longus in the calf aids in pushing off the foot in order to walk or run, and thus this pattern may not be surprising, as it may be imperative to immediately avoid anything that presumably made the other person fearful. In contrast, responding to anger is most relevant when it is directed at the observer (Grezes et al., 2013). Fearful bodily expressions very quickly engage action preparation networks and adaptive response strategies, even without visual awareness or attention (Kret & de Gelder, 2012; Pichon et al., 2012; Tamietto et al., 2009). A similar interaction between the self-relevance of a perceived emotion and the response can be found between eye gaze direction and emotion recognition, where angry facial expressions are easier to recognize with direct eye contact, whereas the opposite is often true for fear (Wieser & Brosch, 2012). In addition, the fact that some of the largest covert activations can be found in the calves, wrist extensors and the lower back are partly in line with previous studies that showed differential activity of these muscles in response to negative stimuli (Coombes et al., 2006, 2009) or pain or fear for pain (Watson et al., 1997; Geisser et al., 2004; Lelard et al., 2013). Similarly, previous studies have found that it is easier to take a step toward a pleasant stimulus and away from an unpleasant one (Chen and Bargh, 1999; Marsh et al., 2005). Furthermore, as the lower back muscle is involved in moving the torso, this might be related to approach-avoidance tendencies (Azevedo et al., 2005; Horslen and Carpenter, 2011; Eerland et al., 2012). In short, these results, taken together with those described in BACS I, indicate that responses to fear and anger can indeed be distinguished by calf, lower back, trapezius, forearm and biceps (de)activation (see Figure 6).

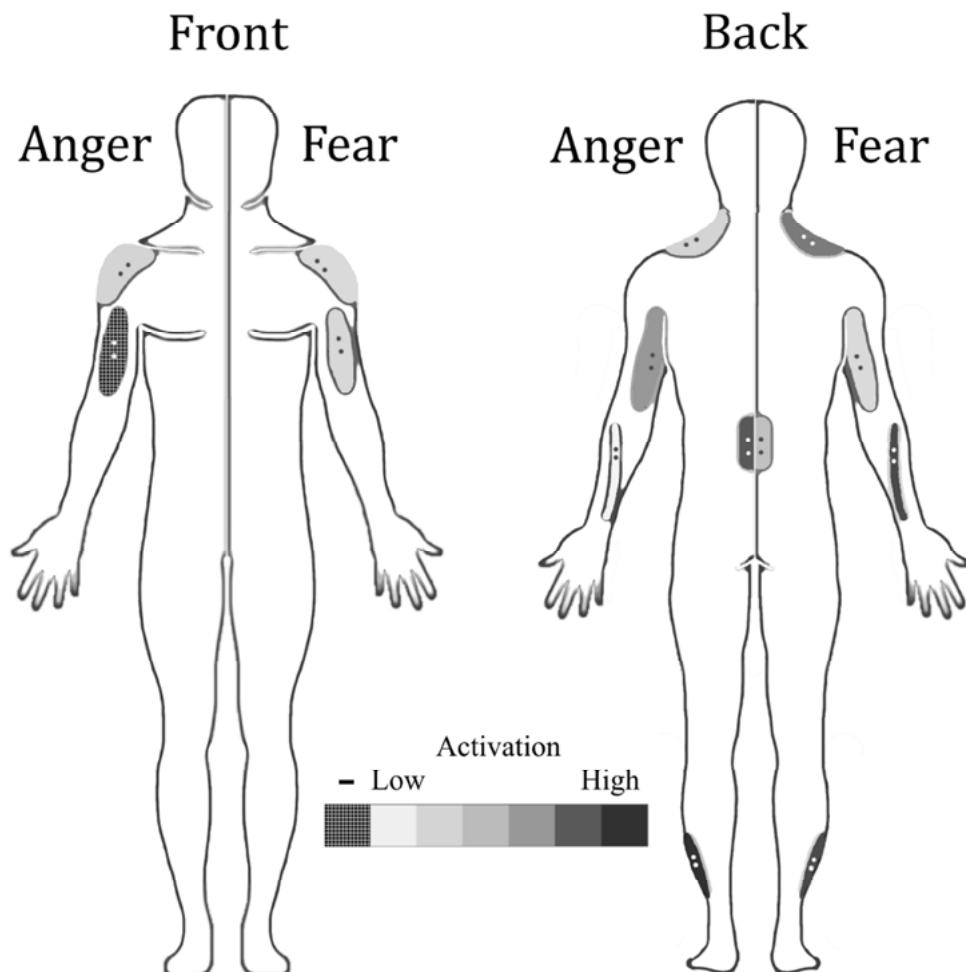


Figure 6 BACS of emotional perception. Schematic overview of muscles that covertly respond to the perception of fearful and angry emotional bodily expressions. Muscles involved in the perception of anger are plotted on the left; those responding to fear perception are plotted on the right. Darker colours indicate a greater involvement, the checker pattern indicates deactivation. Electrode locations are shown with dots.

The BACS now features descriptions of seven muscles during the expression and perception of anger and fear. In order to generalize the BACS it is important to assess the responses of these muscles in relation to other emotions and a neutral condition. As described in Huis in 't Veld et al. (2014), the stimuli used in the present study did not include neutral stimuli containing the same level of movement as their emotional counterparts. It was decided to first expand the BACS by exploring additional muscles, instead of more emotions, as unique muscle activity patterns are difficult to establish

with only four muscles. A follow up experiment, including freely expressed emotions and two control conditions, is currently in preparation. Furthermore, future studies will relate the EMG signal to descriptions of the expressed movement in time and 3D space by using EMG and Motion Capture techniques in concordance. Similar experiments in which participants imitate fixed expressions from video might be improved by using other coding systems such as the Body Action and Posture coding system (BAP; (Dael, Mortillaro, & Scherer, 2012a) or autoBAP (Velloso, Bulling, & Gellersen, 2013). Performing principal component analyses (Bosco, 2010) or calculating which muscles co-contract during the expression of which emotions (Kellis, Arabatzi, & Papadopoulos, 2003), may be suitable methods of statistically appraising which action units are featured for which emotional expressions. Combining these techniques may provide a more complete picture of the specific dynamics of body language and the important contributions of bodily muscles.

From personal fear to mass panic: The neurological basis of crowd perception

Recent studies have investigated the neural correlates of how we perceive emotions of individuals or a group of individuals by using images of individual bodily expressions. However, it is still largely unknown how we perceive the emotion of a dynamic crowd. This fMRI study used realistic videos of a large group of people expressing fearful, happy or neutral emotions. Furthermore, the emotions were expressed by either unrelated individuals in the group or by an interacting group. It was hypothesized that the dynamics between the people in a crowd is a more salient signal than merely the emotion of the crowd. Secondly, it was expected that the group interaction is of special importance in a fearful or 'panic' situation, as opposed to a happy or neutral situation. Using a fast-event related design, it was revealed that observing interactive individuals, more so than independently expressive individuals, activated networks related to the perception, execution and integration of action and emotion. Most importantly, the interactive or panicked crowds, as opposed to the individually fearful crowds, triggered more anticipatory and action preparation activity, whereas the brain was less sensitive to the dynamics of individuals in a happy or neutral crowd. This is the first study to assess the effect of the dynamics between people and the collectively displayed emotion as an important aspect of emotional crowd perception.

Adapted from:

Huis in 't Veld, E. M. J., & de Gelder, B. (2015). *Human Brain Mapping*, 6, 2338 - 2351.

Introduction

In the last decade, many studies have investigated the neuronal correlates of how we perceive the mood of an individual from bodily expressions. But how do we perceive the mood of a crowd? Simmons, Stein, Matthews, Feinstein, and Paulus (2006) used a 'Wall of Faces' paradigm to study what brain regions are recruited when subjects viewed 32 faces simultaneously. Areas such as the ventromedial prefrontal cortex and ventral anterior cingulate cortex (ACC) appear important for the processing of such complex scenes.

However, does the brain perceive a group of people merely as the sum of the individuals in the group? In a task similar to the Wall of Faces paradigm, McHugh, McDonnell, O'Sullivan, and Newell (2010) presented displays consisting of multiple whole body dynamic avatars and found that the emotion of a group is quickly perceived, especially for happiness, fear and sadness. However, these scenarios still do not come close to everyday situations, where movements, interactions and behaviors between other people are very salient signals. For example, observers are able to detect fake or unnatural group behaviors just by subtle body motion cues (Ennis, McDonnell, & O'Sullivan, 2010; McDonnell, Ennis, Dobbyn, & O'Sullivan, 2009) and observers are sensitive to the interaction between group members when judging an individual agents' movement and emotion (Clarke, Bradshaw, Field, Hampson, & Rose, 2005; Hirai & Kakigi, 2009; Manera, Becchio, Schouten, Bara, & Verfaillie, 2011; Neri, Luu, & Levi, 2006). In fact, subtle movement indicators are enough to gauge whether an interaction between two people is a tease or a threat (Sinke, Sorger, Goebel, & de Gelder, 2010).

Previous fMRI studies assessed the underlying neural correlates of these social interactions using stimuli of two humans facing each other (Kujala, Carlson, & Hari, 2012), inviting versus avoiding interactions (Dolcos, Sung, Argo, Flor-Henry, & Dolcos, 2012; Sung et al., 2011) and interacting versus non-interacting (point-light or human) figures (Centelles, Assaiante, Nazarian, Anton, & Schmitz, 2011; Iacoboni et al., 2004; Pierno, Becchio, Turella, Tubaldi, & Castiello, 2008).. These studies indicate that action (extrastriate body area (EBA), hMT+/V5, fusiform gyrus (FG), premotor cortex (PM), precuneus, inferior frontal gyrus (IFG), superior temporal sulcus (STS)) and emotion processing networks (amygdala (AMG), insula, ACC) play a role in the processing of natural social interactions.

Interestingly, all these studies include humans or human figures, but movement alone can be a strong indicator for interaction, even when the agents are non-human like shapes. For example, Castelli, Happe, Frith, and Frith (2000) used animations in which a red and a blue triangle played out different scenarios (chasing, mocking or

surprising each other) or where they moved randomly. Again, areas such as the fusiform gyrus and superior temporal sulcus showed a preference towards the socially interactive stimuli. Additionally, areas related to social perception were found to respond to these kinds of stimuli in similar studies, such as the amygdala, hMT+/V5, dmPFC, posterior cingulate cortex (PCC) and intraparietal sulcus (IPS) (Blakemore et al., 2003; Chaminade, Kawato, & Frith, 2011; Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007; Martin & Weisberg, 2003; Schultz, Friston, O'Doherty, Wolpert, & Frith, 2005; Tavares, Lawrence, & Barnard, 2008).

In conclusion, there is ample evidence that the dynamics between individuals is of equal importance to the emotion of individuals when it comes to accurately judging social interactions. However, not much is known about the neural correlates of perceiving large groups of people, or about the effect of interactions between the people in a crowd. The current study used realistic videos of a large group of people expressing emotion either as individuals or as a group. We tested two hypotheses; firstly whether the brain is sensitive to the difference between individual and interactive expression and secondly, whether this is a function of the emotion expressed. To assess this question, videos showing a crowd of people expressing neutral, fearful or happy bodily expressions, either interacting (for example, "You are at a football stadium together with a group of supporters of your club") or ignoring those around them ("You are happy or fearful, because of personal news you just received, but it has nothing to do with those people around you"), were presented to participants in a fast event-related design. For example, interactively fearful crowds more closely resemble panic situations, whereas interactively happy crowds are more alike to a happy crowd during a sports event. Based on the previous studies it is expected that action perception and body motion networks (among others, the precentral gyrus and the superior and inferior parietal regions; (Grosbras, Beaton, & Eickhoff, 2012)) but foremost those networks involved in both body motion, kinematics and emotion (especially fear) processing, such as the premotor and supplementary motor area (SMA), amygdala, anterior insula, STS, EBA, FG, IFG and the cerebellum (de Gelder, 2006, 2009; Grezes et al., 2007; McAleer, Pollick, Love, Crabbe, & Zacks, 2014; Pichon et al., 2008, 2009, 2012) will be specifically sensitive to the more salient interactively fearful crowds than interactively happy crowds.

Method

Participants

Sixteen right handed participants (3 male; between 19 and 27 years old, $M = 22.7$, $SD = 2.4$) were recruited by an advertisement at Maastricht University. All participants were healthy with no history of neurological or psychiatric illness and had normal or corrected-to-normal vision. All subjects gave informed consent and were paid €10 per hour. The study was performed in accordance to the Declaration of Helsinki and was approved by the local medical ethical committee.

Stimulus materials

Video recordings were made of a group of 17 professional actors (of which 9 were women) expressing happy, fearful, or neutral emotions in either an interactive or individual manner. For the interactive videos, the actors were instructed to express emotion while interacting with the other members of the group. For the individual condition, the actors were instructed to express the emotion while ignoring the other actors. See Figure 1 for example frames. The recordings were made with a HD digital camera (25 frames/second) and edited with Ulead VideoStudio into 2.5 second (s) segments (63 frames, 632 x 416 pixels). The videos were converted to greyscale and low-pass filtered in the spatial frequency domain using Matlab software. This Fourier-based technique filters out high spatial frequencies, resulting in a blurred video clip in which confounding information, such as facial expressions and details on clothing, are removed. The video clips were tested in a validation study in which 18 first year students of Tilburg University categorized the emotion in the clip and indicated whether the people in the group were expressing the emotion interactively or individually. Eight video clips with the best recognition rates (all above 80% correct) for all conditions were selected, resulting in a total of 48 video clips. These video clips were processed further by adding two coloured dots (blue or yellow, lasting 80 ms each) in random frames and in a random location on the frame.

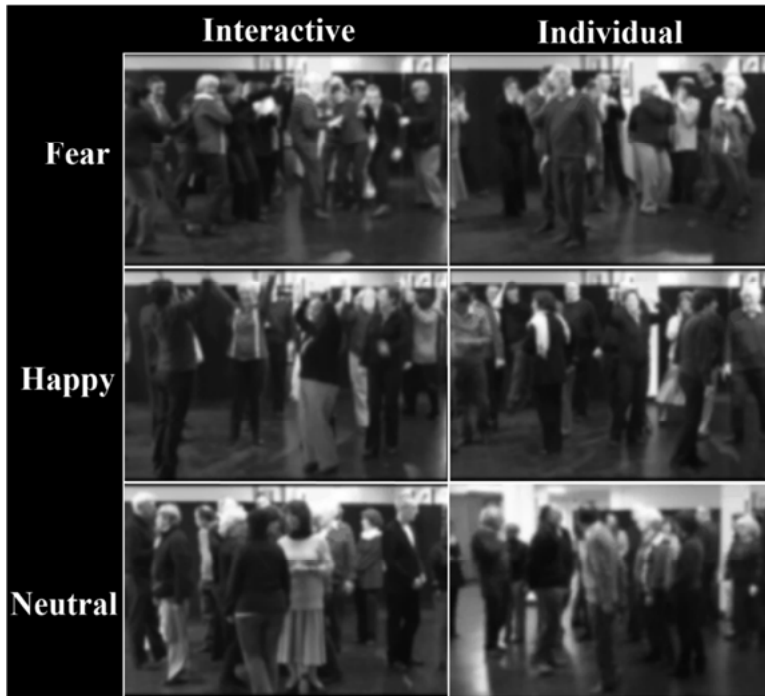


Figure 1. Example frame of each of the stimulus conditions. The videos are blurred using a low pass Fourier-based technique filter.

Twenty-eight other participants from Tilburg University also rated the valence and arousal of these clips on a scale from 1 to 5 using a self-assessment manikin (Bradley & Lang, 1994) and indicated on a scale from 1 to 5 how much movement the video contained. The amount of movement for each video clip was also estimated using a procedure (Pichon et al., 2008) that consists of calculating luminance differences between pixels per frame. Happy videos were seen as more arousing, higher in positive valence and containing more movement than fearful videos, which in turn were more arousing, higher in negative valence and rated as having more movement than neutral videos. Furthermore, interactive fear and happy videos were seen as more arousing and containing more movement than their individual counterparts, while the dynamics did not influence valence or arousal ratings of the neutral videos. Lastly, 15 other participants from Tilburg University rated the amount of movement of still frames taken from the movies. The same pattern of results was found as for the video stimuli. Also, the still frames of the fearful movies were even perceived as having more implied movement than the actual videos. See Figure 2.

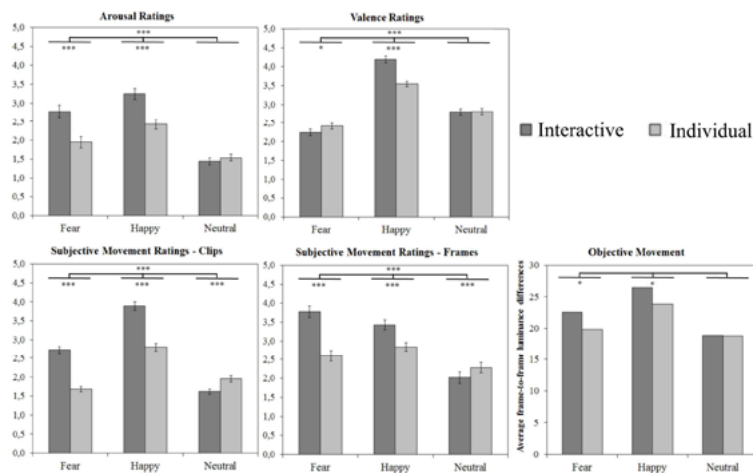


Figure 2. Mean arousal, valence and subjective movement ratings of the stimuli, and mean movement calculated as luminance differences per frame. * $p < .05$, *** $p < .001$.

Experimental design

We created six experimental conditions with a three emotion (neutral, happy and fearful) by two dynamics (interactive or individual) fast-event related design. The experiment was divided into four functional runs of 96 randomly presented trials (48 clips by two repetitions) with a total of 384 trials. Each condition therefore contained a total of 64 trials (eight repetitions of eight unique trials). A trial consisted of the video presentation (2500 ms), an answer screen containing the words “zelfde” (same) or “anders” (different) in Dutch in white letters on a black screen with a duration of 1500 ms, and an inter trial interval of either 2, 4 or 6 seconds showing a white fixation cross on a black background. The forced-choice task for the participants consisted of indicating whether the two dots in the movie were of the same or different color. The response alternatives “same” or “different” appeared randomly left or right of the fixation cross in order to prevent anticipatory responses. The stimuli were back-projected on a frosted screen at the back end of the scanner tunnel and viewed through a mirror attached to the head coil. Stimuli were presented using Presentation software (Neurobehavioral Systems, Inc, version 11.0).

Image acquisition

fMRI images of brain activity were acquired using a head scanner with a magnetic field strength of 3 Tesla (Siemens Allegra, AG, Erlangen, Germany) located at Maastricht University, the Netherlands. High resolution anatomical MRI data were acquired using a three-dimensional (3D) T1-weighted image according to the ADNI sequence protocol: TR = 2250, TE = 2.6, flip angle (FA) = 90°, FoV = 256x256 mm²,

matrix size = 256x256, slice thickness = 1mm, sagittal orientation, total scan time = 8 mins 26 s. The anatomical scan of eight of the participants was acquired during a different run (see Hortensius and de Gelder (2014). The functional images consisted of following repeated single-shot echo-planar imaging sequence: repetition time (TR), 2000; echo time (TE) = 30 ms, (FA) = 90°, field of view (FOV) = 224x224 mm², matrix size = 64x64, slice thickness = 3.5 mm, transversal orientation, number of volumes = 397 per run, total scan time per run = 13 mins 14 s.

Data analyses

Data were pre-processed and analysed using BrainVoyager QX 2.3 (Brain Innovation, Maastricht, the Netherlands). The functional data were slice scan time corrected using cubic spline interpolation, aligned to the first non-discarded scan time, 3-dimensional motion corrected using a trilinear/sinc interpolation and temporal high-pass filtered (GLM-Fourier) with 2 cycles per data point. The first two volumes were discarded. The ADNI scan was transformed into Talairach space (Talairach and Tournoux, 1988). After co-registration the functional runs were also Talairach transformed and spatially smoothed with an 8mm Gaussian kernel. At single subject level, the data of each functional run was deconvolved, using the standard procedure for analysing fast-event related designs in Brain Voyager. In short, the hemodynamic responses to the overlapping events are separated by modelling 10 shifted 'delay' predictors, resulting in a design with 66 predictors, 10 predictors per condition to model the BOLD response at several delays, and an additional 6 z-transformed movement predictors. Then, a random effects multi-subject general linear model was conducted.

As contrasts are not a suitable analysis method for this design, random effects ANOVAs were performed. These analyses show in which areas a main effect of emotion, a main effect of dynamics or an interaction between emotion and dynamics are found. The resulting clusters were corrected for multiple comparisons using a cluster level threshold analysis with an initial p-value of $p < .005$ (Goebel, Esposito, & Formisano, 2006). Four very extensive clusters covering most of the occipital lobe were found for the main effect of emotion using this threshold, so these four clusters were corrected more stringently with a false discovery rate (FDR) of $< .01$. These are indicated in the results (see Table 1). Also, two very large clusters in the inferior occipital gyrus and cerebellum were found for the main effect of dynamics, these were also more strictly corrected with a cluster level threshold analysis with an initial p-value of $p < .001$ (as indicated in Table 2). The ANOVA only specifies in which areas a main or an interaction effect can be found, but does not show which conditions are higher or lower than the others. To assess the underlying pattern of the results, beta values of the clusters were exported and explored in SPSS using repeated measures GLMs with a three emotion (fear, happy, neutral) by two dynamics (interactive,

individual) within-subject design. It is important to note that these statistics are not reported but only used to explore the main and interaction effects and to order the results in the tables.

Results

All participants scored higher than 99% correct on the dot detection task and hence, those results were not further analysed.

Main effect of emotion.

The BOLD responses were higher in the fear condition than in the happy and neutral condition in the left FG, the left insula and the left inferior frontal gyrus (IFG) (see Table 1A). Two other regions showed a preference for both the fearful and happy conditions compared to neutral: the left middle occipital gyrus (MOG), probably corresponding to the hMT+/V5, extending to the middle temporal gyrus (MTG) and the superior temporal gyrus (STG), and the right temporal pole (TP) (see Table 1B). The majority of brain areas were more active during the fear and neutral conditions, as compared to the happy condition. These included the right postcentral gyrus (somatosensory cortex), the right inferior parietal lobule (IPL), the right superior parietal lobule (SPL), the left ventral anterior cingulate cortex (ACC), the left precuneus, the right precuneus and the right superior frontal gyrus (SFG) (see Table 1C). Three regions showed the most activation in response to the happy stimuli and lowest activation in the neutral condition; the right MOG (or hMT+/V5), extending to the right middle temporal, inferior and superior temporal gyri and the right cuneus. In the left cuneus, almost the same pattern was found, except there were no differences between the neutral and the fearful condition (see Table 1D). Finally, three regions showed the highest BOLD response in the neutral condition; the precentral gyrus (premotor cortex), a region in the anterior lobe of the cerebellum and the left SFG (see Table 1E). Also, see Figure 3.

Anatomic region		X	Y	Z	Voxels 1x1x1	F	Peak Voxel <i>p</i>
A. Fear > Happy + Neutral							
Fusiform Gyrus	L	-46	-35	-15	1557	13.49	<i>p</i> = .000066
Insula	L	-28	19	3	191	8.16	<i>p</i> = .001476
Inferior Frontal Gyrus	L	-43	52	-6	108	7.46	<i>p</i> = .002342
B. Fear + Happy > Neutral							
Middle Occipital Gyrus ^a	L	-52	-71	9	2732	33.73	<i>p</i> = .000001
Temporal pole	R	44	7	-36	186	9.26	<i>p</i> = .000737
C. Fear + Neutral > Happy							
Postcentral gyrus	R	35	-26	42	203	7.08	<i>p</i> = .003029
Inferior Parietal Lobule	R	38	-68	33	287	10.42	<i>p</i> = .000365
Superior parietal lobule	R	17	-59	51	591	10.97	<i>p</i> = .000265
Ventral Anterior Cingulate Cortex	L	-7	10	24	346	8.25	<i>p</i> = .001389
Precuneus	R	26	-59	9	230	9.36	<i>p</i> = .000692
Precuneus	L	-10	-62	6	275	8.62	<i>p</i> = .001097
Superior Frontal Gyrus	R	29	43	3	653	9.08	<i>p</i> = .000824
D. Happy > Fear + Neutral							
Middle Occipital Gyrus ^a	R	47	-65	0	3636	27.80	<i>p</i> = .000001
Cuneus ^a	R	17	-89	9	2071	26.18	<i>p</i> = .000001
Cuneus ^a	L	-10	-95	9	429	20.64	<i>p</i> = .000002
E. Neutral > Fear + Happy							
Precentral gyrus	R	29	-14	54	107	9.66	<i>p</i> = .000576
Cerebellum	R	11	-44	-9	247	8.66	<i>p</i> = .001074
Superior Frontal Gyrus	L	-25	40	0	467	11.30	<i>p</i> = .000219

Table 1. Main effect of emotion. Cluster sizes, peak voxel locations in Talairach space, and F and *p*-values of clusters with a significant main effect of emotion. Cluster size threshold corrected, *p* < .005, *a* = correction at FDR < .01.

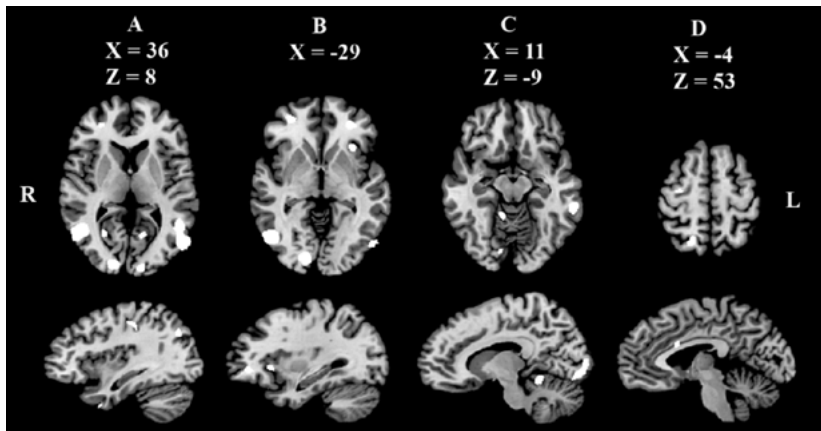


Figure 3. Areas with a main effect of emotion in the whole brain analysis. A) Right SFG, bilateral MOG, bilateral cuneus, right precuneus, left lingual gyrus, right postcentral gyrus, right IPL, and right TP. B) Bilateral SFG, left insula, bilateral MOG, right cuneus. C) Right cerebellum, right cuneus, left FG. D) Right precentral gyrus, right SPL, left ACC.

Main effect of dynamics.

Only areas with a higher BOLD response in the interactive than in the individual condition were found. See Table 2 and Figure 4.

Anatomic region		X	Y	Z	Voxels 1x1x1	F	Peak voxel p
Posterior ACC	R	8	-11	42	425	19.84	$p = .000463$
Fusiform Gyrus	R	38	-47	-15	1203	20.65	$p = .000387$
Fusiform Gyrus	L	-46	-41	-15	366	16.57	$p = .001002$
Inferior Occipital Gyrus ^a	L	-43	-74	3	6056	33.44	$p = .000036$
Lingual Gyrus ^a	R	26	-89	-6	3294	38.13	$p = .000018$
Extrastriate cortex	L	-34	-80	-12	13192	34.82	$p = .000029$
Middle Temporal Gyrus	R	41	-62	9	5775	34.07	$p = .000033$
Supramarginal Gyrus	R	62	-32	24	131	14.24	$p = .001837$
Precuneus	L	-31	-62	36	856	22.15	$p = .000281$
Postcentral Gyrus	L	-49	-35	45	163	13.32	$p = .002367$
Precentral gyrus	L	-25	-14	60	126	16.99	$p = .000904$
Superior Temporal Sulcus	L	-49	-41	18	801	18.00	$p = .000709$
Cerebellum	L	-10	-50	-30	362	20.79	$p = .000376$
Cerebellum	L	-16	-35	-27	430	19.31	$p = .000522$
Cerebellum ^a	L	-40	-65	-27	86	27.77	$p = .000094$

Table 2. Main effect of dynamics. Cluster sizes, peak voxel locations and p-values of clusters with a significant main effect of dynamics. Cluster size threshold corrected, $p < .005$, a = cluster size threshold corrected, $p < .001$.

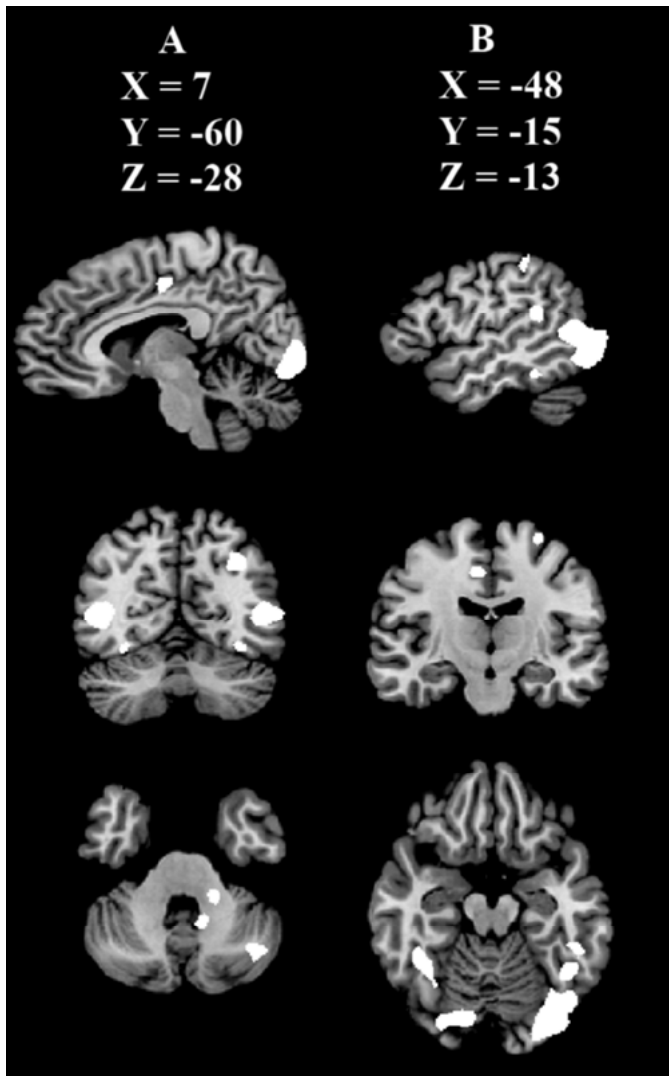


Figure 4. Areas with a main effect of dynamics (Interactive > Individual) in the whole brain analysis as described in Table 2. A) Right ACC, right lingual gyrus, left precuneus, right MTG, right FG, left precuneus, left IOG, left cerebellum. B) Left postcentral gyrus, left STS, left IOG, left FG, right ACC, right posterior ACC, bilateral FG, right MTG, right lingual gyrus.

The interaction between emotion and dynamics.

In a large number of areas, the interaction effect was a result of a stronger response to the interactive fear than to the individual fear condition, whereas there was no such difference in the other two emotional conditions. These include the bilateral parahippocampal gyrus, the bilateral extrastriate visual cortex, the right inferior

temporal gyrus (ITG), a cluster in the right insula, the right precuneus and the left lingual gyrus (see Table 3A). The right lingual gyrus showed an increased BOLD response in the interactive fear condition as compared to the individual fear condition and in the interactive happy condition as compared to the individual happy condition, but no difference between the two neutral conditions (see Table 3B). Two clusters in the left MOG, one of which corresponds to the hMT+/V5, showed a preference for the interactive fearful and neutral conditions as compared to their individual counterparts, without any difference between interactive and individual happy (see Table 3C). Lastly, the insula bilaterally and a cluster in the posterior ACC responded to both interactive fear and the individual neutral condition (see Table 4D) and the cuneus bilaterally activated more strongly in response to the interactive neutral condition (see Table 4E). See Figure 5.

Anatomic region		X	Y	Z	Voxels 1x1x1	F	Peak Voxel <i>p</i>
A. Interactive Fear > Individual Fear							
Parahippocampal Gyrus	R	23	-38	-6	267	8.81	<i>p</i> = .000975
Parahippocampal Gyrus	L	-28	-47	-6	364	10.69	<i>p</i> = .000312
Extrastriate visual cortex	R	41	-74	24	962	10.13	<i>p</i> = .000434
Extrastriate visual cortex	L	-34	-80	24	122	7.12	<i>p</i> = .002929
Insula	R	35	22	15	605	8.90	<i>p</i> = .000920
Precuneus	R	23	-62	42	1483	9.56	<i>p</i> = .000611
Inferior Temporal Gyrus	R	50	-50	0	276	7.68	<i>p</i> = .002013
Lingual Gyrus	L	-19	-89	6	2144	15.06	<i>p</i> = .000030
B. Interactive Fear > Individual Fear + Interactive Happy > Individual Happy							
Lingual Gyrus	R	14	-89	0	6383	26.37	<i>p</i> < .000001
C. Interactive Fear > Individual Fear + Interactive Neutral > Individual Neutral							
Middle Occipital Gyrus	L	-28	-86	6	234	8.11	<i>p</i> = .001524
Middle Occipital Gyrus (hMT)	L	-49	-68	6	1114	11.57	<i>p</i> = .000188
D. Interactive Fear > Individual Fear + Individual Neutral > Interactive Neutral							
Insula	R	41	16	-6	4516	19.20	<i>p</i> = .000004
Insula	L	-37	16	-6	242	8.00	<i>p</i> = .001642
Posterior Dorsal ACC	L	-7	4	27	363	9.69	<i>p</i> = .000565
E. Interactive Neutral > Individual Neutral							
Cuneus	R	14	-83	21	436	12.53	<i>p</i> = .000111
Cuneus	L	-4	-89	36	211	8.65	<i>p</i> = .001079

Table 3. Emotion by dynamics interaction. Cluster sizes, peak voxel locations and *p*-values of clusters with a significant emotion by dynamics interaction effect. Cluster size threshold corrected, *p* < .005.

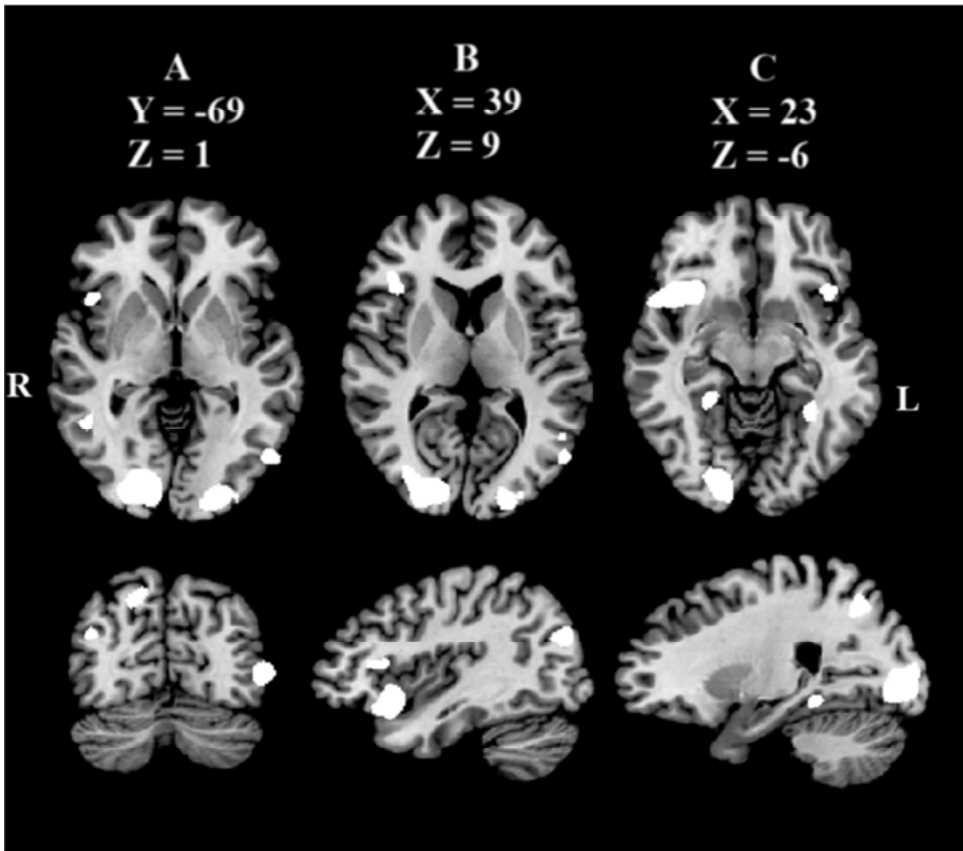


Figure 5. Areas with an emotion by dynamics interaction effect in the whole brain analysis as described in Table 3. A) Left insula, right ITG, bilateral lingual gyrus, right MOG (hMT). B) Right insula, bilateral lingual gyrus, left MOG, left MOG (hMT), right extrastriate area. C) Bilateral insula, bilateral parahippocampal gyrus, right lingual gyrus, right precuneus.

Discussion

The aim of this study was to assess the neural correlates of emotional crowd perception and the effect of the behavioral dynamics between individuals. Firstly, observing emotional crowds activates an extensive network of areas involved in emotional facial and bodily expressions, imitation and emotion contagion (insula, cingulate cortex, IPL, somatosensory areas) (de Gelder, 2006; Iacoboni, 2009; Keysers, Kaas, & Gazzola, 2010; Leslie et al., 2004; Nummenmaa, Hirvonen, Parkkola, & Hietanen, 2008; Tamietto & de Gelder, 2010), motion processing (SPL, MOG), and action perception, preparation and execution (STS, SFG, premotor cortex, cerebellum) (Blake & Shiffrar, 2007; Caspers, Zilles, Laird, & Eickhoff, 2010; Lestou, Pollick, & Kourtzi, 2008).

More importantly however, our first hypothesis pertained to whether the brain is sensitive to the behavioral dynamics of the individuals in a crowd. Indeed, regardless of the emotion of the crowd, observing interactive as compared to individually behaving crowds activated a broad network of areas including those related to the perception of motion, body language, biological motion and social interaction processing; such as the lingual gyrus, supramarginal gyrus, extrastriate cortex, and inferior occipital gyrus (Blakemore et al., 2003; Centelles et al., 2011; Chaminade et al., 2011; Dolcos et al., 2012; Grezes et al., 2007; Iacoboni et al., 2004; Kujala et al., 2012; Pfeiffer, Timmermans, Vogeley, Frith, & Schilbach, 2013; Pichon et al., 2012; Sinke et al., 2010; Tavares et al., 2008). Additionally, interactive crowds more strongly activate networks related to action observation, understanding and execution, such as the precentral and postcentral gyri, the superior and inferior parietal lobules, the STS, MTG, FG, fusiform area and even the cerebellum (Caligiore, Pezzulo, Miall, & Baldassarre, 2013; Caspers et al., 2010; Pelphrey, Viola, & McCarthy, 2004). Interestingly, the cerebellum is crucial for action perception coupling (Christensen et al., 2014) and this response in combination with the precuneus, somatosensory and primary motor cortex activations may indicate that interactive behavior between people signals important determinant of whether emotional states are shared (Nummenmaa et al., 2012) or that something relevant may be happening (Hadjikhani, Hoge, Snyder, & de Gelder, 2008; Schulte-Ruther, Markowitsch, Fink, & Piefke, 2007; Tamura et al., 2013). It was previously found that the precuneus activity increases in response to the speed of a geometric shape when the movement is believed to be intentional, but decreases when it is thought to be random (Zacks, Swallow, Vettel, & McAvoy, 2006). Also, the precuneus, premotor and somatosensory areas are strongly interconnected and in turn linked to the inferior and superior parietal lobules and also to the subcortical areas (thalamus and pulvinar), involved in unconscious emotion processing (Cavanna & Trimble, 2006; Tamietto & de Gelder, 2010). Finally, the dorsal ACC is connected to premotor areas and the limbic system (Etkin, Egner, & Kalisch, 2011) and has been found to integrate emotional and behavioral responses (Pereira et al., 2010).

We also assessed whether there is an interaction between the emotion of the crowd and the behavior dynamics. Behaviorally, interactive fear or 'panic' is experienced as more arousing and less pleasant than individual fear, happy people interacting are seen as more pleasant and arousing than merely a collection of happy individuals, but the dynamics are not of importance for the perception of neutral crowds.

Furthermore, interactive fearful crowds activated a specific network of brain areas consisting of the parahippocampal gyrus (PPA), EBA, the precuneus, insula, lingual gyrus and ITG. The PPA is a well-known area responsive to stimuli of scenes and is involved in encoding the layout of the environment (Epstein & Kanwisher, 1998),

whereas the EBA is sensitive to the perception of bodies and body parts (Downing et al., 2001). The EBA, PPA and ITG in the occipitotemporal cortex are crucial for visual perception, but also play an important role in self-representation, a successful integration of the own body into the environment by integrating visual, spatial and motor-sensory information and preparing the body actions in the environment (Astafiev, Stanley, Shulman, & Corbetta, 2004; Gallivan, Chapman, McLean, Flanagan, & Culham, 2013). This is corroborated by studies showing that the EBA plays a role not only in perceiving a body, but also in action and goal perception (Downing, Peelen, Wiggett, & Tew, 2006; Herrington, Nymberg, Faja, Price, & Schultz, 2012; Jastorff & Orban, 2009) and that damage to the extrastriate cortex produces hallucinations regarding the own body in space (Heydrich & Blanke, 2013). Similarly, both the EBA and the PPA are sensitive to emotion (Atkinson, Vuong, & Smithson, 2012; Peelen, Atkinson, Andersson, & Vuilleumier, 2007; Sinke, van den Stock, Goebel, & de Gelder, 2012). In conclusion, in a panic situation, these areas may be responsible for quickly assessing the gist of the scene in relation to the behaviors of others and more importantly, our own body and its position. Additionally, the insula and the precuneus, with their connections to the limbic, somatosensory and motor systems (Augustine, 1996), may integrate all important emotion and action information to a meaningful whole (Carr et al., 2003; Kurth, Zilles, Fox, Laird, & Eickhoff, 2010) and prepare to take the appropriate action (Zhang & Li, 2012).

Lastly, without taking the dynamics between the individuals into account, many of the regions involved in the processing of fearful crowds overlap with a network important to the perception of danger (Tamura et al., 2013; Zurcher et al., 2013). Specifically, it is noteworthy that the FG, insula and IFG were activated in response to fearful crowds. Insula activation was previously found when participants viewed people facing each other (Kujala et al., 2012), in response to threatening scenes (Nummenmaa et al., 2008) and to stimuli showing a threatening response (Pichon et al., 2012). The insula may therefore play a role in detecting threat in social interactions. It is well connected to other areas involved in emotion processing such as the ACC and vmPFC (Grupe & Nitschke, 2013). In addition, the IFG and FG have frequently been found to be engaged in the perception of social interactions (Centelles et al., 2011; Dolcos et al., 2012; Iacoboni et al., 2004; Kujala et al., 2012) and specifically in threatening interactions (Pichon et al., 2008; Pichon et al., 2012; Sinke et al., 2010) even when there were no humans present in the stimuli (Gobbini et al., 2007; Schultz et al., 2005). Additionally, activity in the IFG, a key region for action observation, imitation (Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005) and action understanding (de Lange, Spronk, Willems, Toni, & Bekkering, 2008), is related to the perception of group-like behavior of dots (Chaminade et al., 2011) and a display containing multiple faces (Simmons et

al., 2006). Most importantly, in the present case the IFG may play a role in risk aversion (Christopoulos, Tobler, Bossaerts, Dolan, & Schultz, 2009).

Note that the majority of studies into the perception of emotional body language or emotional social interactions find amygdala activation (Dolcos et al., 2012; Grezes et al., 2007; Kujala et al., 2012; Pichon et al., 2008; Sinke et al., 2010; Sung et al., 2011; Tavares et al., 2008). A possible explanation for the lack of amygdala activation in the current study pertains to the fact that attention was devoted to the dot-detection task the participants performed. Attention is known to reduce the level of activation of the amygdala as we found in a study using individual video clips (Pichon et al., 2012; see de Gelder, Hortensius, and Tamietto (2012) for a review). A dot detection task was used for a number of reasons. First, as compared to passive viewing, it not only engages the participant but assures participants watched the video. Second, the task is unrelated to the content of the stimuli and thus does not stimulate the participants to overtly think and reason about what is happening in the video.

9 |

Discussion

Overview of the findings

This dissertation touched upon many different facets of social interaction, starting with face identity recognition in healthy participants, subjects with developmental prosopagnosia and an acquired prosopagnosia case, followed by what happens in both the body and brain when emotional bodily expressions are perceived in a social interaction with one or more persons.

In **chapter 2**, we assessed findings of a large sample of healthy controls participants in a student and a middle aged age range on the FEAST, the test battery that we consequently used throughout our research on prosopagnosia. The FEAST consists of a neutral and emotional face memory task, a face and object matching task that allows the user to assess upright face and object recognition ability, a face and house part matching task and a facial expression matching task with human and canine faces. The results provide reference data per gender and age group on all these tasks.

In **chapter 3** we studied 10 DPs and 10 controls using the FEAST and a face body compound identity matching task. DPs showed impaired memory for both neutral and emotional faces and it was found that DPs were impaired in upright, but not inverted, face matching, but they performed at the level of controls on part-to-whole matching. Also, identity matching was improved with the presentation of an emotional body. Lastly, configural perception but not feature-based processing was significantly associated with memory performance.

Similarly, in **chapter 4** we assessed scores on the FEAST in a fairly large group of DPs. It was again found that DPs were impaired in configural processing, but not part-to-whole matching. Also, DPs showed impaired memory for both neutral and emotional faces and furthermore, configural processing again slightly predicted face memory scores. Also, DPs are impaired at emotion recognition as compared to controls, but only for human and not canine facial expressions.

In **chapter 5** we explore face identity and facial and bodily expression recognition (using the FEAST, a bodily expression matching task and an emotional face body compound task) in a new case of acquired prosopagnosia, with damage to the bilateral occipitotemporal/fusiform gyrus but with an intact right occipital face area. Face memory was severely impaired as well as upright face recognition and configural processing. His facial expression recognition was selectively impaired, but he was normally able to recognize bodily expressions. Furthermore, he was influenced by emotional bodies during facial expression recognition, but not the other way around.

Then, moving towards more psychophysiological measures and social interactions, in **chapters 6 and 7** we provided the first reports of the Body Action Coding System by investigating the response of muscles in the neck, shoulders, upper and lower arms, lower back and calves during both the active expression and passive viewing of fearful and angry body language using EMG. The biceps, deltoids, and triceps are recruited strongly for the expression of anger and fear expression predominantly depends on the biceps and the deltoids. The chapters provide patterns of results for both the muscles responsive to emotion without overt activation, and also an overview of which muscles are used overtly for the expression of fear and anger. In conclusion, this study provides more insight into the perception and expression of emotions in the body.

Lastly, **chapter 8** takes us beyond single person perception. In an fMRI study we used realistic videos of a large group of people expressing fearful, happy or neutral emotions. Furthermore, the emotions were expressed by either unrelated individuals in the group or by an interacting group. It was found that observing interactive individuals, more so than independently expressive individuals, activated networks related to the perception, execution and integration of action and emotion. Most importantly, the interactive or panicked crowds, as opposed to the individually fearful crowds, triggered more anticipatory and action preparation activity, whereas the brain was less sensitive to the dynamics of individuals in a happy or neutral crowd.

Face processing and configuration processing in acquired and developmental prosopagnosia.

In chapter one, we gave an overview of both the literature on acquired and developmental prosopagnosia considering their face and object processing abilities. Of course, the name itself implies that people with this condition are blind for faces, and not blind for other things. It is therefore not surprising that also our assessment of the AP and DPs reveal just this: impairments in upright face processing. Combining the DPs in chapter 3 and 4, a total of 31 DPs without any known psychological, psychiatric, neurological problems and without any low level visual deficiencies were tested. Almost all DPs show problems with face memory, but it is interesting to see how they perform on a simultaneous matching task, when memory is taken out of the equation. Using our sample to match task, in principle a simple task in which the participant has to indicate which of the bottom two faces or shoes is of the same identity as the top one, it is consistently found that the DPs are very impaired. However, with maybe a few single exceptions, they are able to recognize shoes equally well as controls and thus our studies strengthen the evidence that prosopagnosia is a face specific condition.

In our brain-lesioned AP case 'EP', of course we also find impaired upright face matching. The AP has damage to the right anterior occipital gyrus, the middle and posterior fusiform gyrus, inferior lingual gyrus and the left temporal and occipital lobes. Using fMRI, we established that EP does not have any face activation in the FFA, which has been damaged. However, he shows face specific activation in the right OFA and right STS, two areas of the three important in the core face processing network. When we look at the cases of 'pure' prosopagnosia as reported in the literature, some cases are a result of anterior temporal lobe damage, which is corroborated by studies finding face selective activation in that part of the cortex (Kriegeskorte et al., 2007; Nestor, Plaut, & Behrmann, 2011; Simmons, Reddish, Bellgowan, & Martin, 2010). However, the majority of cases have damage to the occipitotemporal/fusiform gyrus, just like EP (Barton, 2008; Barton et al., 2001; Busigny et al., 2010; Clarke et al., 1997; de Gelder et al., 2003; Mattson et al., 2000; Rezlescu et al., 2012; Riddoch et al., 2008; Rivest et al., 2009; Rossion et al., 2003; Susilo et al., 2013; Takahashi et al., 1995; Wada & Yamamoto, 2001). It must be noted that in this case, future studies should look deeper into EPs object recognition ability, as his performance on the BORB is normal, but his shoe matching ability is lower than that of controls. EPs case adds to this literature that the FFA is quite a crucial part of the face processing network, and that normal OFA activation is not enough for face recognition (Pitcher et al., 2011c). Interestingly, the opposite is also true. The mere presence of FFA activation in response to faces does not guarantee intact face processing (Wilkinson et al., 2009). In well described case 'PS', the right middle fusiform gyrus is intact and it was found that this area responded normally to the perception of faces. However, it did not recover properly from adaptation as it usually does in healthy controls. The same was found for 'DF' (Steeves et al., 2006), 'CR' and 'SM' (Marotta et al., 2001).

Of course, as also reviewed in the introduction, we are mainly interested in configural processing in AP and DP. As expected, also EP showed a paradoxical face inversion effect, where his inverted face matching accuracy was higher than for upright faces, and on the same level as controls. Almost all pure AP cases where configural processing was tested, have fusiform damage, such as 'S009' (Barton, 2008; de Gelder et al., 2003), 'KC' (Barton et al., 2001; Barton et al., 2002; de Gelder et al., 2003) and 'MK' (de Gelder et al., 2003) or fusiform and occipital lobe/ OFA damage such as with 'PS' (Rossion et al., 2003), Galen (Susilo et al., 2013), 'GG' (Busigny et al., 2010), 'DC' (Rivest et al., 2009), 'FB' (Riddoch et al., 2008). Although see Rezlescu et al. (2012) and Wada & Yamamoto (2001).

In our two studies with DPs, we also clearly find paradoxical face inversion effects. Can the results as found in AP shed light on the configuration processing problems in DP? Recently, it was also found that even though it is possible to locate the FFA in DPs, it shows abnormal activation for configural information (Avidan et al., 2014; Zhang et

al., 2015). All these studies combined point toward a role of the FFA in configural processing of faces. In addition, Kuskowski and Pardo (1999) found a relationship between fusiform activity and successful face memory. To corroborate, we found that impaired configural processing may be related to impaired face memory, as higher face inversion scores were positively related to scores on the face memory tasks. These results are in line with accumulating evidence that the ability to process faces configurally is positively related to face recognition ability (DeGutis et al., 2013; Wang et al., 2012), also in DPs (Richler et al., 2011) and that disrupting the occipitotemporal gyrus also influences configural processing (Yang et al., 2014). Recently, but unfortunately not present in the thesis, we have tested both DPs and EP using the same face and object recognition, configural processing, and facial/bodily expression recognition experiments in the fMRI scanner, to allow the direct comparison of the response and physiopathology between the two disorders.

What about featural processing? As described in Table 1 in chapter 1, AP cases do tend to show impairments in featural processing, which is often related to damage in the OFA (Pitcher et al., 2011b), and see the APs 'DC', 'PS', 'GG', 'FB' and 'MK' in Table 1, chapter 1). In a few APs, it was found that they tend to focus on the mouth, or at least that their eye processing is impaired (see subjects S004, S007, S010, and S011, otherwise known as 'LH' with fusiform damage (Barton, 2008) and 'LR' with middle, inferior and anterior temporal lobe damage (Bukach et al., 2006)). Another way to tackle this question is by using eye gaze. Indeed, whereas normal controls tend to fixate on the center of the face (van Belle et al., 2011), the AP 'GG' focused on both the eyes and mouth and 'PS' focuses very specifically on the mouth (Orban de Xivry, Ramon, Lefevre, & Rossion, 2008). In our two DP samples, we found normal feature processing (also see Bentin et al., 2007). However, DPs can't use this ability to recognize faces in daily life. This indicates that configural processing is not merely lost, but that a remnant of it actively interferes with the feature processing routine (de Gelder & Rouw, 2000a, 2000c). Unfortunately, subjects with prosopagnosia seem unable to successfully recruit this ability to accomplish normal face recognition in daily life. In short, successful face recognition probably depends on a correct cooperation between the networks (Fairhall & Ishai, 2007) and the two routes (Moscovitch & Moscovitch, 2000; Rivest et al., 2009). On a side note, declining face recognition abilities in older participants has also been ascribed to an increased focus on the mouth region (He et al., 2011).

Emotion processing in acquired and developmental prosopagnosia.

To add to the existing literature regarding the overlap of facial identity and emotion recognition processes (Bruce & Young, 1986; Calder & Young, 2005; Haxby et al., 2000), we also assessed facial expression recognition in the AP and DPs.

As can be seen in Table 1 of chapter 1, emotion recognition ability is quite often not assessed in the APs. Sometimes just anecdotal evidence is reported, or it was tested with a very simple, short task. The studies as mentioned above provide conflicting results; however, many APs seem unimpaired in emotion recognition, and those who do often have lesions in the occipital lobe. As EP has normal right OFA activation in response to faces, his comparatively normal facial expression recognition could be attributed to this area (also see Hasson et al., 2003) and Rossion et al., 2003). In addition, as EP has an intact amygdala, hippocampal gyrus and normal STS and OFA activity, activity in these areas might modulate his facial expression recognition and memory for faces (de Gelder et al., 2003; Garrido et al., 2012; Phelps, 2004; Vuilleumier et al., 2001).

In our sample of DPs however, the results seem in line with the suggestion of Calder and Young (2005), indicating that the mechanisms for both abilities overlap to some extent, as we find a less than normal emotion recognition ability even though their scores aren't so far behind controls as to warrant impairments in daily life (Ariel & Sadeh, 1996; Aviezer et al., 2012; de Haan & Campbell, 1991; Duchaine et al., 2006; McConachie & Helen, 1976). However, this goes against the model proposed by Bruce & Young (1986) and Haxby et al. (2000) and also conflicts with those reports that find unimpaired face recognition ability in DP (Dinkelacker et al., 2011; Duchaine et al., 2003; Humphreys et al., 2007; Lee et al., 2010; Nunn et al., 2001; Palermo et al., 2011).

In truth, a likely alternative explanation is that DPs are a very heterogeneous group regarding this ability (Le Grand et al., 2006). If you look at the table of Z scores in our own study in chapter 4, some DPs score normally and others impaired on the facial expression matching task. Other studies also find conflicting reports within samples of cases who can, and cannot, recognize expression (Brunsdon et al., 2006; Dobel et al., 2007; Minnebusch et al., 2007; Schmalzl et al., 2008). This underlines the dangers of overestimating the importance of case studies, especially in such a group as DPs, in which it is to date hard to pinpoint what exactly underlies their face recognition problems neurologically. Future studies could consider thorough testing of the known cases of DPs, grouping them by their specific impairments and trying to find out what defines them. On the other hand, there are also studies that show that it is possible to identify emotional expressions by focusing on features alone (Chen & Chen, 2010; Ellison & Massaro, 1997; Leppanen, Kauppinen, Peltola, & Hietanen, 2007). Individual differences in this ability can thus maybe also account for the conflicting results regarding in emotion recognition in AP and DP; where some AP/DPs can, and others cannot, turn to this featural strategy.

However, the DPs as a group do not differ from the control group on the canine version of the task, which does indicate that there is something going awry for human

faces specifically. A possible explanation could again be found in their impaired configural processing abilities. As previously discussed, emotional expression recognition probably also relies on configural processes (Bartlett & Searcy, 1993; Calder & Jansen, 2005; Calder et al., 2000; Calvo & Beltran, 2014; Durand et al., 2007; Mckelvie, 1995; Palermo et al., 2011; Tanaka et al., 2012; White, 2000).

The role of bodily expressions in prosopagnosia

It was previously established that the presence of emotion can be beneficial for face identity processing (Peelen et al., 2009). When it only comes to faces, there may be a possible role for the FFA, as it is often modulated by emotional expressions, such as an increased activation for emotional than neutral faces or a release of adaptation for both changes in emotion and identity (Fox et al., 2009; Ganel, Valyear, Goshen-Gottstein, & Goodale, 2005; Harry et al., 2013; Kawasaki et al., 2012; Xu & Biederman, 2010). The amygdala may also provide help with face identity recognition, as it is quite robustly activated for faces and strongly connected to the core face network of the OFA, FFA and STS (Carmichael & Price, 1995; Davies-Thompson & Andrews, 2012; Fairhall & Ishai, 2007; Gobbini & Haxby, 2007; Haxby et al., 2000; Morris et al., 1998; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). Indeed, a DP tested by Bentin et al. (2007) benefited from same facial identity in an emotion matching task, van den Stock et al. (2008b) found more FFA activity in controls than DPs for neutral faces, but similar activity levels between the groups for happy and fearful faces and Avidan et al. (2014) found that emotion caused more FFA activity than neutral faces also in DPs. Similarly, configural processing was found to be improved when faces express emotion, as was tested in five APs with occipitotemporal lesions (de Gelder et al., 2003).

If we extend this reasoning, it might not be surprising that in chapter 3, we found that DPs and controls are similarly influenced by fearful bodily expressions when they have to match identity, and in chapter 5 we find again that our AP case is very strongly affected by the presence of fearful (and happy) bodies when he has to assess facial expressions. Not only do the reported results in this dissertation point to normal body processing in DP and AP, the presentation of emotional contextual stimuli might even benefit facial processing. These findings may be related to the fact that there are specialized cortical areas for body processing, such as the fusiform body area (FBA) (Peelen & Downing, 2005) and the extrastriate body area (EBA) (Downing et al., 2001), areas that are also mediated by emotion (Grezes et al., 2007; Pichon et al., 2008, 2009, 2012). These areas were not affected in our AP, and are probably also normal in DP (where normal body recognition (Duchaine et al., 2006) and normal FBA and EBA activity in response to bodies (van den Stock et al., 2008) was already reported previously).

In short, our studies on face and body integration in both DP and AP add to the accumulating evidence indicating that face recognition is sensitive to contextual influences such as facial and bodily expressions (de Gelder et al., 2006; de Gelder & van den Stock, 2011b).

And on that note, we leave face recognition to have a look at other influences of bodily expressions.

The Body Action Coding System

When it comes to facial expressions, the Facial Action Coding System (Ekman & Friesen, 1978) describes what muscles are used for which emotional expressions. This system has been extensively used in research, for example in studies that examined conscious and unconscious facial responses to emotion in clinical populations. This system has also proven to be very valuable in the development of several software systems that allow the automatic recognition of facial expressions, which are used in a wide range of daily life applications, such as human-computer interfacing, gaming, animation and security. However, the role of the body has long been neglected in emotion research. This inspired the question of whether automatic and covert muscle responses to emotion are limited to the face, or whether such activations might also be found in body muscles.

To answer that question, we began the creation of a Body Action Coding System (BACS), based on EMG. Our work on the Body Action Coding System had two main aims; firstly to map which muscles are used during the overt expression of emotions and secondly, whether these muscles are covertly responsive to the perception of emotion. We measured EMG of the upper trapezius descendens in the neck, the anterior deltoids in the shoulder, the biceps and triceps brachii in the upper arms, the wrist extensors in the forearm, the erector spinae longissimus in the lower back and the peroneus longus in the calves during two experiments. In experiment one, participants passively viewed (in a relaxed stance, without movement) videos of actors opening a door and responding angry or fearful, which were projected life-size in front of them. In the experiment two, the participants were asked to imitate the emotional expression of the actors in the same video convincingly with their whole body.

The results showed that it is possible to extract unique patterns of muscle activity for angry versus fearful movements. The biceps were found to be the most important muscle for anger expression, followed secondly by forearm, then by shoulder and lastly by triceps activation. In contrast, a fearful expression was marked by forearm

activity, followed by an equally strong involvement of shoulders and biceps, while activity of the triceps is quite low.

The second aim of the studies was to assess automatic muscle activations in response to the perception of emotion in others, without any overt movement. The perception of a person behaving angry towards the observer caused activation of the biceps and a sudden activation of the muscle in the lower back, normally used for leaning backwards. However, when a fearful person is seen, the trapezius (used for shrugging the shoulders) and the wrist extensors (the most active muscles during fear expression) strongly respond, whereas the biceps is deactivated. Additionally, the muscles in the calf strongly activated in response to both fear and anger, but with very different time patterns. In short, these results indicate that automatic responses to fear and anger can indeed be distinguished by calf, lower back, trapezius, forearm and biceps (de)activation.

In the previous chapters, we already gave an overview of the literature of why we expected that bodily muscles would also show reactive activations in social interactions, just like facial muscles. It was previously established that the stimuli used in the current studies on the Body Action Coding System activate brain areas involved in both the perception and execution of emotions and actions, such as the amygdala, insula, supplementary motor area, inferior frontal gyrus, cerebellum and premotor areas (Grezes et al., 2007; Pichon et al., 2008, 2009, 2012). Automatic responses of muscles in the body may originate from brain areas involved in action preparation, the expression and perception of emotions, social interactions and threat (Carr et al., 2003; Hennenlotter et al., 2005; Leslie et al., 2004) through connectivity of the motor cortex, basal ganglia, amygdala, the brain stem and the spinal cord (Liddell et al., 2005; Morecraft et al., 2007; Sagaspe, Schwartz, & Vuilleumier, 2011; Takakusaki, Saitoh, Harada, & Kashiwayanagi, 2004; Tamietto & de Gelder, 2010).

Interestingly, our findings indicate that not all muscles in the body simply mimic seen behaviors, in contrast to emotional mimicry theories based on facial expressions (Dimberg, 1982). Some muscles very actively involved in movement, like the biceps and wrist extensors, activate in response to the perception of the emotion they are most strongly involved in. In contrast, the activity of postural muscles such as in the lower back, neck and calves, is not large during movement and the covert responses seem more reactive. This reaction might be enhanced by the interactive nature of the videos, in contrast to the more traditional facial EMG studies in which photographs are shown. Another indication that these processes may be more complex than mimicry or motor mapping, are the findings that facial muscle responses also occur without conscious awareness (Tamietto et al., 2009) and in response to non-facial

stimuli such as bodies and voices (Bradley & Lang, 2000; Grezes et al., 2013; Hietanen et al., 1998; Kret et al., 2013; Magnee et al., 2007b).

Furthermore, most muscles deactivate during the actual perception of an emotional behavior of another person (during stimulus presentation). These deactivations may be a function of suppression of specific cells in the primary motor cortex, possibly through the supplementary motor area during action observation, to prevent imitation (Bien, Roebroek, Goebel, & Sack, 2009; Kraskov, Dancause, Quallo, Shepherd, & Lemon, 2009; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010; Vigneswaran, Philipp, Lemon, & Kraskov, 2013). Stamos, Savaki, and Raos (2010) found that action observation inhibited metabolic activity in the area of the spinal cord that contains the forelimb innervations in macaques. In fact, it is known from studies assessing posture that the body can freeze upon the perception of aversive and arousing stimuli (Facchinetti et al., 2006; Lelard et al., 2013; Roelofs et al., 2010; Stins et al., 2011). Other recent studies also support the view that it may be more likely that unconscious emotional muscle responses reflect complex interactive and reactive processes (see Hess and Fischer, 2013 for a review).

The results of the covert and automatic bodily muscle responses again indicate that we are very sensitive to the motions and emotions of others, and what they might mean for us as a person. To extend on this work on social interactions, we performed an fMRI experiment in which we assessed with cortical networks are sensitive to the dynamics of emotional crowds. This effect of interaction might go beyond mere perception and/or mimicry of seen bodily behaviors per se, as previous studies using controlled, non-human like (geometrical) shapes, or in other words interactive behavior without any biological stimuli like faces or bodies, have also found that movement alone can be a strong indicator for interaction (Blakemore et al., 2003; Chaminade et al., 2011; Gobbini et al., 2007; Martin & Weisberg, 2003; Schultz et al., 2005; Tavares et al., 2008). We found that interactive crowds might have a greater emotional impact than crowds of individuals, which may increase action preparation and sympathetic nervous system arousal (Etkin et al., 2011; Gentil, Eskandar, Marci, Evans, & Dougherty, 2009). The finding that the interaction between individuals influences these action perception and execution networks also corroborates psychophysiological findings that interactions between people increase corticospinal excitability (Bucchioni, Cavallo, Ippolito, Marton, & Castiello, 2013; Sartori, Cavallo, Bucchioni, & Castiello, 2011) and influences mu rhythm oscillations, said to reflect mirror neuron activity (Oberman, Pineda, & Ramachandran, 2007). In short, it seems that not only the expressed emotion, but also the dynamics between the individuals are very important characteristics of crowd perception.

Drawbacks of research with dynamic stimuli

An important issue when using dynamic, natural social interactions is the fact that they cannot be well controlled on all levels. We encountered this problem in our EMG and fMRI studies. One methodological issue of the BACS articles pertains to the lack of a comparable baseline condition. In contrast to the use of still photographs of faces, it is very difficult to find a suitable neutral condition with the same movement components when it comes to dynamic bodily expressions. One option is to use neutral actions performed with the arms, such as hair combing, making a call, or lifting a glass to the mouth. However, in the context of the current stimuli in which people opened a door, this would be very unnatural. Unfortunately, the neutral versions of these videos vary greatly from the angry and fearful version with regard to movement and emotional intensity (Pichon et al., 2008), which we felt is unacceptable for the current study. Another option is to use stimuli of people performing an emotion without any context or direction. It was decided to use the stimuli of a person opening a door for two reasons. First, from the perspective of the participant, it is more interactive (as if the person is responding to you), which is a more relevant and natural situation. To illustrate, Grezes et al. (2013) found stronger corrugator activity in response to an angry bodily expressions when they were directed to the participant than when they were not. Even more so than facial expressions, bodily expressions and social interactions alert the perceiver to action tendencies of the other and in turn prepare the observer for action.

Another problem with bodily expressions, as compared with facial expressions, is the variation in the number of possible ways to express a certain emotion. In these studies, the participants imitated the actors in the videos. Even though the actors themselves expressed their emotion freely, and all stimuli showed varied ways of expressing anger and fear, it would not only be interesting but also necessary to see if these results are replicated if participants are asked to express emotion freely themselves. At this moment, we are working on follow up studies of the BACS, in which we included neutral, idle movement and neutral actions such as taking off a shirt, and combing hair.

However, there are several obvious next steps in the development. Firstly; the muscle responses and activations in relation to other emotions need to be assessed. Also, information on which trajectories are made in space and time with what limbs, for example measured with accelerometers, would provide a descriptive level of movement in concordance with the EMG data. Furthermore, this knowledge needs to be imbedded into a user friendly software program which is able to automatically classify both overt and covert emotional responses. By measuring EMG of these muscles wirelessly, while participants are immersed in virtual environments, we aim

to establish distinguishable patterns of muscle activity both during the expression of genuine emotions, as well as during covert emotional responses to realistic social interactions and environmental events, and integrate these in a Body Action Coding System software. We've already finished the data collection of a study in which we recorded EMG activity from six muscles (in the neck, shoulder, arms and lower back) and motion capture simultaneously.

When it comes to our fMRI study, some of the activations could be explained by the differences in arousal, valence or movement of the stimuli, such as the clusters found in the cuneus, the middle occipital gyrus (likely corresponding to the hMT+/V5) and the temporal poles, as they are also important for biological motion detection (Grossman et al., 2000; Watson et al., 1993) and emotion processing and autonomic reactivity (Ongur & Price, 2000). It is possible that merely the higher movement or arousal levels of the fearful and happy stimuli are responsible for activation in these areas (Lane, Chua, & Dolan, 1999). Unfortunately, this is a major problem in dynamic emotion expression research and it is well studied that arousal (Adolphs, Russell, & Tranel, 1999) and movement information such as speed or gait (Chouchourelou, Matsuka, Harber, & Shiffrar, 2006; Roether, Omlor, Christensen, & Giese, 2009) are each by themselves critical for accurate emotion recognition. This means that equalizing stimuli on these inherent dimensions impairs the correct recognition and perception of the emotion. It is important to point out that when images of movement are used; even these still frames contain different levels of implicit motion. This is clearly reflected in the findings that the subjective movement ratings of the inherent movement in the still frames were similar to that of the actual movement in the video clips. However, even though there are differences in movement, valence and arousal in the videos, it is worth stressing that the activity patterns found in the BOLD signal did not match the movement patterns in the videos. For example, even though (especially interactive) happy videos contain the most movement and is high in valence and arousal, only the lingual gyrus shows higher activation for interactive happy than individual happy videos. In short, if the movement, arousal and valence of the stimuli would be the main factor driving the BOLD responses, we should have found most activations in response to happy videos or in response to interactive fear and interactive happy simultaneously. Nonetheless, it would be very beneficial if future studies unravelled the unique contributions of each of these processes. In addition, it would be interesting to more closely assess how people look at the crowds and what exactly they pay attention to. Eye tracking experiments could possibly shed light on the question if people look at the crowds in different ways, and EEG studies could assess when exactly the interaction dynamics influence the perception of the group. Furthermore, a study with motion captured groups could not only provide better controlled stimuli, by changing the position of the individuals without changing the

movement information, but also provides a mean to correlate activity to quantifiable movement aspects (f.e. distance between people, velocity, trajectories, and movement synchronization). Virtual reality also may prove to be a more effective way than presenting videos to more naturally induce emotion, or even create social interactions, in an immersive but still controlled setting.

Clinical implications

The work on prosopagnosia is relatively hard to relate on any real life improvements for these patients any time soon. Overall, both the finding that configural processing is related to face memory and that emotional expression can enhance face memory may have implications for the development of training applications to remediate face recognition disorders. Consistent with the idea that there is configural processing in DP, it strengthens the notion that configural processing would be a good starting point if one aims to improve face recognition, as reported recently (DeGutis, Cohan, & Nakayama, 2014a; DeGutis, Chiu, Grosso, & Cohan, 2014b). For reviews, see (Bate & Bennetts, 2014; DeGutis et al., 2014b).

When it comes to our Body Action Coding System, steps are already taken to implement the system for daily life purposes. This is the first such system based on EMG and the work so far established the feasibility of using EMG as a means to create a coding system, resulting in the description of the activation patterns of seven bodily muscles during the perception and expression of anger and fear in a laboratory setting. Understanding the role of the body in emotional expression is becoming increasingly important, with interest in developing systems for gaming (Savva & Bianchi-Berthouze, 2012; Savva, Scarinzi, & Bianchi-Berthouze, 2012; Zacharatos, 2013), robots (Castellano et al., 2013; Castellano, Villalba, & Camurri, 2007), touchscreen interfaces (Gao, Bianchi-Berthouze, & Meng, 2012) or even teaching (Mayer & DaPra, 2012), and tools for public speaking (Nguyen, Chen, & Rauterberg, 2013). Therefore, there is an increasing interest from other fields (Kleinsmith & Bianchi-Berthouze, 2007; van den Broek, 2012), such as emotion technology, affective computing, artificial intelligence, ICT, or biomedical technology, wanting to incorporate knowledge about physiological responses of the body and their relationship to the emotion of the user in the creation of brain computer interfaces, robots, game characters or virtual reality avatars, software that is able to automatically assess emotional expressions, e-learning or e-therapy, or even day-to-day equipment that is tuned to the emotion of the user. Implementing affective state information through measuring automatic and non-conscious, unintentional muscle activity patterns may serve as input for previously mentioned human-computer or human-robot interfaces, for example gaming consoles or online learning environments, in order to improve a successful user interaction. Also, knowledge

about how body posture influences the state of another can benefit experts in other professions in which successful social interaction is crucial, i.e., teachers, psychologists, or police (see Kleinsmith and Bianchi-Berthouze (2013) for an extensive review).

To that aim, multiple coding systems have been developed that can either interpret or create bodily expressions, based on static postures, motion capture data or videos (see (Calvo & D'Mello, 2010; Karg et al., 2013; Kleinsmith & Bianchi-Berthouze, 2013; Zeng, Pantic, Roisman, & Huang, 2009) for some extensive reviews). However, no system exists yet based on muscle involvement and electromyography (EMG) measurements. Most importantly, only EMG is able to measure responses invisible to the naked eye. If such a system were available, it would enable research on automatic responses without overt movement and build natural emotional expressions based on biologically valid movement data. Even though the different techniques and their respective coding systems all highlight a different aspect of emotional bodily expressions, one of the advantages of surface EMG is the relative ease of use and the availability of affordable recording systems. The action units in the arms and shoulders, such as the wrist extensors, biceps, triceps and anterior deltoids, are easy to locate and measure and provide very strong movement signals. Assessing their activity patterns in comparison to each other enables the discrimination between angry or fearful movements. In addition, the electrode locations of these action units are also very convenient if one uses wireless electrodes or electrodes in a shirt, making it ideal for use in non-laboratory settings, for example classrooms, hospitals or virtual reality environments.

The creation of a BACS would in this regard be very complementary to the FACS, and technological developments enable the use of EMG in these settings, with wireless and easy-to-use systems suitable for a non-laboratory environment already available. Bodily expressions have several advantages compared to facial expressions—they are more interactive, directional, can be recognized from longer distances, and do not automatically convey identity information (de Gelder, 2009). In short, once a BACS is established, it opens up a new array of possibilities to gain further insight into of emotional expression and contagious responses in different cultures, unconscious pain related behavior and empathy. Furthermore, it may prove an interesting tool for research into, and diagnostic tools for, several psychological or neurological disorders such as anxiety, autism, schizophrenia, borderline personality, aggression or behavioral disorders, developmental disorders, and so on (Bakker, Tijssen, van der Meer, Koelman, & Boer, 2009; de Wied, van Boxtel, Matthys, & Meeus, 2012; de Wied, van Boxtel, Posthumus, Goudena, & Matthys, 2009; Magnee, de Gelder, van Engeland, & Kemner, 2007a; Matzke, Herpertz, Berger, Fleischer, & Domes, 2014; Oberman et al., 2007; Oberman, Winkielman, & Ramachandran, 2009; Rozga, King, Vuduc, & Robins,

2013; Sestito et al., 2013) (Aung et al., 2013; Bons et al., 2013; Deschamps, Munsters, Kenemans, Schutter, & Matthys, 2014).

In combination with our fMRI study, we showed that social interactions between people are important, that the perception of emotion and action are closely linked, and that the emotions and social interactions between people in turn influence our own responses to and anticipations of others and the consequences for the self (Wolpert, Doya, & Kawato, 2003). Better understanding of how the brain copes with complex social situations (Pfeiffer et al., 2013; Schilbach et al., 2013) adds a new dimension to understanding social communication and its deficits and is beneficial for the study of, for example, autism (Centelles, Assaiante, Etchegoyhen, Bouvard, & Schmitz, 2012, 2013; Pavlova, 2012; Zurcher et al., 2013).

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Nederlandse Samenvatting

In deze dissertatie worden enkele facetten van sociale interacties behandeld, waaronder het herkennen van identiteit en emotie aan het gezicht in gezonde participanten, mensen met ontwikkelings prosopagnosie (gezichtsblindheid) en verkregen prosopagnosie door hersenschade. Een belangrijk concept in prosopagnosie onderzoek is configuratieve verwerking, in andere woorden, de verwerking van gezichten als een geheel. Mensen verwerken gezichten hoogstwaarschijnlijk als geheel, want normaliter zijn mensen slechter in het herkennen van omgekeerde dan rechtopstaande gezichten, terwijl het omdraaien van objecten weinig invloed heeft. Dit proces lijkt verstoord in prosopagnosie; er is vaak gevonden dat individuen met prosopagnosie beter zijn in het herkennen van omgekeerde gezichten dan rechtopstaande.

Daarnaast wordt er onderzocht wat er gebeurt in het lichaam en de hersenen wanneer emotionele lichaamsexpressies worden waargenomen in sociale interacties tussen twee of meer personen. Het is van het gezicht bekend welke spieren worden gebruikt bij het uiten van welke emoties (Facial Action Coding System). Het is ook vaak gevonden dat het gezicht de emoties van anderen 'imiteert', bijvoorbeeld dat de 'lachspier' in de wang activeert bij het zien van een lach in anderen. Of hetzelfde gebeurt in het lichaam is een belangrijke vraag in het tweede deel van deze dissertatie. Ten slotte wordt met behulp van fMRI onderzocht welke rol de interactie speelt tussen mensen in een groep in neutrale, blijde en angstige (paniek) situaties.

Deel 1: Herkenning van identiteit en emotie

In **hoofdstuk 2** wordt de "Facial Action and Emotion Stimulus Test" (FEAST) gepresenteerd. Deze testbatterij bestaat uit meerdere experimenten ten behoeve van het testen van gezichtsherkenning en emotieherkenning, en geheugen voor gezichten. Deze testbatterij is uitermate geschikt voor het onderzoeken van gezichtsherkenning in bijvoorbeeld prosopagnosie. Deze testbatterij is afgenomen bij een groep van 58 gezonde proefpersonen tussen de 18 en de 62 jaar en de zowel de taken als de resultaten kunnen worden gebruikt als controlegroep voor toekomstige gebruikers van de FEAST.

In **hoofdstuk 3** worden de resultaten van 10 mensen met ontwikkelings prosopagnosie en 10 in leeftijd vergelijkbare controle proefpersonen op de FEAST beschreven. De prosopagnosiegroep was significant slechter in het onthouden van gezichten, zijn slechter in het herkennen van rechtopstaande (maar niet in omgekeerde) gezichten. De patiënten zijn wel in staat om gezichtsdelens te herkennen.

Daarnaast wordt de gezichtsherkenning verbeterd als het gezicht gepaard gaat met een emotionele lichaamsexpressie. De mate waarin gezichten configurationeel worden verwerkt was ook voorspellend voor gezichtsgeheugen: hoe hoger het inversie effect, hoe hoger de score op de geheugentaak.

In **hoofdstuk 4** wordt wederom de FEAST gebruikt om gezichts,- en emotieherkenning te testen in een grotere groep van ontwikkelings prosopagnosie patiënten en controles. Zoals voorheen wordt ook hier gevonden dat gezichtsgeheugen en configurationele verwerking van gezichten is verstoord in deze groep, en dat de mate van configurationele verwerking voorspellend is voor gezichtsgeheugen. In deze studie wordt ook aandacht besteed aan emotieherkenning. De patientengroep is slechter dan de controles in het herkennen van menselijke emotionele gezichtsexpressies, maar is even goed in staat om de emotionele gezichtsexpressies van honden te herkennen. Dit kan betekenen dat de verstoorde configurationele verwerking ook zijn uitwerking heeft op het herkennen van specifiek menselijke gezichtsexpressies.

In **hoofdstuk 5** wordt een scala aan testen, waaronder van de FEAST, gebruikt om gezichts,- en emotieherkenning te onderzoeken in een nog niet in de literatuur gerapporteerde patiënt met verkregen prosopagnosie door schade aan de fusiforme gyrus. Naast de FEAST werd een taak afgenomen om de herkenning van emotionele lichaamsexpressies te testen. Daarnaast werden ‘face body compounds’, oftewel stimuli waarbij het gezicht en het lichaam dezelfde of een conflicterende emotie konden uitdrukken, gebruikt. Het gezichtsgeheugen van deze patiënt is ernstig verstoord, net als gezichtsherkenning en configurationele verwerking van gezichten. Deze patiënt is ook slechter dan gebruikelijk in staat om emotionele gezichtsexpressies te herkennen, maar scoort wel normaal op het herkennen van emotionele lichaamstaal. Verder kan deze patiënt informatie van het lichaam slecht negeren als hem wordt gevraagd de emotie van het gezicht te herkennen, maar bij herkenning van de emotionele lichaamsexpressie heeft het gezicht een vergelijkbare storende invloed als bij controles.

Deel 2: Emotionele sociale interacties

In **hoofdstukken 6 en 7** worden de eerste delen van de Body Action Coding System gepresenteerd, met als doel het onderzoeken welke spieren in het lichaam worden gebruikt bij het uiten van emotie met het lichaam. Daarnaast is een belangrijk doel van deze onderzoekslijn het onderzoeken van hoe deze spieren automatisch en ‘onzichtbaar’ voor het blote oog reageren en activeren in reactie op het zien van angst of boosheid in anderen. Dit werd gedaan door activiteit van spieren in de nek (trapezius) schouders (deltoiden), bovenarmen (biceps en triceps), onderarm

(extensors van de pols) en kuit te meten met behulp van EMG (elektromyografie). In de studies worden twee experimenten beschreven. In experiment 1 kijken de deelnemers video's, levensgroot gepresenteerd met behulp van een beamer, van boze en angstige mensen. De proefpersonen staan ontspannen en kijken de video's zonder te bewegen. In experiment 2 wordt de proefpersonen gevraagd om de lichamelijke emotionele expressie van de acteurs in de video's te imiteren met het eigen lichaam. De hoofdstukken geven vervolgens patronen van activiteit van het lichaam in reactie op het **zien** van emotie in anderen, zonder dat er zelf wordt bewogen, maar ook welke spieren worden gebruikt bij het **uiten** van angst en agressie. Er worden specifieke activatiepatronen beschreven voor beide situaties. Wat betreft het actief uiten van emotie: de biceps wordt het meest gebruikt bij het uiten van boosheid, gevolgd door de onderarmen, en ten slotte bij schouder en triceps activatie. De onderarmen worden het sterkst gebruikt bij het uiten van angst, gevolgd door de schouders en biceps, maar de triceps spelen geen grote rol.

Wanneer je zelf niet beweegt maar je iemand waarneemt die angstig is, reageren de onderarmen sterk, terwijl het zien van iemand die boos is op jou ervoor zorgt dat de rugspieren activeren. Ook zie je dat de spieren in je kuiten, die je normaal gebruikt om weg te stappen, meteen reageren op angst, en ook reageren als iemand zich agressief naar je gedraagt. Het patroon van resultaten laat zien dat meer 'passieve' spieren, die belangrijker zijn voor houding dan bewegen en die dus ook niet erg sterk worden geactiveerd tijdens bewegingen, zoals die in de nek, rug en kuiten, lijken te *reageren* op de emoties van anderen (bijvoorbeeld een ontwijkende, angstige reactie op het zien van agressie). Spieren die erg sterk activeren tijdens beweging, zoals de schouders, biceps, triceps en onderarmen, lijken juist meer te imiteren, zoals de biceps die belangrijk is bij het uiten van en het zien van boosheid, en de onderarmen bij angst expressie en perceptie.

Ten slotte wordt in **hoofdstuk 8** een fMRI onderzoek beschreven waarin deelnemers in de scanner video's van een grote groep acteurs bekijken. Deze acteurs kunnen zich neutraal, angstig of blij gedragen, maar kunnen dit op een individuele wijze doen (dus door de andere mensen in de groep te negeren), of kunnen gezamenlijk neutraal, angstig of blij zijn (een voorbeeld van een gezamenlijke blij situatie is bijvoorbeeld juichen bij een sportwedstrijd, gezamenlijke angst is paniek). Het waarnemen van een groep mensen die gezamenlijk emotioneel is zorgt voor meer activiteit in neurale netwerken die normaliter betrokken zijn bij emotie en actie perceptie en executie. Dit is voornamelijk het geval als de groep mensen in paniek is, wat ook resulteert in meer neurale netwerkactiviteit in die gebieden die verantwoordelijk zijn voor anticipatie en actie preparatie dan een groep mensen die individueel bang is, of individueel/interactief blij is.

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