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Social perception in the real world: employing visual adaptation paradigms in the investigation of mechanisms underlying emotion and trustworthiness perception.

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Abstract

Social context can substantially influence our perception and understanding of emotion and action of observed individuals. However, less is known about how temporal context can affect our judgement of behaviour of other people. The aim of this thesis was to explore how immediate perceptual history influences social perception. Further aims were: (i) to examine whether prior visual experience influences the perception of behaviour of other individuals in a naturalistic virtual environment resembling the real world; (ii) to determine whether our judgement of emotional state or trustworthiness of observed individuals is influenced by perceptual history, and (iii) by cognitive processes such as mental state attribution to the observer; (iv) to investigate whether processing of emotion information from dynamic, whole-body action is dependent on the processing of body identity, and (v) dependent on the body part that conveys it. Here, visual adaptation paradigms were used to examine systematic biases in social perception following prior visual experience, and to infer potential neural mechanisms underlying social perception. The results presented in this thesis suggest that perception and understanding of behaviour of other individuals in the naturalistic virtual environment are influenced by the behaviour of other individuals within the shared social environment. Specifically, in Chapter 3, I presented data suggesting that visual adaptation mechanisms examined thus far in laboratory settings may influence our everyday perception and judgement of behaviour of other people. In Chapters 4 and 5, I showed that these biases in social perception can be attributed to visual adaptation mechanisms, which code emotions and intentions derived from actions with respect to specific action kinematics and the body part that conveyed the given emotion. The results of experiments presented in Chapter 4 demonstrated that emotions conveyed by actions are represented with respect to, and independently of, actors' identity. These finding suggest that the mechanisms underlying processing of action emotion may operate in parallel with the mechanisms underlying processing emotion from other social signals such as face and voice. In Chapter 6, I showed that cognitive processes underlying Theory of Mind, such as mental state attribution, can also influence perceptual processing of emotional signals. Finally, results presented in Chapter 7 suggest that judgments of complex social traits such as trustworthiness derived from faces are also influenced by perceptual history. These results also yielded strong sex differences in assessing trustworthiness of an observed individual; female observers showed a strong bias in perception resulting from adaptation to (un)trustworthiness, while male observers were less influenced by prior visual context. Together these findings suggest that social perception in the real world may be sensitive not only to the social context in which an observed act is embedded, but also to the prior visual context and the observer's beliefs regarding the observed individual. Visual adaptation mechanisms may therefore operate during our everyday perception, in order to adjust our visual system to allow for efficient and accurate judgement of socially meaningful stimuli. The findings presented in this thesis highlight the importance of studying social perception using naturalistic stimuli embedded in a meaningful social scene, in order to gain a better understanding of the mechanisms that underlie our judgement of behaviour of other people. They also demonstrate the utility of visual adaptation paradigms in studying social perception and social cognition.

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CHAPTER 1

General introduction. Multiple bodily signals in social perception

Humans live in a highly complex social environment and spend a significant part of their lives interacting and communicating with others. Effective interaction with other people, during which we accurately interpret and comprehend subtle visual and vocal signals presented by others as cues to their complex mental or emotional states, not only provides substantial benefits, but is also essential for our social functioning.

During the past few decades researchers from fields across Biology, Psychology and Neuroscience have begun to map the complex neural mechanisms underlying the processing of social signals and social interactions. The term "social brain" (Brothers, 1990) is often used to reflect the complex and distributed neutral substrates and processes that allow us to make inferences about other individuals and understand their intentions, feelings and thoughts. Every day, people interpret a large variety of visual social signals including information about the face, body posture and movement, all of which appear in a diverse social context. However, traditionally research on social and affective perception has been dominated by investigating face processing in isolation (see de Gelder et al., 2010 for a review).

Humans are, however, not only remarkably adept in making reliable judgements from a range of social signals, but are also sensitive to the context in which such signals occur (Adolphs, 2003). Multiple approaches, including the study of social signals from different categories like face, body part, whole dynamic body action or vocalization, the interaction between these categories, and the effect of temporal and spatial context on social judgement, are therefore necessary for gaining a better understanding of human social perception and social cognition. In this chapter I will, therefore, review the current literature on the contribution of facial and bodily signals in the perception of emotion and behaviour of other individuals. Furthermore, I will discuss cognitive and neural models influencing our understanding of mechanisms underpinning social perception. Section 1.1 focuses on the processing of facial cues and interactions between processing of facial identity and expressions. In sections 1.2 and 1.3, I discuss the perception and neural processing of bodily emotional expressions and bodily actions, and review the evidence for the need of including dynamic whole-body signals in the study of emotion perception. I will argue that the processing of body identity and emotion may also interact in Section 1.4. Section 1.5 covers the effect of context of emotion perception from faces and bodies, which can significantly influence our judgement of emotions and intentions of other individuals in the real world. Finally, in section 1.6 I argue that including virtual reality environment in the study of social perception may allow for better understanding of how we interpret the behaviour of other people in everyday situations.

1.1 Are faces special?

It has long been argued that faces have a special status in social perception (see McKone & Robbins, 2011 for a discussion). The remarkable range of face shapes, sizes, configurations and complexity of facial muscles structure, make the face a primary social cue that provides information about identity, feelings and intentions. People are drawn to faces from birth, are highly sensitive to face-like patterns, and most importantly are experts in face processing (see Gliga & Csibra, 2007 for a discussion). *Why* faces play a special role in human social perception has fed a debate on whether face processing is domain specific (Kanwisher, 2000; McKone & Kanwisher, 2005). The *domain–specificity* hypothesis suggests that the unique and elaborate processing of faces does not occur for any other type of object and thus has an innate component (de Haan, Humphreys, & Johnson, 2002). In addition a critical period in human development may be necessary for obtaining the expertise in face perception (Le Grand, Mondloch, Maurer, & Brent, 2001, 2003). In contrast, the *domain-general* hypothesis (e.g. Diamond & Carey, 1986) suggests that mechanisms used for face processing are not specialized for faces *per se,* but are involved in the processing of any frequently encountered object category that contains different, but visually similar, exemplars. Evidence suggesting that faces have a special status has come from cognitive psychology, clinical neuroscience and neuroimaging. Studies in cognitive psychology have suggested specific perceptual processes (i.e. configuration-based processing) involved in face perception. Traditionally, the role of facial configuration has been examined by inverting the face, where recognition decreases for upside-down faces (Yin, 1969) or using the face composite-test, where judgement about the top half of the face is influenced by the bottom half of the face (Young, Hellawell, & Hay, 1987). Clinical neuroimaging studies of patients with propopagnosia also provided invaluable insights into the functional organization of neural systems for face processing. Finally, neuroimaging and single cell recordings in primates have highlighted regions of visual cortex that are highly selective for faces. Altogether, findings from these areas suggest specialised visual processing mechanisms that are unique to faces.

1.1.1 A neural system for face perception

Single-cell recordings in macaque monkeys demonstrated the existence of neurons in the superior temporal sulcus (STS) that were highly-selective to faces (Desimone, 1991; Perrett, Rolls, & Caan, 1982). Subsequently, a functional magnetic resonance (fMRI) study in macaques confirmed the existence of face-selective regions in the temporal cortex and more specifically in the STS (Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003). In the human brain, there are also regions where activity is greater for faces than for non-face objects (see Figure 1.2 for a schematic illustration). These well-documented face-selective regions exist in the lateral fusiform gyrus (fusiform face area; FFA), inferior occipital gyrus (occipital face area; OFA) and in the superior temporal sulcus area (sometimes referred to as fSTS; Gauthier et al., 2000; Kanwisher, McDermott, & Chun, 1997; Kanwisher & Yovel, 2006; Puce, Allison, Asgari, Gore, & McCarthy, 1996). These distinct regions play functionally distinctive roles in face processing. Although the degree of specificity in the FFA has been challenged (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999), it remains the most robust face-selective area, responding to a wide variety of face stimuli including faces presented in different orientations, fine drawing of faces, Mooney faces and even animal faces (reviewed in Kanwisher & Yovel, 2006). Therefore, the FFA is considered to be involved in the representation of invariant facial characteristics such as identity (Grill-Spector, Knouf, & Kanwisher, 2004). The OFA on the other hand responds preferentially to parts of the face such as the eyes, nose, and mouth (Pitcher, Walsh, Yovel, & Duchaine, 2007). It plays a critical role in the discrimination of facial expressions at an early stage of visual processing (Pitcher, Garrido, Walsh, & Duchaine, 2008) and has a feed-forward projection to posterior STS (pSTS) and FFA (Davies-Thompson & Andrews, 2012; Haxby, Hoffman, & Gobbini, 2000). The connectivity between OFA and pSTS may underlie processing of changeable aspects of the face such as gaze direction and emotional expressions (Puce, Allison, Bentin, Gore, & McCarthy, 1998).

1.1.2 Models of face identity and emotion processing

The organization of the neural processing of faces is also reflected in models of face perception. An early cognitive model by Bruce and Young (1986) (Figure 1.1. A) proposes two distinct pathways for face processing: one pathway involved in identifying the individual, and a second pathway, for processing changeable aspects of the face such as emotional expressions or gaze direction. The core argument in this model is that certain features of a face are processed independently of other features, so that the processing of one component (e.g. identity) is not influenced by the processing of another component (e.g. facial expression).

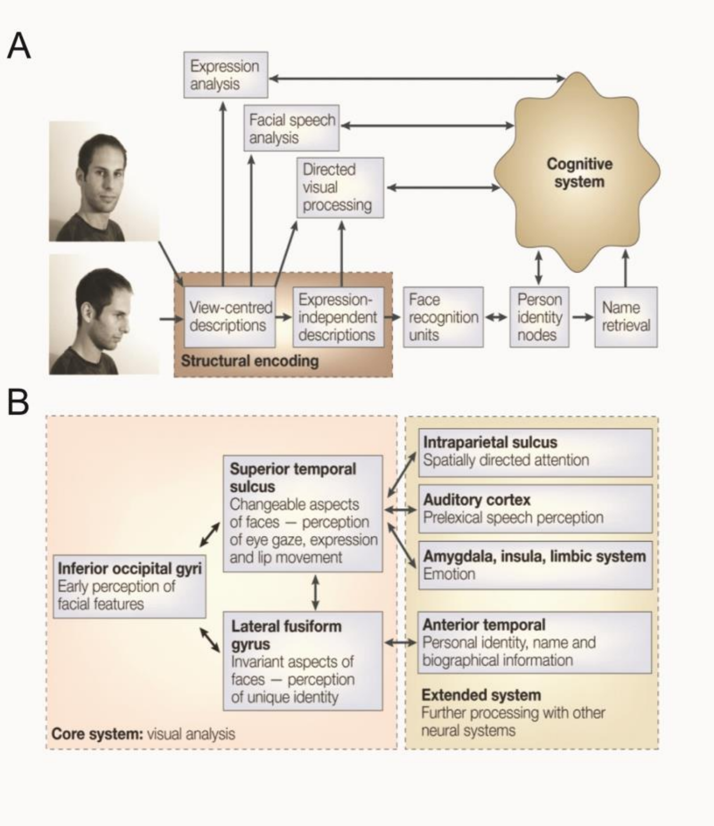


Figure 1.1. The face processing models. Face processing models. (A) The model proposed by Bruce and Young (1986). (B) The model proposed by Haxby, et al. (2000). Figure adapted from Calder (2011).

Subsequently, extending on the work of Bruce and Young (1986), Haxby, et al. (2000) proposed a neural model for face processing (see Figure 1.1. B). Haxby et al.'s model was developed from a review of single-cell recording and neuroimaging data, and located different elements of face processing in specific neural regions. Haxby et al. (2000) delineated the core system consisting of two streams: one located in the FFA processing invariant aspects of the face, and the other located in the STS processing changeable aspects of the face. Although Haxby's model also assumes the relative independence in the processing of facial features from changeable aspects of the face resulting from movement, it also proposed a feed-forward connectivity between OFA, FFA and STS (Haxby, et al., 2000). Evidence for a degree of interdependence in the processing of facial identity and expression, in support of the Haxby et al.'s model, came from behavioural experiments (Campbell, 1996), neuroimaging (Winston, Henson, Fine-Goulden, & Dolan, 2004) and electrophysiology in monkeys (Hasselmo, Rolls, & Baylis, 1989). Nonetheless, both the models and the supporting empirical evidence have recently been challenged (Atkinson & Adolphs, 2011; Calder, 2011; Calder & Young, 2005), and new findings reinforce a proposal for a more interconnected model, where different aspects of face processing may depend on similar visual processing pathways (Calder, 2011) or on the interaction between functionally and anatomically distinct regions (Atkinson & Adolphs, 2011).

1.1.3 Conjoint processing of invariant and changeable aspects of a face

New evidence from monkey neurophysiology and human cognitive and neuropsychological research suggests a degree of overlap in the representation of facial identity and facial expression. Hasselmo, et al. (1989) found cells selective for both face identity and expression in monkey STS. However, a small proportion of these neurons responded conjointly to both facial properties. Another study using single-cell recordings in monkeys indicated that the majority of face-selective neurons in the amygdala responded to both face identity and facial expression (Gothard, Battaglia, Erickson, Spitler, & Amaral, 2007), suggesting that these two components are processed jointly in the amygdala (see also Barraclough & Perrett, 2011 for discussion).

Integrated processing of face identity and facial expression is also supported by results of behavioural experiments. For example, changes in facial identity interfere with participants' judgements of facial expression in studies using the Garner paradigm (Schweinberger, Burton, & Kelly, 1999; Schweinberger & Soukup, 1998). Visual adaptation paradigms (see also Chapter 2) also provide evidence for partially integrated processing of face identity and expression. Adaptation aftereffects for facial expression are more pronounced when the identity of the adaptation and test faces are the same (Campbell & Burke, 2009; Ellamil, Susskind, & Anderson, 2008; Fox & Barton, 2007). In addition, behavioural studies also highlighted the asymmetry in the processing of facial identity and expression; changes in identity influence perception of facial expression, but changes in facial expression do not impact identity recognition (Fox, Oruc, & Barton, 2008; Schweinberger, et al., 1999; Schweinberger & Soukup, 1998).

Neuroimaging data also indicates that face identity and expression processing interact. Using fMRI adaptation, Fox, Moon, Iaria, and Barton (2009) found a functional overlap in the FFA and pSTS, with both of these regions coding both face identity and expression. Using a similar paradigm, Cohen Kadosh, Henson, Cohen Kadosh, Johnson, and Dick (2010) also reported that FFA and OFA are involved in the perception of both facial identity and facial expression. In addition, Baseler, Harris, Young, and Andrews (2012) recently found increased connectivity between FFA and pSTS when the same identity face is presented with varying expressions and gaze direction, suggesting that pSTS may play a critical role in monitoring changes in a particular individual's emotions. Taken together, data obtained in recent neuroimaging studies suggests interplay between brain regions involved in high-level face perception, which may indicate a more interactive processing of invariant and changeable aspects of the face than Haxby et al.'s (2000) model suggests.

Transcranial magnetic stimulation (TMS) studies also provide evidence suggesting a more integrative processing of facial expression and facial identity. The integration of these two types of information may take place in the right OFA. For example Pitcher, et al. (2008) demonstrated that TMS applied over right OFA impaired participants' discrimination of facial expressions at an early stage of processing, around 60-100 ms post stimulus onset. Similar findings were later reported by Cohen Kadosh, Walsh, and Cohen Kadosh (2011), who found that TMS over right OFA also disrupted participants' ability to match faces on the basis of both the identity and expression. These two findings suggest that right OFA may integrate information across identity and expression. Since perception of facial identity relies on configural cues, while facial expressions involve integration of both featural and configural cues (e.g. Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Pitcher, et al., 2007; Rhodes, Michie, Hughes, & Byatt, 2009), OFA may play a role in computing the relations between facial features (Cohen Kadosh, et al., 2011) and thus be involved in processing both of these cues. The OFA has also been suggested to play a role in facial trustworthiness judgements (Dzhelyova, Ellison, & Atkinson, 2011) suggesting that the OFA is involved not only in the initial structural encoding of faces, but also at the later stages of face processing.

Recent data discussed above argues against the original proposal for separate visual systems for processing facial identity and facial expression (Bruce & Young, 1986) and against a strict feed-forward hierarchical model of face perception (Haxby, et al., 2000). Instead, it is suggested that invariant and changeable aspects of the face may be processed via similar processes (Calder, 2011). Moreover, a more interactive model for high-level face perception has been proposed (Atkinson & Adolphs, 2011), where processing of various facial cues depends on the interplay between several neural regions, and the nature of this interplay may be sensitive to the demands of the task.

1.2 Are bodies special?

Faces are, however, not the only socially meaningful stimuli. During social interactions individuals monitor signals from the face, body and voice of their companions. Similar to faces, bodies provide cues to identity, emotion, intention, age and gender (Atkinson, Dittrich, Gemmell, & Young, 2004; de Gelder & Van den Stock, 2011a; O'Toole et al.; Rice, Phillips, Natu, An, & O'Toole, 2013) and bodies may be more reliable sources of this information over longer viewing distances or when facial information is not fully available.

Both human bodies and faces capture people's attention and the visual system assigns them attentional priority, suggesting that both bodies and faces are particularly significant and salient cues (Downing, Bray, Rogers, & Childs, 2004). There are also a number of similarities in the perception of faces and bodies. Bodies, like faces, are processed configurally, which has been demonstrated by the body-inversion effect, where bodies presented upside-down are relatively more difficult to recognize (Reed, Stone, Bozova, & Tanaka, 2003). Visual adaptation (see also Chapter 2) to body identity shares similar perceptual characteristics with face identity aftereffects; they both depend on the strength of the adaptor, and transfer across different stimuli size (Rhodes, Jeffery, Boeing, & Calder, 2013). These studies suggest that similar mechanisms may underlie visual processing of faces and bodies.

Body expressions of emotions are also easily recognized (Atkinson, et al., 2004) and recent studies suggested many similarities in the recognition and production of facial and body expressions of emotion. For instance, people show a similar facial mimicry (Dimberg, 1982) when observing both facial and body (Magnée, Stekelenburg, Kemner, & de Gelder, 2007) expressions of emotion, suggesting that body and face emotion may be processed together. In addition, similar to the face action coding system (Ekman & Friesen, 1978), others have recently developed action and posture coding systems (Dael, Mortillaro, & Scherer, 2012; de Gelder & Hortensius, 2014; Huis in 't Veld, Van Boxtel, & de Gelder, 2014) allowing for a measurement of specific muscle groups, different articulations of body parts and direction and orientation of body movement that underlie whole body expressions of emotion. This recent data suggests that there is a link between observing emotional expressions and muscle responses to the observed emotion in the body, like there is in the face.

1.2.1 A neural system for body perception

Studies in humans and non-human primates revealed the existence of specialized brain networks dedicated to the processing of bodies and body parts. Neurophysiological recordings in macaque monkeys, for instance, demonstrated that some neurons in the inferior temporal cortex (IT) show selective response to human and monkey bodies and hands (Desimone, Albright, Gross, & Bruce, 1984; Wachsmuth, Oram, & Perrett, 1994). Other studies also reported cells in monkey STS that respond exclusively to body actions and body postures (Barraclough, Xiao, Oram, & Perrett, 2006; Jellema, Baker, Wicker, & Perrett, 2000; Perrett, Hietanen, Oram, & Benson, 1992; Wachsmuth, et al., 1994), with some body postures only eliciting the response when they were embedded in context (i.e. preceded by a meaningful action; Jellema & Perrett, 2003a, 2003b).

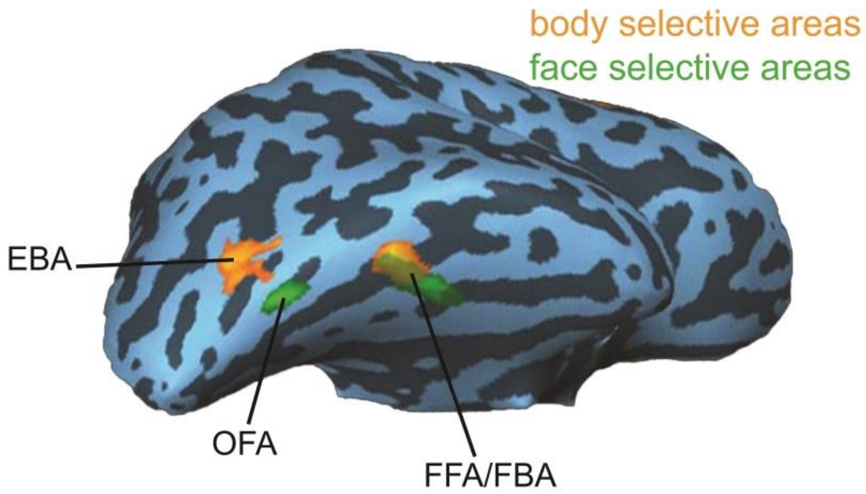


Figure 1.2. Human brain regions sensitive to visual depiction of faces and bodies. Figure adopted from Taylor, Wiggett, and Downing (2007).

Functional magnetic resonance imaging (fMRI) studies in humans provided perhaps the most compelling evidence for the existence of body-selective brain regions. These studies compared responses to images of bodies and body parts to images of faces, objects and object parts (Downing, Jiang, Shuman, & Kanwisher, 2001). A region in the lateral occipotemporal cortex labelled the extrastriate body area (EBA) responds strongly to photographs and line drawings of bodies, stick figures and silhouettes, indicating that the body representation in this region is abstract and can be derived from different visual features (Downing, et al., 2001). The EBA has also been proposed to be involved in mapping morphological features of human bodies and thus potentially represent body identity (Urgesi, Candidi, Ionta, & Aglioti, 2007). A later study, however, reported that the EBA shows no differential response for familiar, unfamiliar or one’s own body (Hodzic, Muckli, Singer, & Stirn, 2009) suggesting that this region is involved in body detection but not identification.

A recent MEG study by Meeren and colleagues (Meeren, de Gelder, Ahlfors, Hamalainen, & Hadjikhani, 2013) that investigated the cortical dynamics of body perception, suggested that the EBA plays a dominant role in the early visual processing of bodies, which may underpin detection of bodies and spatial relations between body parts. Because the EBA responds selectively to body parts, it has also been argued that this area is involved in analysis of the low-level visual features of human bodies, and in creating the representation of the shape and posture of human bodies (Downing & Peelen, 2011; Peelen & Downing, 2007; Taylor, et al., 2007). By creating such a representation of body form, the EBA also plays a critical role in the visual representation of body actions; it encodes various static postures that comprise an action when presented in a sequential order (Downing, Peelen, Wiggett, & Tew, 2006; Zimmermann, Toni, & de Lange, 2013; Zimmermann, Verhagen, de Lange, & Toni, 2013). As the EBA responds to both sequentially and randomly ordered static frames of bodily actions, it is not involved in the processing of dynamic information of human actions (Downing, et al., 2006). However, the EBA also projects to the STS which plays a crucial role in the perception of behaviour of other individuals (Allison, Puce, & McCarthy, 2000, reviewed in section 1.3).

A second body-selective region, anatomically distinctive from the EBA, has been identified in the fusiform gyrus. The fusiform body area (FBA) responds more strongly to whole body images and stick figures depicting bodies (Peelen & Downing, 2005) than to other kinds of objects, and has been suggested to be involved in creating a holistic body representation (Peelen & Downing, 2007). The FBA, moreover, might distinguish between familiar and unfamiliar bodies (Hodzic, et al., 2009), although its involvement in representing body identity is still unclear (see Ramsey, van Schie, & Cross, 2011). Interestingly, some evidence suggests that the FBA may partially overlap with the FFA (see Figure 1.2; Kanwisher, et al., 1997; Peelen & Downing, 2005), suggesting that perception of faces and bodies may be partially processed by the same neural structures (although see Downing, et al., 2001). Indeed, a small number of studies reported finding responses to body stimuli in the FFA (Cox, Meyers, & Sinha, 2004; Hadjikhani & de Gelder, 2003; Spiridon, Fischl, & Kanwisher, 2006). Using a high-resolution fMRI Schwarzlose, et al. (2005) tested the selectivity of the FFA and the FBA for face and body stimuli respectively. The two regions overlapped significantly in majority of scanned participants (all but 2) and were adjacent. However, the analysis were the voxels showing the overlapping selectivity for faces and bodies were omitted revealed a strong selectivity in these distinct (but adjacent) regions with FFA being specialised for the processing of faces and FBA for the processing of bodies. However, recent evidence from a MEG study (Meeren, et al., 2013) points towards the two regions being spatially (although adjacent) and functionally distinct with different temporal organization.

1.3 A human neural system for action perception

In our busy social environment, one of the fundamental functions of the brain is to resolve who the individuals in our proximity are, what they are doing and what their intentions are. Characteristic kinematics of human movements provide information not only enabling us to recognize actions of other people, but also to predict the consequences of their actions and infer about their intentions (Decety & Grezes, 1999; Runeson & Frykholm, 1981). Observed actions may therefore be represented and understood at multiple levels: (i) the kinematic level, informing about the movement trajectory; (ii) the goal level, informing about the purpose of the action; and (iii) the intention level, reflecting the reason for executing the action (Grafton & Hamilton, 2007; Kilner, 2011). These levels have been proposed to be organised hierarchically, where the kinematic level is dependent upon the goal of an action, and the goal being dependent on the intention behind the behaviour (Kilner, 2011).

In order to examine actions at the kinematic level, and thus delineate contribution of the motion information for the visual representation of actions, point-light displays have been frequently employed in electrophysiological and psychophysical studies. Point-light stimuli reduce the visual information of a movement to only kinematic information such as the spatial and temporal component of the motion. Gunnar Johansson (Johansson, 1973) was the first to show that people could immediately recognize complex actions, such as walking or dancing, from solely action kinematics.

Studies in humans and non-human primates revealed that specialized brain networks are dedicated to the processing of biological motion. These networks involve regions in both ventral ("what") and dorsal ("where) streams of the visual system (Giese & Poggio, 2003; Milner & Goodale, 1995; Ungerleider & Mishkin, 1982). The ventral pathway analyses biological movement by recognizing the individual, static key frames (Beintema & Lappe, 2002) of the action and "snapshots" of the body shapes, and matching them to the motion patterns characteristic for each specific action (Giese & Poggio, 2003). Neurons selective for complex shapes (Logothetis, Pauls, & Poggio, 1995) and body form information (Barraclough, et al., 2006) have been identified using single-cell recordings in monkey inferotemporal cortex (IT; Logothetis, et al., 1995) and in the STS (Barraclough, et al., 2006). In humans, brain regions selectively responding to body shapes that also respond to dynamic displays of bodies have been found in the extrastriate and fusiform body areas (e.g. Kontaris, Wiggett, & Downing, 2009; Michels, Lappe, & Vaina, 2005; see also section 1.2.1) and in the STS region (e.g. Allison, et al., 2000; Blakemore & Decety, 2001 for a review).

The dorsal pathway is thought to be specialized for processing motion information by analysing optic flow patterns (Giese & Poggio, 2003). Brain regions involved in this pathway consist of motion-selective areas analysing the local structure of optic flow (MT/MST; e.g. Shadlen, Britten, Newsome, & Movshon, 1996) and motion pattern neurons located in the STS (Giese & Poggio, 2003). It is well documented that in humans the STS region plays a crucial role in the processing of biological motion. Several studies using fMRI and PET techniques found that STS showed activation for the perception of biological motion produced by mouth movements (Puce, et al., 1998), hand actions (Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti et al., 1996) and complex whole-body actions (Bonda, Petrides, Ostry, & Evans, 1996; Grezes et al., 2001; Grossman & Blake, 2002; Grossman et al., 2000; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001). In addition, the STS has been found to play a role in the representation of intentional and goal-directed actions (Jellema, et al., 2000; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004) and is also activated by static photographs depicting implied motion (Barraclough, et al., 2006; Kourtzi & Kanwisher, 2000) suggesting that this region may provide a description of the body action with respect to the purpose and goal of the executed movement.

Evidence for the involvement of the STS region in the processing of bodily actions comes also from single-cell recording in monkeys. Numerous studies found that the STS cell populations respond selectively to the sight of head and torso orientation, hand actions and well as whole-body actions (Barraclough, Keith, Xiao, Oram, & Perrett, 2009; Jellema, Baker, Oram, & Perrett, 2002; Jellema & Perrett, 2002; Perrett et al., 1989; Perrett et al., 1984). The neural representation of biological motion in the monkey STS also extends to the perception of implied motion. Populations of STS cells have been found to respond to static postures when these were embedded in a meaningful context (i.e. preceding movement of the same body part (Jellema & Perrett, 2003a) or when they followed a particular action (Jellema & Perrett, 2003b). The above findings suggest that the STS may provide a representation of bodily actions in terms of their causality, consequences or purpose, and thus contribute to the understanding of naturally occurring behaviour of observed individuals (Jellema & Perrett, 2005).

The separation in the processing of body form and body motion signals is, however, still under debate. One of the difficulties in testing this dissociation empirically comes the fact that these signals are closely linked and quickly integrated (Vangeneugden, Peelen, Tadin & Bettelli, 2014). Jastorff & Orban (2009) for instance, showed that the initial integration of the body form and kinematics cues occurs in the EBA and FBA, which might be sufficient for the automatic processing of human actions. Dorsal regions, namely pSTS became involved when a more detailed analysis of action kinematics was necessary (Jastorff & Orban, 2009). Additional support for the model by Giese and Poggio (2003) and for a distinct neural mechanisms underlying processing of body form and body motion information come from a recent combined fMRI, psychophysical and TMS study by Vangeneugden, Peelen, Tadin & Bettelli (2014). Using these multiple techniques, the researcher showed that the EBA was involved in the processing of the cue invariant information about the body form while the pSTS carried information about the body motion. This double dissociation was furthermore evident in the TMS experiment, where stimulation over the EBA disrupted body form discrimination, and stimulation over the pSTS affected body motion discrimination (Vangeneugden, et al., 2014). The two pathways are therefore considered to separately contribute to the action recognition and thus to the understanding of other's behaviour.

1.3.1 Mirror-neuron system

Another set of action selective neurons is located in the premotor cortex (area F5; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Giese & Poggio, 2003; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). The majority (80%) of neurons in the primate area F5 have purely motor functions; they participate in planning, selecting and executing actions. However, approximately 20% of neurons in this region have both visual and motor responses, as they discharge both when the monkey executes an action (such as grasping) and when the monkey observes the same movement performed by the experimenter or a conspecific (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, et al., 1996; Rizzolatti, Fadiga, Gallese, et al., 1996). These neurons have been called "mirror neurons" as they seemed to match an observed action with an individual's own motor repertoire. Mirror neurons within area F5 have been classified into two groups: "highly congruent" and "broadly congruent" (Gallese, et al., 1996). Highly congruent mirror neurons fire when the observed and executed actions are identical with respect to the movement goal and the specific action employed to execute the goal (e.g. grasping an object with a precision grip). Broadly congruent mirror neurons can be triggered by dissimilar motor acts that share the same goal (e.g. getting a peanut with the hand or mouth). This led to the suggestion that mirror neurons allow the observer to understand the goal of an action and build the representation of the action from the kinematic level to more abstract levels of intentions (Rizzolatti & Fabbri-Destro, 2008). Subsequent studies also demonstrated the existence of mirror neurons in the inferior parietal lobule in monkey brains, supporting the notion that these neurons not only encode the observed motor act, but also enable the observer to infer intentions derived from actions (Fogassi et al., 2005). Understanding of the observed behaviour may therefore rely not only on the visual recognition of specific action kinematics, but also on the context in which the action is executed.

Additional evidence from neurophysiology (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010) and neuroimaging (e.g. Grezes & Decety, 2001; Keysers & Gazzola, 2010; Molenberghs, Cunnington, & Mattingley, 2012; Rizzolatti, Fadiga, Matelli, et al., 1996) studies suggests that a mirror neuron system exists in the parieto-frontal regions in the human brain. Cortical areas that form the core of the human mirror neuron system include ventral inferior frontal gyrus (IFG) and inferior parietal lobule (Rizzolatti & Craighero, 2004). Inferior parietal area is reciprocally connected with the STS (Harries & Perrett, 1991), which provides a visual input to the mirror system. Together, these three areas (ventral premotor cortex, inferior parietal lobule and STS) are often described as the action-observation network (AON) (Grèzes, Armony, Rowe, & Passingham, 2003; Kilner, 2011). Neurons within the STS region are subject to visual adaptation (Barraclough, et al., 2006) and thus the visual analysis of actions may be sensitive to the temporal context in which an action is observed. Biases in the action recognition mechanisms resulting from perceptual history are likely to influence the interpretation of the behaviour of other individuals, which is sub-served by the AON. How temporal visual context influences action understanding has not yet being delineated.

1.3.2 Processing of body identity and action information

As outlined above, understanding of behaviour of other individuals relies on multiple brain networks with some of these networks being sensitive to visual adaptation. In the Giese and Poggio (2003) model, action recognition requires analysis of the body posture and motion information. However it is not yet clear whether processing of body identity (derived from postural and kinematic cues, see section 1.4.1) interacts with processing of body action. Recent data by Wiggett and Downing (2011) suggests that processing of body actions may be independent from the processing of body identity. Using an fMRI adaptation paradigm they tested action- and identity-specific adaptation effects. In their study, significant, widespread action adaptation was found across lateral and ventral occipital cortex, but there was no identity adaptation in any of the brain regions. The lack of identity adaptation may, however, be explained by the participants' familiarity with the presented stimuli and the variation in the low-level features being greater across different actions than between different body shapes (Wiggett & Downing, 2011).

Additional evidence suggesting dissociation in the processing of body identity and body action comes from the neuroimaging and TMS studies. For instance, Kontaris, et al. (2009) suggested that body-selective areas in the extrastriate cortex (involved in the body identity recognition) are functionally dissociated from the action-observation areas. In their fMRI study participants were shown recording of their own hand movements while performing the same or different movement in a scanner. Observation and execution of the same movement suppressed the activity in the pSTS, compared to the condition where participants viewed a different action to the executed action. In contrast EBA and FBA responded equally to the compatible and incompatible conditions, suggesting that the visual representation of body parts in those two regions is decoupled from the motor system (Kontaris, et al., 2009). In another study TMS was administered over EBA or ventral premotor cortex (vPMC) when participants discriminated the identity or the implied action of the presented body part (Urgesi, et al., 2007). Identity (form) discrimination was impaired when the EBA was targeted by the TMS, and action (motion) was impaired after TMS on vPMC, suggesting a dissociation in the processing of body identity and visual discrimination of actions.

However, it may be possible that processing of socially meaningful, emotional actions may be partially dependent on the processing of the actor's identity. A degree of interaction between processing of these two signals have been proposed in face (e.g. Haxby, et al., 2000) and voice processing models (e.g. Belin, Fecteau,

& Bedard, 2004). Understanding of the emotional state of others may depend on mirror mechanisms (Gallese & Goldman, 1998), and mirroring mechanisms, to a certain degree, depend on the agent's identity. Empathy, for instance, which relies on the capacity to simulate the feelings of others (De Vignemont & Singer, 2006), is modulated by the participant's similarity (Krebs, 1975) and familiarity (Cialdini, Brown, Lewis, Luce, & Neuberg, 1997) with the agent, or an affective link between the participant and the agent (Singer et al., 2006). It may therefore be possible that in perception of emotional actions, changes in motor behaviour are tracked with respect to the identity of observed individual.

1.4 Can processing of body identity and emotion interact?

1.4.1 Perception of identity from bodies

Perception of a person in action may most importantly provide information about his/her intentions but not necessarily about their identity. Indeed, identity recognition from bodies is significantly poorer than from faces and faces and bodies together (O'Toole et al., 2011). Nonetheless, recent findings suggest people successfully use various cues such as body size, shape, or proportions to successfully derive identity information from even from static bodies (Hill, Hahn, & O'Toole, 2014). Although the shape and structure of the body provide cues towards one's identity, traditionally gait and other gesture-based movement have been most diagnostic in person recognition. These idiosyncratic or "identity-diagnostic" body motions have been referred to as *dynamic identity signatures* (O'Toole, Roark, & Abdi, 2002). Nonetheless, there is still a limited amount of work investigating how people use visual cues, beyond faces, to recognize other individuals.

A small number of studies using biological motion stimuli investigated whether identity information can be derived from motion cues (e.g. Kozlowski & Cutting, 1977; Loula, Prasad, Harber, & Shiffrar, 2005; Westhoff & Troje, 2007). A few studies reported that people can successfully recognize themselves (Loula, et al., 2005), friends (Kozlowski & Cutting, 1977) and a small number of newly learned identities (Westhoff & Troje, 2007) from biological motion. One study tested the role of visual and motor experience in identity recognition (Loula, et al., 2005). Participants were better at identifying themselves than friends from various point light displays suggesting that both motor and visual experience contribute to identity recognition from body movement. Moreover, identity identification in this study was action dependent, with the best accuracy reported for expressive actions such as dancing, suggesting that analysis of specific kinematic cues may facilitate identity perception from body actions (Loula, et al., 2005).

1.4.2 Perception of emotions from bodies and actions

Our understanding of how we process identity and emotion information from bodies is also limited, as typically scientists have focused on studying emotional signals from faces. This is somewhat surprising, given that early emotion researchers discussed whole-body expressions of emotion in detail. Darwin's classic paper "*The expression of the emotions in man and animals*" (Darwin, 1872/1965) highlighted the importance of postural cues to emotion recognition. More recently (Frijda, 1988) emphasised the link between emotion and action, and highlighted the role of bodily emotional signals. There are, however, a number of reasons why the study of bodily expressions of emotion has been neglected (de Gelder, et al., 2010). One argument is that, perhaps unjustifiably, over four decades ago Ekman (Ekman & Friesen, 1967) argued that bodily expressions of emotions only provide information about the quantity, and not about the specificity of the expressed emotion. However, both specific posture and body shape cues (Aronoff, Woike, & Hyman, 1992; Atkinson, Tunstall, & Dittrich, 2007) and body kinematics (Omlor & Giese, 2007; Roether, Omlor, Christensen, & Giese, 2009; Wallbott, 1998) provide information about the type of emotion being expressed and its intensity. It has been argued that the physical characteristics of the bodily movement, such as speed, acceleration, force or jerk, provide more information about the arousal and intensity of the expressed emotion, whereas more subtle relationships between the position of the joints inform about the type of the expressed emotion (Pollick, Paterson, Bruderlin, & Sanford, 2001; Roether, et al., 2009; Saw Ada, Suda, & Ishii, 2003). Secondly, the recognition of body expressions of emotion is also harder than recognition of facial expressions. The configuration of the human body has more degrees of freedom and the body shape varies significantly during articulated movements (Schindler, Van Gool, & de Gelder, 2008).

However, there is a considerable body of evidence showing that emotions conveyed by bodily actions are easily recognised. Atkinson, et al. (2004) found that different emotions can be reliably identified from both full-light and point-light displays. Although in this study actors were not instructed on how to act out specific emotions, the analysis of the motion information revealed that the same emotions were expressed through similar patterns across different individuals (Atkinson, et al., 2004). Indeed, emotions can also be portrayed and recognized from stylized movements. Dittrich, Troscianko, Lea, and Morgan (1996) found that complex emotions such as fear, anger, disgust, grief or joy can be identified when expressed through dance routines. Later, Pollick, et al. (2001) showed that emotions could be accurately perceived from hand movements alone, such as knocking or drinking. Clarke, Bradshaw, Field, Hampson, and Rose (2005) moreover showed that a range of emotions can be recognized in point-light displays of actors engaged in interpersonal dialog. Interestingly, perception of some social emotions could be affected by the social context; the recognition of love and joy in the above study was impaired by the absence of the acting partner.

Interpretation of behaviour of one individual can therefore be influenced by the presence or absence of other individuals within the same social scene. Whether our understanding of behaviour of other people is affected by the behaviour of other individuals is also one of the questions I attempt to answer in this thesis.

FMRI studies investigating brain responses to bodily expression provide indirect evidence that similar brain mechanisms underpin the processing of emotional signals from bodies and faces. Studies using still images (Hadjikhani & de Gelder, 2003; van de Riet, Grezes, & de Gelder, 2009) and dynamic whole-body expressions of emotion (Atkinson, Vuong, & Smithson, 2012; Grèzes, Pichon, & de Gelder, 2007; Pichon, de Gelder, & Grezes, 2008) found that the fusiform gyrus (FG) and amygdala (AMG), previously associated with processing of facial expressions, are also responsive during processing of bodily emotional signals. Video-clips of moving body parts such as hand gestures expressing anger have also been shown to activate FG, STS and temporoparietal junction (TPJ; Grosbras & Paus, 2006).

A direct comparison of the brain responses to images of face and body expressions of emotions (de Gelder, 2013; van de Riet, et al., 2009) also highlighted some differences in the processing of facial and body emotions. Two studies revealed that FG, EBA, AMG, STS and TPJ all respond to facial and bodily emotional signals, but AMG was more active during perception of facial expressions, while STS, EBA and motion areas V5/MT were more activated by bodily expressions (de Gelder, 2013; van de Riet, et al., 2009). Overall, these studies highlight that even static images of bodily emotional expressions activate action-perception structures (de Gelder, 2013). Building on these findings, de Gelder (2013) proposed that perceiving snapshots of bodily expressions of emotion triggers action preparation in the observers. This proposal is also in line with evidence from monkey physiology studies, where cells in the macaque temporal cortex responded to articulated static body postures when these were embedded into a meaningful context, suggesting that cells in this region may be involved in representing expectations regarding an observed individual's behaviour and future actions (Jellema & Perrett, 2003a, 2003b). Therefore, it is important to investigate emotion processing mechanisms using dynamic stimuli.

The proposal that viewing bodily expression of emotion enables preparation of adaptive responses in the observer, has been highlighted in the de Gelder (2006) model for perception of emotion from bodily cues (Figure 1.3). According to the model, interpretation of emotional signals from the body relies on brain networks specialized in visual, motor and emotional processing. Body emotion visual information is first processed by the subcortical system (in red on Figure 1.3) responsible for reflex-like emotional response, and by the cortical system consisting of the areas involved in the visuomotor perception of the bodily expressions (in blue). Both systems have feed-forward connection to the "body awareness" system; brain structures involved in gaining awareness of the bodily states (in green). Connections between the cortical and body awareness systems allow for a detailed analysis of the affective stimulus and for a decision on how to respond towards that stimulus (de Gelder, 2006). The model, however, does not take into account the role of an actor's identity in the interpretation of emotional signal. Body identity may be processed in the fusiform gyrus (FBA; Hodzic, et al., 2009; Ramsey, et al., 2011; Urgesi, et al., 2007) within the visuomotor system of EBL processing (de Gelder, 2006), so in principal the perception of bodily expressions partially takes into account the actor's identity.

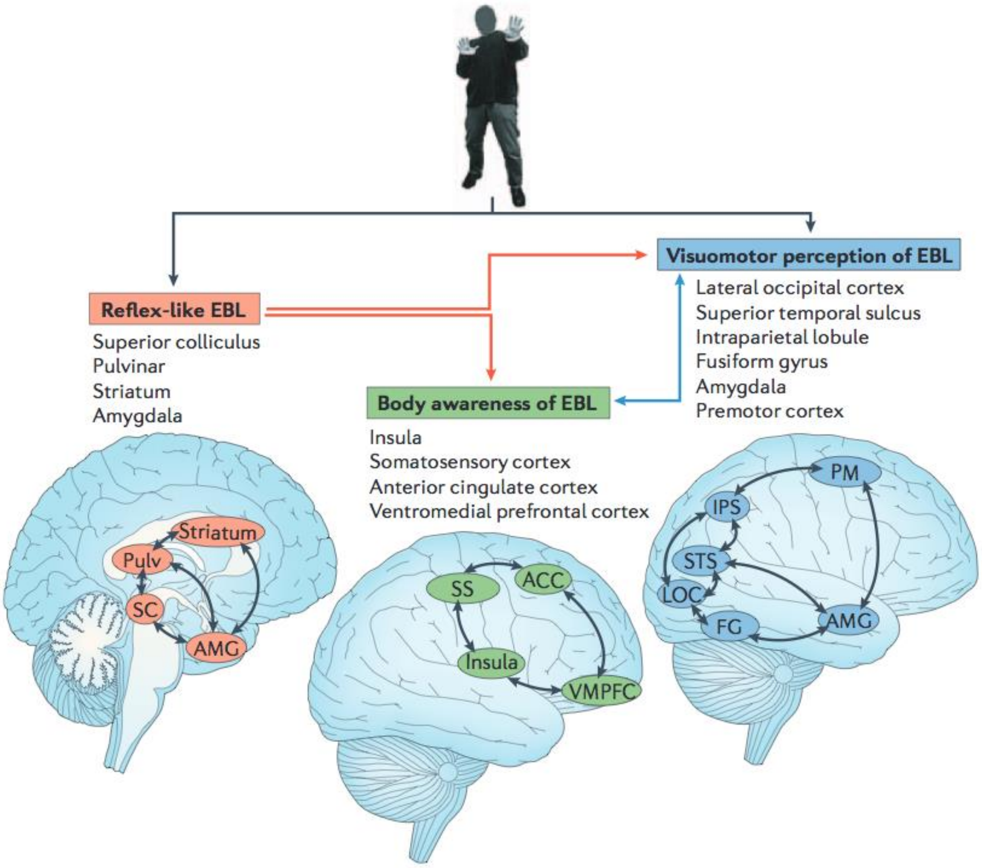


Figure 1.3. Neural networks involved in perception of emotional body language (EBL) by de Gelder (2006). Visual information regarding bodily expression of emotion is first processed by the subcortical reflex-like system (red) involved in the rapid automatic perception of EBL and the preparation of adaptive reflexes, and by the cortical (blue) visuomotor perception system. Both systems have feed-forward connections with the body awareness system (green), and further reciprocal connection between visuomotor and body awareness systems allow for a detailed processing of the affective stimulus. Figure obtained from de Gelder (2006). Copyright by Nature Publishing Group.

1.5 Integration of social signals from faces and bodies

In previous sections I have argued for many similarities in the neural processing of faces and bodies and for the similarities in processing of emotional signals from these cues. The question now is, to what extent information derived from the face can influence the processing of body information and how is our perception of faces influenced by seeing it in the context of the body? Indeed, in real life, faces are usually observed in a context of both the head and a whole body, so it is likely the processing of these cues interacts. There is some evidence suggesting that face processing mechanisms may influence processing of body information. For instance, body-inversion effect (discussed in section 1.2) is reduced for headless bodies, but not for bodies missing other body parts, such as an arm or leg (Yovel, Pelc, & Lubetzky, 2010). Subsequently, fMRI adaptation experiments suggested that this effect is mediated by the activation in the face selective brain areas (FFA) and not in the body-selective brain areas, indicating that face processing mechanisms may be involved in the processing of other stimuli from which the face can be inferred (Brandman & Yovel, 2010). In a similar fashion, a behavioural adaptation study by Ghuman, McDaniel, and Martin (2010) showed that prolonged viewing of headless gender-specific bodies influences the perception of gender from faces. Based on these cross-category, body-to-face aftereffects authors suggested that observation of bodies may lead to a top-down activation of neural representation of face-specific features. The effect of contextual cues on the activation of a specific neural population has also been demonstrated in a fMRI study by Cox, et al. (2004), who showed higher FFA responses to bodies with blurred faces than for headless bodies presented above blurred faces. Cox, et al. (2004) suggested that contextual information may be integrated during object perception via top-down mechanisms. In this case, integration would take place at the semantic level and/or at the level of object representations, which may already contain information about the context in which the given object is likely to occur (Cox, et al., 2004).

However, perceptual integration of facial and bodily cues to emotion is also very rapid, and occurs automatically, even when participants are instructed to attend only one of these cues (Aviezer, Trope, & Todorov, 2012a; Meeren, van Heijnsbergen, & de Gelder, 2005). Meeren, et al. (2005) created face-body compound images, where the expressed emotion was either matched (e.g. fearful body and fearful face) or mismatched (e.g. fearful body and angry face). They found that when face and body conveyed congruent emotion, the recognition of the facial expression was quicker and more accurate. Analysis of the electrophysiological correlates (ERP) moreover showed that such modulation occurred as early as 115 ms post stimulus onset indicating that emotions signalled by faces and bodies are processed and integrated automatically (Meeren, et al., 2005). In consequence, perception of facial expressions is influenced by bodily expressions of emotions (Aviezer, et al., 2012a; Aviezer, Trope, & Todorov, 2012b;

Meeren, et al., 2005; Van den Stock, Righart, & de Gelder, 2007) and vice versa; there is evidence that judgement of body expressions is dependent on the valence of the facial expression associated with the observed body (Willis, Palermo, & Burke, 2011). In recent years there has been a growing body of evidence indicating that other contextual cues, such as voices and background scenes which in real life co-occur with faces and bodies, also affect how we perceive and process facial and bodily expressions (Kret & de Gelder, 2010, 2013; Van den Stock & de Gelder, 2012; Van den Stock, Vandenbulcke, Sinke, & de Gelder, 2014). The influence of such cross-categorical context on emotion perception may suggest that the emotion system is not category specific, and therefore there may exist a common representation of emotion for faces and bodies.

There are several possible mechanisms underlying the cross-categorical influences of faces and bodies on emotion perception. It is possible that some facial expressions presented in isolation may appear ambiguous and can be attributed positive or negative valence (de Gelder, 2006). Bodily expression, however, may provide an appropriate context in which facial expression can be accurately categorised (Aviezer, et al., 2012a). The influence of the body emotion on face emotion recognition may also be due to the close proximity in the underlying neural network for processing both of these signals (see Figure 1.2). It is also possible that perception of emotion is not sensitive to specific body parts.

1.6 Immersive Virtual Environment technology in social perception research

The need for studying the contextual effects on social perception and social cognition has recently been emphasised (de Gelder & Hortensius, 2014). Still, thus far most of our understanding of the processing of social signals comes from highly-controlled laboratory settings, where stimuli are often presented in an impoverished format and in isolation. In contrast, in the real world, interpretation of emotion, behaviour and intention of other individuals occurs within a rich social and temporal context, which may influence our perception. Investigating social perception using naturalistic and dynamic stimuli is crucial for understanding how perception and cognition interact in a complex, real world environment and allows for verification whether results of laboratory studies translate into the natural conditions. In addition, some research questions can only be fully answered using naturalistic tasks and materials, which parallel the real world with its temporal and spatial irregularities (Spiers & Maguire, 2007). A virtual reality environment provides a powerful tool for studying social perception in a highly controlled setting that resembles the real world. Perception of three-dimensional objects and movies may also differ from the perception of two-dimensional stimuli (Snow et al., 2011), suggesting that not all results from the laboratory may translate to everyday perception.

In recent years virtual reality has been successfully employed in studying visual and social perception (Chou, Weingarten, Madden, Song, & Chen, 2012; Gaebler et al., 2014), and in various aspects of social psychology including, for instance, social interactions (Giannopoulos, Wang, Peer, Buss, & Slater, 2011), embodiment (Peck, Seinfeld, Aglioti, & Slater, 2013) or social identity (Slater et al., 2013). Advancement in computer processing moreover allow for conducting psychophysical experiments in virtual reality environments allowing for high control and high ecological validity. Therefore these techniques seem suitable for investigating action perception mechanisms, which would advance our knowledge about processing of social signals in our natural, social environment.

1.7 Aims of the thesis

The overall aim of this research is to examine how temporal context influences social perception. Throughout this thesis I employed visual adaptation paradigms (see Chapter 2) in order to investigate whether perceptual history can bias our perception of social signals such as the emotional state and trustworthiness of other individuals in a real-world situation. Visual adaptation paradigms enable inferences to be made about the neural mechanisms that underpin the perception of specific properties of visual stimuli. With this in mind, the experimental studies in this thesis were developed to further our understanding of the neural and cognitive processes underlying the perception of emotions and trustworthiness from whole-body actions and faces.

Specific research questions:

> Does prior visual experience influence our perception of the behaviour of other individuals in a naturalistic environment?

In Chapter 3, using immersive virtual reality and orthosteroscopic presentation I investigated whether action adaptation biases our judgements of the behaviour of other individuals within the same social scene. Specifically, I tested whether our perceptual weight-judgement of boxes lifted by actors is biased by prior observation of different actors performing similar tasks. In order to compare the biases in action perception in naturalistic and laboratory settings I tested the effects of action adaptation in three viewing conditions: life-size stereoscopic presentation, life-size presentation without stereoscopic depth information, and small-scale presentation without stereoscopic depth information.

> Is our perception of the emotional state of other individuals derived from observing their actions sensitive to visual adaptation mechanisms?

If adaptation to natural actions biases our perception of behaviour of other individuals, it is possible that social judgments derived from dynamic bodily actions are also subject to biases induced by visual adaptation. In Chapter 4 I examined the biases in the perception of emotions derived from whole-body actions resulting from visual adaptation.

> Is processing of emotion from whole-body action dependent on the processing of body identity?

Evidence from neuroimaging and psychophysical studies suggest that processing of facial expression may depend on the processing of facial identity. Does similar interaction exist for the processing of body action and identity? In Chapter 4 I tested the role of identity in the coding of emotion derived from body actions and examined the characteristics of emotional action adaptation aftereffects for same-identity and different-identity conditions.

> Is emotion perception category-specific?

Does perception of emotion rely on mechanisms that are specific to the body part that conveys it? To investigate whether processing of emotional body actions influences the perception of facial expression in Chapter 5 I tested the cross-category, body-to-face adaptation aftereffects.

> Is adaptation to emotional expression influenced by the knowledge regarding the emotional state of the observed actor?

Chapter 6 presents a series of experiments examining whether adaptation to facial expressions is modulated by Theory of Mind (ToM) processes. Here I examined whether attribution of the mental state, i.e. knowledge about the emotional state behind the expressed emotion, modulates the magnitude of facial expression aftereffects. This was tested by adaptation to genuine and faked emotional expressions.

> Is perception of complex social traits such as trustworthiness biased by perceptual history?

Finally, in Chapter 7 I examined whether complex social trait judgements such as trustworthiness perception derived from faces are susceptible to visual adaptation. Previous research (Stirrat & Perrett, 2010) also suggested that women may be more sensitive to facial cues to trustworthiness, therefore I tested the effects of adaptation to (un)trustworthiness in male and female participants.

CHAPTER 2

General Methods. Adaptation as a method for studying social perception

"Sense-perception, as realized in actual perceiving, is a mode of qualitative change. This explains why the affection continues in the sensory organs (…) not merely while they are actually engaged in perceiving, but even after they have ceased to do so. (…) When persons turn away from looking at objects in motion (…) they find that the visual stimulations still present themselves, for the things really at rest are then seen moving. Sensory organs are acutely sensitive to even a slight qualitative difference (…) and that sense-perception is quick to respond to it; but also reacts upon it."

Aristotle

(On Dreams)

The recent sensory history immediately creates a context in which our current perceptual experience is interpreted. The human visual system shows a considerable plasticity when dealing with such context in a constantly changing environment. A striking and easily measurable form of such plasticity is that caused by visual adaptation. During adaptation, response properties of the neurons that encode the adapted stimulus change, and responses to the subsequent test stimuli are also altered (Kohn, 2007). The effect of adaptation on the subsequent perception is perceptually manifested by inducing *aftereffects* – visual illusions that typically bias perception of the test stimulus towards the opposite of the adapted stimulus (Barlow, 1972; Barlow & Levick, 1965; Mollon, 1974). There are numerous examples that illustrate the significant changes in perception induced by visual adaptation, such as a description of a motion aftereffect first reported by Aristotle (Anstis, Verstraten, & Mather, 1998), and more recently face aftereffects (Leopold, O'Toole, Vetter, & Blanz, 2001; Webster, Kaping, Mizokami, & Duhamel, 2004; Webster & MacLin, 1999b) where judgment of facial categories such as gender or expression is strongly biased by prior exposure to a face manipulated along these dimensions.

One of the functions of adaptation is to provide adaptive adjustments that the visual system makes after a prolonged exposure to a given stimulus. These adjustments sometimes lead to a shift in perception and sometimes may lead to a renormalization, where the adapted stimulus appears more average (Webster & MacLin, 1999b). Such renormalization is based on the properties of the currently observed image, which following prolonged exposure will serve as a baseline for perceiving new incoming stimuli. For instance, as we continuously observe them, distorted faces appear more average (Webster & MacLin, 1999b) and blurred images appear more focused (Elliott, Georgeson, & Webster, 2011). Such recalibration increases the visual system's sensitivity to changes in the surrounding visual environment and therefore, can have functional advantages.

2.1 Functional benefits of adaptation

Some of the advantages of adaptation can be observed at the visual coding level, enabling the visual system to best adjust to the regularities in the environment. These advantages can occur at the behavioural level, with recently emerging psychophysical evidence for improved perceptual performance following adaptation (e.g. Clifford, Wyatt, Arnold, Smith, & Wenderoth, 2001; Keefe, Dzhelyova, Perrett, & Barraclough, 2013; Oruc & Barton, 2011). Adaptation for instance maximises the range of information that can be represented within the neural response (Webster, McDermott, & Bebis, 2007). As the range of stimuli that each neuron will respond to (its tuning function) is limited, adaptation can center tuning around the stimulus that is currently encoded (Kohn & Movshon, 2004). Consequently, this adjustment of tuning functions towards the mean stimulus level leads not only to an improvement in visual sensitivity (e.g. as in light adaptation, where the sensitivity adjusts to the mean level of brightness) but also to an improvement in visual discrimination (Webster, et al., 2007). Improvement in discrimination of novel or rare stimuli is achieved by suppressing responses to the frequent or persistent stimuli while sparing the response to the novel stimuli characteristics (Kohn, 2007). Improved discrimination following adaptation has been reported for a variety of stimulus properties, for instance motion (Phinney, Bowd, & Patterson, 1997), orientation (Clifford, et al., 2001) and more recently for more complex stimuli such as facial gender (Yang, Shen, Chen, & Fang, 2011) and even facial trustworthiness (Keefe, et al., 2013).

Adaptation also improves coding efficiency by altering the tuning properties of the activated neurons (Kohn, 2007). While encoding common or persistent stimuli, neurons become more narrowly tuned, maximizing the amount of information that is conveyed in each spike. Such reduction in redundancy leads to savings in energy spending, as action potentials are metabolically expensive (Lennie, 2003).

Finally, adaptation provides the visual system with perceptual constancy; it allows for a stable representation of object properties by ignoring the variations in the stimulus caused by changes in external environment (Webster, 2011). This is evident, for example, in colour constancy, where adapting to the average colour or brightness within the natural environment can lead to a better representation of a colour of a given object by removing the distortions caused by the changes in luminance (due to e.g. changes in seasons) (Webster & Mollon, 1997). The same process may also play a role in providing perceptual constancy within the observer by compensating the variations (e.g. changes in visual sensitivity due to aging) that arise from the observer (Webster, et al., 2007). Adaptation may readjust the visual response to the structure of natural images, so that the adapted images appear more natural or better focused (Webster, Georgeson, &

Webster, 2002). Adaptation thus not only regulates how things look, but may also allow the visual system to make predictions about the world by establishing the norm-based codes for a given stimulus based on its average representation (Leopold, et al., 2001). Adaptive norm-based coding mechanisms operate on the assumption that the stimulus is coded by pairs of neural populations adaptively tuned to above- and below-average values for the similar class of stimuli (Rhodes & Jeffery, 2006). Norm based coding has been proposed to underlie our face identity perception, where the average identity is coded implicitly in the tuning of face coding neurons (Leopold, et al., 2001; Rhodes & Jeffery, 2006). Based on this prediction, each new face is represented relative to how much it deviates from the norm or the prototype. Faces that lie further away from the average elicit stronger neural signal (Leopold, Bondar, & Giese, 2006), which allows for a better recognition and detection of outliers in the constantly changing environment.

2.2 Mechanisms of perceptual adaptation

The most commonly observed property of visual adaptation is that it causes a change in sensitivity to the observed stimulus (Webster, et al., 2007). This effect arises from the reduction in cell's firing rate (which reduce the cell's response) to the adapted stimulus (Kohn, 2007). Studies on adaptation suggest that the visual system undergoes an active recalibration of its sensitivity based on the immediate temporal context. However, because the visual system has a wide range of ways in which it can adjust to recent perceptual history, it is possible such adaptations operate differently at successive stages of sensory processing (Kohn, 2007). A number of cellular mechanisms have been proposed to possibly underlie changes in neural sensitivity resulting from adaptation.

Theoretical studies have suggested that adaptation may result in a short-term synaptic depression due to the depletion of presynaptic vesicles (Chance, Nelson, & Abbott, 1998). Evidence for this mechanism in *in vivo* studies, is, however, very limited. Another synaptic mechanism that has been proposed to be mediated by adaptation is a change in the strength of synaptic inhibition (Barlow, 1990; Barlow & Foldiak, 1989). Changes in synaptic inhibition may explain adaptation effects in the retina, but not in the cortical brain (Kohn & Movshon, 2004). The Fatigue Hypothesis was also proposed to explain the occurrence of adaptation aftereffects (Graham, 2001). Here, prolonged response to a specific stimuli pattern causes the depletion of neurotransmitters in cells that responded selectively to this pattern (Kohn & Movshon, 2004). Adaptation aftereffects can, however, still occur long after the simulation has finished, and can even re-appear following periods of darkness suggesting that aftereffects exhibit "storage" (Watamaniuk & Heinen, 2007). This evidence indicates that neurotransmitter depletion cannot be the mechanism underlying adaptation. Intracellular recordings in V1 have also shown that adaptation can cause both attractive and repulsive shifts in tuning of the adapted cells (Teich & Qian, 2003). Reduction in the cell excitation results in narrow tuning, while reduction in both excitation and inhibition of the adapted cell can cause the repulsive shift in preferences. It has been proposed that such plasticity can be achieved by changing synaptic weights or hyperpolarization of the presynaptic neurons (Kohn, 2007). These models are helpful in explaining how adaptation can alter tuning of the adapted cells differently at different stages of sensory processing.

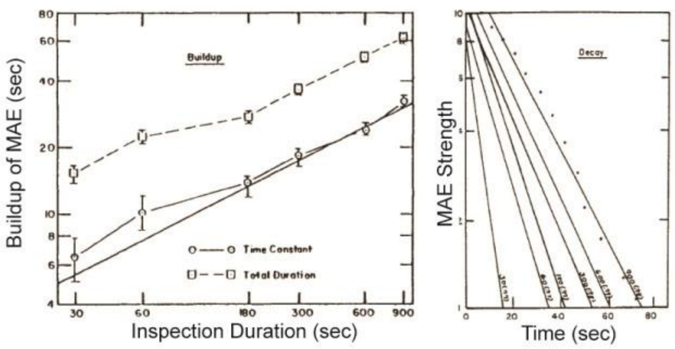
Since adaptation re-centers tuning around the prevailing stimulus, only the test stimuli that share similar properties with the adaptor are expected to evoke weaker responses (Kohn, 2007). Indeed, visual aftereffects are selective and therefore reflect narrow (or broad) tuning of the neural population that encodes given stimulus dimensions. Physiological measurement of these tuning curves and behavioral measurement of perceptual biases following exposure to stimuli that vary along given dimensions thus allows for the investigation of the perceptual mechanisms using psychophysical techniques.

2.3 Timescale of adaptation

Adaptation aftereffects operate on multiple timescales, and changes in neural responses can occur following brief adaptation lasting milliseconds (e.g. Leopold, et al., 2001) to more prolonged ones ranging from seconds to minutes (e.g. Carbon et al., 2007). Similarly, perceptual changes following adaptation can be brief, or can operate over longer durations including hours, days and weeks (Carbon & Ditye, 2011b). This diversity in the duration of adaptation suggests that different forms of adaptation may serve different functions at different timescales (Webster, 2011).

With traditional aftereffects, the magnitude of aftereffect depends on the duration of adaptation and the duration of the test stimulus or the delay between the presentation of the adapting and test stimuli (Hershenson, 1989; Leopold, Rhodes, Muller, & Jeffery, 2005). Recent studies indicated that high-level adaptation to face identity (Rhodes, Jeffery, Clifford, & Leopold, 2007), gender of biological motion (Troje, Sadr, Geyer, & Nakayama, 2006a), hand actions (Barraclough, et al., 2009) and whole body action aftereffects (Barraclough, Ingham, & Page, 2012) show similar dynamic properties. These include logarithmic build up with the exposure to the adapting stimulus, exponential decay over time, and a power-law relationship between the duration of the adapting stimulus and the decay time (see Figure 2.1).

a Dynamics of motion aftereffect (Hershenson, 1989)



b Dynamics of face identity aftereffect (Leopold et al., 2005)

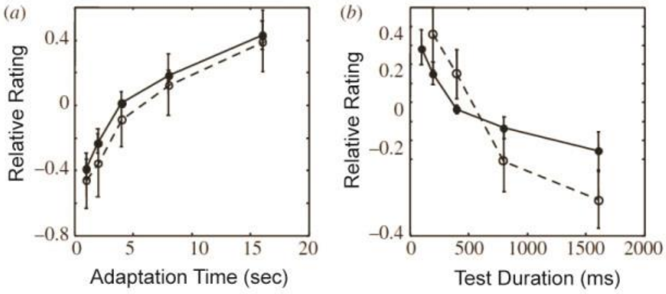


Figure 2.1 Dynamics of motion and face identity aftereffects. Dynamics of the a) motion aftereffect (Hershenson, 1989). Aftereffect magnitude increases with the duration of the adaptation phase (left) and decreases with time post-adaptation (right). Dynamics of b) face identity aftereffect (Leopold et al., 2005), where aftereffect also increases with the increase of the adaptation duration (left) and decrease with the increase of the duration of test stimulus (right).

On one hand, shared temporal characteristics for aftereffects arising from adaptation to distinct neural properties suggest that adaptation may occur in a similar fashion at different stages of the cortical hierarchy. Any differences in temporal dynamics for specific class of adapted stimuli may, on the other hand, inform about the specificity of adaptation mechanisms at different levels of sensory processing. In case of high-level face aftereffects, for instance, traditionally such aftereffects have been observed following relatively long exposures to the adapting stimuli (at least 1 second; e.g. Hsu and Young (2004). However, less is known about the temporal dynamics of aftereffects that occur following very brief adaptation. It has been argued that aftereffects arising from brief adaptation are particularly interesting as they are likely to be associated with adaptation in the higher level areas (Fang, Murray, & He, 2007; Suzuki, 2001). Manipulating the duration of adaptation may therefore allow for targeting neural processes at different stages of visual processing. Indeed, in one study, brief adaptation (500 ms) resulted in view-independent aftereffects, while longer adaptation (5 sec) led to position-specific afterffects suggesting that the different adaptation latencies can affect different neural populations (Kovacs, Zimmer, Harza, & Vidnyanszky, 2007a). In another study, different type of information derived from faces (expression or identity) required different adaptation durations to result in perceptual aftereffects, suggesting that global and featural processing of faces operates on multiple timescales (Van Rijsbergen, Jannati, & Treves, 2008).

Adaptation can also act over hours, days, and even weeks. A classic example for such long-lasting aftereffects is a McCollough effect – a colour aftereffect contingent with the spatial orientation of the adapted patterns (McCullough, 1965), which has been shown to persist up to a few days post-adaptation (Jones & Holding, 1975). Long-term adaptation has also been shown for properties beyond colour (see also Table 2.1), such as orientation. Zhang, Bao, Kwon, He, and Engel (2009) asked participants to wear a specialized head-mounted video camera that could filter the visual display in real time and deprive them of a specific orientation. Following 4 hours of such adaptation, participants showed increased sensitivity to the deprived orientation, and this effect was still measureable 24 hours post adaptation. These results elegantly demonstrated how adaptation allows the visual system to adjust its sensitivity to be able to respond accordingly to small changes in the visual characteristics of the environment providing a benefit to the observer. The authors interpreted these results as providing support for the proposal that the visual system is constantly in some state of adaptation to the surrounding environment, and that prolonged deprivation may in turn release such adaptation and thus increase sensitivity to specific features (Zhang, et al., 2009). In a similar fashion, long term visual adaptation has been recently proposed to underlie more permanent changes such as shifts in face preferences (Carbon, 2010; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003) and even aesthetic preferences (Carbon, 2011; Carbon, Leder, & Ditye, 2007).

However, long-lasting aftereffects can also be induced by relatively brief adaptation indicating that adaptation, aside from acting at the perceptual level, can also alter the mental representation of a given stimulus (see Strobach & Carbon, 2013 for a review). In the real world adaptation can act as a fast recalibration process that can influence our social perception (Kloth & Schweinberger, 2008) and in turn influences our interaction with other individuals. One study investigating a temporal delay on the effects of adaptation (see Table 2.1. for an list of studies reporting long-lasting aftereffects) focused on the gaze direction judgement (Kloth & Schweinberger, 2008), which is an important social signal. The study revealed that after adapting to a specific gaze direction for 88 seconds, participants showed an impaired classification of the adapted direction of the gaze (i.e. typical gaze direction aftereffect) even after 7 minutes post adaptation. This research demonstrated potentially different mechanisms underpinning short and long-term adaptation.

Differential neural mechanisms for short and long-term face viewpoint adaptation have also been proposed. Long-term fMRI adaptation leads to viewpoint-dependent adaptation in face selective areas, which is sensitive to the degree of rotation of the adapted stimulus, while short-term adaptation causes viewpoint-independent adaptation in the same areas (Fang, et al., 2007). Interestingly, in the same study right superior temporal sulcus (rSTS) only showed an adaptation effect following long-term adaptation, suggesting that adaptation at different timescales may reflect selectivity of different neural populations. Furthermore, Carbon and colleagues systematically examined the decay (or persistence) of face aftereffects and demonstrated that perception of configural information from faces was still biased after 5 min (Carbon, Strobach, et al., 2007), 80 min (Carbon & Leder, 2006), 24 hours (Carbon & Ditye, 2011b) and even one week (Carbon & Ditye, 2011b) post adaptation, further suggesting that adaptation can alter not just immediate perception, but also the mental representation of the adapted stimulus and even form long-term changes which may underlie memory and learning. It is likely that aftereffects that operate on different timescales depend on different cellular mechanisms (see Barraclough & Perrett, 2011 for a review). It is therefore important to differentiate adaptation effects that take place at different stages of visual processing; with short-lasting aftereffects likely to operate at the perceptual level, and long-lasting effects likely to be involved in generating stimulus familiarity and potentially underlying long lasting changes in representations, which may contribute to such phenomena as the other-face effect (Webster & MacLeod, 2011b).

Table 2.1 Examples studies reporting long-lasting, “sustainable”, aftereffects.

Study	Adapted property	Adaptation duration	Adaptation- test delay	Test duration	Long-lasting aftereffect overview
Vernon (1934)	Tilted lines	10 min	Up to 15 min	Unlimited (participants asked to respond immediately)	Aftereffects occurred for a “appreciable” period of time – still measureable after 5min
Hammer (1949)	Figural aftereffect (tilted lines)	Between 5 – 160 sec, in 30 sec steps	0 – up to 180 sec	Unlimited (participants asked to respond immediately)	Aftereffect magnitude depended on the adaptation duration, reached zero after 90 sec delay
Hershenson (1989)	Motion	30-900 sec	N/A	Unlimited (participants stopped the test display once they reported no aftereffect)	Following 15 min adaptation aftereffects still measured up to 80 sec.
Leopold, et al. (2001)	Face identity	5 sec	150 – 2400 ms	200 ms	Aftereffects were diminished for intervals greater than 300 ms, but adaptation continued to influence perception after even 2400 ms.
McKone, Edwards, Robbins, and Anderson (2005)	Face distortion	5 sec and 160 sec	Up to 15min, 24 hrs	200 ms	Following 160 sec aftereffects still measured after 15 min delay, 24 hrs removed the aftereffect, 5 sec adaptation survived 10 sec delay, 20 sec delay filled with visual stimuli removed the aftereffect.
Carbon, Strobach, et al. (2007)	Face distortion (familiar faces)	36 min	5 min, 24 hrs	Until response	Aftereffects significant after both delays: AE after 24hrs were weaker, but still reliable.
Kloth and Schweinberger (2008)	Gaze direction	1.5 min (88.8 sec plus 5 sec top up)	0 – up to 10 min	400 ms	Aftereffects decreased exponentially over time, but remained significant until 7min post adaptation.
Carbon and Ditye (2011b)	Face distortion (familiar faces)	25 min	5 min, 24 hrs, 1 week	Until response	Aftereffects significant after all delays.

2.4 High-level aftereffects

Adaptation paradigms employed for studying high-level and socially meaningful stimuli such as faces (see Clifford & Rhodes, 2005 for a review) or body actions (e.g. Barraclough & Jellema, 2011; de la Rosa, Streuber, Giese, Bulthoff, & Curio, 2014) allow for probing mechanisms underlying processing of more abstract perceptual attributes. Faces, for example, vary highly in their morphology which allows for differences in physical appearance across identities, genders or ethnicities (e.g. Bruce & Young, 1986). Additionally, short-term changes in facial configurations co-occurring with expressing different emotional states or changes in gaze direction are important social signals. Adaptation can be used to target both invariant (e.g. Leopold, et al., 2001; Rhodes & Jeffery, 2006) and changeable (e.g. Fox & Barton, 2007; Hsu & Young, 2004) aspects of the face which makes it a powerful tool for studying social perception.

Indeed, adaptation has been employed to examine processing of multi-dimensional facial judgements such as facial age (Schweinberger et al., 2010), attractiveness (Rhodes, et al., 2003) or trustworthiness (Keefe, et al., 2013; Wincenciak, Dzhelyova, Perrett, & Barraclough, 2013; see chapter 7). Evidence from auditory adaptation to vocal identity (Zäske, Schweinberger, & Kawahara, 2010), gender (Schweinberger et al., 2008) and affect (Bestelmeyer, Rouger, DeBruine, & Belin, 2010) moreover provide evidence that adaptation is not restricted to the processing of visual information, and occurs also for high-level non-linguistic auditory stimuli. Adaptation has also been used to characterise mechanisms underlying biological motion gender (Troje, et al., 2006a) and emotion (Roether, et al., 2009), and more recently goal-directed hand actions (Barraclough, et al., 2009) and whole body walking actions (Barraclough, et al., 2012; Barraclough & Jellema, 2011).

It is, however, important to elucidate whether adaptation to high-level stimuli can be distinguished from adaptation at earlier stages of visual processing. There are a number of strategies that allow for distinguishing high-level aftereffects from the low-level ones. For instance, face and action aftereffects show transfer across changes in position, image size (Barraclough & Jellema, 2011; Leopold, et al., 2001) and orientation (Barraclough, et al., 2009; Rhodes, et al., 2003) suggesting that high-level aftereffects are non retinotopic, and probably result from adaptation of selective neurons in the cortex (Leopold, et al., 2006). Face aftereffects have also been found to depend more on the perceptual category that the stimuli belong to (i.e. identity or gender boundary) rather than purely on the structural similarities between the stimuli (Bestelmeyer et al., 2008) which is encoded by lower-level neurons coding the physical characteristics of different face patterns. Adaptation to high-level stimuli is also more dependent on the awareness of the adapted stimulus, and is mostly eliminated when the face is masked by binocular suppression (Moradi, Koch, & Shimojo, 2005). Face aftereffects can also be induced following visualization, where participants are only asked to imagine faces belonging to the predefined category (DeBruine, Welling, Jones, & Little, 2010; Hills, Elward, & Lewis, 2010). Adaptation to emotional expressions conveyed by faces and actions moreover transfer across different identities (Fox & Barton, 2007; Roether, et al., 2009) further suggesting that emotion specific aftereffects may depend on the more abstract, semantic representation of affect, which is not coded with respect to a particular individual. Recent evidence for cross-category aftereffects (Ghuman, et al., 2010; Little, Feinberg, DeBruine, & Jones, 2013; Palumbo, D'Ascenzo, & Tommasi, 2014; Weigelt, Koldewyn, & Doehrmann, 2010), where aftereffects transfer across two different categories representing the same attribute (e.g. face and body gender or emotion) provide further evidence that aftereffects may occur at the semantic level and independent of the physical properties of the stimulus that convey the given attribute.

However, it is still not clear whether aftereffects can occur at the conceptual and abstract level. Kovacs et al. (2006) found no evidence for the transfer of gender aftereffects across two body parts – faces and hands – suggesting that processing of human body parts is shape-selective. Similarly, in a study by Fox and Barton (2007) adaptation to facial affect did not occur for the non-facial images (e.g. Darwin's pictures of emotional dogs), and did not transfer across two separate modalities, i.e. visual and auditory. Recent evidence suggests that under certain conditions aftereffects can be induced by objects belonging to different global categories (Javadi & Wee, 2012; Palumbo, et al., 2014) and even by two separate sensory modalities i.e. visual and auditory signals (Skuk & Schweinberger, 2013). This indicates that adaptation is not only a property of the early stages of sensory processing but is a mechanism operating throughout the sensory processing hierarchy.

2.5 Dissociating adaptation from other cognitive and perceptual biases

Stimulus repetition may have several behavioural consequences on subsequent perception; it is therefore important to distinguish the effect of adaptation from other perceptual and cognitive biases.

Repetition priming

Repetition priming (Tulving & Schacter, 1990a) typically results in faster and more accurate responses to the stimulus when that was preceded by the same (or contextually similar) stimulus. Therefore behavioural consequences of priming are different to those induced by perceptual adaptation; the priming stimulus shows a positive, facilitatory effect on the test stimulus. Recent behavioural, electrophysiological and neuroimaging data (Kaiser, Walther, Schweinberger, & Kovács, 2013; Walther, Schweinberger, Kaiser, & Kovács, 2013) suggest that priming and adaptation affect slightly different stimuli; priming is observed for unambiguous stimuli whereas adaptation affects the perception of ambiguous stimuli. Different regions of the visual cortex may also be sensitive to either adaptation or priming (with adaptation affecting most object and face selective areas, and priming affecting only face selective areas; cf. Kaiser, et al., 2013), suggesting that those two phenomena possibly rely on exclusive neural mechanisms (Walther, et al., 2013).

Negative priming

Adaptation may result in an inhibited response towards the adapted property. Similar inhibitory processes are observed following negative priming (Fox, 1995; Tipper, 1985), which results in slower and less accurate responses toward the test stimulus, when that was preceded by a stimulus that was effectively ignored. Since both stimuli in negative priming paradigms are presented in rapid succession and participants are asked to ignore the probe, it is unlikely that negative priming will contribute towards effects observed following adaptation.

Reverse priming

Reverse priming relates to the priming in the opposite direction of the prime i.e. participants may show slower responses to the test stimulus which is similar to the previously observed object (Glaser & Banaji, 1999). Reverse priming occurs when the primes are extreme, and it is analogous to the contrast effects (see below). Therefore it is likely to provide an automatic correction for the bias induced by the preceding prime (Glaser & Banaji, 1999). However, reverse priming is expected when the prime is presented for a very brief duration (up to 200 ms) and is stronger with longer stimulus onset asynchrony (SOA; Heij, Dirkx, & Kramer, 1990).

Contrast effect

The contrast effect is a cognitive phenomenon often encountered in social judgement, which may also influence participants' responses towards social stimuli. Contrast effect relies on the principle of trade-off contrast, where the surrounding objects may bias the perception and judgment of the target stimulus (Simonson & Tversky, 1992). This may be problematic in adaptation studies, as here participants may develop a cognitive strategy to judge the test stimulus as simply being different from the previously observed adaptor. To deal with this issue, judgement of the test stimuli may be tested on multiple response options or in free-naming paradigm, giving participants an opportunity to select the most appropriate label for the observed percept (Rutherford, Chattha, & Krysko, 2008). Enabling participants to freely choose the response that best reflects their perception of the test stimulus, allows for examining the relationship between the tested stimuli categories. Additionally, Hsu & Young (2005) tested whether facial expression aftereffects can be explained by a criterion shift, where participants develop a tendency to classify the stimulus based on a contrast produced by placing this stimulus in a temporal context of another stimulus (e.g. adapting face). By varying the duration of adaptation phase they found that expression aftereffects were dependent upon the induction (adaptation) time. These findings suggested that high-level afterffects result predominantly from the adaptation of neural populations tuned to particular expressions and not from the criterion change (Hsu & Young, 2005).

Sequential Contrast

Sequential contrast results in an effect very similar to the adaptation aftereffect, where the test stimulus is "repelled away" from the prime in the orthogonal (or opposite) direction (Suzuki & Cavanagh, 1998). Sequential contrast, however, relies on a very different timescale; traditionally it is induced following a very brief prime presentation (approximately 30ms) and only remains measureable up to 150-300 ms (Suzuki & Cavanagh, 1998). Interestingly, contrast effects also show an initial increase in strength with an increase in SOA. Examining the temporal dynamics of adaptation aftereffects can help distinguish adaptation from potential sequential contract effects.

Representational momentum

An observer's perception of a last frame of a dynamic display may often be displaced forward in the direction of the observed trajectory. This displacement has been termed representational momentum (RM) (Freyd & Finke, 1984; Hubbard, 2005) and has been suggested to have an adaptive function role in helping the observer to optimally respond to changing stimuli. As with adaptation, in order for the representational momentum to occur, the final image in a sequence needs to be semantically related to the preceding display. In contrast to adaptation where the adaptors are usually portraying a stimulus at peak intensity, in RM the intensity of the stimuli may differ throughout the display.

Perceptual learning

Another form of perceptual plasticity is perceptual learning, defined as the improvement in the ability to perform a specific perceptual task following practice (Gibson, 1969). Adaptation can be distinguished from perceptual learning as the two phenomena have different underlying mechanisms. Adaptation results from the prolonged exposure to the particular stimulus, while perceptual learning results from a practice of a specific task (Ahissar & Hochstein, 2004). Unlike adaptation, which can transfer across different stimulus categories, perceptual learning is often specific to the stimuli presented during practice (Gold, Bennett, & Sekuler, 1999). However, as many perceptual tasks (e.g. perceptual discrimination) involve prolonged or repetitive exposure to specific stimuli, it is likely that adaptation contributes to perceptual learning.

Adaptation-induced increased sensitivity to novel stimuli may have an effect on task performance, which would contribute to perceptual learning. Moreover, long-term recalibration following adaptation may also reflect a form of learning (Webster, Werner, & Field, 2005).

2.6 Psychophysical adaptation paradigms

2.6.1 Adaptation paradigms examining bias in perception

Throughout this thesis (excluding Chapter 5) experiments have been conducted using adaptation paradigms and followed the procedure broadly described below. Similar procedures consisting of a test-adaptation-test cycle have been widely employed in studies of perceptual aftereffects (e.g. Barraclough, et al., 2012; Barraclough & Jellema, 2011; Bestelmeyer, et al., 2008; Fox & Barton, 2007; Rhodes, et al., 2007; Rhodes, et al., 2003; Skinner & Benton).

Participants first looked at, and judged, the *test stimulus*, which had neutral characteristics (with respect to adaptors) or was ambiguous (i.e. containing features belonging to both opposite adapters). I called this phase the *pre-adaptation phase,* which served as a *baseline* for calculating the adaptation aftereffects. Next, participants completed the *adaptation phase*, where they were exposed to an adapting stimulus for a prolonged time. Adapting stimuli were manipulated along the examined dimension. Following each presentation of the adapting stimulus participants observed the same test stimulus again. Finally, in some instances, where the experiment was conducted over a longer time period (Chapters 4 and 5), participants completed the *post-adaptation phase*, which followed the same procedure as the *pre-adaptation phase*. Participants' responses for the pre- and post-adaptation blocks were averaged and served as a *baseline* for calculating the adaptation aftereffects. Differences in participants' responses towards the test stimuli between the *baseline* and *adaptation* phases, and following two opposite adaptors allowed for the measurement of perceptual bias induced by the adaptation.

2.6.2 Adaptation procedure testing discrimination following adaptation

In order to quantify the magnitude of the cross-category emotion aftereffects, in Chapter 5 I employed a psychophysical method based on *Fechner's psychophysics* (Ehrenstein & Ehrenstein, 1999). Psychophysics allow for a systematic examination of *psychological* judgement given by the participant to stimuli varying along *physical* dimensions. It is therefore a mathematical approach for measuring the internal representation of the external physical world using experimentally derived data.

2.6.3 Basic concepts of psychophysics

Data obtained in the psychophysical experiments can be plotted on a psychometric function (see Figure 2.2 A). Here, cumulative responses of an experiment are plotted as a function of a stimulus level. Responses can be measured as percentage of correct responses (usually in a forced choice design) or as a percentage of yes responses (in a yes-no design). The point on the psychometric function (i.e. interval between the two stimuli) representing the intensity of the stimulus, where participants are making each of the two responses equally often is called the point of subjective equality (PSE; Ehrenstein & Ehrenstein, 1999). Determining the PSE individually for each participant also provides control over the intensity of the stimuli selected for the experiments, that they can be tailored to the individual differences among observers. In the adaptation experiments reported in Chapter 5, I used the PSE to determine the strength of the adapting and test stimuli for each participant.

To measure the effect of adaptation on the perception of a test stimulus a common way is to look at the shift in the central tendency in the psychometric function (Figure 2.2 B) and shift in the PSE (Morgan, Dillenburger, Raphael, & Solomon, 2012). Without adaptation, the observer would be expected to classify an ambiguous stimulus (e.g. neutral expression) as happy or sad with equal probability. However, after (e.g. emotion) adaptation the psychometric function is shifted away from the adapted emotion, so the stimulus containing less happiness appears happy following sad adaptation. The magnitude of the shift in the psychometric function following adaptation to two opposite emotions, can inform about the strength of the emotion aftereffects.

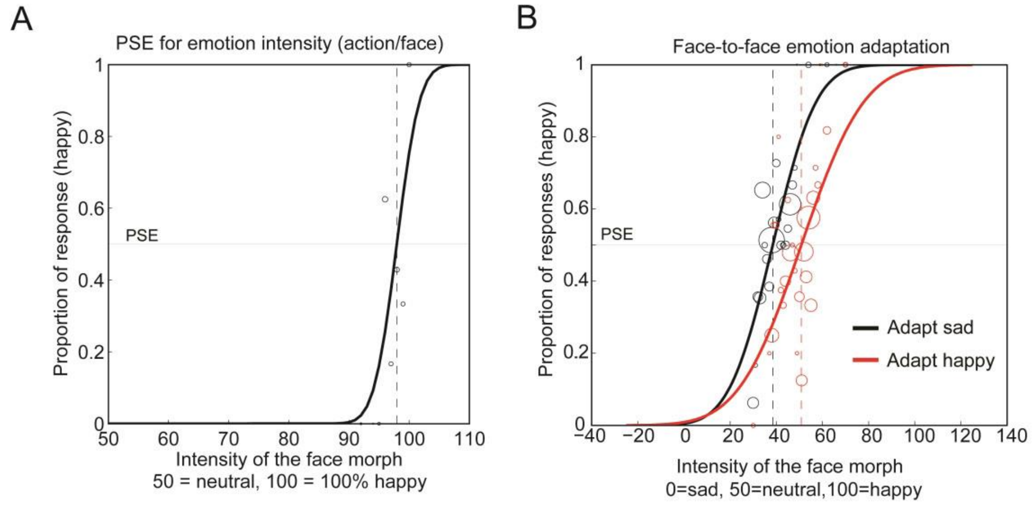


Figure 2.2 Example of a psychometric function. (A) The example illustrates the proportion of time where a stimulus (face morph) is perceived as happy and the corresponding stimulus intensity. The threshold (PSE) is defined as the intensity at which the stimulus is judged as happy at 50% of the time. (B) The example of a shift in psychometric function following adaptation to sad (black line) or happy (red line) facial expression. Negative shifts following sad adaptation are shifts "down" where stimuli containing less happiness are perceived as happy, whereas positive shifts following happy adaptation are shifts up, where stimuli containing more happiness are perceived as happy.

Effects of adaptation can also be measured as a change in threshold for detecting differences in stimuli. This threshold is referred to as the just noticeable difference (JND) and reflects the smallest difference between two stimuli that leads to a change in experience (Treutwein, 1995). The slope of the psychometric function determines the JND. The JND is calculated as half of the stimulus intensity range (plotted on x axis) between the points on the psychometric function corresponding to 75% and 25% of responses given to the stimulus (e.g. 75% and 25% of happy responses plotted on y axis on Figure 2.2).Traditionally the threshold is considered to be a perceptible difference between the stimuli that the observer can detect in ~75% of the trials. Adaptation to a given stimulus property may for instance result in a selective improvement in discriminating thresholds for the adapted property (Keefe, et al., 2013; Yang, et al., 2011).

2.6.4 Psychophysical procedures

There are several methods for estimating the psychometric function using psychophysical procedures. Popular methods include the *method of limits* and the *method of adjustments*. In a method of limits the experimenter varies the strength of the stimulus in small ascending or descending steps, and on each trial the observer reports whether the stimulus differs from the standard. The stimuli are adjusted until the observer reports that the threshold has been reached. The method of adjustment is similar, however, here the observers adjusts the stimulus level and sets it to apparent equality with a standard. A slightly more time-consuming method is the *method of constant stimuli*. Here, the whole psychometric function is sampled over a large predetermined number of trials, where the stimuli strength varies across the whole range. This method is free from any initial assumption, but requires a large number of trials in order to obtain measures for each point in the psychometric function. The most common psychophysical procedure is to use a *staircase* (see Figure 2.3). The staircase starts with high stimulus strength and after a predetermined number of correct responses the stimulus strength is decreased. Whenever the observer responds incorrectly to the stimulus, a reversal is made and the stimulus strength is increased. Both the staircase steps and the reversal rules can be predetermined; the staircase follows an up-down procedure, where the stimulus strength is increased or decreased on a trial-by-trial basis based on the participant's responses. The staircase procedure targets the point on the psychometric function where the stimulus can be classified as either similar or dissimilar to the standard. This makes the staircase particularly useful for determining the PSE in appearance-based tasks (Kingdom & Prins, 2010).

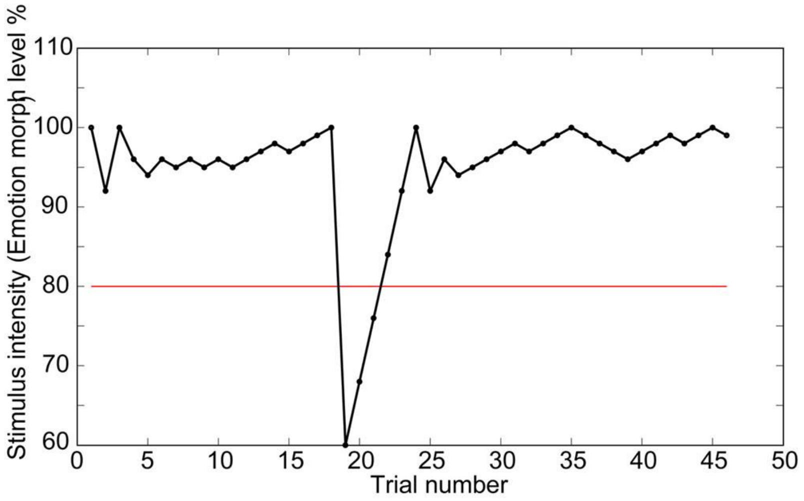


Figure 2.3 Example of two interleaved staircase procedure. To calculate the intensity of the test stimulus at which it is perceived as equally intense as the standard (action) stimulus participants complete two staircases: one descending (first ~19 trials plotted on the figure), where the initial intensity of the stimulus was high and was gradually reduced, and one ascending (remaining ~25 trials), where the initial intensity of the stimulus was low and was gradually increased. The initial staircase step size i.e. the difference of the intensity level between the first and next stimulus, was set to 8%, and was halved on each of the first 3 trials. After 12 reversals, where the staircase alternates between presenting stimuli of a slightly lower and higher intensity and the observer is likely to responds similarly to both stimuli, the procedure stops.

For all psychophysical experiments in this thesis, I used a staircase procedure with interleaved reversal rule (1-up, 1-down, 1-up, 1-down). Strength of the adapting stimuli was determined individually for each participant by calculating separate PSE for each adaptor. Adaptation aftereffects have been calculated as a difference in PSE for the test stimuli between pre-adaptation and adaptation conditions, as well as following two different adaptation conditions.

CHAPTER 3

Action adaptation in naturalistic viewing conditions

Some of the data presented in this chapter has been presented at the following conference:

Keefe, B., Wincenciak, J., Ward, J., Jellema, T., Barraclough, N.E. (2012). Adaptation aftereffects when seeing full-body actions: Do findings from traditional 2D presentation apply to 'real-world' stereoscopic presentation? *Perception,* 41 ECVP Abstract Supplement, page 72.

3.1 Abstract

When observing actions of other individuals we automatically interpret the specific movements in terms of goals, intentions or belief. Accurate understanding of the meaning of other people's behaviour is essential for successful social interaction. Our perception of actions of other individuals can, however, be biased by the temporal context in which an observed action was embedded (e.g. Barraclough & Jellema, 2011). In recent years visual adaptation has been employed in the study of action coding mechanisms and the biases in action perception induced by prior visual experience. However, the majority of that work has taken place under highly controlled, laboratory conditions. In this study I used a perceptual-weight judgement task to test whether action understanding is subject to adaptation under more naturalistic viewing conditions. Stimuli were presented under three different conditions: life-size stereoscopic presentation, life-size presentation without stereoscopic depth information, and small-scale presentation without stereoscopic depth information. Following adaptation to an actor lifting heavy or light boxes, or standing still, participants judged the weight of different boxes lifted by test actors. Results of the study showed that adaptation significantly influenced the perceived weight of the test box. The biases in weight judgement following adaptation were equally strong across all three presentation conditions. These findings suggest that adaptation can systematically bias our perception and interpretation of behaviour of other people in our everyday life.

3.2 Introduction

Humans have adapted to live inside social groups where complex social interactions are elements of everyday life are an essential part of society. A crucial component of everyday social exchange is observing the behaviour of other people and making sense of their intentions, beliefs or desires. People developed an astonishing ability to understand these mental states of other's just by looking at their nonverbal behaviour. For instance, we can successfully judge whether a person is honest or deceitful by observing the characteristic kinematics of his/hers executed actions (Grezes, Frith, & Passingham, 2004; Grèzes, Frith, & Passingham, 2004). Accurate interpretation of this action information is fundamental for our social functioning.

In natural environments, actions are executed within a rich temporal and social context. In order to fully understand actions, they need to be interpreted with respect to the context in which they appear. A significant number of experimental studies, however, have focused on eliminating the effects of contextual sources of information and examined action perception mechanisms using impoverished stimuli such as point-light display (e.g. Atkinson, et al., 2004; Dittrich, et al., 1996). These stimuli can be highly controlled and finely manipulated, but do not represent the normal visual input that is available when we are watching the behaviour of others in the real world. Alternatively, video clips of actors embedded in a natural context can be used to examine visual processing of actions (e.g. Grezes, et al., 2004; Hamilton, Joyce, Flanagan, Frith, & Wolpert, 2005). These stimuli may be difficult to control experimentally, but provide a richer representation of the body movement and can contain useful contextual and scene information.

There is a body of evidence suggesting that social and temporal contexts can influence our perception and understanding of actions of other individuals. The same action embedded in different contexts can for example signal different intention (Iacoboni et al., 2005). Inferring the purpose of an unusual action can also be facilitated by providing a plausible explanation for such action (Brass, Schmitt, Spengler, & Gergely, 2007). Social context in which an observed action is embedded has also been proposed to be integrated with, and can influence action recognition mechanisms (de la Rosa, et al., 2014). Finally, evidence from visual adaptation studies (Barraclough & Jellema, 2011; Barraclough, et al., 2009) suggests that our perception of human actions is strongly influenced by the immediate prior visual experience. As shown in the adaptation studies, visual action recognition mechanisms are sensitive to prior perceptual history. Following adaptation, these systems, may provide biased information about actions downstream to subsequent brain regions involved in understanding the intentions of others, e.g. "mirror" areas (Grafton, 2009). It is, however, possible that these later stages can also be adapted.

In this study I investigated how action understanding under natural viewing conditions is influenced by the perceptual history. Participants adapted to whole body actions embedded in a natural social scene and subsequently performed an action understanding task. The action understanding task was a weight-judgement task: participants viewed a video clip of an actor lifting a box and placing it on a table and were asked to judge the weight of that box. This task seems natural, but is not always easy (Runeson & Frykholm, 1981) as it requires participants to perform a detailed assessment of the kinematics of the observed action (Hamilton, et al., 2005). Different kinematic features such as the type of grasp or the duration of the lift can provide information about the box weight. However, the most informative cues seem to come from the velocity of the early part of the lift (Hamilton, et al., 2005). These subtle changes in the kinematics of the observed movement can be reliably discriminated by the participants and used to infer the characteristics, such as weight, of the observed objects.

Previous studies have also shown that performing weight judgement engages the mirror neuron system (Hamilton, Wolpert, & Frith, 2004; see also Chapter 1, section 1.3.1). Accurate assessment of the observed lifts is biased by participants lifting boxes themselves, suggesting that it requires in the observer the ability to simulate or to build an internal model of similar actions (Hamilton, et al., 2004). In two fMRI studies activity in the inferior frontal gyrus (IFG) was recorded when participants either judged the beliefs of an actor based on his/hers box-lifting behaviour (Grèzes, et al., 2004) or when motor processing modulated the perceptual judgement of observed actions (Hamilton, Wolpert, Frith, & Grafton, 2006). In addition disrupting the activity of the IFG with a repetitive transcranial magnetic stimulation (rTMS) impaired participants' ability to judge the weight of boxes lifted by an observed person (Pobric & Hamilton, 2006). Together these results suggest that perceptual weight-judgement is a complex action-understanding task that is achieved through the motor simulation.

Observation of and interpretation of such a complex body action engages multiple brain networks that underlie visual recognition (e.g. Giese & Poggio, 2003) and understanding of an action (e.g. Gallese & Goldman, 1998; Rizzolatti & Craighero, 2004). Visual processing of body actions takes place over two cortical streams; a ventral stream projecting from V1 through V2 and V4 to the inferior temporal cortex dealing predominantly with object recognition, and a dorsal stream extending from V1 to the inferior parietal cortex coding the location of the stimulus relative to the observer (Decety & Grezes, 1999; Giese & Poggio, 2003; Milner & Goodale, 1995). Understanding of the goal of an action has been proposed to rely on more anterior regions identified as Action Observation Network (AON; Grèzes, Armony, Rowe, & Passingham, 2003; Kilner, 2011; see also Chapter 1, section 1.3.1). The AON includes areas that make up the mirror neuron system; ventral inferior frontal gyrus (IFG) and inferior parietal lobule (Rizzolatti & Craighero, 2004) and the STS, which responds to the perception of biological motion (Allison, Puce & McCarthy, 2000). Previous studies (Barraclough, et al., 2009) have shown that observation of a hand lifting boxes can result in action adaptation biasing the weight-judgement of subsequently lifted boxes. Whether the bias in the weight judgement following adaptation is driven by the adaptation in the visual action processing mechanisms or by the adaptation in the mirroring system is, however, still unclear.

Most of our understanding of the mechanisms underlying action perception comes from studies conducted in highly controlled experimental conditions. There is a growing interest and the need for complimentary results obtained in such well-controlled laboratory setting with findings from more naturalistic settings (e.g. Sanchez-Vives & Slater, 2005; Spiers & Maguire, 2007). Comparing the findings from the laboratory studies with those from studies of real world experiences are critical for verifying whether results obtained in experiments hold true under natural conditions. This notion is particularly important as it is often assumed that the findings obtained using simplified stimuli will generalize to the real world. Secondly, some research questions can be best answered using naturalistic stimuli with naturally occurring temporal irregularities and meaningful context (Spiers & Maguire, 2007). An increasing number of studies examining social perception have therefore started using movies of natural actions (e.g. Barraclough & Jellema, 2011; de la Rosa, et al., 2014; Grèzes, et al., 2004) and virtual reality environments (e.g. Han, Jiang, Humphreys, Zhou, & Cai, 2005) in order to test mechanisms of action understanding in conditions that resemble our complex natural world.

There are clear benefits of employing virtual reality technology in the study of social perception. Virtual reality allows for simulating the experimental setting with a good ecological validity and control. Three-dimensional movies presented via stereoscopic display have also been found to evoke stronger experience in the observer and have resulted in increased inter-subjective correlations of cortical networks than the same 2D movies (Gaebler, et al., 2014).

Recent studies on visual and social perception that employed virtual reality have also largely confirmed results of laboratory studies (see Chou, et al., 2012 for a review). One study that used virtual reality goggles during fMRI examination of brain processing of gaze perception (Pelphrey, Viola, & McCarthy, 2004) found a similar pattern of activation in the fusiform gyrus and STS as studies using static facial images (see Allison, et al., 2000 for a review). These results may suggest that neural coding of social stimuli presented in 2D and in 3D is largely similar. On the other hand, a recent study investigating the visual processing of 2D images and natural 3D objects using fMRI repetition paradigm found different results for these two types of stimuli (Snow, et al., 2011). Two dimensional images produces typical, repetition suppression effects whereas no repetition effects were observed for naturally presented real objects. These results suggest that neural mechanisms for the perception of natural, ecologically valid stimuli may differ from those underlying perception of 2D images of the same objects.

3.3 The current study

In the light of the above, this study tested whether adaptation to whole-body actions occurs under naturalistic viewing conditions. Stimuli were videos of natural actions, where actors lifted and placed on the table boxes of varying weights. Participants' performed a perceptual weight-judgement task after adapting to three different action contexts: actor lifting heavy or light boxes, or actor standing still. Stimuli were presented under three different viewing conditions: life-size stereoscopic presentation (3D), life-size presentation without stereoscopic depth information (2D), and small-scale presentation without stereoscopic depth information (small 2D). Following previous work reporting adaptation induced aftereffects in weight-judgement tasks (Barraclough, et al., 2009) it was predicted that adaptation to movies of actors lifting heavy boxes would result in test boxes appearing lighter and adaptation to actors lifting light boxes would result in text boxes looking heavier. In order to create a natural context, adapting and test actors were always of a different identity embedded within the same social scene. Similarly sized adaptation aftereffects across the three viewing conditions would suggest that adaptation to one individual's actions can bias the perception of behaviour of other individuals in the same social environment.

3.4 General methods

3.4.1 Participants

Twenty four participants (13 female, age, *M*=22.5 years, *SD*=3.9) took part in the study; all were naive to the purpose of the study. Participants were University of Hull students or staff and received payment for participating in the experiments. All had normal or corrected to normal vision and stereoacuity better than 40 arcsec. Experiments were approved by the ethics committee of the Departments of Psychology at the University of Hull and were performed in accordance with the ethical standards laid down in the 1990 Declaration of Helsinki.

Assessment of participants' stereoacuity

Participants were tested for stereoacuity at the screening session which took place before the first experiential session. Stereoacuity was measured using an anaglyph random dot stereogram that allowed to measure stereopsis to 40 arcsec. The binocular cues in the stereogram indicated five circles receding in depth. Participants viewed the stereogram on a 22" screen CRT monitor (Philips 202P40, 1600x1200 pixels, 100Hz refresh rate) wearing red/cyan glasses and were asked to report whether they saw an emerging image. Once they reported seeing ‘circles’ or ‘rings’, they were asked to count how many circles appeared in the image.

3.4.2 Stimuli

Stimuli were video clips filmed using a custom built 3D camera. The camera was composed of 2 Panasonic TM900 digital cameras (each filming at 1920x1080 pixels, and 50 fps progressive scan) mounted on a solid aluminium plate and set to a 66mm parallel inter axial distance (IAD). During filming the 3D camera was placed at a height of 1.22m, and at a distance of 4.1m from the virtual screen plane; all objects were viewed at a depth behind the screen plane (i.e. uncrossed disparity). Four actors (2 males, 2 females) were filmed while lifting boxes onto a table from the floor (see Figure 3.1). All boxes (see Figure 3.1) were of the same size and colour and their weight was manipulated by filling each box with sand bags of a desired weight. This way there was no visual cues to the weight of each box.

Adapting actions consisted of movies of actors lifting 8, 2kg (light adaptation) or 18kg (heavy adaptation) boxes. Boxes were placed in a line (along the depth dimension), so actors lifted one box after another. The adaptation control condition consisted of movies of actors standing still in front of a box for 30 seconds. Test actions were lifts of a box weighing 6, 8, 10, 12 or 14kg. For all adapting and test actions actors were always informed about the weight of the boxes prior to lifting. Both adapting and test actions were filmed at 90° angle, with actors facing right. In pilot testing, the actions of one female actor whose lifts of the 2kg boxes were perceived as the lightest and lifts of the 18kg boxes were perceived as the heaviest were selected for the adapting stimuli. Actions of the remaining three actors were used as test stimuli, so that the identity of the adapting and test actor was always different.

Using video editing software (Sony Vegas Pro 10), stimuli were created by superimposing the adapting and test action movies so that both actions appeared to occur in the same room. Using this procedure I generated 45 videos (3 test actors x 3 adaptation conditions [heavy, light, control] x 5 test box weights).

3.4.3 Stimulus presentation

Stimuli were presented in three viewing conditions: life-size 3D, life-size 2D and small scale 2D. For the life-size 3D and 2D presentation testing took place in the Hull Immersive Visual Environment (HIVE) auditorium at the Department of Computer Science, University of Hull. Stimuli were presented on a 2.44m x 5.33m rear projection screen (2 x Mirage 2000 Christie Digital DLP projectors, effective full screen resolution: 2,240x1,024 pixels, 100Hz refresh rate). Stimuli were viewed through active LCD shutter glasses (nuVision 60 GX, McNaughton Inc., triggered by StereoGraphics Infra-Red emitters). Participants sat on an adjustable chair at a height of 1.22m and 4.1m from the screen plane (to the cyclopean eye). Stimuli viewed from this position were orthostereoscopic such that the stereo image of the actors and environments were viewed in real world dimensions. Participants with interpupillary distances (IPDs) greater or less than the interaxial distance (IAD) of the camera (66mm) would be expected to perceive depth that is compressed or expanded from orthostereoscopic projection, respectively. Distortions in perceived depth induced in participants with IPDs greater or less than the IAD of the camera would be too small to be reliably detected based on normal stereoacuity (10 arcsec, Howard & Rogers, 2002). For life-size 2D participants viewed only the left video channel through the LCD shutter glasses. Small scale 2D stimuli were presented on a Philips 202P40 22” CRT Monitor (1,600x1,200 pixels, 100Hz refresh rate), where participants sat approximately 43cm away from the screen such that the actors subtended approximately the same area of visual space as for the large screen presentations.

3.4.4 Design and experimental procedure

Adaptation top-up paradigm was used in the experiment. In this paradigm, participants first adapt to the adapting stimulus for over several seconds (20-150 seconds, cf. Weigelt, Muckli, & Kohler, 2008). Here participants adapted for 30 seconds. Following this phase, a classic event-related adaptation takes place, where a short, (e.g. 5-sec long) presentation of an adapting stimulus is inserted between each of test stimuli. The adaptation is therefore ‘topped-up’ on every trial. This way a stable adaptation is maintained throughout the testing block. This design type allows for capturing the maximal effect of adaption in a blocked design and it considered to reveal mid- to long-term effect of adaptation (Weigelt, et al., 2008).

A PC running MATLAB 2010a (The MathWorks, Natick, MA) and Psychtoolbox (Brainard, 1997) controlled the experiments, displayed the stimuli and recorded participant responses. A custom built movie playback engine (mex3Dplayer) was used to display 3D videos. Participants took part in 3 testing sessions to test the 3 viewing conditions on different days; order of testing session was counterbalanced across participants. Each testing session consisted of three blocks with a control block (no adaptation) always occurring first, and two adaptation blocks (adapt heavy and adapt light) counterbalanced across participants and testing sessions. Each block consisted of 15 randomised trials (3 test actor identity x 5 test box weight). Each adaptation block begun with an adaptation phase where a movie of an adapting actor consecutively lifting 8 boxes (weighing 2 kg in light adaptation and 18kg in heavy adaptation) was played three times (24 lifts). The first experimental trial began as soon as the adaptation phase had finished. Each trial (see Figure 3.1) began with 2 seconds of adapting and test actors standing still in order to allow for stereo fusion (Hoffman, Girshick, Akeley, & Banks, 2008). Next, the during the adaptation top-up adapting actor consecutively lifted 8 boxes. Boxes were placed in a line, so the actor lifted one box after another and placed them on a table in front of her (see Figure 3.1). In a light adaptation all boxed weighed 2kg and in a heavy adaptation condition they weighted 18kg. Then, following 1 second of inter-action interval (IAI) where both actors stood still, the test actor lifted their box. Once the test action was finished the screen turned black for 1.5 second during which participants responded. Participants were asked to indicate the weight of the test (2, 4, 6, 8, 10, 12, 14, 16, or 18kg) box by pressing an appropriate number on a wireless numberpad. If no response was given during this interval an error beep was played and the trial was repeated at a random point later in the block. The control block (no adaptation) begun with both adapt and test actor standing still in front of a one box for 30 seconds. Next, the test actor lifted the box and participants were asked to respond during the 1.5 seconds interval from when the screen turned black.

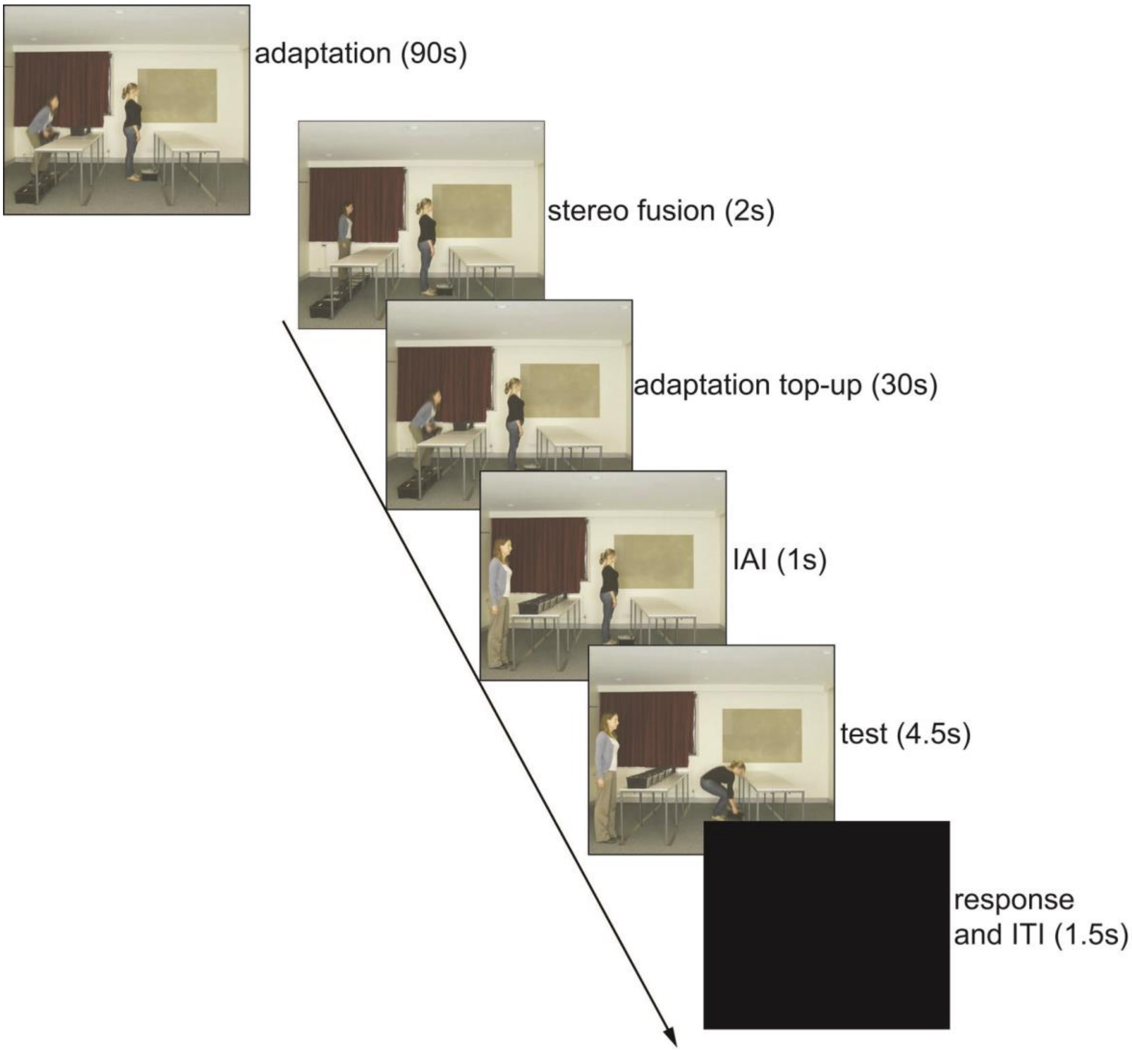


Figure 3.1 A schematic illustration of the experimental procedure. Each testing block begun with a 90 sec adaptation, where the adapting actor lifted heavy or light boxes or stood still in the control condition. Each experimental trial begun with 2 sec of both actors' inactivity followed by the adaptation top-up where the adapting actor lifted and placed onto a table 8 boxes. After 1 sec of inter-action

interval (IAI) test actor lifted one box. Once the test action was completed the screen turned black for 1.5 sec.

3.4.5 Data Analysis

First, mean rating of each test box weight was calculated for each participant in each adapting and viewing condition. To examine whether experimental manipulation (heavy and light adaptation) affected weight judgement of all test boxes, I averaged ratings of each test box across participants for each adapting and viewing condition. These average ratings are illustrated in Figure 3.2. As observed rating of test boxes correlated highly with physical weight of the boxes in all experimental conditions (all slopes<.40, all $R^2>.88$), I then averaged the ratings of all test boxes. This step created a single value representing test box rating for each participant and each adapting and experimental condition. Next, aftereffects were calculated for each viewing condition and each participant. Heavy aftereffects values were calculated by subtracting the test box rating in the control condition from the test box rating in the heavy adapting condition. Light aftereffects values were calculated by subtracting the test box rating in the in the control condition from the test box rating in the light adapting condition. These values were used for the main analysis.

3.5 Results

Average ratings of each test box in each adapting and experimental condition are illustrated in Figure 3.2.

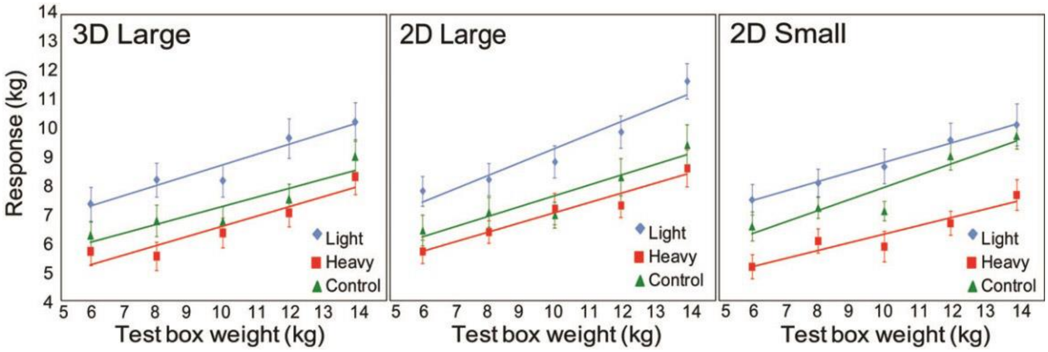
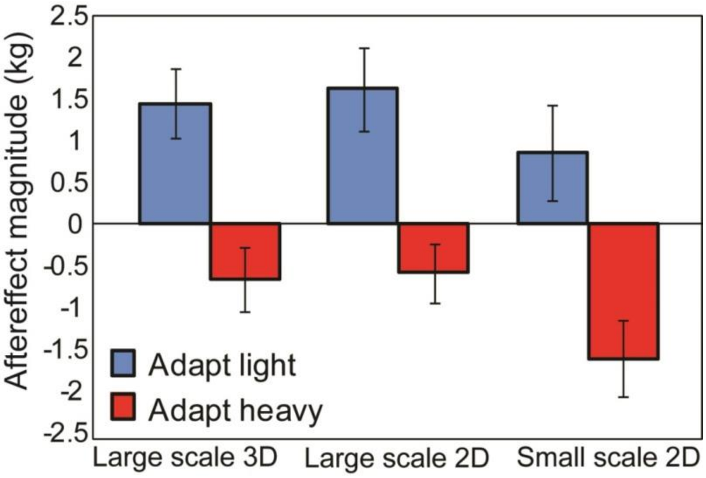


Figure 3.2 Mean weight rating for each of the test boxes in each viewing condition. Blue lines represent test box rating following light adaptation (2kg),

red lines represent rating following heavy adaptation (18kg) and green lines represent rating in the control condition (no adaptation). Error bars represent SEM.

Aftereffects were analysed using a 2x3 within-subjects ANOVA with factors of adaptation condition (heavy, light) and viewing condition (3D, 2D life-size, 2D small scale). The magnitude of these aftereffects is illustrated in Figure 3.3. Weight judgements of the test boxes were significantly affected by the adapting stimulus (ANOVA, main effect of adaptation condition, $F(1,23)=68.38$, $p< .001$, $\eta_p^2 = .75$). Test actors appeared to lift heavier boxes (M=1.3, SD=.30) following adaptation to light boxes, while test actors appeared to lift lighter boxes (M=-.96, SD=.37) following adaptation to heavy boxes. The viewing condition did not have a significant effect on the magnitude of these aftereffects ($F(2,46)=2.23$, $p=.119$, $\eta_p^2 = .09$)[1], nor was there an interaction between adaptation condition and viewing condition ($F(2,46)=.32$, $p=.727$, $\eta_p^2 = .01$), indicating that the biases in weight judgement following adaptation were equally strong across all presentation formats.



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[1] Although the viewing condition did not have any effect on the weight judgement of test boxes as revealed by the 2x3 ANOVA, upon visual inspection of Figures 3.2 and 3.3 it appears that in the 2D small scale viewing condition test boxes were overall judged as lighter than in the large scale conditions. Consequently, the heavy adaptation may have had a marginally stronger effect on weight judgment in the 2D small scale condition as suggested by Figure 3.3. The study could have potentially been underpowered to detect this effect. However, additional studies investigating the characteristics of these weigh-judgement aftereffects (see Keefe, Wincenciak, Ward, Jellema, & Barraclough, 2012, *ECVP Supplement*) suggested that adaptive mechanisms systematically influence action perception regardless of the presentation format.

Figure 3.3 Weight judgement adaptation aftereffect magnitude (kg). Positive values indicate that following adaptation test boxes appeared heavier; negative values indicate that following adaptation test boxes appeared lighter. Error bars represent SEM.

3.6 Discussion

The results of this study demonstrated that adaptation to videos of an actor lifting heavy or light boxes resulted in subsequent repulsive action aftereffects, where the perceived weight of the box lifted by the test actor was biased away from the adapted weight. Specifically, the test actors appeared to be lifting heavy boxes following adaptation to actor's lifting light boxes, and test actors appeared to be lifting light boxes following adaptation to heavy lifts. These biases in action perception were equally strong across all three viewing condition: large scale 3D, large scale 2D and small scale 2D. Together these findings suggest that our perception and judgement of behaviour of other individuals can be affected by the temporal context. Here, participants' interpretation of the behaviour of one individual in a shared social scene biased their perception of subsequent actions performed by other individuals. As these biases occurred when participants observed actions in a naturalistic, life-size virtual reality environment, it is likely that our every-day interpretation of behaviour of other people is also sensitive to similar social biases.

The similarities between action aftereffects in 2D and large scale 3D conditions also suggest that similar mechanisms may underlie visual processing of action of other individuals in the naturalistic and laboratory conditions (see also Chou, et al., 2012 for a review). The study was, however, not designed to determine the potential loci of action adaptation in a naturalistic environment. Previous studies, using 2D video clips of hand-lifting actions have shown that recognition and interpretation of the whole-body weight lifting actions requires the engagement of multiple brain networks involved in action recognition (e.g. Giese & Poggio, 2003) and action understanding processes (e.g. Gallese & Goldman, 1998; Rizzolatti & Craighero, 2004). Adaptation to body actions is also likely to occur at multiple states of these networks (e.g. Kohn, 2007). For instance, Barraclough and colleagues (Barraclough & Jellema, 2011; Barraclough, et al., 2009) reported that action adaptation still occurs at the high-level, view-independent stage of action processing, possibly in the STS region (Barraclough, et al., 2009). In addition, in a recently study using repetition suppression (RS) paradigm in an fMRI experiment, Wiggett and Downing (2011) reported that action adaptation resulted in a widespread adaptation across the action recognition network including EBA, FBA, FFA, pSTS and motion selective region (hMT+). Since actors in the present experiment were always facing the same direction, it is possible that adaptation at the lower, view-dependent level of visual processing contributed to the aftereffects observed here. However, action aftereffects transferred across different actors, who differed significantly in body shape and action kinematics, so it is unlikely that adaptation at the lower level of visual system can fully explain the effects observed here.

In addition, visual analysis of body actions requires the analysis of the goals behind the executed movement (e.g. Gallese, Fadiga, Fogassi, & Rizzolatti, 2002; Gallese & Goldman, 1998; Iacoboni, et al., 2005), which has been proposed to rely on activity within the mirror neuron system and its connectivity with the STS region (Gallese, Keysers, & Rizzolatti, 2004). Perceptual weight-judgement tasks have also been reported to rely on the motor simulation and activity in the mirror neuron system (Hamilton, et al., 2004; Pobric & Hamilton, 2006). It is possible that the biases of the weight judgement following adaptation observed here could also have arisen from adaptation in both action recognition regions and beyond, at the higher cortical levels encoding the goal of an action (Hamilton & Grafton, 2006). This is, however, still an empirical question and the data of the present study does not address the underlying neural mechanisms of action adaptation.

The present study provided evidence that our perception of behaviour of other individuals is affected by the immediate perceptual history. Specifically, in a naturalistic social scene the interpretation of actions of one individual can be biased by our interpretation of other individuals within the same scene. However, the design of the current study does not allow for identifying whether these distortions in perception arise from the adaptation induced biases in the perception of specific action kinematics, i.e. adaptation in action recognition mechanisms, or/and are due to the biases in action understanding i.e. adaptation in the mentalizing system. This question along with other questions dealing with the characteristic of adaptation aftereffects to whole-body actions have been answered in subsequent studies conducted in our lab which are not part of this thesis (see Keefe, Wincenciak, Ward, Jellema, & Barraclough, 2012 for details). Nonetheless, results of this study are the first to show that our naturalistic viewing of the behaviour of people is influenced by visual adaptation occurring due to the presence of other individuals within the social environment.

CHAPTER 4

Adaptation to emotional body actions

This chapter is largely based on work that has been submitted for publication:

Wincenciak, J., Ingham, J., Jellema, T., Barraclough, N.E. (submitted). Interdependent processing of identity and emotion in whole body actions. *Cognition.*

And presented at the following conferences:

Wincenciak, J., Ingham, J., Jellema, T., Barraclough, N.E. (2013). Two systems for emotional action processing: with and without identity, 35th European Society for Cognitive Psychology Conference, Budapest, Hungary

Wincenciak, J., Ingham, J., Jellema, T., Barraclough, N.E. (2012), "Emotional action aftereffects indicate dual emotion coding mechanisms" *Perception,* 41 ECVP Abstract Supplement, page 53.

Wincenciak, J., Ingham, J. S, Barraclough, N. E. (2011), "Visual adaptation to emotional actions" *Perception,* 40 ECVP Abstract Supplement, page 213.

Please note: Data in Experiment 1 has been collected by Jenny Ingham during her Nuffield Summer Bursary.

4.1 Abstract

Accurate perception of an individual's identity and emotion derived from their action and behaviour is crucial for successful social functioning. Here, I examined the biases in perception of emotion of other individuals resulting from adaptation to emotional body actions and I tested the role of identity in the coding of emotion derived from body actions. After adapting to actors performing actions in either a happy or sad manner participants were asked to interpret the emotion of the neutral, test action. Results of the experiments showed that participants systematically judged the test actions as conveying the opposite to the adapted emotion. The magnitude of these emotional action aftereffects was dependent upon adapting and test stimulus similarity. The largest aftereffects occurred when adapting and test actors had the same identity and were performing the same action. Aftereffects transferred across identity, but not across action. Both identity-dependent and identity-independent aftereffects increased logarithmically with adaptation duration, as with previously observed high-level aftereffects. Critically, identity-independent aftereffects declined logarithmically with increasing intervals between adapting and test stimulus, as with other high-level aftereffects, while identity-dependent aftereffects did not decline (up to 10 s). Altogether, these results demonstrate the existence of extensive biases in the perception of emotional human behaviour resulting from our immediate perceptual history. Furthermore, the findings reported here suggest that processing emotion from body actions is partially dependent on the processing of body identity. These findings are consistent with models of face processing suggesting interdependence in the processing of invariant and changeable aspects of social cues.

4.2 Introduction

In the previous chapter I reported that adaptation to whole body actions embedded in a natural social environment results in a subsequent bias in the perception of behaviour of other individuals within the same scene. I showed that these biases also occur when the stimuli are presented in a naturalistic, virtual reality environment and thus are likely to shape our interpretation of behaviour of other people in everyday life.

The question now remains, what other aspects of social perception are subject to visual adaptation? In particular, I wanted to investigate whether the perception of emotional states of other individuals, derived from observing their actions, is also influenced by the perceptual history. Previous studies (Roether, et al., 2009) have already reported that adaptation to happy and sad walking actions results in high-level emotion-specific aftereffects. These have, however, only been tested with computer-generated walkers whose kinematics were based on point-light data for only one, generic, walking action. Humans, on the other hand, express and successfully recognize emotion from a variety of body movements (e.g. Atkinson, et al., 2004; Dittrich, et al., 1996). Therefore, the results of Roether and colleagues (2009) do not distinguish adaptation to emotional actions occurring at the action kinematic level from higher action-independent level of emotion processing. In light of the above, in this chapter I tested adaptation to emotions expressed in various natural whole body actions.

Human bodies also differ significantly in body shape and specific kinematics. These idiosyncratic body features and body kinematics enable us to successfully recognize different individuals from their movements (Kozlowski & Cutting, 1977; Loula, et al., 2005). In a similar vein, human faces differ in shape and facial configurations (Bruce & Young, 1986) and human voices possess individual acoustics parameters (Brunelli & Falavigna, 1995) that enable person identification. While face (Bruce & Young, 1986; Haxby, et al., 2000) and voice processing (Belin, et al., 2004; Spreckelmeyer, Kutas, Urbach, Altenmüller, & Münte, 2009) models have been developed to explain how identity and emotion information are linked in social cognition, our understanding of how we process these signals from body actions is limited.

Evidence from single unit recordings in monkeys (e.g. Gothard, et al., 2007; Hasselmo, et al., 1989; Perrett, et al., 1984), human neuroimaging (e.g. Baseler, et al., 2012) and electrophysiological (Martens, Leuthold, & Schweinberger, 2010) psychophysical studies (e.g. Atkinson, Tipples, Burt, & Young, 2005; Campbell & Burke, 2009; Fox & Barton, 2007; Ganel & Goshen-Gottstein, 2004; Schweinberger & Soukup, 1998) have also suggested that processing of facial expression may depend, to some extent, on the processing of facial identity. Visual adaptation studies, for instance, reported that facial expression aftereffects transfer across different facial identities, but are significantly smaller than aftereffects measured for the same individuals (Campbell & Burke, 2009; Fox & Barton, 2007). These studies show that processing of facial expression is sensitive to changes in face identity and suggest interdependence in the processing of those two types of information from the face. In a similar fashion, evidence from Garner's selective attention (e.g. Ganel & Goshen-Gottstein, 2004; Schweinberger & Soukup, 1998) and rating paradigms (Dobel et al., 2008) revealed asymmetric dependencies between different aspects of face processing; while invariant facial features such as identity and sex can be perceived independent of expression, they may influence the processing of facial expressions (e.g. Atkinson, et al., 2005; Schweinberger & Soukup, 1998). However, there has been no research investigating the relationship between the processing of these signals from body actions. Neural and computational models of visual processing of actions (Fleischer, Caggiano, Thier, & Giese, 2013; Giese & Poggio, 2003) have also not been developed to take into account conjoint processing of emotion and identity. Therefore, the second aim of the experiments described within this chapter was to investigate whether identity modulates the perception of emotional cues from body actions.

Finally, characteristics of adaptation aftereffects can be used to determine the properties of the underlying visual processing mechanisms of complex social stimuli. Traditionally, aftereffects for high-level social stimuli such as faces (Leopold, et al., 2005) or actions (Barraclough, et al., 2012) show similar characteristics as aftereffects for low-level stimuli (Hershenson, 1989). The properties of aftereffects for dynamic social stimuli are, however, still largely untested. In order to examine the properties of emotional action aftereffects, I performed a series of experiments testing the temporal characteristics of these aftereffects.

4.3 The current study

Since biases in action understanding following adaptation were similarly sized across laboratory and virtual environment settings, as reported in Chapter 3, all experiments reported here have been conducted using 2D stimuli presented on a small screen. Across all experiments, participants adapted to whole body actions performed in either a happy or sad manner, then subsequently rated test actions carried out in a neutral manner. I tested the role of identity by varying the similarity between the identity of the adapting and test actors. In addition, I tested the role of specific action kinematics in the perception of emotion from body movement by varying the action type between the adapting and test stimuli. Following previous work (Kohn & Movshon, 2004; Verhoef, Kayaert, Franko, Vangeneugden, & Vogels, 2008) it was predicted that the magnitude of the aftereffects would decrease as similarity between the adapting and test stimuli decreased. Aftereffects that remained significant when the adapting and test actions differed in identity would suggest partially interdependent processing of identity and expression (cf. Campbell & Burke, 2009; Ellamil, et al., 2008; Fox & Barton, 2007), while aftereffects that transferred across different actions would suggest that emotions derived from body movements are coded beyond action specific neural mechanisms. Finally, in order to differentiate emotional action aftereffect from other potential mechanisms (see Chapter 2), I performed experiments testing the temporal dynamics and decay of emotional action aftereffects and experiments ruling out the potential contribution of response bias in adaptation aftereffects reported here.

4.4 General methods

4.4.1 Participants

Participants were University of Hull staff and students and received course credit or payment for participating. Participants had normal or corrected to normal vision. All participants were naïve to the purpose of the study except authors JI (Experiment 1) and JW (experiments 2 and 3). Excluding authors' data from the analysis did not influence the significance of any results and thus any conclusions drawn. Experiments were approved by the ethics committee of the Department of Psychology, University of Hull, and performed in accordance with the ethical standards laid down in the 1990 Declaration of Helsinki.

4.4.2 Stimuli

Two sets of emotional action stimuli (Figure 4.1) were made by filming actors conveying happy, sad and neutral actions in varying degrees of intensity. Stimulus set 1: Sixteen actors (8 female) were filmed (Canon XL1s, 720 x 576 pixels, 25fps, progressive scan) performing 4 different actions: lifting a box, putting down a box, sitting down on a chair, and walking to the right. Actors wore plain clothes and were filmed with their head at a three-quarter rear view (the face turned away from the camera), so that facial expressions could not be seen. Film was edited to generate 320 (16 actors x 4 actions x 5 emotions) 2s movies. Movies were rated by 14 independent observers (11 females, age *M*=21.9, *SD*=4.58) on a 5-point Likert scale, where 5=very happy and 1=very sad. The 64 actions (16 actors x 4 actions) rated as being most happy (*M*=4.27, *SD*=0.50), and the 64 actions rated as being most sad (*M*=1.65, *SD*=0.46) were used as adapting stimuli. The 64 neutral actions (*M*=2.88, *SD*=0.28) were used as test stimuli. Stimulus set 2: Sixteen new actors (8 female) were filmed in a chroma-green room (Panasonic, HDC-TM900, HD format 1920x1080 pixels, at 50fps progressive scan) walking diagonally so that facial expressions could not be seen (Keefe et al., 2014). Movies were edited to key out the green screen, and generate

48, 2s movies (16 actors x 3 emotions: happy, sad, neutral). Movies were rated by 10 independent observers on two independent 9-point Likert scales, where 1=neutral, 9=very happy/very sad, to ensure that the adapting actions conveyed the appropriate emotion (for detials of the ratings see Keefe, et al., 2014). Happiness ratings: happy actions *M*=5.31, *SD*=1.34; neutral actions *M*=2.77, *SD*=0.47). Sadness ratings: sad actions *M*=4.56, *SD*=1.02; neutral actions *M*=2.89, *SD*=0.56). The happy and sad actions were used as adapting stimuli; the neutral actions were used as test stimuli.

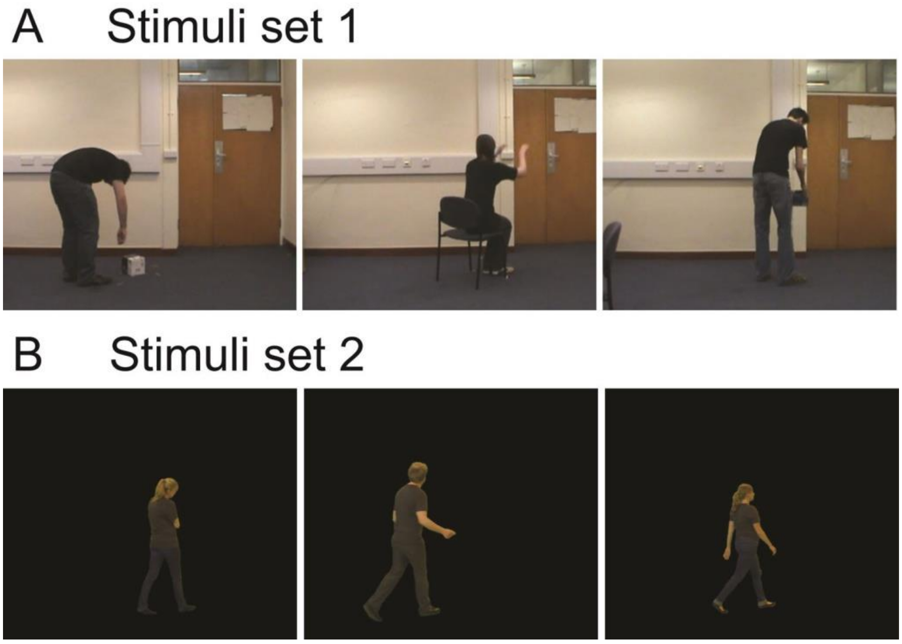


Figure 4.1 Example frames from movies used as adapting and test stimuli. A) Images from stimuli set 1 showing sad picking up a box, happy sitting down and neutral putting down a box (left to right). B) Images from stimuli set 2 where the background was keyed out and actors performed walking actions in a sad, happy and neutral manner (left to right).

4.4.3 Design and experimental procedure

As experiments in Chapter 4 followed a fully factorial design I used a traditional adaptation-test design, where multiple stimuli can serve as the adaptors. This paradigm is also typically used in psychophysics (Kohn, 2007). Here on each trial adapting stimulus, presented for several seconds (e.g. 16 sec), was followed by a brief inter-stimulus interval (ISI) and a test stimulus. As I measured participants' response to the test stimuli in a 2AFC design (happy or sad), I presented the happy and sad adapting stimuli in a pseudo-random order within each of the experimental blocks. Blocked design, with separate happy and sad adaptation blocks could instead bias participants to always respond with same response option. Because of this, I couldn't employ the adaption top-up design.

A PC running MATLAB 2006a (The MathWorks Inc., Natick, MA) and the Cogent toolbox (www.vislab.ucl.ac.uk/cogent.php) was used to control the experiment and display movies in the centre of a 22" CRT monitor (Philips 202P40, 1600x1200 pixels, 100Hz refresh rate), and record participant responses. Participants sat approximately 57cm from the screen and stimuli (subtending approximately 22.3 degrees x 16.6 degrees at the eye) were presented on a mid-grey background. To help preclude low-level retinotopic dependent adaptation, participants freely viewed all stimuli thereby preventing stereotypic eye-movements. All experiments followed a standard adaptation procedure where adapting movies were followed by a blank inter-stimulus interval (ISI) containing a small yellow fixation cross, followed by a single test movie. Participants indicated whether the test movie conveyed happy or sad emotions (2 AFC: experiments 1 and 3) or happy, sad, disgusted or surprised emotions (4 AFC: Experiment 2) on a labelled keypad.

4.4.4 Data Analysis

For each experiment and each participant and condition, I calculated the mean aftereffect (see individual sections). Even though aftereffects with complex social stimuli are typically quite variable (Barraclough, et al., 2012; Barraclough & Jellema, 2011) a very small number of participants showed exceptionally large aftereffects. These effects may reflect a potential problem in the conduct of the task by these individuals (for example rating the adapting stimulus, and not the test stimulus). Data was therefore discarded from those outlying individuals with aftereffects more than 2 SD from the mean aftereffect. Whenever data from outlying participants have been excluded, and whether its exclusion influenced the significance of the results, this has been described in the respective results section.

4.5 Experiment 1: The role of identity and action kinematics in the emotional action aftereffects.

Experiment 1 tested if exposure to movies of actors portraying different emotions through their whole body actions resulted in emotional action aftereffects. The adaptation paradigm was adapted from Fox and Barton (2007), who investigated the role of identity in emotion perception from faces. The effect of stimulus similarity on the magnitude of emotional action aftereffects was tested by varying the similarity between actions executed in the adapting and test stimuli, and by varying the similarity between the actors carrying out these actions.

4.5.1 Method

Participants

Twenty participants (14 females, 6 males, mean age=23.9 years, *SD*=8.2) took part in the experiment.

Stimuli

Stimuli were obtained from stimulus set 1. Two male and 2 female actors performing 3 actions (lifting a box, sitting down, and walking) were selected for the experiment. Actions performed in a happy and sad manner were used as adapting stimuli, while actions performed in a neutral manner were used as test stimuli.

Design and experimental procedure

Stimuli were presented across 5 blocks, each containing 24 trials. In an initial control block without adaptation, 12 test video clips were presented twice in pseudorandom order. The same 12 video clips were later were subsequently rated in each of the adapting blocks. In 4 counterbalanced adaptation blocks, 4 different pairings of adapting and test stimuli were employed (same identity/same action, same identity/different action, different identity/same action, different identity/different action). On any one trial, adapting videos (happy and sad actions) were repeated 8 times (16s duration), followed by a 0.3s ISI, and then a test stimulus presented for 2s. Each test stimulus was presented following both happy and sad adaptation stimuli. Inter-trial interval was 5s. Participants classified each test video as either happy or sad (scored as: 1=happy, 0=sad). Mean estimates of the emotion perceived in the test stimuli were calculated separately for the control, happy and sad adaptation conditions across 4 stimulus similarity conditions. To calculate the ‘happy’ and ‘sad’ aftereffects I subtracted the estimates of test stimuli in the control condition from the happy and sad adaptation conditions.

4.5.2 Results

Data from two participants (both female, both age 20) were discarded from the analysis as one showed outlying data (>2 SD from mean aftereffect) and one did not engage in the task. Removal of this data did not change the significance of the following analysis. Aftereffects were tested using a within-subject Analysis of Variance (ANOVA) with factors of adaptation emotion (happy, sad) and stimulus similarity (same identity/same action, same identity/different action, different identity/same action, different identity/different action). Adaptation to happy and sad emotional action videos generated significantly different aftereffects (F(1, 17)=11.261, p<.005, η_p^2=.40; see Figure 4.2), where test actions were judged as conveying the opposite emotion to the adapting stimuli. As the similarity between the adapting and test stimuli decreased, so did aftereffect magnitude (interaction between adaptation emotion and stimulus similarity: $F(2.1, 35.7)=4.25$, $p<.05$, $\eta_p^2=.20$, Greenhouse-Geisser correction applied); there was no main effect of stimulus similarity ($F(2.1, 35.8)=0.83$, $p>0.05$, $\eta_p^2=.05$, Greenhouse-Geisser correction applied).

Happy and sad aftereffects were significantly different only in those conditions where the adapting and test stimuli contained the same action, irrespective of identity: same identity/same action ($t(17)=4.48$, $p<.001$; different identity/same action ($t(17)=2.85$, $p<.05$). For conditions where the adapting and test stimuli contained different actions, happy and sad aftereffects were not significantly different from each other, indicating that adaptation to emotional action adaptation does not transfer from one action type to another.

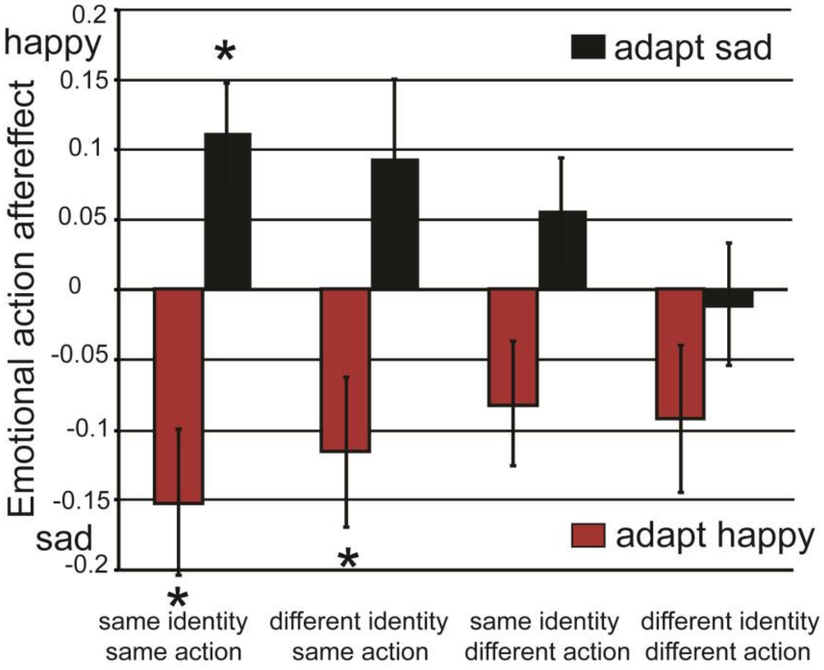


Figure 4.2 Emotional action aftereffects for different pairings of adapting and test actions. Positive values indicate that adaptation made the test actors appear happier (than in the no-adaptation condition), negative values indicate that adaptation made the test actors appear sadder. Error bars represent standard error of the mean (SEM). Asterisks indicate significance at $p<.05$.

4.6 Experiments 2a and 2b: Dynamics of emotional action aftereffects.

In Experiment 1 I found that the emotional action aftereffect magnitude depended upon the similarity between the adapting and test stimuli. The largest significant aftereffects were seen for the same identity/same action condition and the different identity/same action condition, suggesting both identity-dependent and identity-independent emotional action aftereffects. To establish how these aftereffects relate to previously studied visual aftereffects I measured the dynamics of identity-dependent and identity-independent emotional action aftereffect in two experiments. Previous research has shown that motion (Hershenson, 1989), face (Leopold, et al., 2005; Rhodes, et al., 2007), biological motion (Troje, Sadr, Geyer, & Nakayama, 2006b) and action (Barraclough, et al., 2009) aftereffects build up logarithmically with adaptation duration and decay exponentially with time. I tested the effect of adapting stimulus duration and the duration of the inter-stimulus interval (ISI) between the adapting and test stimuli on aftereffect magnitude in two separate factorial experiments (2a: same identity/same action; 2b: different identity/same action). I predicted that if emotional action aftereffects showed similar dynamics as found for these other previously tested aftereffects, then exposure to emotional actions would result in visual adaptation. This would distinguish an adaptation mechanism from other potential mechanisms like visual object priming, forward masking or post-perceptual effects (cf. Barraclough, et al., 2012)

4.6.1 Methods

Participants

Eighteen new participants (11 females, 7 males, mean age=20.4 years, *SD*=3.8) took part in Experiment 2a; a further eighteen new participants (12 females, 6 males, mean age=24.7, *SD*=6.7) took part in Experiment 2b. All participants were naive to the purpose of the experiment.

Design and experimental procedure

Adapting stimuli were taken from the stimuli set 1 and consisted of 64 movies of actions (16 actors x 4 actions) performed in both a happy and sad fashion (128 stimuli in total). In both experiments I varied the number of times the adapting stimulus was presented in immediate succession (1, 2, 4, 8 repeats), and varied the ISI between the adapting and test stimuli (200, 400, 600, 1600ms in 2a; 400, 800, 1600, 3200ms in 2b). In each experiment, therefore, there were 32 different adaptation conditions (4 adaptation repeats x 4 ISIs x 2 emotions) that were presented in a pseudorandom order. The choice of ISIs in Experiment 2a was based upon previous measures of the duration of face identity aftereffects

(Leopold, et al., 2005) and whole body aftereffects (Barraclough, et al., 2012) where significant aftereffect declines were observed over 1600ms. For Experiment 2b I extended the range of tested ISIs to 3200ms to better sample the possible decline in aftereffect over time.

Test stimuli consisted of the 64 movies of actions (16 actors x 4 actions) performed in a neutral fashion. In Experiment 2a the identity of the actor and the type of action performed in the adapting and test movies were identical on every trial. In Experiment 2b, the type of action performed by the actor in the adapting and test movies was identical on every trial, however, the identity (and gender) of the actor was always different. Between trials there was a 5s inter-trial interval. In total, each participant viewed each of the 32 adaptation conditions 10 times (320 trials in total). Each experiment was conducted across five blocks of testing conducted over 2 separate, approximately 1 hour, testing sessions.

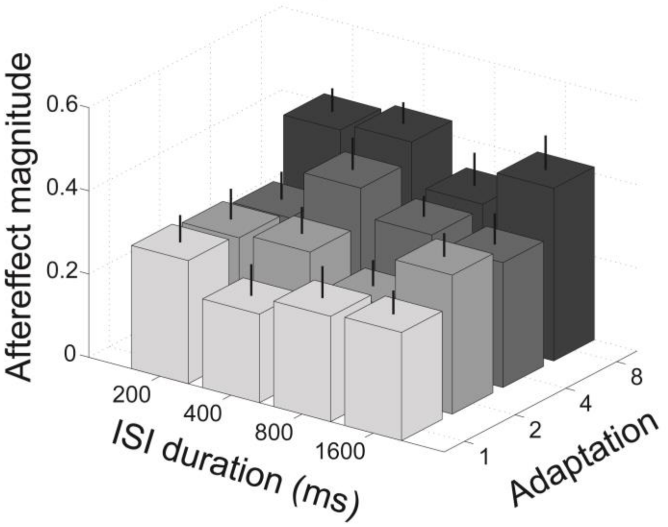
Analysis

Participant responses were scored on a scale where 1 indicated that the participant interpreted the test actor as appearing sad and 0 indicated that the participant interpreted the test actor as appearing happy. Mean judgments of emotion (happy or sad) of the test stimuli for each of the 32 conditions (2 emotions x 4 adaptation repeats x 4 ISIs) were calculated separately for each participant. In Experiment 1 I established that there was both a happy and a sad emotional action aftereffect (see Figure 4.2), in Experiments 2a and 2b I used a different estimate of the aftereffect. Following previous measures of emotion aftereffects using facial stimuli (e.g. Fox & Barton, 2007; Fox, et al., 2008), for each experimental condition, I subtracted the mean ratings of the test actor following adaptation to sad stimuli from the mean ratings of the test actor following adaptation to the happy stimuli. This difference value represents the magnitude of the aftereffect, i.e. the differential influence of the emotion of the preceding actor on the perception of emotion conveyed by subsequent test actors. For this analysis positive values indicate a typical, “repulsive” aftereffect, where following adaptation, the emotion conveyed by test actors look like the opposite of the emotion conveyed by the adapting actors. Negative aftereffect values indicate that following adaptation, the emotion conveyed by test actors was rated as similar to the emotions conveyed by the adapting actors; this effect would be akin to visual object priming (Tulving & Schacter, 1990b). Although this method precludes identifying the relative contributions of happy and sad actions to emotional aftereffect dynamics, it reduces systematic biases, maximises any action emotional aftereffect, and eliminates the necessity for a ‘no-adaptation’ condition thereby allowing me to test many experimental conditions (32) within a limited testing period (2 hours).

4.6.2 Results

Mean aftereffects for sixteen different conditions were calculated in both experiments 2a and 2b and are plotted on Figure 4.3. Data from one participant (female, age 20) in Experiment 2a was discarded from the analysis as outlying data. Repeating the analysis with this data did not change the significance of the results when testing with ANOVA. For both Experiment 2a and 2b, all aftereffects were positive, indicating that under all conditions adaptation had a repulsive effect. The dynamics of the emotional action aftereffects, however, appeared to be different in the two experiments (see Figures 2a and 2b). As the groups of participants, and the durations of the ISIs between the two experiments were different, I analysed the two experiments separately using 2-way ANOVAs (4 adaptation repeats x 4 ISI durations).

For Experiment 2a (same identity) the duration of the adapting stimulus had a significant effect on the aftereffect magnitude (main effect of adaptation repeats: $F(2.2, 35.2)=5.44$, $p<.005$, $\eta_p^2=.25$; Greenhouse-Geisser correction applied). There was no significant effect of ISI duration (Main effect of ISI: $F(3, 48)=1.04$, $p=.38$, $\eta_p^2=.07$) nor a significant interaction between adaptation repeats and ISI duration (adaptation repeats x ISI: $F(9,144)=0.83$, $p=.59$, $\eta_p^2=.05$).


a Same identity

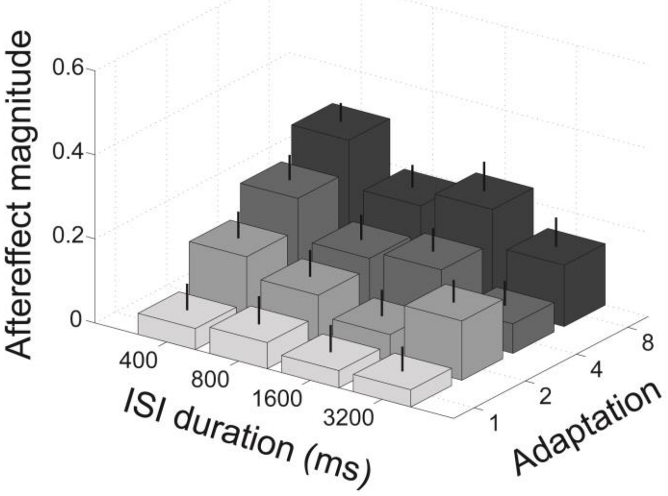

b Different identity

Figure 4.3 Emotional action aftereffect magnitude as a function of adaptation repeats and ISI for Experiment 2a (a) and Experiment 2b (b). All aftereffects showed positive values typical of repulsive aftereffects, where test stimuli look less like the adapting stimuli. Error bars indicate SEM.

For Experiment 2b (different identity) the duration of the adapting stimulus also had a significant effect on aftereffect magnitude (main effect of adaptation repeats: $F(3,51)=9.94$, $p<.001$, $\eta_p^2=.37$). Although a reduction in aftereffect magnitude with ISI was apparent from Figure 2b, this was not significant (main effect of ISI: $F(3,51)=1.95$, $p=.132$, $\eta_p^2=.10$) nor was the interaction between adaptation repeats and ISI (adaptation repeats x ISI: $F(9,153)=0.90$, $p=.52$, η_p^2

=.05). The reason for the lack of significance of ISI on aftereffect magnitude in Experiment 2b may be due to a number of factors.

First, following 1 repeat of the adapting stimulus there was little aftereffect at any ISI. Indeed significant aftereffects are only found following 4 or 8 adaptation stimulus repeats (one-sample t-tests, $p<.0031$, Bonferroni correction applied). This contrasts with the analysis of the same identity aftereffects measured in Experiment 2a, where significant aftereffects were found following 1, 2, 4 and 8 adaptation stimulus repeats (one-sample t-tests, $p<.0031$, Bonferroni correction applied). The small and non-significant aftereffects in Experiment 2b obtained after 1 and 2 repeats may have contributed to the non-significant main effect of ISI. Second, the range of ISIs that I tested for both Experiments 2a and 2b may have been too restricted, I may have found a significant decline in the magnitude of both same identity and different identity aftereffects if I had chosen a greater range of ISIs. The ISIs for Experiment 2a where chosen based upon significant declines in aftereffect magnitude over similar time periods seen with other whole body actions (Barraclough, et al., 2012). Having found no decline with the range of ISIs used in Experiment 2a (200-1600ms), I extended the range of ISIs for Experiment 2b (400-3200ms). Both same identity and different identity emotional aftereffects, however, might decline over longer ISIs.

In order to better predict the duration of emotional action aftereffects I fitted logarithmic functions to only those aftereffects that were significant in both experiments (following 4 and 8 adaptation repeats). I extrapolated the decay functions (logarithmic trendlines plotted on a semi-log plot, see Figure 4.4) in order to determine the point at which the aftereffect declined to zero. I estimated the duration of the aftereffects only in different identity condition (Experiment 2b) as the aftereffects seemed to decay as a function of inter-stimuli interval only in this experiment. I calculated the predicted x value (inter-stimulus interval duration) from the trendline equation available for each of the plots:

$$\text{Equation: } y = (c * LN(x)) + b$$

For the data plotted in 4 adaptation repeats condition, the equation values equalled:

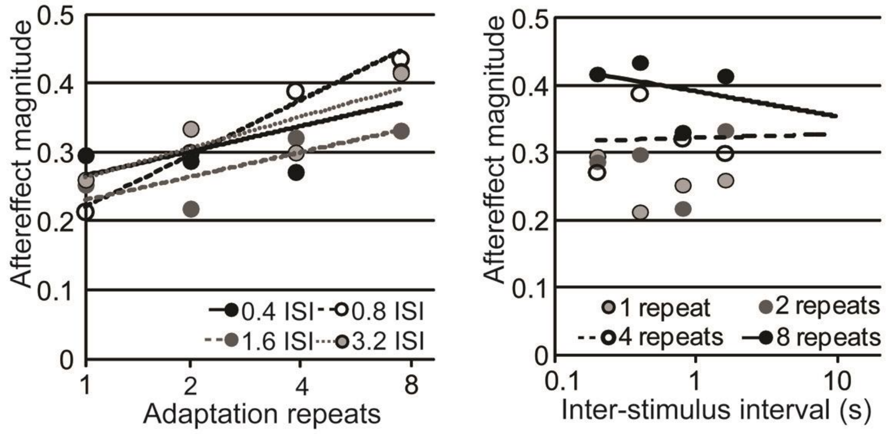
$$y = (0.067 * LN(x)) + 0.6222$$

suggesting that the aftereffects would decay to zero after approximately 10.8 seconds. For data plotted in 8 adaptation repeats, the equation values equalled:

$$y = (0.064 * LN(x)) + 0.6732$$

suggesting that the aftereffects would last approximately 37.0 seconds. The use of this technique to estimate the duration of aftereffects, however, is prone to some error, particularly for the condition following 8 adaptation repeats where the decay function is sampled far from where it crosses zero (37s). For 4 adaptation repeats my prediction was likely to be more accurate, as I was sampling the decay function much closer to where it crosses zero (10.8s). I tested the decay of the emotional action aftereffects over this ISI in Experiment 3.

a Same identity aftereffects



b Different identity aftereffects

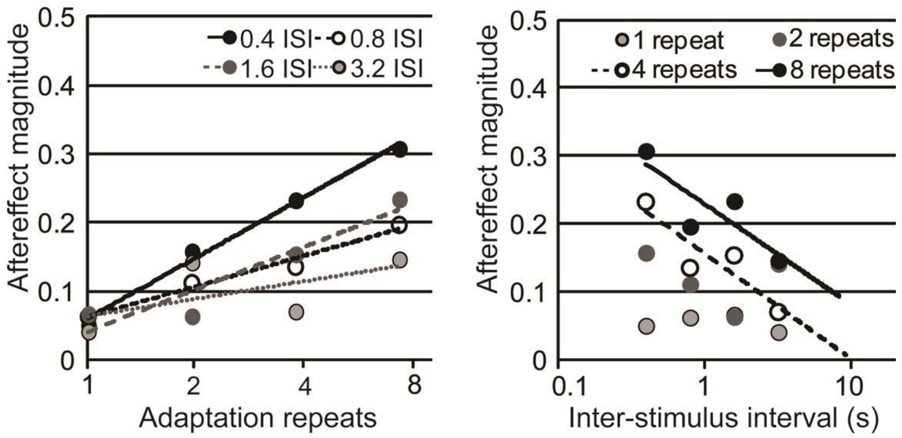


Figure 4.4 Same identity (a) and different identity (b) aftereffects. Aftereffect build up with adaptation repeats (for different ISIs) are illustrated on the left, and aftereffect decline with ISI (for different adaptation repeats) are illustrated on the right. Logarithmic functions are fitted to data on each sub-plot.

4.7 Experiment 3: Aftereffects duration tested with longer inter-stimulus intervals.

In Experiment 3 I tested the prediction for the duration of the emotional action aftereffects. The data from experiments 2a and 2b gave a strong indication for the magnitude of emotional adaptation aftereffects following 4 repeats of the adapting stimulus. At short ISIs (400ms) I expected to see significant same and different identity aftereffects. With an ISI of 10.8s, I expected to see no decline in the same identity aftereffect, but I expected the different identity aftereffect to have disappeared.

4.7.1 Methods

Participants

Twenty four new participants (16 females, 8 males, mean age=21.5 years, *SD*=3.1) took part in the experiment; all were naïve to the purpose of the experiment except for the experimenter.

Stimuli

Stimuli were selected from stimulus set 1. Four male and 4 female actors performing 4 actions (lifting a box, putting down a box, sitting down, and walking) were used in the experiment. Actions performed in a happy and sad manner were used as adapting stimuli, while actions performed in a neutral manner were used as test stimuli.

Design and experimental procedure

Stimuli were presented across 2 counterbalanced blocks, where on each trial adapting and test stimuli were paired up to create same identity/same action and different identity/same action stimulus similarity conditions. Adapting stimuli (happy and sad actions) were repeated 4 times (8s duration). Inter-stimulus intervals, determined in prior testing, were 0.4s and 10.8s. Each test stimulus was presented following happy and sad adaptation. A 5s interval was included between trials. Participants classified videos of test actions as either happy or sad (2AFC) as for Experiment 1. Mean estimates following happy and sad adapting stimuli, and for each of the 4 different conditions (identity x ISI), were calculated separately, and aftereffect magnitudes were calculated by subtracting responses following sad adaptation subtracted from response following happy adaptation.

4.7.2 Results

Data from two participants (male, age 19; female, age 20) were discarded from the analysis as they showed outlying data (>2 SD from mean aftereffect). Aftereffects were analysed using ANOVA with within-subject factors of identity (same, different) and ISI duration (0.4s, 10.8s). The same identity aftereffect was larger than the different identity aftereffect, as seen in the previous two experiments (Figure 4.5; ANOVA, main effect of identity, $F(1,21)=5.74$, $p<.05$, $\eta_p^2=.25$ for same and different identity respectively). Importantly there was a significant interaction ($F(1,21)=4.77$, $p<.05$, $\eta_p^2=.18$) between identity and ISI, in which the different identity aftereffect declined over time, whereas the same identity aftereffect persisted. There was no main effect of ISI ($F(1,21)=.07$, $p=.79$, $\eta_p^2=.00$). Including the outlying data from the two participants who showed strong priming effects influenced only the identity x ISI interaction which became a trend ($F(1,23)=3.66$, $p=.06$, $\eta_p^2=.14$). The different identity emotional action aftereffect therefore appeared to show similar characteristics to other high level and action aftereffects (Barraclough, et al., 2012; Leopold, et al., 2005; Troje, et al., 2006). The same identity emotional action aftereffect, however, showed a very different pattern, even marginally increasing over time, suggesting a different underlying mechanism.

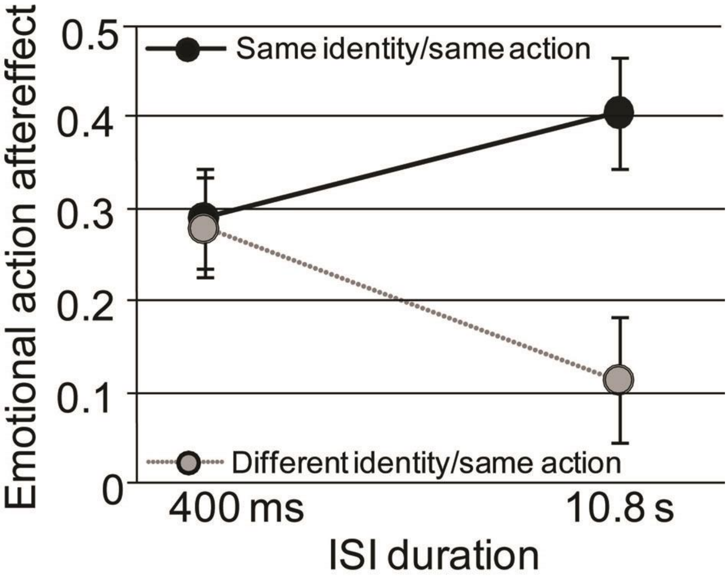


Figure 4.5 Emotional action aftereffects as a function of ISI. Error bars represent standard error of the mean (SEM).

4.8 Experiment 4: Control for change in response criterion

In Experiment 4 I clarified that the emotional action aftereffects were due to a bias in perceptual processing rather than a bias in decision making (Hsu & Young, 2004; Webster, et al., 2004). Participants could in principle have reasoned that since the test stimulus was clearly different from the adapting stimulus, they should select the response option that was different from the adapting stimulus. If indeed adaptation causes test stimuli to appear less like the adaptor (Leopold, et al., 2001), then perceptual adaptation to one emotion (e.g. happy) would result in an increase in the likelihood of the opposite emotion (sad) being selected rather than any other emotion options. In contrast, the application of a same/different decision rule would result in all different emotion categories being selected, rather than just the opposite one. These predictions were tested across the two conditions that generated significant aftereffects in Experiment 1 (same action/same identity and same action/different identity). Further, to ensure that aftereffects were not dependent upon any particular set of video stimuli, stimuli for this experiment were selected from a different set of stimuli (set 2).

4.8.1 Method

Participants

Fifteen new participants (6 females, 9 males, mean age=24.9 years, *SD*=3.2) took part in the experiment, all were naïve to the purpose of the experiment except the experimenter and one individual (male, age 28) tested also during Experiment 3. Removal of this data did not change the significance of the following analysis.

Stimuli

Stimuli were obtained from stimulus set 2. Eight male and 8 female actors performing walking were selected for the experiment. Walking actions performed in a happy and sad manner were used as adapting stimuli, while walking actions in a neutral manner were used as test stimuli.

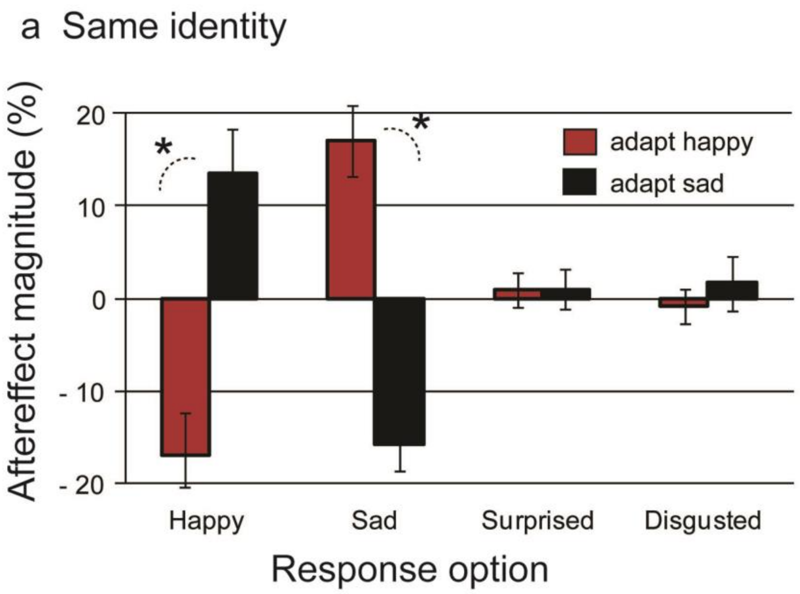
Design and experimental procedure

Stimuli were presented across 4 blocks; an initial control block without adaptation (16 test stimuli presented twice in a pseudorandom order), followed by 2 counterbalanced adaptation blocks (where on each trial adapting and test stimuli were paired to create same identity/same action and different identity/same action combinations of stimulus similarity), and a final control block identical to block 1. Adapting stimuli (happy and sad actions) were repeated

4 times (8s duration); ISI was 0.4s. Each test stimulus was presented following happy or sad adaptation. The inter-trial interval was 5s. Participants classified videos of actions as happy, sad, surprised or disgusted following adaptation to action videos of happy and sad actors (4AFC). For each participant, and each block, the percentage responses for each of the 4 possible emotions (happy, sad, surprised, and disgusted) were calculated (cf. Skinner & Benton, 2010). Responses to both control blocks were averaged. Aftereffects were calculated by subtracting the percentage response from the control blocks from responses to the same stimuli following happy and sad adaptation for same and different identity conditions separately.

4.8.2 Results

Aftereffects were tested using ANOVA with within-subject factors of adaptation emotion (happy, sad), stimulus similarity (same identity/same action, different identity/same action) and response emotion (happy, sad, surprised, disgusted). Both the same and different identity aftereffects resulted from shifts in the perception of action emotion (rather than a shift in a response rule/criterion) as they were judged as conveying the 'opposite' to the adapted emotion rather than 'another' emotion (adaptation emotion x response emotion, $F(1.81, 25.4)=27.20$, $p<.001$, $\eta_p^2=.66$, Greenhouse-Geisser correction applied, Figure 4.6). As suggested by Figure 4.6, the same identity aftereffects were significantly bigger ($M=15.8$) than the different identity aftereffects ($M=6.0$). This was confirmed by a three-way interaction (adaptation emotion x stimulus similarity x response emotion, ANOVA, $F(3,42)=14.49$, $p<.001$, $\eta_p^2=.50$). No other effects reached significance. Post-hoc paired t-tests revealed that adaptation only affected the classification of test stimuli as happy (same identity: $t(14)=5.88$; different identity: $t(14)=3.11$, both $ps<.0125$) and sad (same identity: $t(14)=7.25$; different identity: $t(14)=3.38$, both $ps<.0125$) and had no effect on the choice of surprised or disgusted labels (all $ps>.27$).



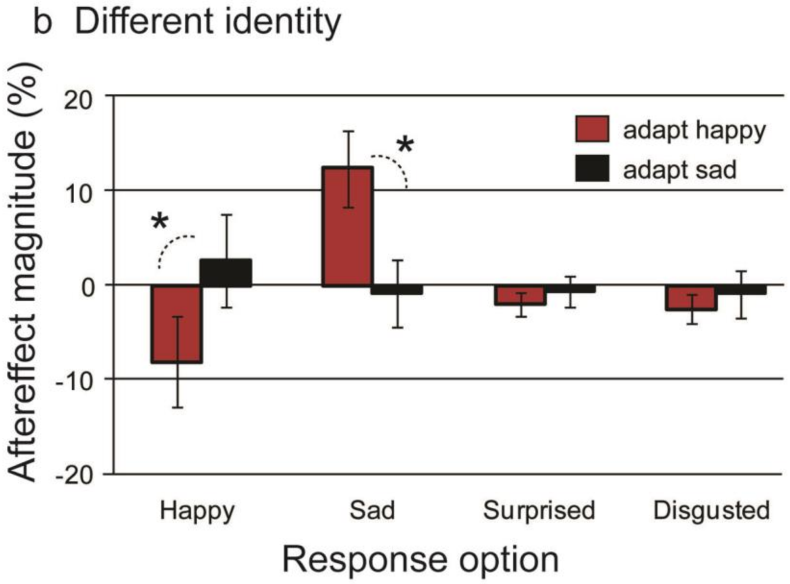


Figure 4.6 Mean percentage change in the classification of the emotion conveyed by test stimuli following happy and sad adaptation. Positive values, more often selected emotion; negative values, less often selected emotion. The identity of the actors in the adapting and test stimuli were either the same (a) or different (b). Error bars represent standard error of the mean (SEM). Star (*) indicates significance level after Bonferroni correction, *p*<.0125.

4.9 Discussion of Chapter 4

This study showed that adaptation to emotional whole body actions substantially biases the perception of the emotion conveyed by subsequent actions. Following adaptation to happy actions, subsequent actions appear somewhat sad; following adaptation to sad actions, subsequent actions appear somewhat happy. The magnitude of these emotional action aftereffects was dependent upon the similarity between the adapting and test stimuli. The largest aftereffects occurred when adapting and test actors had the same identity and performed the same action. Aftereffects, albeit slightly smaller, also occurred when the adapting and test actors had different identities and performed the same action. Differences in the aftereffects magnitude between the same identity and different identity conditions indicate involvement of both identity-dependent and identity-independent neural populations in the coding of emotional actions. These findings parallel results of Fox & Barton (2007) and Campbell and Burke (2009) and suggest partially integrated processing of identity and emotion from whole body actions.

However, aftereffects never occurred when the adapting and test actors were performing different actions. Different actions have different kinematics, and bodily expressions of emotion are dependent upon the characteristic kinematics of the action (e.g. see Roether, et al., 2009). The failure of adaptation to one set of characteristic movements to exert an influence on the perception of a very different set of movements, suggests that body emotion is coded within action specific neural mechanisms.

Both the same identity and different identity aftereffects increased in magnitude as the adapting action was repeated. However, the decline in the magnitude of the same identity and different identity aftereffects with increasing ISIs was notably different. The identity-independent aftereffect seems to decline significantly over approximately 10 seconds, very much like a typical high-level aftereffect (Barraclough & Jellema, 2011; Leopold, et al., 2005). In contrast, the identity-dependent aftereffect appeared to last much longer, similar to aftereffects seen with other social stimuli such as gaze direction (Kloth & Schweinberger, 2008) and face configuration (e.g. Carbon & Ditye, 2011b, 2012).

Lastly, control experiments indicated that aftereffects resulted from the adaptation of high-level visual coding mechanisms. Although adaptation in low-level visual processing mechanisms, such as processing of colour, motion, orientation or spatial frequency (see Hole, 2011 for a review), was likely to be occurring simultaneously, it is unlikely to be a dominating factor here. This is because emotional action aftereffects showed several of the characteristics of previously observed high-level aftereffects. Firstly, similarity between adapting and test stimuli determined aftereffect magnitude (see Kohn, 2007; Verhoef, et al., 2008). Secondly, for the different identity aftereffect, adaptation appears to decline over a period similar to other high-level action and face aftereffects (e.g. Barraclough, et al., 2012; Leopold, et al., 2005). Finally, the dominating effect here was the effect of high-level emotion adaptation, as the aftereffect was predominantly determined by the emotion conveyed by the adapting actor. Low-level retinotopic dependent adaptation is also unlikely to explain observed here effects, as adapting and test stimuli were dynamic, with naturally occurring differences in expressions of emotions and kinematics across actors, and actors were never presented in precisely overlapping retinotopic locations. Finally, in Experiment 4 I ruled out that the adaptation aftereffects resulted from a post-perceptual response bias (discussed in Hsu & Young, 2004). Theoretically, participants could have employed a response strategy where, following viewing actions conveying particular emotions, when judging the subsequent test action they would select the response that was simply different from the adapted emotion. Such post-perceptual mechanisms could mimic the repulsive aftereffects when tested with a 2AFC task. This is unlikely, because: first, such a post-perceptual mechanism would not be dependent upon the duration of the adapting stimuli, and would occur even after one repeat of the adapting stimulus. However, single adapting stimulus repeats resulted in very small non-significant aftereffects, and both same identity and different identity aftereffects were influenced significantly by the duration of the adapting stimulus, consistent with the typical dynamics of high-level aftereffects (Barraclough, et al., 2012; Leopold, et al., 2005). Second, Experiment 4 demonstrated that participants' judgements of the test stimuli were specific to the adapted emotion category (happiness or sadness). Participants indicated that the test stimuli were of the opposite emotion (sadness or happiness), rather than any other emotion, even though they could select any emotion from the six basic emotions.

The similarity between the aftereffects observed here with emotional action adaptation and those seen with emotional face aftereffects (Campbell & Burke, 2009; Ellamil, et al., 2008; Fox & Barton, 2007) suggest that similarly acting, processing systems might underlie the coding of emotion and identity information from actions (see also Haxby, et al., 2000). Action representation within the STS can be modulated by emotional body language (Grèzes, et al., 2007), and adaptation within this region (cf. Grossman, Jardine, & Pyles, 2010) is likely to underlie the identity-independent emotional action aftereffects. The neural substrates underlying our ability to recognise actor identity from body form and motion have not been well delineated, but may involve the extrastriate body area (EBA; Saxe, Jamal, & Powell, 2006; Urgesi, et al., 2007) along with regions in the anterior temporal lobe (although see Downing & Peelen, 2011). Adaptation in more anterior regions of the temporal cortex that takes into account actor identity may underlie the identity-dependent aftereffects; although this suggestion is more speculative. Furthermore, anterior cortical regions do not show the same adaptation characteristics as the more posterior cortical regions (cf. Verhoef, et al., 2008). The less common longer lasting aftereffects observed here, also seen with faces (e.g. Carbon & Ditye, 2011b, 2012; Kloth & Schweinberger, 2008) and voices (e.g. Schweinberger, et al., 2008; Zäske, et al., 2010), may result from the effects of adaptation on later stages of processing inducing a longer term recalibration. Such long lasting aftereffects may shift the observer's reference point according to their recent experience in order to optimize the sensory processing of the external world over longer period of time.

The effects observed here are likely to result from adaptation of high level visual coding mechanisms, as emotional action aftereffects show several of the characteristics of previously observed high-level aftereffects. First, similarity between adapting and test stimuli determined aftereffect magnitude (see Kohn, 2007; Verhoef, et al., 2008). Second, the adaptation aftereffects observed here did not result from a response bias towards selecting any test emotion as long as it was different from the adapting emotion (discussed in Hsu and Young, 2004). Finally, the dominating effect here was the effect of high-level emotion adaptation, as the aftereffect was predominantly determined by the emotion conveyed by the adapting actor. Low-level retinotopic dependent adaptation is unlikely to explain the effects observed here, as adapting and test stimuli were dynamic, with naturally occurring differences in expressions of emotions and kinematics across actors, and actors were never presented in precisely overlapping retinotopic locations. Together, these results rule out other possible low-level or post-perceptual explanations for emotional action aftereffects that accounted for some other demonstrations of high-level perceptual aftereffects (e.g. Butler, Oruc, Fox, & Barton, 2008; Xu, Dayan, Lipkin, & Qian, 2008).

In summary, experiments reported here suggest partially interdependent processing of identity and emotion from whole body actions. These results indicate that neither complete segregation nor fully conjoint processing underlie the coding of emotions and identity from actions. This arrangement parallels recent data on the processing of face and voice information that suggest that rather than completely separate processing of emotion and identity (e.g. Bruce and Young, 1986), representations of emotion and identity can interact (e.g. Baseler, et al., 2012; Belin, et al., 2004; Gobbini & Haxby, 2007; Vuilleumier & Pourtois, 2007). Different characteristics of the identity-dependent and identity-independent aftereffects may suggest that perception of emotional actions not only recruits both identity-dependent and identity-independent neural populations, but may also involve two separate processing mechanisms. One of these mechanisms processes emotion irrespective of actor identity, while the other processes emotion taking into account actor identity. The latter identity-dependent mechanism might undergo a longer-term recalibration following adaptation, perhaps accounting for a durable integration of identity and emotion information in the processing of dynamic social stimuli.

CHAPTER 5

Cross-category emotion adaptation

5.1 Abstract

Some recent neuroimaging studies have suggested the existence of a shared representation of emotion conveyed by bodies and faces. Cross-category visual adaptation paradigms have also been used to investigate the interaction between face and body processing. To date, they have provided mixed evidence of shared processing of different social traits from these cues. In this Chapter, I investigated whether adaptation to emotion conveyed by bodily actions influenced face perception. Participants adapted to happy and sad whole body actions or faces, then judged the emotion conveyed by static test faces that varied along a morph continuum between happy and sad. I also tested whether identity had any effect on any putative aftereffects by varying the identity of the adapting and test stimuli. Participants took part in four experimental sessions in which they completed forced-choice adaptive staircase procedures. Points of subjective equality (PSEs) for test faces following each adaptation condition were calculated from a psychometric function fitted to the data. Adaptation aftereffects were calculated by subtracting PSEs in no-adaptation baseline conditions from PSEs for each of the adaptation conditions. Emotional adaptation to faces influenced face perception irrespective of the identity of adapting and test faces, although adaptation aftereffects were bigger for the same than in the different identity conditions, consistent with previous research. There was no evidence for adaptation to bodies influencing face perception. These results suggest the adaptation to emotion may be category-specific and adaptation to emotions conveyed by the whole body action may depend on the specific action kinematics or body parts that convey a given emotion.

5.2 Introduction

In previous chapters I employed visual adaptation paradigms to investigate how our perception of emotions from whole body actions is influenced by temporal context. Perceptual aftereffects resulting from adaptation to whole body actions also suggest that perception of emotion from these dynamic cues is partially dependent upon an actor's identity and executed action. However, it is not clear whether emotion adaptation reported here was specific to the stimulus category that conveyed it, i.e. whole body action, or whether adaptation could occur at more abstract, stimulus-independent level. Emotion adaptation aftereffects that transfer across different stimuli categories, such as faces and bodies, would suggest that emotion may be processed in an abstract, category-independent manner.

Support for the category-independent processing of emotional signals comes from neuroimaging studies (see Heberlein & Atkinson, 2009 for a review). For instance, bodily and facial emotional expressions represented in point-light stimuli modulate neural activity in brain regions such as the right EBA, FFA and left FBA (Atkinson, Vuong, & Smithson, 2012). Crucially, in this study neutral expression conveyed by bodily and facial movements showed stimulus category-selective activation (i.e. activated a neural population that coded the specific stimulus type), while expressions of anger and happiness modulated the activity of face and body selective regions regardless of the stimulus category. Similarly, Peelen, Atkinson, and Vuilleumier (2010) proposed the existence of supra-modal representation of emotion in high-level brain areas including the medial prefrontal cortex (MPFC) and the STS. Here, the authors compared brain activity patterns to emotions expressed across different visual cues (dynamic facial expressions and whole body expressions of emotion) and across different sensory modalities (visual: faces and bodies, and auditory: emotional voices). These results suggested that MPFC and STS processed emotion information regardless of the sensory cues. However, one study that directly compared the brain activity for the viewing of dynamic faces and bodies also reported that the STS (along with other regions) showed a greater activity for body stimuli compared to face stimuli (Kret, Pichon, Grezes, & de Gelder, 2011).

These studies, however, compared brain responses to dynamic facial and dynamic body stimuli. Whether a similar pattern or results would emerge for the comparison of static versus dynamic cues is unclear, as separate neural mechanisms may underlie processing of these cues. Indeed, studies examining neural mechanisms involved in the processing of static and dynamic facial expression often report that dissociable neural structures underlie perception of these stimuli types. Viewing dynamic faces not only resulted in higher activation in brain regions associated with emotion processing such as amygdala (LaBar, Crupain, Voyvodic, & McCarthy, 2003), but compared to static expressions, dynamic facial expressions resulted in greater activity in the brain regions specialised for processing motion (V5; Zeki et al., 1991), facial and body actions (STS; Allison, et al., 2000; Kilts, Egan, Gideon, Ely, & Hoffman, 2003; Schultz & Pilz, 2009) and in motor areas (right ventral premotor cortex; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004). More recently, Pitcher, Dilks, Saxe, Triantafyllou, and Kanwisher (2011) extended these findings and noted that right posterior STS (pSTS) responded much more strongly to dynamic faces compared to static faces, and that right anterior regions of the STS (aSTS) responded only to dynamic faces. In a similar fashion, viewing static and dynamic body expressions of emotion also activate partially distinct neural population. In contrast to static bodies, perception of whole body expressions of emotion resulted in additional activation in the STS-temporo-parietal junction and premotor cortex (Grèzes, et al., 2007; Pichon, et al., 2008). These results suggest that, although there is a considerable overlap in the neural systems involved in emotion processing from different cues, additional, specialised networks contribute to the recognition of emotional signals from different stimulus categories.

Behavioural experiments (reviewed in section 1.5 of Chapter 1) also suggest that there may exist a common representation of emotion for faces and bodies. Visual adaptation studies, however, have so far provided mixed support for this notion. For instance, Fox and Barton (2007) investigated the influence of different emotional adaptor types such as static faces, animal bodies, words and sounds on the classification of emotion in static, test faces. While strong and significant aftereffects were observed following adaptation to emotional faces, emotional bodies and sounds did not elicit significant aftereffects. More recently Skuk and Schweinberger (2013) tested the effect of emotional adaptation in unimodal (voice), bimodal (dynamic face and voice) and cross-modal (dynamic face) conditions on the perception of voice emotion. These results provided limited support for the multimodal nature of emotion processing, as cross-modal aftereffects transferring from vocal to visual stimuli were observed only in male participants.

The evidence for cross-modal and cross-category aftereffects for other social judgements is also mixed. In cross-modal adaptation studies, aftereffects did not transfer between faces to voices in the perception of sex (Schweinberger, et al., 2008), but adaptation to specific voice identity influenced subsequent perception of facial identity (Hills, et al., 2010). Recently, Little, et al. (2013) reported cross-modal aftereffects where exposure to masculinised or feminized voices influenced judgement of faces and vice versa, but these effects were observed only for the same-sex stimuli. Even within visual modality, there is mixed evidence that adaptation transfers across different stimuli categories. For instance, adaptation to male or female hands did not influence the perception of subsequent faces (Kovacs, et al., 2006). In contrast, adaptation to sex and identity conveyed by static bodies influenced subsequent judgement of these traits in faces (Ghuman, et al., 2010; see Weigelt, et al., 2010 for a review) and adaptation to frontal and profile faces influenced perception of sex in subsequent bodies (Palumbo, et al., 2014).

5.3 The current study

Given the mixed evidence for the cross-category aftereffects, in the current study I investigated whether adaptation to emotional whole body actions transfers across stimulus category and influences the perception of emotion in static faces. As the results reported in Chapter 4 suggest that emotional action aftereffects are weakened when the adapting and test stimuli are of different identities, I also examined whether cross-category emotion aftereffects are dependent on the actor's identity. In addition, as previous studies suggested that adaptation effects for various social traits are smaller when adapting and test stimuli vary in sex (e.g. Bestelmeyer, et al., 2008; Little, deBruine, & Jones, 2005; Little, et al., 2013), stimuli selected for this study portrayed male and female actors. Following Ghuman, et al. (2010), participants in this study adapted to emotional whole body actions and were asked to judge emotion in faces created by morphing along a continuum between a neutral and an emotional expression (happiness or sadness). In order to ensure that participants associated the face with the body action portrayed by the same actor, I selected one male and one female actor whose action and facial expressions were used as both adapting and test stimuli.

5.4 Methods

5.4.1 Participants

Participants were University of York and University of Hull students and staff (6 females, 6 males, mean age =25.6 years, *SD*=3.5) and all received payment for participation. All participants had normal or corrected to normal vision and were naive to the purpose of the study. Experiments were approved by the ethics committees of the Department of Psychology, University of York and the Department of Psychology, University of Hull, and were performed in accordance with the ethical standards laid down in the 1990 Declaration of Helsinki.

5.4.2 Stimuli

Action stimuli were selected from a database of whole body actions (Keefe et al., 2014). All stimuli were edited (Sony Vegas Pro 11) to last for 2 seconds and were rated by 10 independent observers on two independent 1-9 Likert scales, where

1=neutral, 9=very happy/very sad. Video clips of two actors (1 male, 1 female) performing walking actions in a happy and sad way, were used as the adapting stimuli. Video clips were selected to closely match the intensity of expressed emotion; mean rating for happy actions for male actor: *M*=7.2, *SD*=1.75, for female actor *M*=6.7, *SD*=1.76, mean ratings for sad actions for male actor: *M*=6.3, *SD*=1.76, for female actor: *M*=5.8, *SD*=2.52. For the purposes of the experiment, video clips were converted to grey scale and matched for mid luminance and contrast using custom build software (Image Manipulation Software, University of St. Andrews). Exemplar frames from the action stimuli are illustrated in Figure 5.1a.

Face stimuli were photographs of the same two actors. Both actors posed 7 emotions (fear, surprise, disgust, contempt, anger, sadness and happiness), and a neutral expression. Each expression was captured against a uniform white background, from a frontal viewpoint, with actor's eyes directed straight ahead, using Panasonic TM900 HD camera with a built-in flash. Actors wore matched clothing (the same as for the filming of action stimuli) and had no glasses, makeup or jewellery. Prior to expressing each emotion actors underwent a mood induction procedure (MIP), known as autobiographical recall, which effectively elicits given affective states (Jallais & Gilet, 2010; Westermann, Spies, Stahl, & Hesse, 1996 for a review). Actors were also coached on how to display each of the emotions according to Action Unit (AU) Descriptions.

Photos of neutral, happy and sad expressions were selected for the experiment. Photos were converted into bitmap format and matched for white balance using The Gimp software, and matched for mid luminance and contrast using custom build software (Image Manipulation Software, University of St. Andrews). Next, images were horizontally aligned and scaled to the same interpupillary distance. Morphed continua of expressions were created using PsychoMorph (Tiddeman, Burt, & Perrett, 2001). In order to control for individual differences in posing expressions, I first generated the average shape of happy, sad and neutral expressions for both actors. I then transformed each actor's expression by adding 100% of the linear difference in shape between the actor's individual expression and the average expression (cf. Harris, Young, & Andrews, 2012). This method allowed me to standardise the expressed emotion across both actors. In this way I ensured that any differences in magnitude of the emotion aftereffect were due to the change in identity and not due to the difference in the way two actors displayed emotional expressions. Next, the expression continua were generated by morphing between happy and neutral, and sad and neutral expressions, separately for each actor (see Figure 5.1b). To ensure that the face stimuli conveyed a comparable intensity of expression to the video stimuli, I extended the expression continua by creating caricatures of happy and sad expressions conveying up to 150% happiness and sadness. For each actor and expression I created 75 morphed faces (giving a continuum of 151 faces ranging from sad, via neutral to happy). Images were then converted to grey scale and masked with an oval to cover any external facial features.

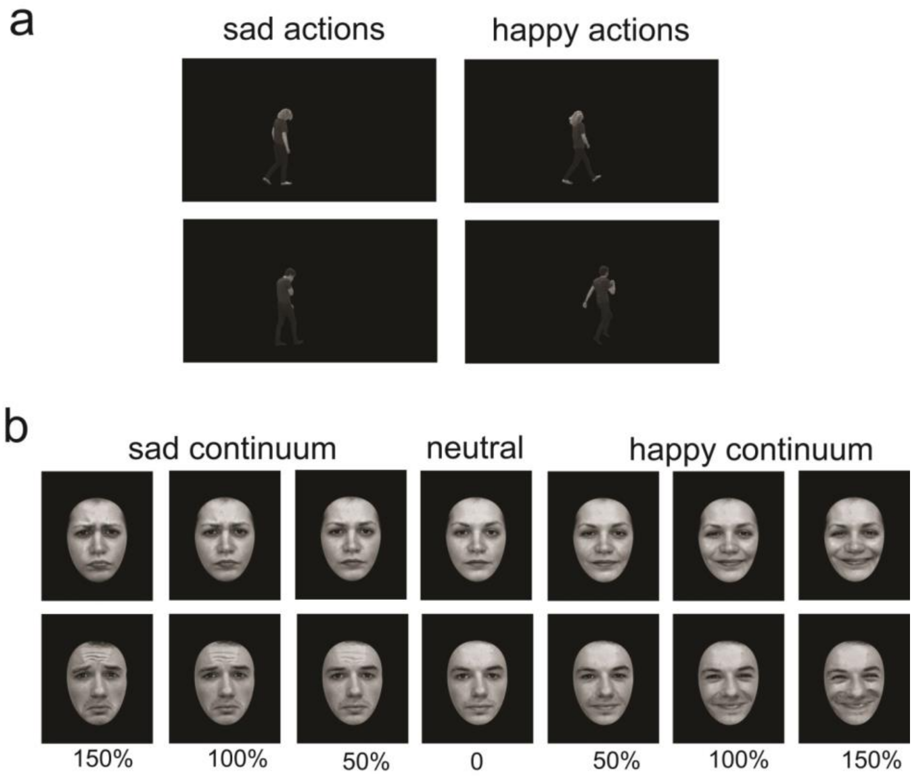


Figure 5.1 Example of stimuli used in the experiment. (a) Frames from the happy and sad action stimuli performed by female (top) and male (bottom) actors, (b) Example of facial stimuli from the expression continua for female (top) and male (bottom) actors.

5.4.3 Stimuli calibration

To ensure that any difference in the aftereffect magnitude between face and action adaptation conditions was not caused by the difference in the strength of the adaptors, the intensity of the emotion in the face adapting stimuli (i.e. the strength of the face morph) was matched with the intensity of the emotion in the action stimuli. This step was necessary, as dynamic displays of emotions may be perceived as more intense than static displays (Ambadar, Schooler, & Cohn, 2005; Biele & Grabowska, 2006). Stimuli calibration was done individually for each participant to account for any individual differences that may influence the perception of emotion intensity. For each participant, face morphs that were perceived as equally happy or sad as the actions were later used as adapting stimuli.

Stimuli calibration took place during the first testing session and was completed using an adaptive staircase method. A PC running MATLAB 2010a (The MathWorks, Natick, MA) and Psychtoolbox (Kleiner et al., 2007) was used to display the stimuli and record participants' responses. Each participant completed two separate blocks, one for happy and one for sad stimuli. In each block participants completed a forced-choice task while stimuli were selected on the basis of interleaved staircases: 2 for male stimuli and 2 for female stimuli. The order of the blocks was counterbalanced across participants and all male and female staircases were interleaved within each block. For each staircase, happy or sad (male and female) video clips were set as standard and the face stimuli were set as comparison. The order of standard (action) and comparison (face) was randomised. On each trial, participants saw a video clip of male or female adapting action displayed for 2s and one of the face stimuli from the morph continuum. Face stimuli were displayed for 500ms; as short presentation of face stimuli produces equally reliable measurement of social judgement as unlimited viewing time (e.g. Willis & Todorov, 2006), so the difference in the duration of action and face stimuli was not expected to influence the intensity judgement. Participants were asked to judge which stimulus (the action or the face) was more happy or more sad, and indicated their response on a keyboard. The inter-trial interval was set to 2s.

Each staircase began with the presentation of a happy or sad stimulus of 125% intensity. The initial staircase step size was set to 8%, which then halved on each of the first 3 reversals. Staircase reversal rules were 1-up, 1-down and 1-up, 1-down for each gender face. The staircases quit after 12 reversals. The maximum number of trials per staircase was set to 50, but the majority of staircases resulted in approximately 30 trials per staircase type providing approximately 60 trials per psychometric function. From each staircase (happy/sad, male/female) I calculated a point of subjective equality (PSE), where the face stimulus was perceived as equally happy or sad as the action stimulus. Values of the PSEs represented the strengths of the face morphs, which were then used as adapting stimuli in the main experiment.

5.4.4 Design and experimental procedure

In Chapter 5 I used Feshner Psychophysics (Ehrenstein & Ehrenstein, 1999) to quantify the magnitude of cross-category emotion aftereffects. I was able to do it, as here I morphed the test stimuli (i.e. facial expressions) along the adapted dimension (from happy to sad). Using this method I could also represent aftereffect as a shift in the intensity the stimulus, at which it is perceived as being neutral. This way I was also able to precisely measure the effect of adaptation without participant's conscious awareness. The study design was based on Ghuman, et al. (2010) who tested the cross-category sex and identity adaptation.

Participants completed four experimental sessions, testing each of the adapting conditions, on four different days. In two sessions, participants adapted to face stimuli and rated subsequent face stimuli of either the same (face adaptation/same identity) or a different (face adaptation/different identity) actor. In the two remaining sessions, participants adapted to action stimuli and rated the subsequent face stimuli of either the same (action adaptation/same identity) or a different (action adaptation/different identity) actor. The order of sessions was counterbalanced across participants.

Pre-adaptation phase.

The experiment was performed on a PC running MATLAB 2010a (The MathWorks, Natick, MA) and Psychtoolbox (Kleiner et al., 2007). Schematic illustration of the experimental procedure is presented on Figure 5.2. Each session began with a pre-adaptation baseline block, to determine the value of the male and female faces, that were perceived as happy or sad with equal probability. In the baseline block participants completed four forced-choice adaptive staircases (two for female and two for male faces; starting with either happy or sad morphs). On each trial, a briefly presented blue fixation cross (200ms) was followed by a test face (presented for 200ms). Participants were asked to judge whether the test face was happy or sad by pressing the appropriate key on the keyboard. The inter-trial interval with a green fixation cross presented in the centre of the monitor was set to 2s. Possible starting points for each staircase were 20% happy or 20% sad male or female face. The initial step size was set to 8%, which was halved on each of the first 3 reversals. The staircase reversal rule was 1-up, 1-down and 1-up, 1-down for each gender face. The staircase quit after 12 reversals. The maximum number of trials per staircase was set to 50, but the majority of staircases resulted in less than 30 trials per staircase type providing approximately 60 trials per psychometric function.

Adaptation phase.

Next, participants completed one of the adapting conditions, during which test stimuli were selected on the basis of eight interleaved staircases (male or female actor x happy or sad adaptation x happy or sad staircase starting points). On each trial, first an adapting stimulus was presented for 8s. The adapting movie was played 4 times, while the adapting face was displayed for 8s. In the same identity blocks the test face was always of the same actor as in the adapting movie or face, while in the different identity blocks the test face was always of a different actor. After a brief inter-stimulus interval (blue fixation cross, 200ms) a test face was displayed for 200ms. The screen then went blank and participants responded whether the test face was happy or sad. Following their response a green fixation cross was displayed for 2s indicting an inter-trial-interval (ITI). The possible intensity of the test face, i.e. starting points for each staircase were 20% happy or 20% sad. To avoid low-level adaptation in the face adaptation condition, the test face was 75% of the size of the face adapting stimulus. The staircase parameters were the same as for the baseline conditions. Finally, participants completed a post-adaptation baseline block, which followed the same procedure as the pre-adaptation baseline block.

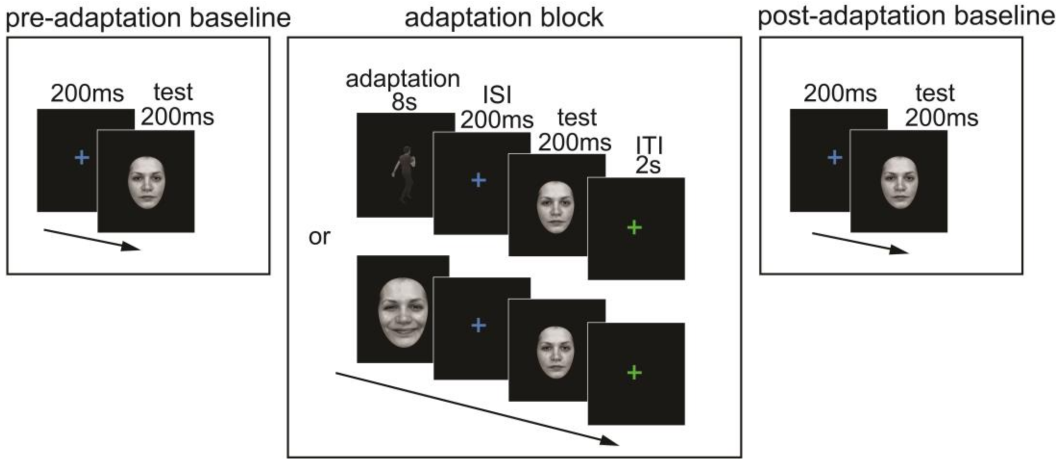


Figure 5.2 A schematic illustration of the experimental procedure.

5.4.5 Data analysis

For each participant and each condition I computed the PSEs by first fitting cumulative Gaussian psychometric functions to the data. PSEs values indicated the % of the face morph that was judged as happy or sad with equal probability. PSEs were calculated separately for male and female actors in each of the conditions. For each testing session, PSEs from pre-adaptation and post-adaptation baselines were averaged to produce a single value, which was then used to calculate the aftereffects. The aftereffects were calculated by subtracting PSE values in the baseline conditions from the PSE values in the adaptation condition. Positive aftereffects represented shifts in the PSE towards more happy stimuli, while negative aftereffects represented shifts in the PSE towards more sad stimuli. Aftereffects were calculated separately for male and female actors and each adapting condition (action/face adaptation, same/different identity). Aftereffects values were used in the main analysis.

5.5 Results

Since I only used two actors as adapting and test stimuli, in order to check that both male and female actors produced comparable aftereffects I analysed the shifts in PSE using a within-subject 2x2x2x2 ANOVA with factors of adapting stimulus type (face, action), identity (same, different), adapting emotion (happy, sad) and actor (female, male). ANOVA revealed that the main effect of actor was non-significant ($F(1,11)=1.51$, $p=.245$, $\eta_p^2=.121$) and none of the interactions involving the actor reached significance (all $F_s<1.50$, all $p_s<.246$), suggesting that adaptation to both actors resulted in similar aftereffects. Therefore, for the main analysis I averaged aftereffect across the two actors; the aftereffect values for each adapting condition are illustrated in Figure 5.3. The within-subject 2x2x2 ANOVA with factors of adapting stimulus type (face, action), identity (same, different), adapting emotion (happy, sad), revealed that adaptation to happiness and sadness generated significantly different aftereffects (main effect of adapting emotion, $F(1,11)=54.56$, $p<.0001$, $\eta_p^2=.832$). Importantly, a significant interaction between adapting emotion and adapting stimulus type ($F(1,11)=51.51$, $p<.0001$, $\eta_p^2=.824$) indicated that aftereffects were stronger for the same category condition (face adaption) than for the different category (action adaptation). A post-hoc paired sample t-test revealed that happy and sad aftereffects were significantly different from each other only in the face adaptation condition (happy AE; $M=3.5$, $SD=.372$, sad AE; $M=-4.4$, $SD=4.62$, $t(11)=7.51$, $p<.0001$) and not in the action adaption condition (happy AE; $M=-1.3$, $SD=1.83$, sad AE; $M=-.89$, $SD=2.46$, $t(11)=1.72$, $p=.112$).

Adaptation also resulted in stronger aftereffects in conditions where adapting and test actor were of the same identity as suggested by a significant interaction between adapting emotion and identity ($F(1,11)=7.44$, $p=.020$, $\eta_p^2=.403$). This effect was further clarified by a significant 3-way interaction between adapting emotion, identity and adapting stimulus type ($F(1,11)=6.64$, $p=.026$, $\eta_p^2=.377$), suggesting that in the face adaptation condition aftereffects were greater for the same identity than for different identity condition, but identity had no effect in the action adaptation condition, where adaptation did not result in any significant aftereffects. An interaction between adapting stimulus type and identity approached significance ($F(1,11)=4.15$, $p=.066$, $\eta_p^2=.274$). No other effects reached significance (all $F_s<.41$, all $p_s<.534$).

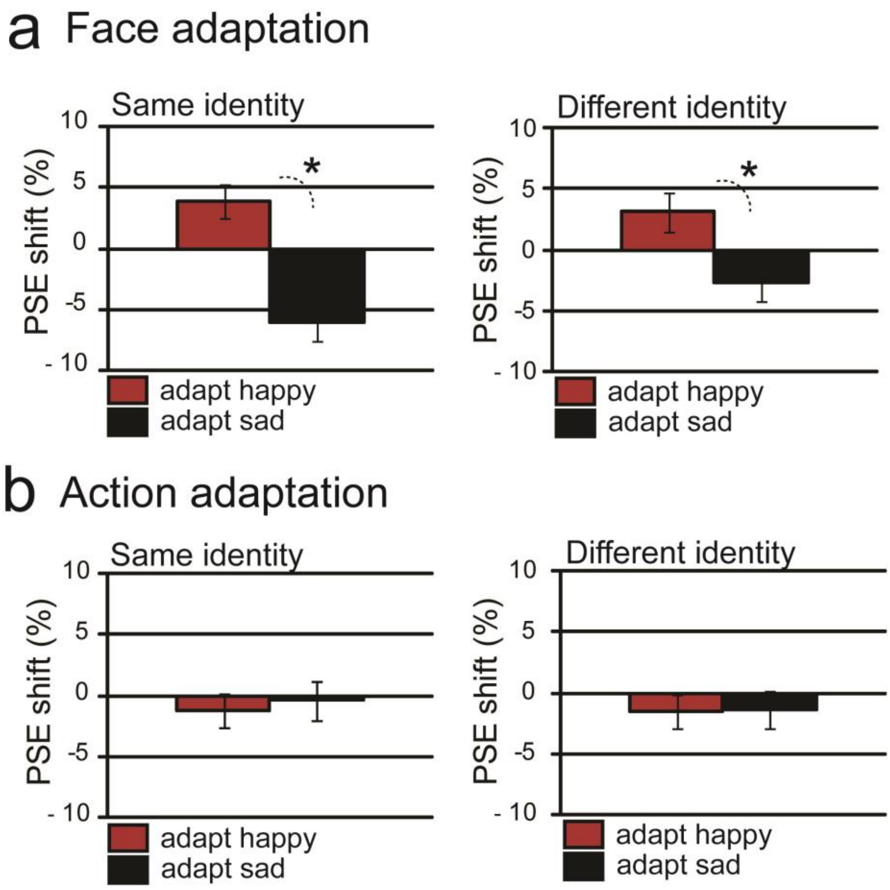


Figure 5.3 Shift in the point of subjective equality (PSE) following adaptation to happy (red) or sad (black) faces (top) and actions (bottom). Zero represents no effect of adaptation, positive values indicate PSE shift towards more happy faces and negative values indicate PSE shift towards sad faces. Error bars represent SEM. Asterisk represent a significant difference between conditions (p<.001).

5.6 Discussion of Chapter 5

The results of this experiment demonstrated that adaptation to emotional whole body actions does not influence the emotion perception in subsequent static faces. Adaptation did not cross perceptual category even when the adapting and test actors were of the same identity. In contrast, adaptation to facial expressions of happiness and sadness influenced subsequent emotion perception in test faces the effects of adaptation were stronger for the same identity condition, where adapting and test stimuli depicted the same individual. These results confirmed previous findings reporting identity-dependent and identity-independent facial expression aftereffects (Campbell & Burke, 2009; Fox & Barton, 2007; Pell & Richards, 2013; Skinner & Benton, 2012), and demonstrated the stimuli manipulation and the experimental design I employed in this study successfully elicited adaptation aftereffects in the same-category condition.

The lack of cross-category whole body action-to-face adaptation cannot be attributed to the difference in the strength of the action and face adaptors. The intensity of the emotional expression in the face adapting stimuli was matched with the intensity of the action adapting stimuli individually for each participant. In contrast, this null result could be explained by a dissociation in the processing of static and dynamic stimuli. Adapting action stimuli portrayed dynamic whole body walking actions, while test stimuli were always static faces. Previous neuroimaging studies highlighted the considerable overlap in the neural systems underlying perception of emotion from faces and bodies (de Gelder, et al., 2010; Heberlein & Atkinson, 2009), but also delineated specific brain regions that are involved in the processing of dynamic and static faces and bodies (Atkinson, et al., 2012; O'Toole et al., 2014). For instance, viewing dynamic expressions, in contrast to static body and facial expressions, resulted in a greater activity in the pSTS (Grèzes, et al., 2007; Pitcher, et al., 2011) and premotor areas (Grèzes, et al., 2007; Sato, et al., 2004). In addition, activity in the pSTS was increased for viewing emotional point-light body action in contrast to point-light facial expression (Atkinson, et al., 2012). Perceptual adaptation is likely to operate at multiple stages of the cortical hierarchy ranging for areas encoding simple features of the stimulus to high-level regions encoding complex stimuli (see Webster, 2011 for a review). It is possible that in the current study, viewing emotional whole body actions resulted in the adaptation solely in regions that respond to emotional action e.g. in the pSTS (Atkinson, et al., 2012; Grèzes, et al., 2007). Here, adaptation would have not influenced the processing of static faces. This finding may also suggest that processing of some emotions (e.g. happiness and sadness) from static facial expression and dynamic whole body action may rely on distinct neural mechanisms.

Another possible explanation for the lack of cross-category adaptation may be that perception and recognition of emotion from whole body actions is dependent upon the specific kinematics or body parts that convey it. This proposal is also in line with the results of Experiment 1 reported in Chapter 4, where adaptation did not transfer across different adapting and test actions. Adapting actions in this study were happy and sad walking action. Previous research has suggested that recognition of basic emotion from gait typically depends on a relatively small number of posture and kinematic features (Roether, et al., 2009). The most diagnostic features for the recognition of happiness and sadness from gait have been proposed to include the speed of an action, head inclination and elbow and shoulder angle (Roether, et al., 2009). Moreover, in an important experiment Roether and colleagues (2009) examined whether adaptation to happy and sad walking actions performed by artificial walkers that exhibited only the most prominent posture and kinematic features that were necessary for the recognition of these two emotions, would result in a similar effects as adaptation to natural happy and sad walks. The result suggested that adaptation to artificial walkers had a significant influence on the perception of subsequent neutral actions. There was no difference in the magnitude of adaptation aftereffects between the artificial and natural gait conditions, suggesting that emotion recognition from dynamic actions may rely only on a limited number of postural and kinematic cues. Critical features necessary for the perception of happiness and sadness in gait delineated by Roether and colleagues were readily visible in the action stimuli used in this study. Therefore, it is possible that adaptation occurred at the visual processing level that is sensitive to specific action kinematics and not at more abstract, category-independent level.

Despite rich evidence for the influence of body emotion on the perception of face emotion (Aviezer, et al., 2012a, 2012b; Meeren, et al., 2005; Van den Stock, et al., 2007), the results of the present study suggest that viewing emotional whole body actions does not have an effect of subsequent perception of emotion in static faces. The discrepancy between the finding of previous studies and the current experiment may, however, be due to differences in the methods employed to study the interaction in the processing of emotion form faces and bodies. Firstly, traditionally the influences of the body emotion on the classification of the face emotion have been investigated using static body postures and static facial expressions (e.g. Aviezer, et al., 2012a, 2012b; Van den Stock, et al., 2007), while body stimuli used in this study were dynamic actions. There are well-documented differences in the processing of static and dynamic expressions (e.g. Kilts, et al., 2003; LaBar, et al., 2003; Sato, et al., 2004), which could have contributed to the null result observed here. Secondly, previous studies often embedded facial expressions on body expressions of emotion creating congruent or incongruent compound stimuli, where emotions expressed by the face were either matched or mismatched with body expressions (Aviezer, et al., 2012a, 2012b; Meeren, et al., 2005; Van den Stock, et al., 2007). Results of these studies suggest a rapid and automatic perceptual integration of the information conveyed by the body and the face that may enable a better evaluation of the biologically important signals (Meeren, et al., 2005). Neural networks processing these two types of stimuli may, however, still be distinct.

To date, visual adaptation studies have provided mixed support for the existence of shared representation of bodies and faces (e.g. Ghuman, et al., 2010; Kovacs, et al., 2006; Palumbo, Laeng, & Tommasi, 2013; Weigelt, et al., 2010). The results of this study contribute to this debate and suggest that representation of emotional information may be category-specific.

Neuroimaging studies that compared the brain reposes to dynamic body and dynamic facial expression of emotion have highlighted shared networks that processed emotional information regardless of the stimulus category (Atkinson, et al., 2012; Peelen, et al., 2010). It is therefore possible that the lack of cross-category adaptation observed here may be attributed to the significant dissimilarity between the adapting and test stimuli, and in particular to the absence of dynamic information in face stimuli.

CHAPTER 6

Adaptation to genuine and faked facial expressions

6.1 Abstract

Aftereffects following adaptation to facial expressions are well documented, but less is known about which aspect of the stimulus is adapted: the facial expression *per se* or the emotional state of mind suggested by the expression. To investigate this further, in this study I used both genuine and faked facial expressions of joy and anger, matched for intensity, as adapting stimuli. In each trial, participants first assessed whether the facial expression was faked or genuine, and received feedback about their judgment. This allowed participants to form a belief regarding the emotional state of the adapted actor. Next, participants adapted to the same stimulus for either 5 sec, 500 ms or 8 sec, in a between-subject design. Responses to the neutral test expression of the same actor were measured in a 2AFC design (angry or happy) or on a 5-point Likert scale (including neutral). This manipulation allowed me to test whether an internal state attribution to the observed actor modulated the adaptation to facial expressions. Following 5 sec and 500 ms adaptation aftereffects to genuine expressions were significantly larger than those to faked expressions, when measured on a rating scale, but not in a 2AFC paradigm. This 'advantage' for genuine expressions disappeared following 8s adaptation, where equally strong aftereffects were obtained. These findings suggest that adaptation to facial expressions is influenced by emotional state attribution, but that this effect is short-lasting. These findings also raised an interesting question as to whether the scale on which the effects of perceptual adaptation are measured can influence the strength of perceptual bias resulting from adaptation.

6.2 Introduction

Accurate face perception is fundamental for social interaction. Information derived from faces enables us to appraise the intentions and mental states of our conspecifics and adjust our behaviour accordingly. The face is also central to our affective expression; rapid muscular changes permit facial expressions to evolve over short period of time, which in turn allows us to communicate our emotional states to others (Ekman, 1993; Plutchik, 1982). However, facial expressions not only reflect our automatic appraisal of environmental events (Frijda, 1988), they also enable us to act in accordance with the situational demands and comply with social norms. The smile, for instance, has been identified as particularly versatile; serving over 18 different functions (Ekman 2001). It may signal a genuine expression of enjoyment and amusement (Ekman, 2001), positive behavioural intent (e.g. greeting smiles; Eibl-Eibesfeldt, 1972), or in-group favouritism (Beaupré & Hess, 2003), but it may also mark embarrassment and shame (Keltner, 1995).

Human beings, moreover, have the ability to deliberately pose various facial expressions. They can use this ability to censor their expressions to hide or falsify their true feelings. Smiles, for example, can be expressed to mask negative emotions (Ekman, 2001). Deliberate control over one's emotional expressions has an important adaptive function; it allows for control over our social exchange. It also plays a role in emotional development; children as young as 4 years, smile in order to mask their disappointment after receiving an unattractive gift (Cole, 1986), adjusting their behavioural response to the situational context.

Accurate interpretation of honest and simulated expressions may, however, be difficult. In order to understand what another individual is actually feeling, one needs to observe not only the emotion overtly expressed, but also any subtle cues that may indicate that the expressed emotion is simulated and faked (Gosselin, Kirouac, & Doré, 1995). Since the aim of deliberately posed expressions is to convince the observer/encoder that the displayed emotion is actually felt, it is likely that faked expressions are convincing reproductions of the genuine ones.

6.2.1 Genuine vs. faked expressions

The (dis)similarity between genuine and faked expressions of emotions has been extensively studied (e.g. Duchenne, 1862/1990; Frank, Ekman, & Friesen, 1993; Gosselin, et al., 1995). Three major morphological and perceptual differences between the two have been identified: faked expressions are more asymmetrical than genuine expressions (Ekman, Hager, & Friesen, 1981), they have a more irregular timing of muscular contraction (Hess, Kappas, McHugo, Kleck, & Lanzetta, 1989) and the two expressions activate different facial muscles.

French anatomist Duchenne first observed that orbicularis oculi muscle surrounding the eye is activated in smiles that occur in spontaneously experienced enjoyment, but not when the smiles are posed (Duchenne, 1862/1990; Frank, et al., 1993). This, *Duchenne marker*, is a hallmark of genuine smiles, which involve the contraction of the muscle around the eye, the orbicularis oculi, pars lateralis (Frank, et al., 1993). It corresponds with Action Unit 6 ("cheek raiser") in Ekman, Friesen, and Hager's (2002) Facial Action Coding System (FACS); it is responsible for narrowing the eye aperture, appearance of wrinkles ("crow's feet") in the external corner of the eye, raising the cheek and lowering the eye cover fold. The Duchenne smile is also characterised by the synchrony between orbicularis oculi and zygomatic major muscles, so that they reach the maximal contraction at the same time and equally on both sides of the face (Niedenthal, Mermillod, Maringer, & Hess, 2010).False, or non-Duchenne smiles, on the contrary, are expressed deliberately in order to convince observers that the positive affect is felt, when in fact it is not.

6.2.2 Recognition of genuine and faked expressions

People have an exceptional ability to infer others' complex mental and emotional states from subtle visual cues. The majority of research on the recognition and processing of facial expression has, however, employed prototypical examples of basic emotions *in isolation* (Ekman, 1994). These, may significantly differ from our everyday experience (Niedenthal, et al., 2010). In real life there is a great diversity of individuals, social contexts and motivations behind expressed emotions. In consequence, people are often required to interpret ambiguous, deliberate and blended expressions, which in their function and visual appearance differ from prototypical expression. Being able to accurately judge the authenticity and interpret the meaning of observed expressions may be challenging and less is known about the perceptual and cognitive processes involved in recognition of deliberate and faked expressions.

Processing of faked facial expressions is more cognitively demanding than processing of genuine expression. Calvo, Gutierrez-Garcia, Avero, and Lundqvist (2013) measured visual attention patterns of participants viewing genuine (enjoyment) smiles and faked (non-enjoyment) smiles. Observation of the latter resulted in longer and more frequent fixations of the eye and mouth regions suggesting an increased attentional engagement required for correct interpretation of an expression incongruent with actor's emotional state. Especially the eye region is critical for the accurate interpretation of observed expressions. When judging the authenticity of briefly presented blended expressions, where the emotion signalled by the eyes is incongruent with the emotion signalled by the mouth (i.e. top half of the face is taken from the expression of anger and bottom half depicted happiness), the integration of the information carried by the eye region with the rest of the face enables accurate discrimination of the expression (Calvo, Fernández-Martín, & Nummenmaa, 2012). Processing of ambiguous, blended expressions and prototypical expressions also relies on different neural activation patterns. Identification of prototypical expressions occurs at early stages of visual processing, between 180-430 ms post stimulus onset, while detection of ambiguity and judgement whether the given expression is genuine is delayed until later stages of processing (430-720 ms post stimulus onset; Calvo, Marrero, & Beltrán, 2013). Processing of non-prototypical expressions is therefore more time-taking and more challenging.

6.2.3 Processing of facial expressions from the embodied cognition perspective

Theories of embodied cognition argue that emotion recognition is not only based on the explicit, cognitive appraisal of the visual characteristics of an expression, but also involves the integration of the sensory–motor experience elicited in the observer with the visual representation of an expression (Gallese, 2007; Goldman & de Vignemont, 2009; Goldman & Sripada, 2005). Such integration facilitates the reconstruction of the mental state of the observed individual through simulation and appears to be critical for the recognition of emotions displayed by others (Adolphs, 2002a; Atkinson & Adolphs, 2005; Gallese, 2007). Niedenthal, et al. (2010) built on this knowledge and proposed the simulation of smiles model (SIMS), according to which perceptual cues, experimental cues obtained through embodied simulation, and conceptual knowledge are used to interpret emotional expressions. The model highlights the importance of internal, motor and somatosensory simulation while recognizing facial expressions. This subjective affective response in the observer contributes to the correct interpretation of the authenticity of the observed expression.

6.3 The current study

In a series of experiments I investigated to what extent the attribution of mental states modulates the perception of facial expressions using a visual adaptation paradigm. The study was designed to address the question whether, and if so, to what extent, top-down Theory of Mind (ToM) processes can interact with the processing of facial expressions.

First, adaptation may occur not only to the facial expression *per se* (i.e. its perceptual characteristic), but also to the emotional state of mind derived from that expression. Genuine and fake expressions exhibit similar facial characteristics, but their underlying emotional states are quite different: happiness in case of a genuine facial expression of happiness, no-happiness in case of a faked facial expression of happiness. For a faked expression of happiness, it is usually not known what the real emotion is (if any), we only know that it isn't happiness. For the aim of the current experiment this is sufficient.

Adaptation may possibly occur not only to the perceptual representation of the emotion (i.e. the literal facial features) but also to the representation of the other's emotional state of mind. It is currently hotly debated whether or not such a representation of the other's emotional state of mind involves one's motor system and associated viscera-sensory experiences. According to embodied cognition theories (Gallese, 2007; Niedenthal, et al., 2010), a representation of other's emotional state of mind would indeed be underpinned by the sensory-motor experience that is associated with motor simulation of the observed expression. However, the traditional ToM approach does not reserve a special role (or any at all) for the motor system in attributing mental or emotional states of mind to others (Baron-Cohen, 1995).

It has been argued that ToM processes modulate the sensory processing of social stimuli. Teufel and colleagues (Teufel et al., 2009; Teufel, Gutmann, Pirow, & Fischer, 2010) proposed that early stages of visual processing of social stimuli are modulated by the mental state attribution. Using a gaze adaptation paradigm (Teufel et al., 2009) and gaze following paradigm (Teufel, Alexis, Clayton, & Davis, 2010), Teufel and colleagues showed that ToM processes influence the basic gaze-perception system. When participants believed that the actor could see through a pair of goggles, this mental state attribution facilitated gaze processing. However, when participants believed that the actor could not see through the goggles, the effects of adaptation were reduced. The belief regarding actor's ability to see influenced the magnitude of adaptation aftereffects (Teufel, Fletcher, & Davis, 2010).

Recently de la Rosa and colleagues (de la Rosa, et al., 2014) showed that adaptation to body actions is also sensitive to the social context. Priming participants with hitting or waving actions prior to the visual adaptation task significantly modulated the action adaptation aftereffects. These results suggest that visual action recognition is modulated by high-level processes such as interpretation of, and the expectations about, the observed action.

If perception of facial expressions is modulated by the belief regarding the emotional state of the actor, then we would expect such modulation to affect the adaptation to facial expressions. According to (Teufel, et al., 2009) participants' belief regarding the genuineness or fakeness of the adapted expression influences the strength of adaptation aftereffects, where more pronounced aftereffects would be observed in a genuine condition. This prediction was tested across six experiments, where participants adapted to either genuine or faked expressions of happiness and anger. In order to ensure that participants attributed the correct emotional state to the actor displayed in the adapting stimuli, on each trial they explicitly evaluated whether the presented expression was genuine or faked and then received feedback as to whether they were correct or not. Adaptation to genuine and faked expressions was measured across 3 different adaptation durations in order to examine the time-course of the top-down (knowledge/belief) modulation of the perception of facial expressions.

Additionally, participant's responses were recorded on two different scales (2AFC and a rating scale) in order to examine how robust facial expression aftereffects are across different scoring methods.

6.4 General methods

6.4.1 Participants

A total of 125 undergraduate students (97 females, 28 males, age, *M*=20.8 years, *SD*=3.4) from the University of Hull took part in six experiments. All participants had normal or corrected to normal vision, were naive to the purpose of the study and provided written consent prior to the experiment. Participants received course credits for taking part in the experiment. The study was approved by the Ethics Committee of the Department of Psychology, University of Hull, and was performed in accordance with the ethical standards laid down in the 1990 Declaration of Helsinki.

6.4.2 Stimuli

Custom made digital colour photographs of neutral facial expressions and of genuine and faked facial expressions of happiness and anger of four professional actors (2 females: CL, MA and 2 males: BR, LO) were taken by a professional photographer of “Accademia Aramus”, a cultural association in Rome, Italy. These images were used across all experiments. In order to capture genuine expressions of happiness and anger, actors underwent the Stanislavsky mood induction technique (Gosselin, et al., 1995; Stanislawski, 1975), which involves the retrieval and re-experience of past experiences where they felt the targeted emotion. For the faked expressions, the procedure described by Duclos and Laird (2001) was used. For faked happy expressions, actors were first trained to relax the muscles around the eyes, as in the neutral expression, in order to avoid the natural contraction of the orbicularis oculi. Actors were asked to maintain this position for 15 seconds, while lifting the lip corners to indicate smiling. For faked expressions of anger, actors were trained to display anger by clenching their teeth and pushing the upper lip against the bottom lip without contracting the eye brow. They were asked to maintain this pose for 15 seconds. All expressions were photographed at peak intensity.

Images were edited using Adobe Photoshop software (Adobe Systems, San Jose, California, USA). Images were aligned horizontally, equalized for luminance and contrast and converted into grey scale bitmaps. A black oval mask covering any external facial features was then applied to the images. All stimuli are illustrated in Figure 6.1. For the adaptation experiments, images of neutral facial expressions were used as test stimuli and genuine and fake expressions were used as adapting stimuli. In order to ensure that any observed adaptation aftereffect were due to adaptation at the retinotopic level all test stimuli (subtended 520 x 580 pixels) were 30% smaller than adapting stimuli (743 x 829 pixels) (cf. Webster & MacLeod, 2011b).

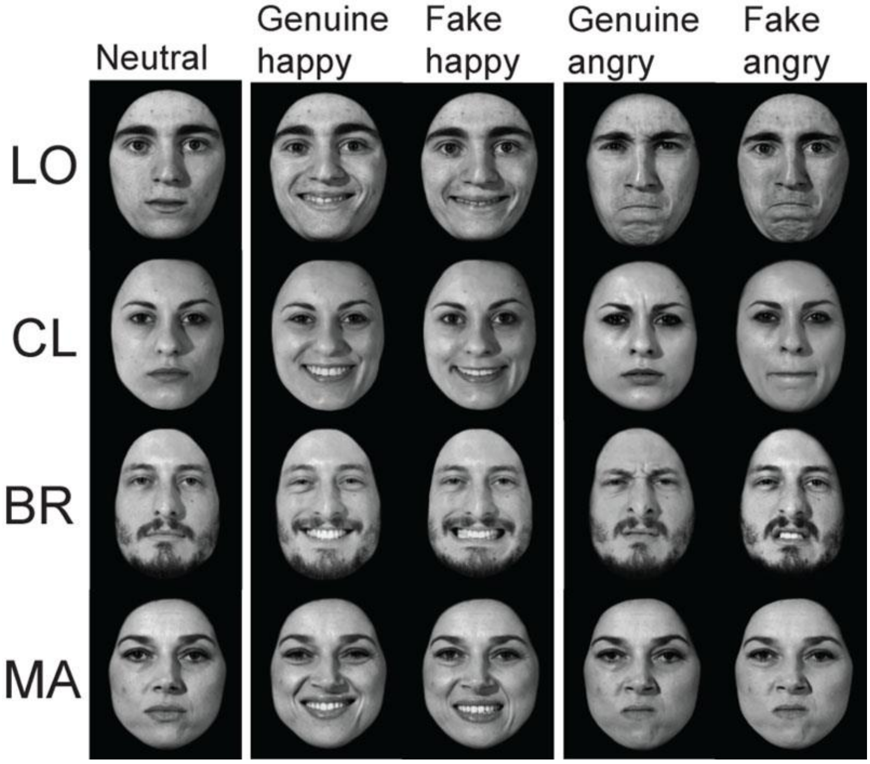


Figure 6.1 Stimuli used in the adaptation experiments. Photographs depict four actors (LO, CL, BR and MA) portraying neutral, and happy and angry expressions, both genuine and faked.

Calibration of the genuine and fake adaptation stimuli

Genuine facial expressions may be perceived as more intensive than faked expressions (Gosselin, et al., 1995), which may affect the strength of the adaptation aftereffect resulting from the exposure to these two types of stimuli. To assure that any difference in the magnitude of emotion aftereffects between genuine and faked conditions was not due the difference in the strength of the adapting stimuli, genuine and faked stimuli were matched for perceived intensity in the calibration experiment.

Twenty-five participants (21 females, age *M*=20.8 years, *SD*=3.7) who did not participate in any of the following adaptation experiments completed the intensity matching task. Participants were presented with a target face depicting a 100% (peak) fake expression in the upper half of the display and five test faces below it (see Figure 6.2). The test faces were blends of 100% genuine and neutral expressions created in 10% steps. Faces were morphed using Sqirlz Morph 2.0 software (http://www.xiberpix.net/SqirlzMorph.html). The test faces varied from 60% emotion (60% expression and 40% neutral) to 100% (pure genuine expression. Faces were presented in an increasing fashion form left to right. Participants were asked to choose the face from the bottom display that matched the intensity of the top face by pressing the corresponding number on the keyboard. Stimuli were presented on the screen until participants' response. Following their response the screen turned blank for 5 seconds until the next trial. The task consisted of 8 trials in total (4 actors x 2 emotions).

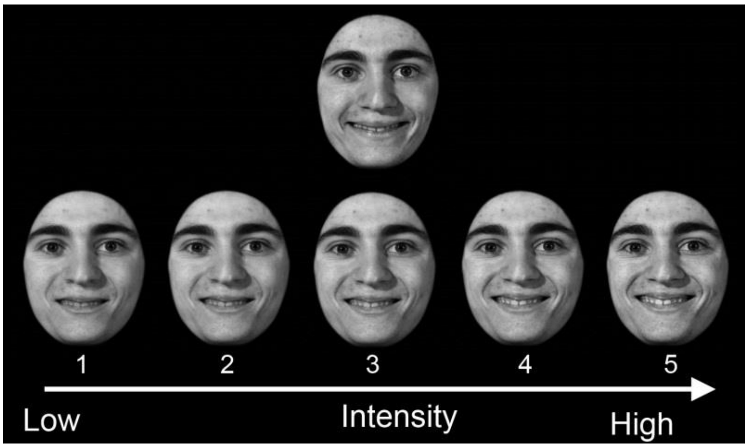


Figure 6.2 Illustration of a single trial in the intensity matching task. Top image displays a faked expression of happiness at the maximum intensity available (called 100%). Bottom images represent a section of a morphing continuum between the genuine expressions of happiness at 60% intensity (far left) and 100% intensity (far right), in 10% steps.

In all experiments the faked adapting emotions were shown at 100% intensity and the genuine adapting stimuli were selected on the basis of average values obtained from the intensity matching experiment presented in Table 6.1

Table 6.1 Mean ratings of the intensity for the genuine happy and angry expressions which were perceived of equal intensity as happy and angry faked expressions based on the judgement of 25 observers. Bottom row contains the percentage (in steps of 10%) of the maximum intensity of the genuine expression selected for the adaptation experiments

Actor		LO		CL		BR		MA	
		Happy	Angry	Happy	Angry	Happy	Angry	Happy	Angry
Mean ratings of the matched expression (%)	*M*	78.8	82.0	83.6	70.0	84.0	73.2	76.8	87.6
	SD	6.6	11.9	8.6	10.8	9.1	12.8	11.8	10.9
Intensity of blends selected for the adaptation experiment (%)		80	80	80	70	80	70	80	90

6.4.3 Design and experimental procedure

Experiments in Chapter 6 followed a traditional adaptation-test design. Here, participants completed one experimental block, where different types of adapting stimuli (e.g. genuine or faked happy and sad expressions) were presented in a pseudo-random order. This was done to ensure that participants were not biased to respond to the test stimulus with the same response option. Therefore, adaptation-top up design was not suitable for these experiments. In every experiment in Chapter 6 participants also completed a pre-adaptation block, where they rated the test stimuli presented in isolation (i.e. without the preceding adapting stimulus). I included this pre-adaptation block, as I wanted to calculate the aftereffects separately in genuine and faked conditions.

All experiments were controlled by a PC running E-prime (Psychology Software Tools, Inc., Pittsburgh). Stimuli were displayed in the centre of a 22" screen CRT monitor (Philips 202P40, 1600x1200 pixels, 100Hz refresh rate). Participants sat approximately 50 cm away from the screen; they entered responses on the keyboard.

Pre-adaptation phase.

All adaptation experiments began with a pre-adaptation block, where participants judged the emotion portrayed in each of the neutral test stimuli. Each trial started with a brief fixation cross (250 ms), which was followed by a neutral test stimulus presented on the screen for 250 ms. Participants responded by pressing the appropriate key on the keyboard, in a 2AFC format (happy or angry, Experiments 1, 3 and 5), or on a 5-point Likert scale ranging from slightly angry (1) via neutral (3) to slightly happy (5), (Experiments 2, 4, and 6). Following the response, the screen remained blank for 5 sec. Each of the test images was displayed twice in a random order (8 trials in total).

Adaptation phase.

Directly following the pre-adaptation phase, 4 practice trials of the adaptation experiment were completed (2 actors x emotions), followed by 16 randomised experimental trials (4 identities x 2 facial expressions (happiness, anger) x 2 intentions (fake, genuine). Each trial began with an explicit judgement task (see Figure 6.3), where participants assessed whether the displayed stimulus portrayed a genuine or a faked expression. This ensured that participants were actively engaged in assessing the emotional state of mind behind the displayed facial expression. If this kind of information was simply provided to the participants, for example by presenting the label 'fake' or 'genuine' on the screen, then they would not be actively engaged in the classification of the expression. However, a judgment about the authenticity of an expression can be quite difficult to do if only one facial expression (either fake or genuine) is presented and no comparison can be made. Therefore, simultaneously a comparison face was presented depicting the same actor expressing the same emotional expression (happiness or anger), but with the opposite intention. The target face, which participants were asked to evaluate, was presented centrally and the comparison face was presented in the right bottom corner of the display. Participants were asked to determine whether the expression depicted in the target face was genuine or faked by pressing one of two marked keys on the keyboard (z="genuine" or m="faked"). Both stimuli remained on the screen until a response was made. Directly following the response, feedback ("correct" or "incorrect") was displayed for 3 sec. The trial was repeated if participants responded incorrectly, until the correct answer was given. Following a correct judgement participants were presented with an adapting stimulus for 5 sec, which was always the same face as in the immediately preceding fake/genuine judgement task. Next, after a brief fixation cross (250 ms) participants saw a smaller test stimulus (displayed for 250 ms) depicting the same actor, but with a neutral expression. Participants were asked to indicate their judgement of the emotion expressed in the test stimulus (2AFC in Experiments 1, 3 and 5, and 5-point rating scale in Experiments 2, 4, and 6). Once the response was registered the screen remained black for a further 5 sec before the next trial began.

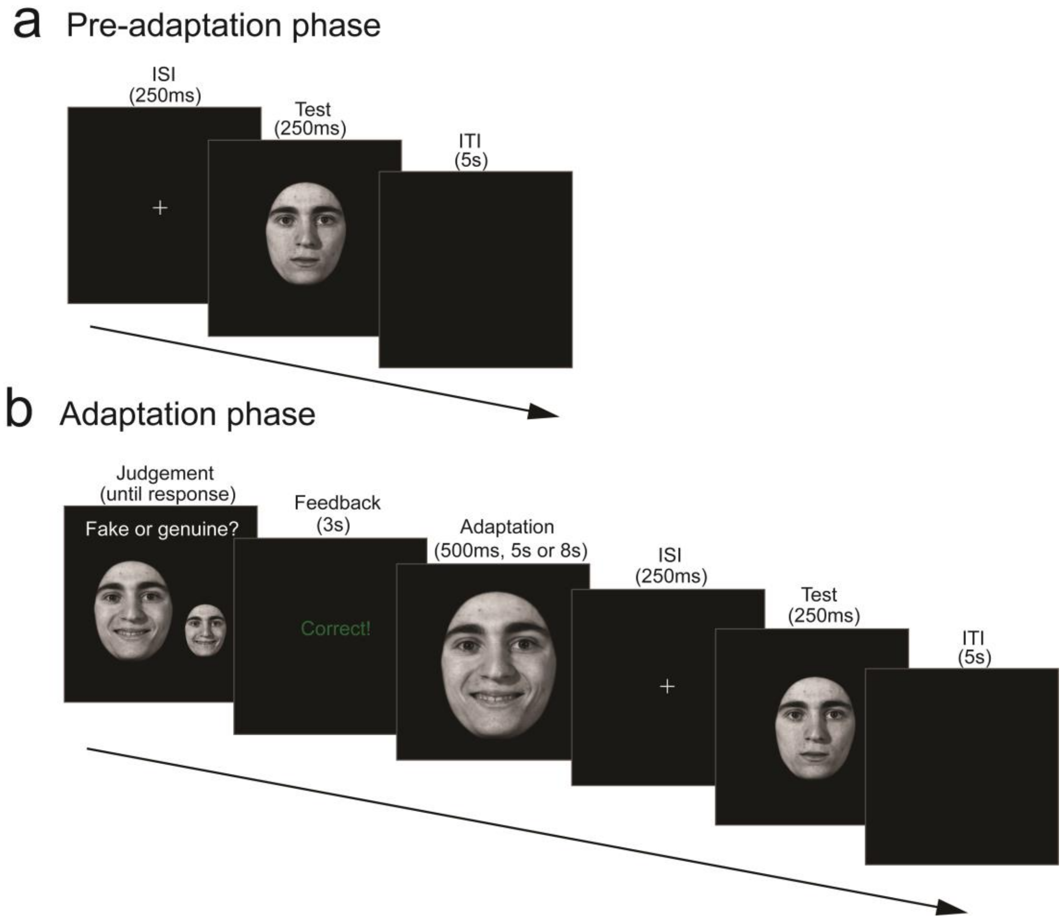


Figure 6.3 Illustration of a single trial of the pre-adaption phase (a) and a single trial of the adaptation phase (b). Similar experimental protocol was employed in experiments 1-6. Duration of the adapting stimulus differed across experiments (500 ms in Experiments 1-2, 5 sec in Experiments 3-4, 8 sec in Experiments 5-6).

6.4.4 Data reduction and analysis

Trials of which RTs exceeded 3500 ms were considered outliers and were removed from the analysis (across 6 experiments 4.3% of trials were excluded). Face expression aftereffect are well documented (c.f. Webster, 2011 for a review). However, a small number of participants in this study showed a very strong non-repulsive adaptation aftereffect (similar to object priming) suggesting that they had not judged the expression of the test stimulus, but responded to the adapting stimulus. Therefore, participants whose mean aftereffect values exceeded 2 SD of the mean aftereffect were excluded from the analysis (1 participant in Experiment 3; female, aged 21 and 1 participant in Experiment 4; female aged 21). Removal of the data of these participants did not significantly change the results.

Ratings of the test stimuli from the pre-adaptation phase were used to calculate the magnitude of the happy and angry aftereffects in the genuine and faked adaptation conditions. Aftereffects were calculated by subtracting ratings of the test stimulus following adaptation to happy and angry (genuine and faked expression), from ratings of the test stimuli in the pre-adaptation phase individually for each participant. Moreover, to illustrate the magnitude of these aftereffects, ratings following happy adaptation have been subtracted from ratings following angry adaptation in genuine and faked conditions. Positive values of these aftereffects indicate that the adaptation had a repulsive effect, where the emotion of the test stimulus was classified as opposite to the emotion of the preceding adapting stimulus.

6.5 Experiments with 5 seconds adaptation

Adaptation to expressions of happiness and anger are known to result in significant repulsive aftereffects (e.g. Fox & Barton, 2007; Webster, et al., 2004). However, the facial expressions tested so far in the literature were always genuine expressions, in which the facial expression and the emotional state of mind of the actor are congruent. Therefore, from these studies it cannot be determined whether adaptation occurred to the facial expression *per se* (such as a U-shaped mouth and lifted eyebrows in an expression of happiness, and a slightly inverted U-shaped mouth and lowered eye brows in an expression of anger), or to the emotional state of mind (happiness or anger), or to both. Further, from these studies it can also not be determined whether the explicit knowledge about the other's emotional state of mind influenced/modulated the judgement of the test stimulus.

As far as I know no adaptation studies have been performed with faked emotional expressions as adapting stimuli. However, the use of faked expressions should allow to disentangle these two aspects and determine which aspect was adapted and what the influence is of the attribution of an emotional state of mind to the actor. In all experiments reported here, the observer knew that the emotional state of mind of those actors displaying a faked expression of happiness was not happiness. Similarly, the observer knew that the emotional state of mind of the actors displaying faked expressions of anger was not anger.

Since genuine and faked expressions share similar perceptual characteristics, both types of adapting stimuli might be expected to elicit typical, repulsive aftereffects. However, if adaptation of the emotional state of mind had occurred, then the fake and genuine conditions should differ in the magnitude of their aftereffects. Thus, if the judgment of the test stimulus was influenced solely by adaptation to perceptual facial features, aftereffects in the fake and genuine conditions would be of a similar magnitude. However, if the judgment of the test stimulus was influenced by adaptation of the observer's representation of the actor's emotional state of mind then a reduced aftereffect would be found in the fake conditions. Alternatively, it could be that there was no adaptation of the observer's representation of the actor's emotional state of mind, but the explicit knowledge about the actor's state of mind did influence the judgment of the test stimuli.

Optimal, and typically employed, timescales for adaptation and test phases in face adaptation studies are approximately 5 seconds for the adapting and 200-500 ms for test stimuli (Fox & Barton, 2007; Leopold, et al., 2001; Skinner & Benton, 2010). Longer adaptation duration leads to a stronger aftereffect, whereas longer test duration abolishes the effects of adaptation (Leopold, et al., 2005). Therefore in the following experiments duration of the adapting stimuli was set to 5 seconds and duration of test stimuli was 250 ms.

6.5.1 Experiment 1: 2AFC response option

Methods

Participants

Twenty five participants (19 females, age, *M*=20.5 years, *SD*=3.6) completed Experiment 1.

Experimental procedure

The experiment followed a standard procedure described in the General Methods. Duration of the adapting stimulus was set to 5 seconds, and participants responses were measured using a 2AFC task.

Data reduction and analysis

Fifteen trials (2.5%) were removed from the analysis, as the RT exceeded 3500 ms. Ratings of test stimuli in the pre-adaptation phase were used to calculate the aftereffect magnitude (see General Methods). Average ratings of the neutral expression in the pre-adaptation phase and in the adaptation experiment portrayed by each actor are plotted in Figure 6.4.

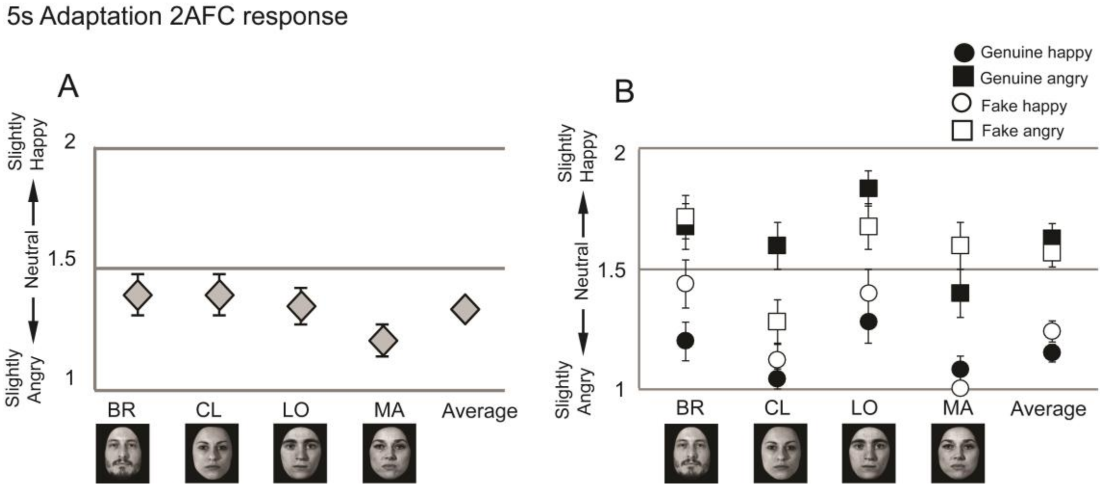


Figure 6.4 (A) Average ratings of the neutral expressions obtained in the pre-adaptation phase in Experiment 1. (B) Ratings displayed for each individual actor, and as an average across all four actors. Error bars represent 1SEM.

Results

Magnitude of the aftereffects is illustrated in Figure 6.5. A repeated measures 2x2 ANOVA with within-subject factors of intention (genuine, faked) and facial expression (happy, angry) revealed a significant effect of adapting facial expression on the judgement of the test stimuli ($F(1,23)=71.99$, $p<.001$, $\eta_p^2=.76$), where the neutral test stimuli appeared slightly angry following happy adaptation ($M=-.18$) and slightly happy following angry adaptation ($M=.27$). There was no effect of intention on the judgement of the test stimulus ($F(1,23)=.69$, $p=.413$, $\eta_p^2=.03$). The interaction between facial expression and intention was non significant ($F(1,23)=1.62$, $p=.216$, $\eta_p^2=.07$).

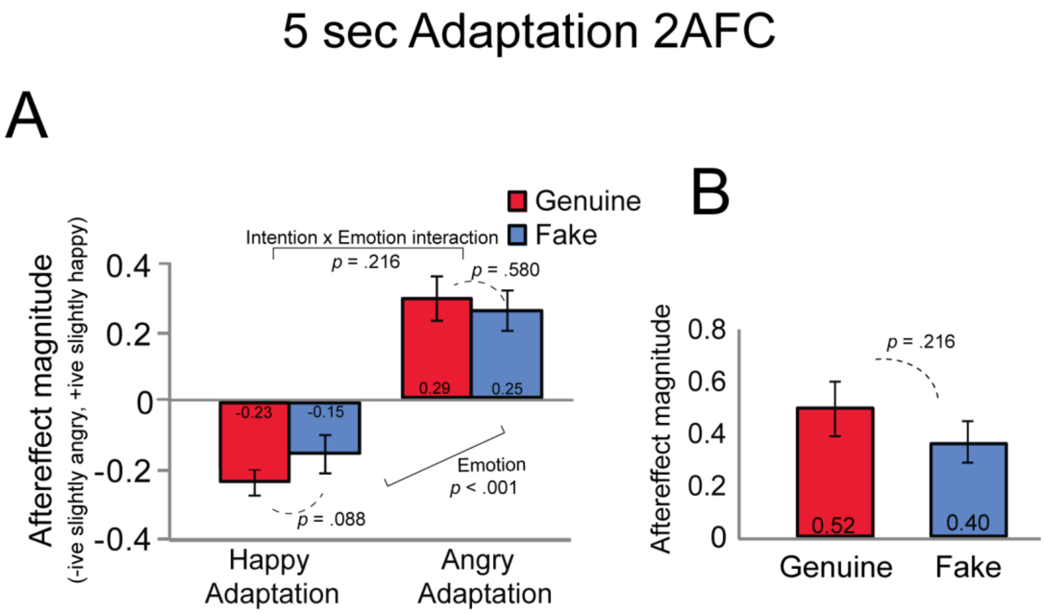


Figure 6.5 (A) Aftereffects following happy and angry adaptation after subtracting the ratings obtained in the pre-adaptation phase from those in the adaptation experiment. (B) For illustrative purposes, aftereffects are shown as a difference in ratings of the test stimuli following happy and angry adaptation. Error bars represent 1SEM.

6.5.2 Experiment 2: 5-point response option

The use of the two alternative forced-choice (2AFC) paradigm in some aspects of face perception research has recently been criticised by Scott, Clark, Boothroyd, and Penton-Voak (2013). These authors argued, that using this method in order to asses stimuli that differ along a single dimension may artificially induce effects that otherwise would not be detected, e.g. when tested with different methods such as rating scales. DeBruine (2013) has subsequently experimentally tested and disproved this claim, showing that a 2AFC paradigm produced similar effects as the rating paradigm. What is more, unlike argued by Scott, et al. (2013), DeBruine (2013) found that the 2AFC scale was also more conservative that the rating scales. This dispute in the literature regarding what is the appropriate measure for assessing perception of social stimuli highlights the need for testing alternative methodologies examining social perception. In this light I tested whether the effect of adaptation to genuine and faked expression, using identical stimuli and procedure, measured on a 5-point Likert scale would produce similar results as in a 2AFC paradigm.

Methods

Participants

Twenty participants (16 females, age, *M*=21.7 years, *SD*=6.3) completed Experiment 2.

Experimental procedure

Experiment followed a standard procedure described in the General Methods. Duration of the adapting stimulus was set to 5 seconds, and participants responses were measured on a 5-point Likert scale.

Data reduction and analysis

Twenty nine trials (6.4%) were removed from the analysis, as the RT exceeded 3500 ms. Ratings of test stimuli in the pre-adaptation phase were used to calculate the aftereffect magnitude (see General Methods). Average ratings of the neutral expression in the pre-adaptation phase and in the adaptation experiment portrayed by each actor are plotted in Figure 6.6.

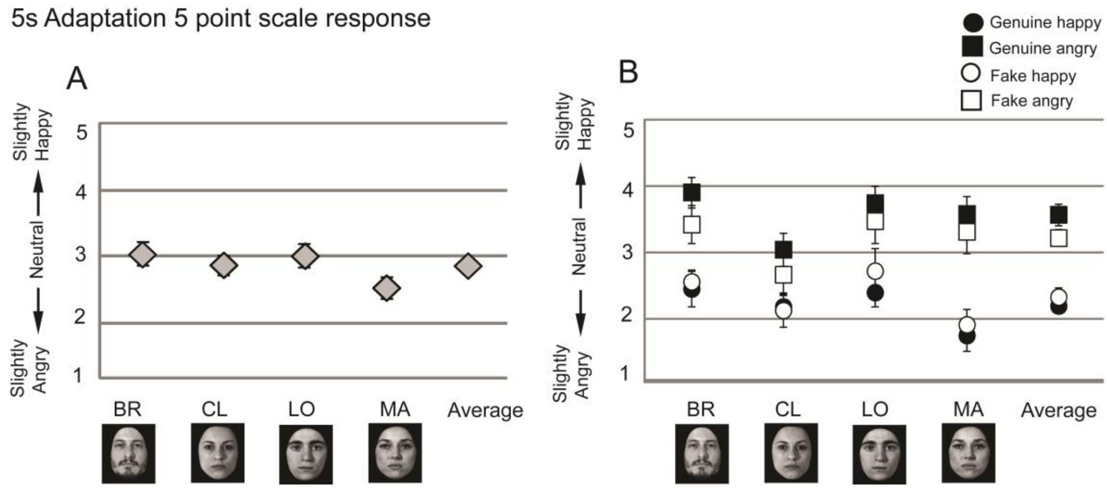


Figure 6.6 (A) Average ratings of the neutral expressions obtained in the pre-adaptation phase in Experiment 2. (B) Ratings displayed for each individual actor, and as an average across all four actors. Error bars represent 1SEM.

Results

Aftereffects are presented in Figure 6.7. A repeated measures 2x2 ANOVA with within-subject factors of intention (genuine, faked) and facial expression (happy, angry) revealed a significant effect of adapting facial expression on the judgement of the test stimuli ($F(1,18)=75.23$, $p<.001$, $\eta_p^2=.81$), where the neutral test stimuli appeared slightly angry following happy adaptation ($M=-.56$, $SD=.12$) and slightly happy following exposure to angry adaptors ($M=.43$, $SD=.15$). There was a significant interaction between the facial expression and intention ($F(1,18)=6.16$, $p=.023$, $\eta_p^{2=}.26$), indicating that the mental state attribution influenced the emotional judgement of the test stimuli. There was no main effect of the intention $F(1,18)=.27$, $p=.613$, $\eta_p^2=.01$).

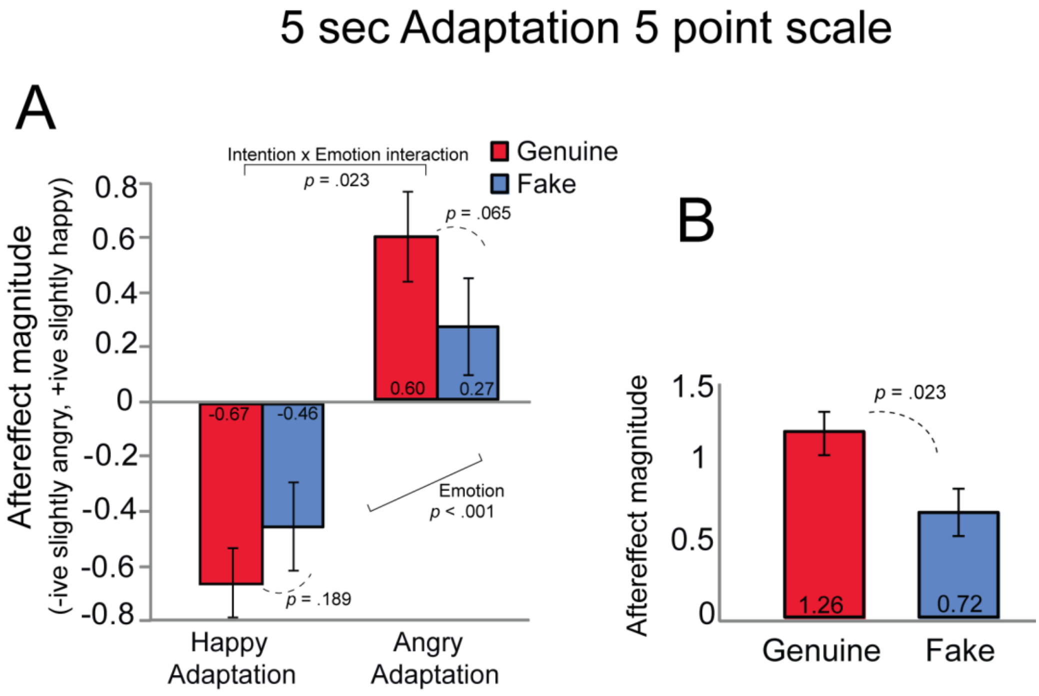


Figure 6.7 (A) Aftereffects following happy and angry adaptation after subtracting the ratings obtained in the pre-adaptation phase from those in the adaptation experiment. (B) For illustrative purposes, aftereffects are shown as a difference in ratings of the test stimulus following happy and angry adaptation. Error bars represent 1SEM.

6.5.3 Discussion

Experiments 1 and 2 investigated whether adaptation to facial expressions of emotion occur to the facial expression (perceptual level) or to the emotional state of mind of the observed actor (mentalizing level). Additionally, the study tested whether mental state attribution to the actor would modulate the effects of adaptation. Adaptation to both genuine and fake expressions resulted in significant, repulsive aftereffects suggesting that adaptation occurred for the perceptual characteristics of expressions of happiness and anger, and not for the representation of the actor's emotional state of mind.

All participants correctly identified genuine and faked expressions in the judgement task preceding the adaptation. Is it likely that this judgment was based purely on the differences in morphological and perceptual features that differentiate those two types of expressions (Ekman & Friesen, 1974; Frank, et al., 1993; Niedenthal, et al., 2010), and not on the corresponding somatosensory experience that participants could have felt when observing genuine or fake stimuli (Niedenthal, et al., 2010). Upon debriefing, the majority of participants indeed reported relying on the physical differences in the eye and mouth regions between the two images when making the decision regarding the intention depicted by the stimuli.

Aftereffects in the genuine and fake conditions measured in a 2AFC paradigm were equally sized, suggesting that knowledge regarding the emotional state of the observed actor did not modulate the perceptual processing of facial expression. In a rating scale paradigm, however, adaptation to genuine expressions resulted in significantly stronger aftereffects than adaptation to the faked expressions. It is possible that a 2AFC paradigm is more conservative than a 5-point scale in detecting subtle changes in judgments of social stimuli (see also DeBruine, 2013). Allowing participants to select a “neutral” option from the rating scale may also provide a more sensitive measure for detecting any biases in the judgment of the test stimuli following adaptation. Since the “neutral” option represented a correct response towards the test stimuli, measuring aftereffects as deviation from the correct answer may be more appropriate (see also Teufel, et al., 2009).

It is possible that the advantage of genuine adaptation observed here with the rating paradigm was facilitated by the mental state attribution task that preceded each adapting stimuli. Such modulation of mental state attribution on the effect of perceptual adaptation may be relatively small and thus undetectable by the conservative 2AFC paradigm (DeBruine, 2013). Modulatory effects of ToM processes on the perceptual processing of social stimuli have been previously reported (Teufel, Alexis, et al., 2010; Teufel, et al., 2009; Teufel, Fletcher, et al., 2010). However, it is not clear whether this modulatory effect of top-down processes on the processing of facial expressions can be enhanced or eliminated by reducing or increasing the duration of adaptation phase. Perceptual adaptation typically depends on the duration of the adapting stimuli, with stronger aftereffects occurring following longer adaptation (e.g. Leopold, et al., 2005). Therefore, to test whether the explicit knowledge about the actor’s state of mind had a bigger influence on the judgment of test stimuli when the adaptation phase was short, in the next experiment I reduced the duration of adapting stimuli.

6.6 Experiments with 500 ms adaptation

There are reports that brief, 300-500 ms long adaptation periods may be sufficient to evoke aftereffects for various facial characteristics including face view (Fang, et al., 2007) and face gender (Kovacs, Zimmer, Harza, & Vidnyanszky, 2007b). Aftereffects resulting from short adaptation may, however, exhibit different properties and may result from adaptation in different cortical regions (Fang, et al., 2007). For instance, Kovacs, et al. (2007b) have shown that in face gender adaptation viewpoint-invariant aftereffects were observed following both short-term (500 ms) and long-term (5 sec) adaptation, whereas adaptation of position-specific neural mechanisms required longer exposure to the adapted stimulus.

Ability to accurately recognise the true emotion from facial expression may also be dependent upon the duration of inspection. Calvo, Gutierrez-Garcia, et al. (2013) suggested that fake smiles are often misinterpreted as genuine, as the mouth region, which is perceptually similar in both expressions, is likely to be inspected within the first fixation. This may be because the U-shape of the mouth is readily accessible to the visual system and speeds up the process of expression classification regardless from the information conveyed by the eyes (Calvo, et al., 2012). Therefore, when the duration of the adapting facial expression is very short, the knowledge regarding the emotion behind that expression may have a greater influence on subsequent perception. To test this prediction in the next two experiments I reduced the duration of adaptation phase to 500 ms.

6.6.1 Experiment 3: 2AFC response option

Methods

Participants

Nineteen participants (15 females, age, *M*=21.4 years, *SD*=3.9) completed Experiment 3.

Experimental procedure

The experiment followed a standard procedure described in the General Methods. Duration of the adapting stimulus was set to 500 ms, and participants' responses were measured in a 2AFC response paradigm (where 1=slightly angry, 2=slightly happy).

Data reduction and analysis

Ten trials (2.1%) were removed from the analysis, as their RTs exceeded 3500 ms. Ratings of test stimuli in the pre-adaptation phase were used to calculate the aftereffect magnitude (see General Methods). Average ratings of the neutral expression portrayed by each actor are plotted in Figure 6.8.

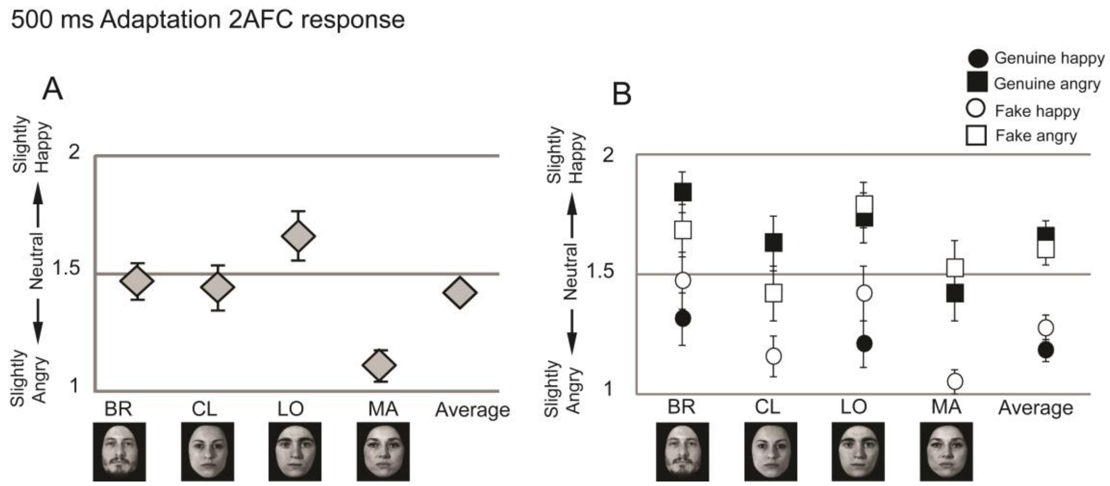


Figure 6.8 (A) Average ratings of the neutral expressions obtained in the pre-adaptation phase in Experiment 3, (B) Ratings displayed for each individual actor, and as an average across all four actors. Error bars represent SEM.

Results

Aftereffects following adaptation to happy and angry, genuine and faked expressions were calculated by subtracting average ratings of the test stimuli following adaptation from the ratings in the pre-adaptation phase (see General Methods). These values were entered into a 2x2 ANOVA with within-subject factors of intention (genuine, faked) and facial expression (happy, angry). Magnitude of these aftereffects is illustrated in Figure 6.9.

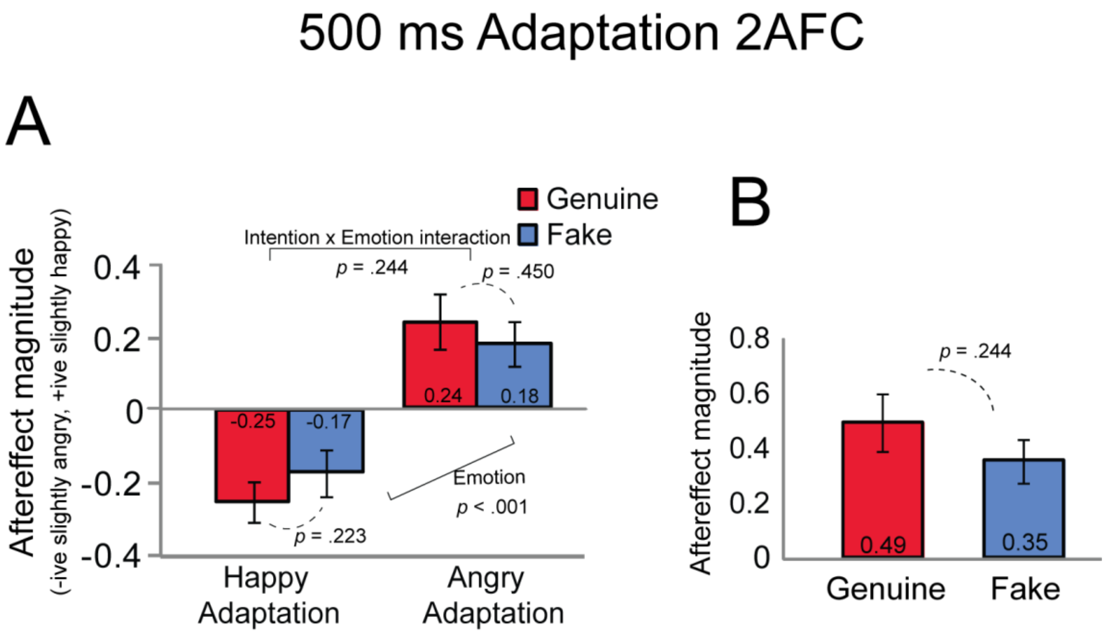


Figure 6.9 (A) Aftereffects following happy and angry adaptation after subtracting the ratings obtained in the pre-adaptation phase from those in the adaptation experiment. (B) For illustrative purposes, the aftereffects are shown as a difference in ratings of the test stimuli following happy and angry adaptation. Error bars represent 1SEM.

Analysis showed a typical adaptation effect (main effect of facial expression, $F(1,18)=33.91$, $p<.001$, $\eta_p^2=.65$), where following happy adaptation neutral test stimuli were judged as slightly angry ($M=-.21$), and following angry adaptation neutral test stimuli were judged as slightly happy ($M=.21$). There was no effect of intention on the judgement of the test stimulus ($F(1,18)=.04$, $p=.835$, $\eta_p^2=.002$). The interaction between facial expression and intention was non significant ($F(1,18)=1.45$, $p=.244$, $\eta_p^2=.08$), suggesting that the perception of the emotion displayed in the test stimuli was not influenced by the knowledge regarding the mental state of the observed actor.

6.6.2 Experiment 4: 5-point scale

Methods

Participants

Twenty one participants (16 females, age, $M=21.4$ years, $SD=3.2$) completed Experiment 4.

Experimental procedure

The experiment followed a standard procedure described in the General Methods. Duration of the adapting stimulus was set to 500 ms, and participants responses were measured on a 5-point Likert scale (where 1=slightly angry, 2 =very slightly angry, 3=neutral, 4=very slightly happy, 5=slightly happy).

Data reduction and analysis

Twenty three trials (4.5%) were removed from the analysis, as the RT exceeded 3500 ms. Ratings of test stimuli in the pre-adaptation phase were used to calculate the aftereffect magnitude (see General Methods). Average ratings of the neutral expression in the pre-adaptation phase and in the adaptation experiment portrayed by each actor are plotted in Figure 6.10.

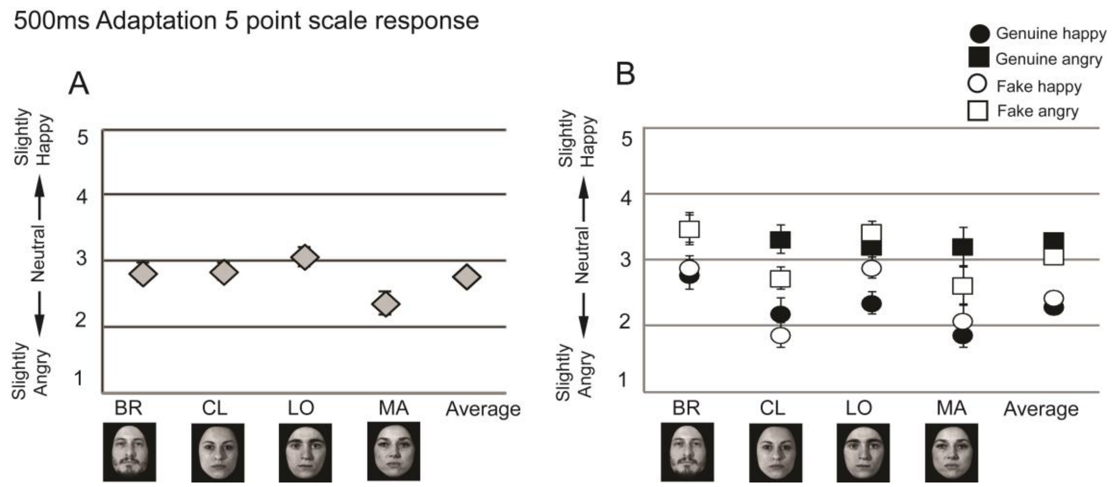


Figure 6.10 (A) Average ratings of the neutral expressions obtained in the pre-adaptation phase in Experiment 2. (B) Ratings displayed for each individual actor, and as an average across all four actors. Error bars represent 1SEM.

Results

Results illustrating the ratings of the test stimuli following adaptation and the magnitude of the observed aftereffect are shown in Figure 6.11. A repeated measures 2x2 ANOVA with within-subject factors of intention (genuine, fake) and facial expression (happy, angry) revealed a significant main effect for facial expression ($F(1,20)=59.89$, $p<.001$, $\eta_p^2=.75$), where the neutral test stimuli appeared slightly angry following happy adaptation ($M=-.33$) and slightly happy following exposure to angry adaptors ($M=.46$). The interaction between facial expression and intention was also significant ($F(1,20)=7.96$, $p=.011$, $\eta_p^2=.28$), indicating that the mental state attribution influenced the emotional judgement of the test stimuli. There was no main effect of the intention *F*(1,20)=2.74, *p*=.113, η_p^2=.12).

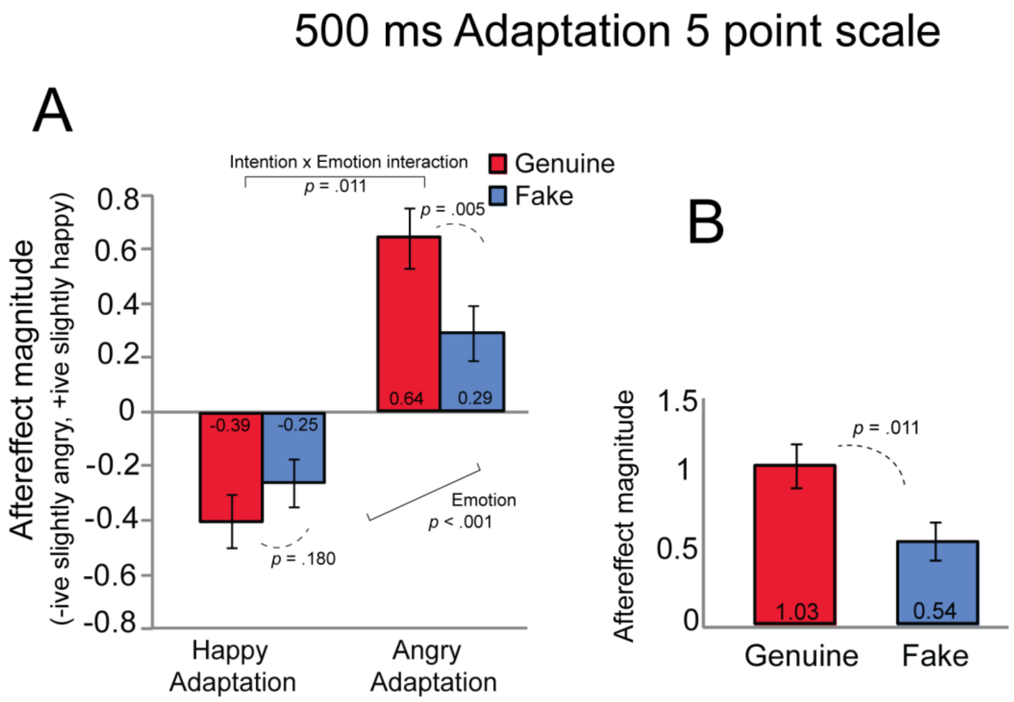


Figure 6.11 (A) Aftereffects following happy and angry adaptation after subtracting the ratings obtained in the pre-adaptation phase from those in the adaptation experiment. (B) For illustrative purposes, the aftereffects are shown as a difference in ratings of the test stimuli following happy and angry adaptation. Error bars represent 1SEM.

6.6.3 Discussion

Results indicated that the very brief adaptation to emotional expressions induced significant aftereffects resulting in a bias in the perception of the neutral test stimuli. This result is somewhat surprising, but not inconsistent with findings reported in the literature on perceptual aftereffects. Extreme short adaptation have been previously reported to produce significant aftereffects for shape perception (Suzuki, 2005) and face perception (e.g. Kovacs, et al., 2007b). Adaptation to emotional expressions can even result in expression aftereffects when the adapting stimulus is presented outside visual awareness (Adams, Gray, Garner, & Graf, 2010).

Stronger aftereffects observed in the genuine condition, measured on a rating scale, may have resulted from the modulatory effect of ToM processes on the perception of facial expression. Participants knowledge regarding the fakeness of the adapting stimulus, could have therefore reduced the strength of the adaptation to fake happiness and anger. In the 2AFC paradigm, however, both genuine and fake aftereffects were of a similar magnitude. To elucidate the results of the 500 ms adaptation study and 5 sec adaptation study, in subsequent experiments I have increased the duration of the adaptation phase. It is possible, that if the influence of ToM processes on processing of facial emotion is small, as suggested by the inconsistent results between 2AFC and rating scale paradigms, the advantage of the adaptation to genuine expression may be abolished with longer exposure to the adapting stimuli.

6.7 Experiments with 8 seconds adaptation

Increasing the duration of the genuine and fake adapting stimuli, may have two possible effects on the magnitude of facial expression aftereffects. First, it is possible that during longer inspection of the adapting stimuli, participants will be able to better recognize the emotional state behind the observed expression through embodied simulation (Gallese, 2001, 2003). The knowledge regarding the emotional state of the observed expression may therefore be combined with participant's own sensory – motor experience (Niedenthal, et al., 2010). If that is the case, increasing the adaptation duration will have a positive effect on the adaptation to genuine, but not to faked expressions.

However, it is also possible that adapting stimuli did not induce in participants the experience of genuineness or fakeness (Niedenthal, et al., 2010). As both types of stimuli share many physical and perceptual features, adaptation could have occurred only at the perceptual level in the visually responsive neural populations. The difference in the magnitude of genuine and fake aftereffects could have been due to the modulatory effect of the ToM process (i.e. attribution of the mental state) on the perceptual processing of facial expressions. This effect, may however, be transient. By increasing the duration of the adaptation phase I will be able to test how strong is the top-down modulation of conceptual knowledge on the sensory processing of faces.

6.7.1 Experiment 5: 2AFC response option

Methods

Participants

Twenty participants (17 females, age, *M*=20.5 years, *SD*=2.4) completed Experiment 5.

Experimental procedure

The experiment followed a standard procedure described in the General Methods. The duration of the adapting stimulus was set to 8 seconds, and participants' responses were measured in a 2AFC task.

Data reduction and analysis

Eleven trials (2.2%) were removed from the analysis, as the RT exceeded 3500 ms. Ratings of test stimuli in the pre-adaptation phase were used to calculate the aftereffect magnitude (see General Methods). Average ratings of the neutral expression in the pre-adaptation phase and in the adaptation experiment portrayed by each actor are plotted in Figure 6.12.

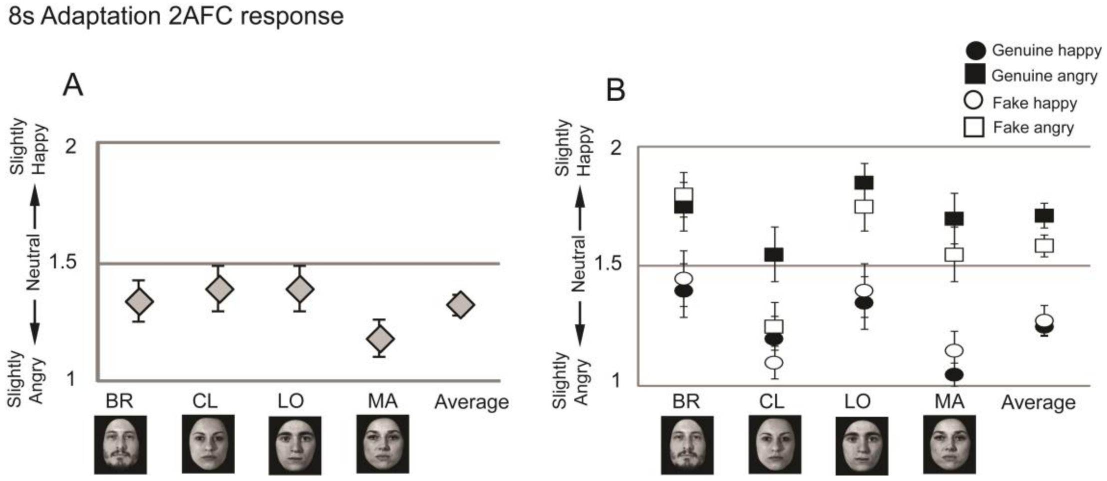


Figure 6.12 (A) Average ratings of the neutral expressions obtained in the pre-adaptation phase in Experiment 5. (B) Ratings displayed for each individual actor, and as an average across all four actors. Error bars represent 1SEM.

Results

Aftereffects are illustrated in Figure 6.13. A repeated measures 2x2 ANOVA with within-subject factors of intention (genuine, faked) and facial expression (happy, angry) revealed a significant effect of adapting facial expression on the judgement of the test stimuli ($F(1,19)=29.18$, $p<.001$, $\eta_p^2=.61$), where the neutral test stimuli appeared slightly angry following happy adaptation ($M=-.08$) and slightly happy following angry adaptation ($M=.23$). The was no effect of intention on the judgement of the test stimulus ($F(1,19)=3.73$, $p=.069$, $\eta_p^2=.16$). The interaction between facial expression and intention was non significant ($F(1,19)=.19$, $p=.667$, $\eta_p^2=.07$).

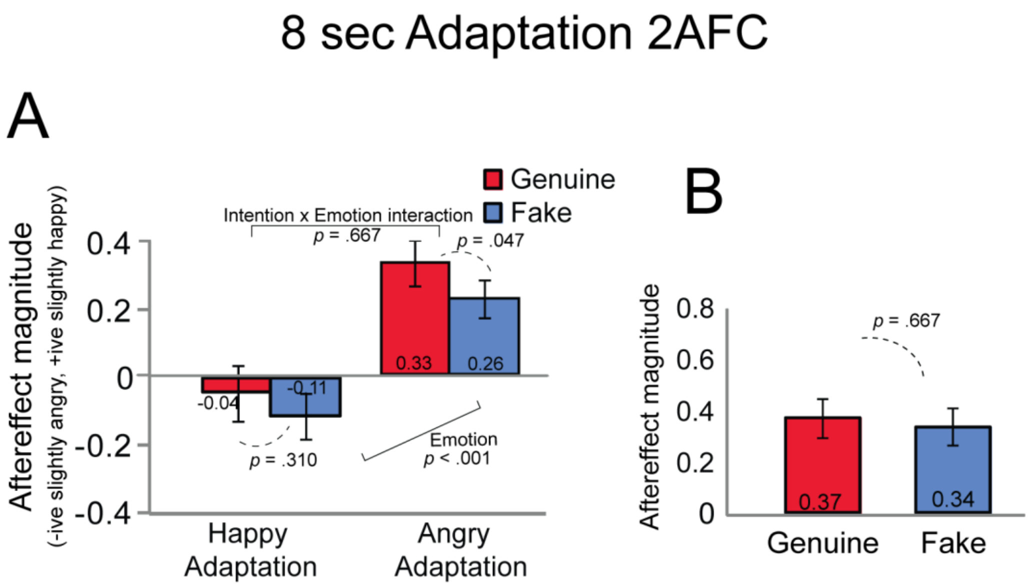


Figure 6.13 (A) Aftereffects following happy and angry adaptation after subtracting the ratings obtained in the pre-adaptation phase from those in the adaptation experiment. (B) For illustrative purposes, the aftereffects are shown as a difference in ratings of the test stimulus following happy and angry adaptation. Error bars represent 1SEM.

6.7.2 Experiment 6: 5-point response option

Methods

Participants

Twenty participants (15 females, age, *M*=19.6 years, *SD*=0.9) completed Experiment 6.

Experimental procedure

The experiment followed a standard procedure described in the General Methods. The duration of the adapting stimulus was set to 8 seconds, and participants responses were measured on a 5-point Likert scale.

Data reduction and analysis

Forty two trials (8.8%) were removed from the analysis, as the RT exceeded 3500 ms. Ratings of test stimuli in the pre-adaptation phase were used to calculate the aftereffect magnitude (see General Methods). Average ratings of the neutral expression in the pre-adaptation phase and in the adaptation experiment portrayed by each actor are plotted in Figure 6.14.

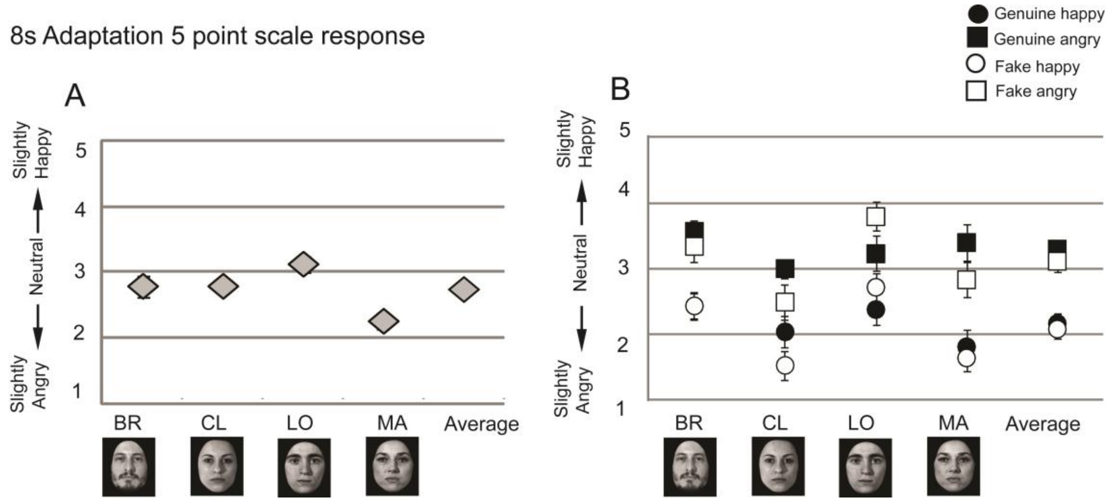


Figure 6.14 (A) Average ratings of the neutral expressions obtained in the pre-adaptation phase in Experiment 6. (B) Ratings displayed for each individual actor, and as an average across all four actors. Error bars represent 1SEM.

Results

Aftereffects are illustrated in Figure 6.15. A repeated measures 2x2 ANOVA with within-subject factors of intention (genuine, faked) and facial expression (happy, angry) revealed a significant effect of adapting facial expression on the judgement of the test stimuli ($F(1,19)=38.48$, $p<.001$, $\eta_p^2=.67$), where the neutral test stimuli appeared slightly angry following happy adaptation ($M=-.51$) and slightly happy following exposure to angry adaptors ($M=.44$). There was no effect of intention on the judgement of the test stimulus ($F(1,19)=1.35$, $p=.259$, $\eta_p^2=.07$). The interaction between facial expression and intention was non significant ($F(1,19)=.46$, $p=.505$, $\eta_p^2=.02$).

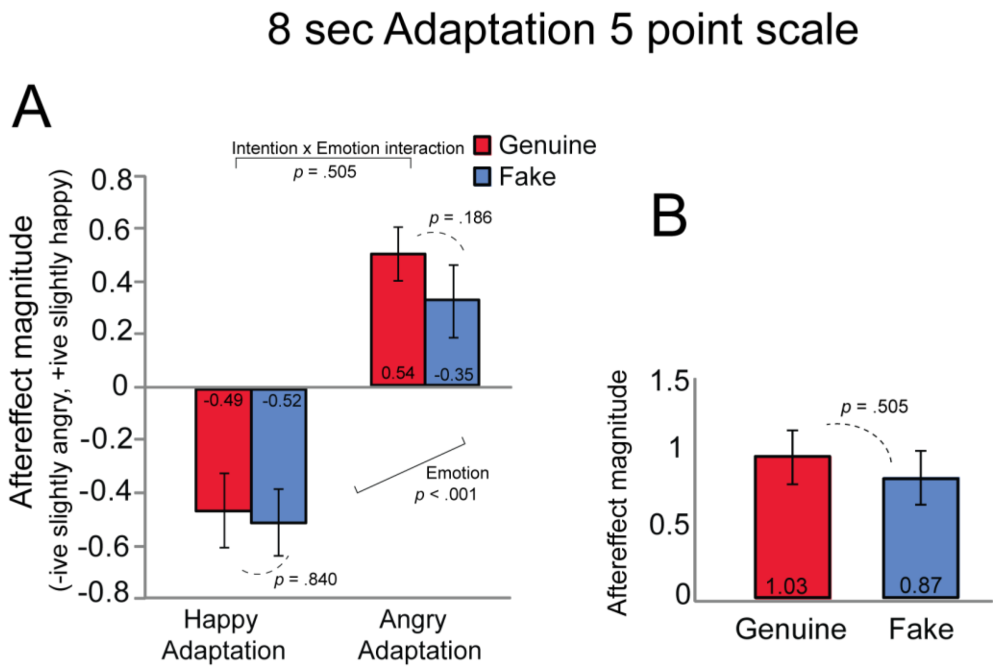


Figure 6.15 (A) Aftereffects following happy and angry adaptation after subtracting the ratings obtained in the pre-adaptation phase from those in the adaptation experiment. (B) For illustrative purposes, aftereffects are shown as a difference in ratings of the test stimulus following happy and angry adaptation. Error bars represent 1SEM.

6.7.3 Discussion

The aim of Experiments 5 and 6 was to elucidate the inconsistent results among Experiments 1-4, where the advantage of adaptation to genuine expression was only observed for measurement taken on a rating scale. This advantage could have been due to the small influence of ToM processes on the perception of facial expression. Results of two experiments were similar and showed that adaptation to genuine and faked expression resulted in equally strong aftereffects. Therefore, the advantage of the adaptation to genuine expression, observed in Experiments 2 and 4, is likely to be due to the top-down modulation of the mental state attribution (i.e. knowledge regarding actor's intention) on the processing of facial emotional expression. Such modulation may, however, be short lasting, as following longer duration (8s) adaptation to both genuine and faked expressions resulted in aftereffects of similar magnitude.

Genuine expressions used in the study were matched for intensity to the faked expressions, so the difference in the magnitude of aftereffects could not be solely due to the difference in the strength of the adaptors. Aftereffects in both conditions following long 8 seconds adaptation were equally strong, which suggests that the method of matching the intensity of those two types of expression was successful.

6.8 General Discussion of Chapter 6

In Chapter 6 I examined the influence of ToM processes, specifically emotional/mental state attribution to the observer, on the perceptual processing of facial expressions. Across 6 experiments I tested whether knowledge regarding the observed individual's emotional state affected the subsequent perception of emotion of this individual. By measuring the biases in perception on two different scales, 2AFC and rating scale, and over 3 different adaptation durations, I also tested how robust is such top-down modulation. Data collected across two scales produced a slightly different pattern of results, which prevents the drawing of a clear conclusion regarding the strength of top-down inferences on perception. The source of potential discrepancy in the results and the cognitive mechanisms that could underpin the observed results are discussed below.

First, face expression aftereffects were found with both genuine and faked adapting facial expressions and following short (500 ms) and longer (5 and 8 sec) adaptation. These aftereffects are unlikely to arise solely from adaptation to local facial features such as shape or curvature of the mouth (Xu, Dayan, Lipkin, & Qian, 2008), but are likely to involve also high-level adaptation in the cortical areas involved in face processing (Leopold, et al., 2001). In our experiments, both happy and angry adapting faces induced aftereffects of a similar magnitude. This effect was of similar magnitude for all four actors used in the experiments. On one hand, the U-shaped mouth of a happy expression is a reliable indicator of happiness. However, the shape of the mouth in an angry expression is mostly flat, just as in a neutral expression. On the other hand, the difference in the eyebrow position is more pronounced between the angry and neutral expression, than between happy and neutral expressions. In this study, aftereffects following adaptation to anger were equally pronounced as aftereffects resulting from adaptation to happiness. This suggests that the aftereffects most probably did not depend solely on adaptation to one, most salient physical facial characteristic. The test stimuli were also smaller than the adapting stimuli and participants were allowed, and indeed advised, to freely observe and move their eyes across the adapting and test faces to ensure that the adaptation did not occur at the retinal level (Webster, 2011). This was done to limit adaptation in the low-level processing areas. Together it suggests that adaptation was likely to occur in the high-level cortical regions for face processing (fusiform cortex, STS; Winston, et al., 2004).

Second, the 2AFC scale, due to its dichotomous nature, may not be able to pick up on subtle differences in the perception of stimuli in way the 5-point scale does. An overall adaptation aftereffect can very well be detected by the 2AFC scale, but modulations of these aftereffects may be overridden by the dichotomy. The 5-point scale is in that respect more 'senstitive'. Although some evidence from face perception studies suggest that ratings of faces collected using 2AFC and rating scales are highly correlated (DeBruine, 2013; Quinn, Lazare, Hancock, & Watt, 2013), it has also been suggested that 2AFC paradigm may result in a more conservative measure of some facial attributes (DeBruine, 2013).

I will now discuss possible explanations for the reduced aftereffects obtained when adapting to faked facial expressions.

(i) Different sensory-motor experiences: embodied cognition.

Relying on theories of embodied cognition (Gallese, 2001; Goldman, 2006; Goldman & de Vignemont, 2009), an important component of emotion recognition is the sensory-motor experience associated with the observed expression within the observer. Visual representation of the expression triggers a congruent emotional response in the participant via mechanisms of facial motor mimicry (Niedenthal, et al., 2010). Automatic mimicry is indeed triggered by the observation of both positive and negative facial expressions (Dimberg, 1982; Dimberg, Thunberg, & Elmehed, 2000) and can elicit changes in emotional state in the observer (Schneider, Gur, Gur, & Muenz, 1994). Such sensory-motor experience may be able to facilitate the discrimination between genuine and faked expressions (Niedenthal, et al., 2010).

If emotion recognition involves simulating the viewed expression or executing similar motor program by the observer, then mirror neuron systems are likely to be involved (Atkinson & Adolphs, 2005). Supporting evidence for this proposal came from fMRI studies where largely similar neural networks, predominantly involving premotor areas, superior temporal cortex, insula and amygdala, were active when participants observed and imitated static (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003) and dynamic facial expressions (Leslie, Johnson-Frey, & Grafton, 2004). Perception of genuine expressions is also likely evoke stronger experience in the observer than perception of faked expressions, as the meaning behind these expressions is matching the perceptual cues (Niedenthal, et al., 2010). Therefore it is possible that the stronger sensory-motor experience in the observer could have facilitated adaptation to genuine expression of happiness and anger.

(ii) Interaction between perceptual and mentalizing systems.

An interaction between perceptual and metalizing systems may provide another possible explanation for the difference in the magnitude between genuine and fake aftereffects. According to Teufel, Fletcher, et al. (2010)'s perceptual metalizing model of social perception, basic sensory processing of social stimuli is influenced by ToM processes. Here, person knowledge or explicit attribution of mental states (processed in ToM system; mPCF, TPJ; (Saxe, 2006; Saxe & Baron-Cohen, 2006) determines the STS activity and consequently influences perceptual processing of socially relevant information (Teufel, Fletcher, et al., 2010). The STS in turn provides visual input to the mirror neuron system (inferior parietal lobule, IPL; Allison, et al., 2000; Iacoboni & Dapretto, 2006) and thus influences the perception-action coupling and the implicit ToM (Teufel, Fletcher, et al., 2010).

Support for an integration of bottom-up, stimulus driven information, and top-down, context information provided by ToM comes from studies investigating perception of gaze direction. Teufel and colleagues used the gaze-adaptation paradigm to demonstrate that mental state attribution (belief that the actor was or was not able to see) influenced gaze processing. Specifically the “seeing” condition resulted in significantly stronger gaze direction aftereffects than the “non-seeing” condition (Teufel, et al., 2009). Using a representational momentum paradigm Hudson, Liu, and Jellema (2009) also found that perception of social cues (such as gaze direction) signalling an actor’s intentions (i.e. agentive motion) influenced judgments made about the actor’s movements, presumably due to intentional attributions to the actor. Similarly, a perceptual history during which participants automatically attribute emotional/mental states to the actor may bias subsequent emotion perception of that individual (Jellema, Pecchinenda, Palumbo, & Tan, 2011; Palumbo & Jellema, 2013).

Results of the current study fit within this framework providing additional support for the bi-directional relationship between metalizing and perceptual systems in the analysis of social stimuli (facial expressions). However, increasing the duration of adapting stimuli in experiments 5 and 6 removed the disadvantage of adaptation to faked expressions. This may suggest that the modulation by ToM processes of sensory processing of facial expressions may be short lasting. Alternatively, it is possible that during the extended adaptation, participants could have updated their belief regarding the authenticity of the observed expression, or the memory of the actor faking his/her expression may have faded away. Feedback from the implicit ToM system (e.g. reduction in the sensory-motor experience of the genuine expression) to the explicit ToM system (Teufel, Fletcher, et al., 2010) could have resulted in both expressions being perceived as genuine, and thus removed the reduction in aftereffects in the fake condition.

(iii) Perceptual differences between genuine and fake expressions.

Genuine and fake adapting stimuli were matched for the perceived intensity, so the difference in the magnitude of aftereffects in these two conditions should not be due to the difference in the strength of the adaptors. Overall, perceptual feature characteristics for the expressions of joy and anger were also very similar between genuine and faked expressions. In case of joy, for instance, both types of expressions displayed characteristic U-shapes of the mouth, and this region is particularly informative for the recognition of happiness (Smith, Cottrell, Gosselin, & Schyns, 2005). The difference between genuine and faked expressions lay predominantly within the eye region. The integration of facial information necessary for correct recognition of facial expression also tends to proceed from the eyes downwards (Schyns, Petro, & Smith, 2007). Although, the duration of our adapting stimuli (500 ms - 8 sec) allowed for a full integration of all diagnostic features, the perceptual decision regarding the expressed emotion could have could have been influenced by the eye region.

In addition, it is possible that the stimuli did not evoke in participants the experience of genuineness or fakeness. According to the SIMS model proposed by Niedenthal, et al. (2010) such experience is necessary for the observer to classify the observed expression as fake. Duchenne smiles (i.e. genuine signals of happiness) when expressed deliberately, as opposed to being spontaneous reactions, can be misinterpreted as fake. In a recent study participants' facial mimicry measured by electromyography (EMG) was greater for spontaneous than deliberate smiles, regardless of whether these smiles were Duchenne or non-Duchenne (Krumhuber, Likowski, & Weyers, 2014). If facial mimicry and sensory-motor experience associated with the observed expressions are necessary for the accurate interpretation of the authenticity of the smile, it is possible that participants in this study did not feel the emotion behind the observed expression.

Participants in this study were able to correctly identify which expressions were genuine and which were faked. In principle, they could have learned this skill in a short practice session and made their judgements based on the presence or absence of the wrinkles around the eye region, and not based on their subjective experience. The stimuli used in this study were also not created using the FACS systems (Ekman & Friesen, 1976) and morphing of the genuine expressions could have contributed to these expressions appearing less genuine. In addition, on each trial participants received feedback regarding their judgement of the genuineness or fakeness of the adapting stimulus; if they responded incorrectly they were shown the same faces and prompted to respond again.

Results of this study also raised an interesting question as to whether the scale on which the effects of perceptual adaptation are measured can influence the strength of perceptual bias resulting from adaptation. Similar concerns have recently emerged in research on social perception and decision making (DeBruine, 2013; Frederick & Mochon, 2012; Quinn, et al., 2013; Scott, et al., 2013) highlighting the importance of addressing potential distortions in judgement introduced by different scoring methods.

CHAPTER 7

Adaptation to facial trustworthiness

This chapter is largely based on work that has been published:

Wincenciak, J., Dzhelyova, M., Perrett, D.I. & Barraclough, N.E. (2013). Adaptation to facial trustworthiness is different in female and male observers. *Vision Research*, 87: 30-34.

And presented at the following conference:

Wincenciak, J., Dzhelyova, M., Perrett, D.I. & Barraclough, N.E. (2014). Adaptation to facial trustworthiness is different in female and male observers. Human Behavior and Evolution Society in Natal, Brazil. July 2014.

7.1 Abstract

Face adaptation paradigms have been used to investigate the mechanisms underlying the processing of various facial characteristics including identity, sex and emotion. Judgements of facial trustworthiness have also been influenced by visual adaptation, however, these (un)trustworthy face aftereffects have only been shown following adaptation to emotional expression and facial masculinity or femininity. In this study I investigated how exposure to trustworthy and untrustworthy faces influenced the perception of the trustworthiness of subsequent test faces. In a mixed factorial design experiment, I tested the influence of adaptation to female and male faces on the perception of subsequent female and male faces in both female and male observers. Female observers showed typically repulsive aftereffects, where novel faces were more likely to be judged as untrustworthy after viewing trustworthy faces and were more likely to be judged as trustworthy after viewing untrustworthy faces. These aftereffects were unaffected by manipulating the sex of the adapting or test stimuli. In contrast, recent visual experience did not influence male observers' perceptions of the trustworthiness of new faces. This sex difference suggests that different mechanisms may underpin male and female observers' perception of facial trustworthiness and suggest that, in assessing trustworthiness of other individuals, male observes may be less influenced by prior visual context.

7.2 Introduction

In previous chapters I presented results showing how prior visual context can influence our judgement of other individuals' behaviour and emotional state. In our everyday life we also derive complex social traits such as competence (e.g. Ballew & Todorov, 2007) and trustworthiness (Winston, Strange, O'Doherty, & Dolan, 2002) merely from observing other individuals' faces. These judgements guide decision making during social interactions and influence our pro-social behaviour. Inaccurate assessment of other peoples' trustworthiness can therefore significantly impact social and economic exchange. Trustworthiness conveyed by a person's face, for example, is used by observers when making trust decisions and whether to invest money with that person (e.g. van't Wout & Sanfey, 2008). Although people are remarkably consistent at judging trustworthiness of other individuals even after a very brief exposure (Todorov, Pakrashi, & Oosterhof, 2009; Willis & Todorov, 2006), it is not yet clear how assessments of this useful social information are affected by prior visual experience. Therefore in this chapter I investigated how adaptation to faces conveying different degrees of trustworthiness dimensions influences our judgement of trustworthiness of other individuals.

7.2.1 Perception of facial trustworthiness

Social cognition models (Fiske, Cuddy, & Glick, 2007; Oosterhof & Todorov, 2008) suggest that people evaluate social traits of other individuals on two universal dimensions: warmth and competence. While warmth dimension captures traits related to a person's intentions such as sincerity or friendliness, the competence dimension reflects traits related to their abilities (Fiske, et al., 2007). More recently Oosterhof and Todorov (2008) proposed that the best approximation for the warmth dimension is perceived trustworthiness. Trustworthiness judgements rely on detection of subtle facial features resembling expressions that signal approach or avoidance behaviour (Todorov, Baron, & Oosterhof, 2008) and on facial structure (Stirrat & Perrett, 2010; Todorov, Said, Engell, & Oosterhof, 2008). For instance, neutral faces that have been exaggerated along the untrustworthiness dimensions resemble faces with angry expressions, while exaggerating faces along the trustworthiness dimension produces faces with happy expressions (Oosterhof & Todorov, 2008). Therefore judgement of facial trustworthiness is often proposed to be an overgeneralization of perception of emotional expression (Montepare & Dobish, 2003). Nonetheless, trustworthiness can also be conveyed by facial structure and variations in the size or shape of individual facial features (Todorov, Baron, et al., 2008) or facial width (Stirrat & Perrett, 2010). Wider faces, with shallow cheeks, wider chins or lower eyebrows are for instance perceived as less trustworthy. Manipulating faces of sexually dimorphic features can also alter their perceived trustworthiness, where more masculine faces are usually judged as less trustworthy (Buckingham, DeBruine, Little, Welling, Conway, Tiddeman, et al., 2006; Oosterhof & Todorov, 2008).

Although judgements of facial trustworthiness appears to rely on complex structural and expressive cues, people's rapid assessments of facial trustworthiness are highly consistent and correlated with judgements made with longer exposures (Todorov, et al., 2009; Willis & Todorov, 2006). Findings from behavioural (e.g. Willis & Todorov, 2006) and neuroimaging data (e.g. Adolphs, 2002b; Winston, et al., 2002) also suggest that evaluating faces on trustworthiness happens spontaneously and automatically. To date, only a small number of studies have tested whether trustworthiness judgements can be influenced by the temporal context. Todorov, et al. (2009) for instance, primed participants with subliminally presented trustworthy or untrustworthy faces and measured their judgement of subsequently presented neutral faces. Although participants were not aware of the presence of the prime, their evaluation of test faces was biased towards the trustworthiness level of the prime.

Perception of facial trustworthiness is also susceptible to visual adaptation, but so far this has only been demonstrated following adaptation to other facial characteristics. For example, adaptation to angry or happy faces biases evaluation of subsequent neutral faces so that they appear more or less trustworthy respectively; in contrast, adaptation to fearful faces has no effect on perceived facial trustworthiness (Engell, Todorov, & Haxby, 2010). This research supports proposals that evaluations of facial trustworthiness and judgements of specific emotional expressions derived from faces rely on some common facial features and thus may in part be processed by overlapping neural mechanisms (Oosterhof & Todorov, 2009; Todorov, Baron, et al., 2008; Todorov & Engell, 2008; Todorov, Said, et al., 2008). Furthermore, perception of facial trustworthiness has also been shown to be biased following adaptation to masculine and feminine faces (Buckingham, DeBruine, Little, Welling, Conway, Tiddleman, et al., 2006). In this study participants adapted to both masculinised and feminised versions of male faces, and were required to rate the attractiveness or trustworthiness of subsequent test male faces. Adaptation to both masculinised and feminised faces appeared to affect the perceived trustworthiness of subsequent faces. Buckingham et al. argued that this adaptation mechanism may contribute to the development of longer term face preference judgements.

It is not yet clear, however, if adaptation occurs following exposure to faces that differ in perceived levels of trustworthiness. If facial trustworthiness adaptation follows the typical pattern as seen for previously tested face aftereffects where subsequent stimuli appear less like the adapting stimulus, then we would expect to find that adaptation to untrustworthy faces causes subsequent faces to appear more trustworthy, and adaptation to trustworthy faces causes subsequent faces to appear more untrustworthy. Aftereffects resulting from trustworthiness adaptation might have implications for the development of longer term judgments of the trustworthiness of other individuals from daily experiences of faces (e.g. see Carbon & Ditye, 2011a).

7.3 The current study

To investigate whether we adapt to facial trustworthiness, here I compared the effect of adaptation to untrustworthy and trustworthy faces in order to assess whether facial trustworthiness adaptation biased subsequent perception of facial trustworthiness. Previous research has indicated that the perception of facial trustworthiness is contingent on the sex of the face (e.g. Dzhelyova, Perrett, & Jentzsch, 2012). I therefore measured the effect of adaptation to both trustworthy and untrustworthy female and male faces and its effect upon the perception of female and male test faces in both female and male observers, all within one factorial design experiment.

7.4 Methods

Participants

Participants were University of Hull students and staff (24 females, mean age=22.5 years, *SD*=4.71; 24 males, mean age=23.9, *SD*=6.01), all received course credit or payment for participating. All participants had normal or corrected to normal vision and were naive to the purpose of the study. Experiments were approved by the ethics committee of the Department of Psychology, University of Hull, and performed in accordance with the ethical standards laid down in the 1990 Declaration of Helsinki.

Stimuli

Face stimuli were obtained from The Perception Lab, University of St Andrews. The original set of stimuli included ninety-nine faces (49 male) of Caucasian students, age range 17 to 25, displayed on a white background with a neutral expression, minimal makeup and no jewellery, and were horizontally aligned and scaled to the same interpupillary distance. Each face was rated for trustworthiness using a 7-point Likert scale by independent observers. Adapting faces (illustrated in Figure 7.1) were prototypes generated by averaging (Rowland & Perrett, 1995) separately the 8 most untrustworthy and the 8 most trustworthy faces of each sex from the bank of 99 images. Control adapting faces (both male and female) were also generated by averaging the untrustworthy and trustworthy prototypes. Test faces were a subset of 50 images (25 females, 25 males, age range: 18-24) from the original set of 99. The images were selected to cover the whole range of trustworthiness ratings. In order to ensure that adaptation to low-level visual properties did not contribute to any measure of trustworthy aftereffects, all adapting stimuli (subtended 356x455 pixels) were presented twice the size of the test stimuli (subtended 178x240 pixels).

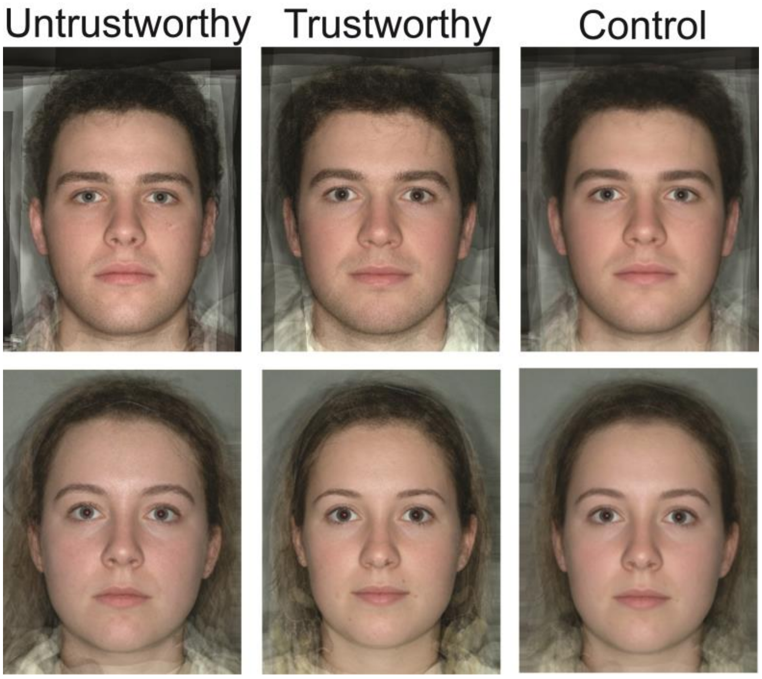


Figure 7.1 Male (top) and female (bottom) untrustworthy (left), trustworthy (middle) and control (right) adapting stimuli.

Design and experimental procedure

In this experiment six adapting conditions (i.e. male and female untrustworthy, trustworthy and control face) were presented in separate, counterbalanced blocks. Because of this blocked design I was able to employ the adaption top-up design. Participants first adapted for 30 seconds to one of the adapting stimuli. Following this phase, a classic event-related adaptation took place, where a short presentation of an adapting stimulus was interleaved with the presentation of each of the test stimuli. The adaptation was therefore ‘topped-up’ on every trial and maintained throughout the testing block.

The experiment was controlled by a PC running MATLAB 2006a with the Cogent toolbox. Stimuli were displayed in the centre of a 22” screen CRT monitor (Philips 202P40, 1600x1200 pixels, 100Hz refresh rate). Participant responses were recorded on the number pad of the keyboard.

The experiment consisted of six blocks of 50 trials. Each block began with a single 30 second long adaptation, followed by a testing phase consisting of alternating presentation of ‘top-up’ adaptation and test stimuli (Figure 7.2). Between the adaptation and testing phase instructions were briefly (1000ms) displayed indicating that the testing phase was about to begin. All stimuli were presented on a mid-grey screen throughout.

In each block one of the six prototype faces (male or female x trustworthy, untrustworthy or control, see Figure 7.1) was used as the adapting stimulus for both the adaptation and the adaptation top-up. All 50 test stimuli (25 female, 25 male) were seen once in each of the 6 blocks. Each of the 50 trials during the testing phase consisted of first a 5 sec presentation of the adapting stimulus, a brief inter-stimulus interval (ISI, duration 500ms) then the presentation of one of the smaller test stimuli (duration 250ms). Following the presentation of the test stimulus participants indicated their judgement of the untrustworthiness of the test face using an 8 point Likert scale where 1=very trustworthy and 8=very untrustworthy. Once a response was registered the screen remained grey for a further 1 sec before the beginning of the next trial. Test stimuli were presented in a random order within each block. After completing each block of 50 trials, participants were offered a short break before proceeding to a subsequent block. Order of testing blocks was counterbalanced using a Latin square method in order to eliminate position effects for the different adapting stimuli.

In order to ensure that the faces used as test stimuli lay on the continuum of (un)trustworthiness between the trustworthy prototypes and the untrustworthy prototypes I performed an additional rating experiment. A second set of independent observers (14 females, mean age=20.5 years, SD=3.40; 14 males, mean age=23.9, SD=5.46) rated both the female and male untrustworthy, trustworthy and control prototypes together with the 50 individual test faces on a 1-8 Likert scale (1=very trustworthy, 8=very untrustworthy). Each original face was shown once and prototype faces were shown 5 times; faces were shown in a random order.

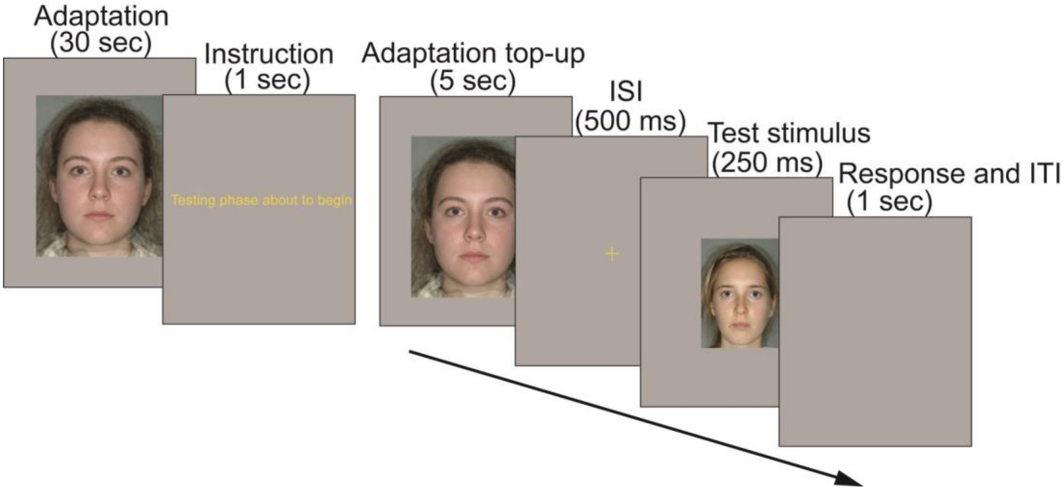


Figure 7.2 A schematic of the experimental procedure. Each testing block began with a 30 sec adaptation followed by the instructions. Next, the testing phase consisted of a 5 sec top-up adaptation, followed by a short inter-stimulus interval (ISI; 500ms) and a presentation of a test face (250ms). Participants rated the trustworthiness of the test stimuli on a 8-point Likert scale. Following their response, the screen remained mid-grey for another 1 sec during the inter-trial interval (ITI).

7.5 Results

Mean trustworthiness ratings for the 6 prototype faces and the 50 test faces were calculated for each participant and then averaged across participants (see table 7.1). Surprisingly many of the original test faces were seen as more untrustworthy than the untrustworthy prototypes, this may have resulted from the averaging process used in the generation of our untrustworthy prototypes. Average faces, for example, can appear more attractive than the originals from which they are made (DeBruine, Jones, Unger, Little, & Feinberg, 2007), and perception of trustworthiness is highly correlated with attractiveness (Oosterhof & Todorov, 2008). Similarly, the male control prototype was rated as almost equally trustworthy as the trustworthy prototype by both male and female raters. Including this prototype in the analysis of the effects of trustworthy and untrustworthy adaptation relative to the control condition would lead to difficulty in the interpretation of the data. Therefore, I decided to drop the use the control stimulus and calculate the effects of adaptation as the difference in the perception of the test stimuli following adaptation to trustworthy and untrustworthy prototypes.

I also wanted to analyse the ratings of those test faces where adaptation to the trustworthy and untrustworthy prototypes would generate opposite aftereffects.

To do this, I assessed the effect of adaptation on those test faces whose rating of trustworthiness was between the values for the trustworthy and untrustworthy prototypes, when rated by both female and male raters. In total there were 14 (7 male and 7 female) test faces that matched this criterion, their mean ratings are also described in table 7.1. Additional 36 faces (18 male and 18 female) that lie outside the continuum between the two types of adapting prototype stimuli were excluded from the main analyses. As these faces were rated as more untrustworthy than the untrustworthy prototype an appropriate assessment of the effect of adaptation in these stimuli was unfeasible. Analysis on these 36 faces, as well as on a complete set of test stimuli (50 faces) revealed a very similar pattern of results as the analysis on the 14 faces that lie between trustworthiness-untrustworthiness continuum. Interpretation of the effect of adaptation on test faces that lie outside this continuum would, however, be very problematic, as the relationship between these faces and the adapting faces is not obvious. In order to provide a clear measurement of the effect of adaptation to trustworthy and untrustworthy faces on the perception of trustworthiness of natural faces, I report the analyses conducted only on the 14 test faces. Face aftereffects have previously been assessed with even smaller number of test stimuli (e.g. Buckingham, DeBruine, Little, Welling, Conway, Tiddleman, et al., 2006; DeBruine, et al., 2007) and this reduction in the number of test faces did not affect my findings.

Ratings of the 14 test stimuli were entered into a 4-way mixed ANOVA with 3 within group factors [adaptation trustworthiness (trustworthy, untrustworthy) x adaptation stimulus sex (female, male) x test stimulus sex (female, male)] and 1 between group factor [participant gender (female, male)]. ANOVA showed that there was a significant effect of adaptation trustworthiness (main effect of adaptation trustworthiness: $F(1,46)=6.87$, $p<.05$, $\eta_p^2=.13$), and importantly a significant interaction between adaptation trustworthiness and participant gender ($F(1,46)=8.88$, $p<.005$, $\eta_p^2=.16$). I also found a significant main effect of test stimulus sex ($F(1,46)=31.45$, $p<.001$, $\eta_p^2=.41$) indicating that male faces were on average judged as more untrustworthy that female faces. No other main effects or interactions were significant (all $F_s<2.19$, all $p_s>.145$, all $\eta_p^2<.05$). As the results of the ANOVA indicated that aftereffects were significantly different in female and male observers, I analysed aftereffects from these 2 groups of participants separately using two 3-way ANOVAs in order to better interpret and understand the effect of adaptation

Table 7.1 Mean ratings (M) and standard deviations (SD) of adapting (untrustworthy, trustworthy and control prototypes) and test faces on a 8-point Likert scale, where 1=very trustworthy, 8=very untrustworthy. * 7 female and 7 male faces that have been used in the main analysis.

		Untrustworthy prototype		**Trustworthy prototype**		**Control prototype**		**Average of 50 test faces**		**Average of 14 test faces***	
		Female faces	Males faces	Female faces	Males faces	Female faces	Males faces	Female faces	Males faces	Female faces	Males faces
Female raters	M	4.62	5.15	2.31	3.46	3.77	3.54	4.57	5.20	3.87	4.27
	SD	1.71	1.57	1.18	1.61	1.59	1.61	1.38	1.01	0.56	0.64
Male raters	M	4.69	5.15	2.38	3.92	2.69	3.92	4.52	5.12	3.68	4.47
	SD	1.25	1.46	1.39	1.85	1.32	1.85	1.32	0.92	0.75	0.31

7.5.1 Female participants

Ratings of test stimuli for female observers were analysed using a 3-way ANOVA [adaptation trustworthiness (trustworthy, untrustworthy) x adaptation stimulus sex (female, male) x test stimulus sex (female, male)]. This analysis showed a significant main effect of adaptation trustworthiness ($F(1,23)=14.75$, $p<.001$, $\eta_p^2=0.39$), and a main effect of test stimulus sex ($F(1,23)=13.33$, $p<.001$, $\eta_p^2=.37$) indicating that female test faces ($M=3.86$) were on average rated as more trustworthy than male test faces ($M=4.74$). No other main effects or interactions were found (all $F_s<1.11$, all $p_s>.30$, all $\eta_p^2<.05$).

In order to illustrate the effect of adaptation I calculated aftereffects (ratings following trustworthy adaptation minus ratings following untrustworthy adaptation) for each condition (see Figure 7.3). All aftereffects were positive on this scale indicating that following adaptation, test faces looked less like the preceding adapting stimuli; this is characteristic of other face aftereffects (see Webster & MacLeod, 2011a for a review).

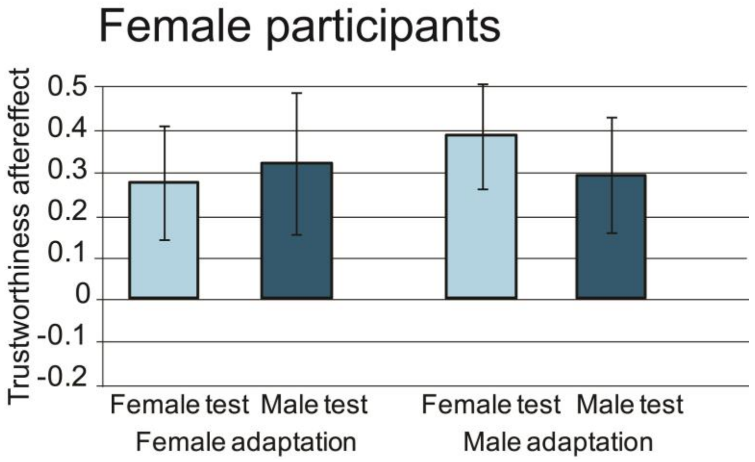


Figure 7.3 The effect of adaptation to (un)trustworthiness on faces in female observers. Positive values indicate 'repulsive' aftereffects where test stimuli are judged as less like the adapting stimuli, negative values indicate priming like effects where stimuli are judged as more like the adapting stimuli. Error bars indicate SEM.

7.5.2 Male participants

I analysed ratings of test stimuli measured in male participants in the same way as for female observers by using a separate 3-way ANOVA [adaptation trustworthiness (trustworthy, untrustworthy) x adaptation stimulus sex (female, male) x test stimulus sex (female, male)]. For male participants adaptation trustworthiness had no effect on the rating of test stimuli (main effect of adaptation trustworthiness: $F(1,23)=.07$, $p=.79$, $\eta_p^2=.003$). There was, however, a main effect of test stimulus sex ($F(1,23)=18.39$, $p<.0001$, $\eta_p^2=.44$) where female test faces ($M=3.82$) were on average rates as more trustworthy than male test faces ($M=4.82$) across all experimental conditions. No other main effects or interactions were found (all $F_s<.78$, all $p_s>.38$, all $\eta_p^2<0.03$). As for female observers I calculated aftereffects (ratings following trustworthy adaptation – ratings following untrustworthy adaptation) for each condition, and these are illustrated in Figure 7.4.

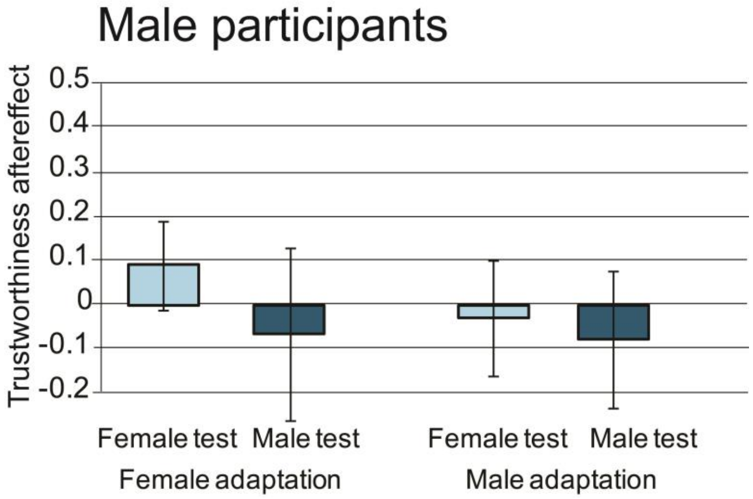


Figure 7.4 The effect of adaptation to (un)trustworthiness on faces in male observers. Positive values indicate 'repulsive' aftereffects where test stimuli are judged as less like the adapting stimuli, negative values indicate priming like effects where stimuli are judged as more like the adapting stimuli. Error bars indicate SEM.

7.6 Discussion of Chapter 7

The results of this experiment suggest that adaptation to face trustworthiness generates different aftereffects depending upon the gender of the observer. Female observers showed typically characteristic adaptation aftereffects. Here, adaptation to untrustworthy and trustworthy faces resulted in typical 'repulsive' aftereffects, where test stimuli are judged as less like the adapting stimuli (e.g. Fox & Barton, 2007; Leopold, et al., 2001; Webster & MacLin, 1999a). Male observers, in contrast, showed no face adaptation aftereffects. For both female and male observers, male test stimuli were always judged as more untrustworthy than our female test stimuli (see Table 7.1). Critically, however, for both female and male observers, there was no interaction between the effect of test stimulus sex and adaptation trustworthiness indicating that the different ratings of these two groups of test stimuli did not influence aftereffects.

Repulsive face aftereffects are thought to involve changes in the sensitivity of cells late in the visual processing hierarchy that selectively code faces (e.g. Chen, Yang, Wang, & Fang, 2010; Webster & MacLeod, 2011a). Prolonged exposure to a face, or faces, with a defining set of characteristics could, in principle, generate a temporary reduction in sensitivity in cells coding those specific facial characteristics (along with other changes in cell tuning functions). Other neural mechanisms coding different facial properties, that do not respond to the adapting face, would retain their sensitivity. One explanation for the facial trustworthiness aftereffects observed here in female observers is that adaptation to untrustworthy faces results in a temporary reduction in the sensitivity of the population of cells that represents untrustworthy faces. The cell population that represents trustworthy faces would have its sensitivity spared. The cell population response to subsequent test faces would then be biased towards the more trustworthy end of the spectrum, leading to the observed aftereffects where the test faces appear more trustworthy. A similar, but opposite process, could occur following adaptation to trustworthy faces. Face trustworthiness is determined by a number of different facial characteristics (Oosterhof & Todorov, 2008, 2009; Stirrat & Perrett, 2010), and so (un)trustworthiness adaptation is likely to affect multiple populations of neurons coding these various features.

For female observers there was no interaction between adaptation trustworthiness and adaptation stimulus sex or test stimulus sex. This indicates that the aftereffects are similarly sized irrespective of the sex of the adapting and test stimuli (see also Figure 7.3). It appears, therefore, that the (un)trustworthy aftereffect in female observers is a general effect and does not take into account the sex of the faces observed, indicating sex-independent coding of facial trustworthiness in female observers.

In contrast to the aftereffects observed in female participants, in male participants adaptation did not produce any repulsive or attractive aftereffects. A possible explanation for these null findings is that the aftereffects that result from adaptation to the trustworthiness of faces by male observers are dominated by other cognitive effects rather than putative (un)trustworthy aftereffects. There is evidence that during judgements of trustworthiness male observers can be less influenced by visual information from the face than female observers. In an investigation of the role of facial width-to-height ratio on perception of trustworthiness, male observers were less influenced by this perceptual information than female observers (Stirrat & Perrett, 2010). In particular subordinate females were most likely to be influenced by facial width-to-height ratio when making judgements of trustworthiness. Stirrat and Perrett's explanation for these findings was that male observers, and especially more dominant males, may be able to effectively ignore facial width-to-height ratios as a cue to another individual's trustworthiness as dominant males can often operate with impunity. For male participants, perhaps small (un)trustworthiness aftereffects are also effectively ignored.

The finding that female observers show typical adaptation aftereffects to untrustworthy and trustworthy faces while male observers show no aftereffects may reflect a different balance in the influence of different processing mechanisms underlying perception of trustworthiness in female and male participants. Although the role of gender of participant in facial trustworthiness perception is most often not studied, there is some electrophysiological evidence that there may be differences in the way facial trustworthiness is processed in female and male observers. In an event related potential (ERP) study of the perception of untrustworthy and trustworthy faces, female observers were faster and more accurate in the perception of facial trustworthiness than male observers (Dzhelyova, et al., 2012). Furthermore, the amplitude of the P1 signal (a positive signal 100ms after stimulus onset) over the right hemisphere was larger in female than male observers during observation of faces. This sex difference in the P1 signal, however, may relate to face processing *per se* rather than the processing of trustworthiness from faces.

The test stimuli that were used to assess the effect of adaptation to trustworthy and untrustworthy faces were a restricted set of 14 rather than all 50 test stimuli originally shown to participants. This was necessary as the rating of the test stimuli by the set of independent observers indicated that, against original predictions, many of the test stimuli were rated as even more untrustworthy than female and male untrustworthy prototypes. This may have resulted from the averaging process used for generating of the untrustworthy prototypes. The morphing technique used to make the prototypes generated average faces (Rowland & Perrett, 1995), and average faces can appear more attractive than the originals from which they are made (discussed in DeBruine, et al., 2007). For example, the average untrustworthy prototypes are likely to be more symmetrical, and have smoother skin than many of the test faces. As the perception of trustworthiness is highly correlated with attractiveness (Oosterhof & Todorov, 2008), the untrustworthy female and male prototype faces may have appeared more attractive and thus more trustworthy than many of the potentially more irregular faces in the original set of 50. Because my measure of the effect of adaptation involved the comparison of the effect of adaptation to prototypes on opposite ends of the trustworthiness-untrustworthiness continuum, it would have been problematic to try and analyse the effect of adaptation on the particularly untrustworthy test faces.

In conclusion, this study found that aftereffects result from prolonged exposure to untrustworthy and trustworthy faces for female participants but not for male participants. These aftereffects were measured while participants assessed photographs of faces, indicating that in female observers immediate prior visual experience to facial trustworthiness can potentially bias judgments made about the trustworthiness of faces in real-life situations. The clear difference in the visual aftereffects induced in female and male observers may indicate that when assessing trustworthiness of other individuals, men may be less influenced by the prior visual context.

CHAPTER 8

General discussion

The ability to accurately interpret behaviour of other individuals is an essential part of our social functioning. In our busy social environment, multiple social cues provide a valuable insight into the richness of the mental and emotional states of our conspecifics. These cues, can however, also influence the way we perceive and judge their actions. Therefore, for better understanding of the dynamics of social perception, it is important to examine the mechanisms underlying our judgements of emotional and social signals within the social and temporal context in which they are likely to occur in the real world (see de Gelder & Hortensius, 2014, for a review).

The main aim of this thesis was to explore how temporal context influences social perception. It is well demonstrated that immediate perceptual history can distort and bias our judgement of emotional and mental states (e.g. Fox & Barton, 2007; Palumbo & Jellema, 2013; Webster, et al., 2004) of other individuals and their actions (e.g. Barraclough & Jellema, 2011; Barraclough, et al., 2009; de la Rosa, et al., 2014; Roether, et al., 2009). The work presented here extended previous findings and examined how prior visual experience shapes our understanding of the emotional and mental state of other people derived from observing their actions. Visual adaptation paradigms I employed in this thesis also provided insight into possible neural mechanisms that may underlie our perception of emotion from dynamic, whole body actions. Focusing on this thesis as a whole, I suggest that the following conclusions can be drawn:

(i) Temporal context can substantially distort our perception of action, emotion and other social traits such as trustworthiness of other individuals in a natural, social environment. This finding supports previous reports suggesting that mechanisms underlying our social perception, measured in laboratory settings, may translate into our perception in the real world.
(ii) Mechanisms underlying perception of emotion from whole body actions may parallel those for the processing of emotional signals from other social cues such as faces and voices. To process the dynamic aspects of social behaviour, such as changes in the emotional state, we may combine information regarding observed individual’s identity with the information regarding their emotional state.
(iii) Judgement of the emotional state of other individuals is not only influenced by the temporal context, but is also subject to influences of cognitive, Theory of Mind processes. Attribution of the mental state to the individual can influence perceptual processing of emotion signals.

In this General Discussion I will summarise the main findings of the experiments within this thesis and expand on the conclusions drawn above.

8.1 Summary of main findings

The focus of the study presented in Chapter 3 was to examine whether adaptation to whole-body actions occurs under naturalistic, resembling the real world viewing conditions. To test this, participants first adapted to a video clip of an actor lifting either heavy (18 kg) or light (2 kg) boxes. Subsequently, they rated the weight of similarly looking boxes lifted by other individuals. Both actions were embedded within the same scene to create a natural context. The experiment was conducted under three viewing condition; life-size stereoscopic presentation, life-size presentation without stereoscopic information and small-scale presentation without stereoscopic presentation. The results revealed that the weight judgement of test boxes was significantly influenced by the preceding adapting action. Specifically, observing an actor lifting heavy boxes resulted in subsequent boxes appearing lighter, whereas observing an actor lifting light boxes resulted in subsequent boxes appearing heavier. These biases in action perception were equally strong for different test actors (including male and female actors) and across different viewing conditions. Overall, these findings suggested that our perception of and interpretation of behaviour of other individuals may be influenced by the preceding temporal context, in which the observed behaviour was embedded.

In Chapter 4 I investigated whether perception of emotional states of other individuals derived from observing their actions is also subject to biases resulting from visual adaptation. As there was no difference in the magnitude of action aftereffects between life-size and small size presentations, as reported in Chapter 3, all the experiments were performed in a standard, laboratory setting. In Experiment 1 I tested the effect of stimulus similarity on the magnitude of emotional action aftereffects by varying the identity of actors and actions they performed between the adapting and test movies. Interpretation of the emotional state of the test actor was biased only in those conditions where the adapting and test actors performed the same action, irrespective of the actor's sex and identity. For conditions where adapting and test actors performed different action, aftereffects were non significant indicating that adaptation to emotional actions transferred across individuals, but not from one action type to another.

To further test the role actor's identity in the emotional action aftereffects and to establish how these aftereffects relate to previously reported visual aftereffects (e.g. Leopold, et al., 2005; Rhodes, et al., 2007; Troje, et al., 2006b) In Experiments 2a and 2b I measured the build up and decay of same identity (i.e. identity-dependent) and different identity (i.e. identity-independent) aftereffects respectively. This was done by measuring the effects of adapting stimulus duration and the duration of the inter-stimulus interval (ISI) on the magnitude of aftereffects. Both identity-dependent and identity-independent aftereffects increased logarithmically with the duration of the adapting stimulus, as with previously observed face (e.g. Leopold, et al., 2005; Rhodes, et al., 2007) and action (e.g. Barraclough, et al., 2009, 2012; Troje, et al., 2006b) aftereffects. However, while identity-independent aftereffect declined logarithmically with increasing ISI intervals, the identity-dependent aftereffect showed no decline. Therefore in Experiment 3 I tested duration of these two aftereffects over longer ISIs, extending them to 10.8 sec. Results of Experiment 3 showed that identity-independent aftereffect declined over time and disappeared over this time frame showing similar characteristics to other high-level aftereffects. However, the identity-dependent aftereffect showed a very different pattern, where it marginally albeit non-significantly, increased over time, suggesting a potentially different underlying mechanisms.

Participants' interpretation of the emotional state of test actors in experiments 1-3 was tested using a two-alternative forced choice paradigm (2AFC). In principle participants could have adapted a cognitive strategy to judge the test emotion as being simply different then the emotion expressed in the adapting movie. To control for this cognitive bias, in Experiment 4 I employed a 4AFC design, where participants could select the label that was either opposite (happy/sad) or unrelated (surprised/disgusted) to the adapted emotion, to describe the emotion expressed in the test movie. Results of this experiment showed that both identity-dependent and identity-independent aftereffects resulted from a shift in participants' perception of the action emotion (rather than from a cognitive strategy), as the test movies were judged as conveying the opposite to the adapted emotion, and not any other emotion.

In Chapter 5 I tested whether adaptation to emotion conveyed by the whole-body action and by facial expressions biases perception of emotion conveyed by the face in a forced-choice adaptive staircase adaptation paradigm. This method allowed me to examine whether representation of emotion is category-independent. Results of this study revealed typical facial expression aftereffects (e.g. Campbell & Burke, 2009; Fox & Barton, 2007; Skinner & Benton, 2012). Here, following adaptation, point of subjective equality (PSE) was shifted towards the adapted emotion indicating the reduced sensitivity to that emotion. This shift was also greater when the adapting and test face portrayed the same individual, then when the faces were of different identities, which is consistent with previous studies (e.g. Campbell & Burke, 2009; Fox & Barton, 2007; Skinner & Benton, 2012). However, there was no evidence for the cross-category emotion adaption, as adapting to emotional whole-body actions had no influence on the sensitivity to emotions expressed in a face. These findings suggest that the emotion adaptation may be category specific.

The focus of experiments presented in chapter 6 was test whether emotional state of mind attributed to the observed actor influenced the magnitude of the emotional expression aftereffects. I tested this by using genuine and faked facial expressions of joy and anger as adapting stimuli. Participants adapted to the expression for either 500ms, 5 sec or 8 sec and interpreted the emotion of neutral test stimulus in either 2AFC design or on a rating scale. Critically, on each trial participants first assessed whether the adapting expression was faked or genuine and received feedback regarding their judgement ensuring they held the correct belief about the emotional state of mind of the actor. On a rating scale, but on in a 2AFC paradigm, following 5 sec and 500ms adaptation, aftereffects to genuine expressions were significantly larger than those to faked expressions. However, this 'advantage' for genuine expressions disappeared following 8 sec adaptation, suggesting that adaptation to facial expressions may be influenced by emotional state attribution, but that this effect is short-lasting.

Finally, in Chapter 7 I investigated whether other complex social traits such as perceived trustworthiness are subject to biases resulting from visual adaptation. Here, participants adapted to male and female trustworthy, untrustworthy and control (i.e. mid-trustworthy) faces and rated the trustworthiness of subsequent male and female faces. Female, but not male, participants showed typical adaptation aftereffects, where they rated novel faces as less trustworthy after viewing trustworthy faces, and as more trustworthy after viewing untrustworthy faces. In contrast, male participants' trustworthiness judgement was unaffected by the adaptation. These results suggested that trait and personality judgements can also by influenced by the prior visual experience, but they also highlighted a potential sex difference in the in the sensitivity to visual context in these complex judgements.

The first objective of this thesis was to assess whether previously established biases in action perception resulting from visual adaptation would translate into our judgement of behaviour of other individuals in a virtual environment resembling the real world. This question is particularly important, as in natural, highly-stimulating and complex environments our visual system needs to constantly adjust to deal with ever-changing situational demands. To date, most of the research investigating the plasticity and adaptive adjustments of the visual system has been conducted in highly controlled laboratory settings, where external noise is minimised. However, in real life, these external influences cannot always be eliminated. In Chapter 3, I presented data suggesting that action understanding mechanisms are subject to visual adaptation. Equally strong biases in the judgment of behaviour of other people were measured when participants were tested both in a laboratory setting and in the 3D virtual reality environment. These findings suggest that our perception in everyday life may also be influenced by prior visual experience. Results of these experiments also suggest that visual adaptation mechanisms may operate to recalibrate our perception of socially meaningful stimuli. One of the functional advantages of adaptation is to allow the visual system to increase its sensitivity towards changes in the surrounding visual environment. Although I only measured the biases in perception, it is possible that adaptation for natural categories such as whole body actions also results in an improved visual sensitivity to similar cues.

The focus of Chapters 4 and 5 was to investigate the effects of adaptation to emotional body actions on subsequent perception of emotion in action and faces. Results of these studies demonstrated extensive biases in the judgement of emotional human behaviour resulting from our immediate perceptual history. Our interpretation of the emotional state of other individuals may therefore be influenced not only by the social and spatial context (see de Gelder & Van den Stock, 2011b for a review), but also by the temporal context, in which an observed act was embedded. Accurate interpretation of the emotional state of our conspecifics is crucial for our social functioning, and it has been suggested that viewing and interpreting the bodily expression of emotion in others triggers the preparation of adaptive responses in the observer (de Gelder, 2006). The data presented in this thesis may suggest that in order to fully evaluate the potential consequences of the observed emotive act, our visual system takes into account immediately prior visual context.

Findings reported in Chapter 4 also suggested that emotions conveyed by whole body actions may be represented both with respect to, and independently of, actor identity. These findings align with our understanding of the mechanisms underlying perception of identity and emotion from faces (Atkinson & Adolphs, 2011; Haxby, et al., 2000) and voices (Belin, Bestelmeyer, Latinus, & Watson, 2011; Belin, et al., 2004). These results also suggest that when assessing the socially meaningful signals from faces and body actions, it is critical to monitor changes in the emotional state of the observed individuals along with monitoring their identity. Such monitoring, with respect to face stimuli, has been recently proposed to involve connectivity between the pSTS and FFA (Baseler, et al., 2012). Whether parallel neural mechanisms are involved in the processing of body emotion and identity, however, still remains unclear.

Results of studies in Chapters 4 and 5 also suggest that processing of emotion from whole body actions may be dependent on the specific action kinematics and body part that convey it. In these experiments, adaptation to a specific emotional action did not influence the perception of subsequent different actions nor faces, even when these were of the same individual. To date, the literature presents mixed results on whether processing of emotional information is category-specific or category-independent. On the one hand, neuroimaging studies suggest the activity of the body and face selective brain regions is modulated by the affective visual stimuli regardless of category (body or face) that conveyed it (Atkinson, et al., 2012). Similarly, emotion signals conveyed by different sensory modalities activate high-level brain areas including the MPFC and STS, where affective information may be represented in a supra-modal fashion (Peelen, et al., 2010). On the other hand, psychophysical adaptation studies have not yet reported reliable cross-modal emotion aftereffects (Fox & Barton, 2007; Skuk & Schweinberger, 2013). However, the lack of cross-category and cross-modal aftereffects does not necessarily suggest that emotions from body and face cues are processed by completely separate neural substrates. A speculative explanation for the lack of cross-category aftereffects may be that adaptation may operate in the lower levels of perceptual processing, and not in the higher levels, where evaluation of the emotional state of the observed individual may take place (see also Chapter 6).

In Chapter 6, I examined whether, and if so, to what extent, top-down Theory of Mind (ToM) processes can interact with the processing of facial expressions. Using both genuine and faked expressions of happiness and anger as adapting stimuli, I investigated whether attribution of the mental state to the observer modulates the perceptual processing of facial expressions. Results of the experiments reported here provided a moderate support for the proposal that adaptation to facial expressions can be modulated by emotional state attribution. These findings are in line with recent work suggesting that forming a belief, or having knowledge regarding observed individual intentions, can wield a top-down influence on the perceptual processing of social cues (Teufel, et al., 2009). The integration of bottom-up, stimulus driven information, and top-down, contextual information and explicit person knowledge in the processing of socially relevant cues have been proposed in Teufel, Fletcher, et al. (2010) metalizing model of social perception. The model emphasises the bi-directional relationship between perceptual analysis of social signals and higher order cognitive function. Together, findings reported in Chapters 3-6 suggest that our perception and understanding of intention and emotion of other individuals can be significantly influenced by the prior visual context and prior knowledge regarding the observed individual. The bias in our perception is likely to arise at the early stages of visual analysis of the observed act.

Finally, in Chapter 7, I investigated whether perception of complex social traits such as trustworthiness is also influenced by visual adaptation processes. Results of this study suggest sex differences in the adaptation to facial (un) trustworthiness, where female observers showed a strong bias in perception resulting from adaptation to trustworthy and untrustworthy faces, while male observers were less influenced by the prior visual context. These findings may reflect a different balance in the influence of different processing mechanisms underlying perception of trustworthiness in female and male participants. Alternatively, there may exist individual differences in the sensitivity to the temporal context when evaluating observed individuals on complex social traits.

8.2 Implications for social perception

In our natural environment, actions are executed within a rich social and temporal context and in order to fully understand intentions, emotional and mental states of observed individuals, we need to interpret the observed behaviour with respect to the context in which it appears. However, to date most of our understanding of mechanisms underlying social perception and social cognition is based on studies investigating perception of facial expressions presented in isolation (see de Gelder & Hortensius, 2014; de Gelder, et al., 2010 for a review) and from action perception studies using impoverished stimuli such as point-light display (e.g. Atkinson, et al., 2004; Heberlein & Atkinson, 2009). Indeed, until recently very little research focused on examining emotion perception from bodily signals and in particular from naturalistic whole body actions (de Gelder & Hortensius, 2014). In consequence our understanding of emotion perception, based predominantly on models of emotion processing from static faces and bodies, may underestimate the role of contextual information in the accurate interpretation of behaviour of our conspecifics in everyday life.

The results presented in this thesis demonstrated the existence of extensive biases in the perception of emotional human behaviour resulting from our immediate perceptual history. These biases are likely to arise from the visual adaptation of mechanisms coding specific action kinematics rather than from post-perceptual, cognitive biases. This mechanism is extremely important for our accurate and successful social functioning, as it suggests that early, visual analysis of socially meaningful stimuli is likely to be influenced by the social and temporal (i.e. what has been observed in the recent past) context in which these stimuli are embedded.

Recent studies investigating the effects of social context on the perception of facial and bodily expressions of emotion, tested how perception of emotional scene, body expressions or vocal prosody can modify our interpretation of emotion derived from these cues (e.g. Aviezer, et al., 2012a, 2012b; Gelder et al., 2006; Meeren, et al., 2005; Righart & de Gelder, 2008a; Righart & De Gelder, 2008b). Results of multiple experiments suggested that the emotional gist of a natural scene, bodily expression and affective prosody influence the recognition of emotional signals from multiple social cues. It has been proposed that this influence is due to a rapid and automatic integration of multiple cues that takes place very early in the processing stream and does not require high-level, semantic analysis of the emotional content (de Gelder & Van den Stock, 2011b). In these studies, however, contextual information was always presented simultaneously, while in this thesis I explored the effects of immediate prior visual context on emotion perception. The findings that emerged from experiments presented here suggest that perception of emotion is dependent on the prior perceptual history and this consideration should play a role in future models of emotion processing from faces and bodies.

Immediate visual context can significantly alter our interpretation of behaviour of other people in everyday situations as suggested by a study presented in Chapter 3. Such context may function to disambiguate the emotional signal conveyed by the body or the face (de Gelder & Van den Stock, 2011b). Bodily expressions of emotion can be harder to recognize than facial expressions, as the configuration of the human body has more degrees of freedom and the body shape can vary greatly during articulated movements (Schindler, et al., 2008). Nonetheless, emotion recognition from dynamic body actions may be facilitated by the fact that the same emotions are often expressed through similar kinematic patterns across different individuals (Atkinson, et al., 2004; Roether, et al., 2009). Visual adaptation of specific action kinematics, that are characteristic of each emotion, may therefore improve recognition of novel emotions by increasing the sensitivity of the visual system to non-adapted movement patterns. Action and emotional action adaptation aftereffects, reported here transferred across different individuals, often of different ages and gender, suggesting that action adaptation in the real world may act to ease perception and recognition of behaviour of newly encountered individuals.

Visual adaptation mechanisms, tested in laboratory settings, have also been shown to have many functional benefits, allowing the observer to better adjust to the dynamic and constantly changing environment (Webster, 2011). Some of the advantages of adaptation have been recently noted for the processing of complex social stimuli such as faces. Following brief adaptation observers are, for instance, better able to discriminate rare stimuli (Keefe, et al., 2013; Yang, et al., 2011) or to establish norms for the processing of novel stimuli based on their average representation (Leopold, et al., 2001). These aspects of adaptation allow for better recognition and detection of outliers in a dynamic environment and may serve an important role for perception in the real world. It is likely that adaptation to actions of other individuals' in our natural environments enables us to better discriminate between potentially threatening or harmful behaviours, and adjust our own behaviour accordingly.

8.3 Outlook for future research

The work presented in this thesis provides a potential starting point for further work on the influence of social and temporal context on social perception. Until recently, little research has been conducted in the area of emotion and trait perception from dynamic body actions. There is much scope for research within this field and the investigation of sources of biases in the perception of behaviour of other people. Below I provide a description of topics that this research was not able to fully address, but that I consider are of importance.

Perception of complex emotions and social traits from whole body actions

Much of the research of body expressions of emotion focuses on perception of limited emotional signals such as threat (e.g. de Gelder, 2006; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; de Gelder, et al., 2010) or basic emotions (e.g. Atkinson, et al., 2004; Dittrich, et al., 1996; Pollick, et al., 2001). In everyday life, however, we are often required to interpret ambiguous, blended and complex emotional signals that may differ from the exemplars used in research. Whether our perception and interpretation of these complex signals relies on similar mechanisms as those for the perception of prototypical emotions is still unclear. In a recent study Thoresen, Vuong, and Atkinson (2012) investigated personality trait attribution derived from gait using point-light display. Their findings suggest that trait judgements may rely on impressions of emotion, age and masculinity, which are conveyed by a small number of specific kinematics. It is therefore possible that our judgement of complex social traits such as trustworthiness, competence or dominance from whole body actions, are also largely based on the features that signal valence (i.e. expression) and dominance, as it has been proposed for faces (Oosterhof & Todorov, 2008; Todorov, Said, et al., 2008). Identifying specific motion and body form parameters that are crucial for making reliable trait inferences from actions would allow scientists to model the structure of body action evaluation.

Integration of emotional signals from multisensory cues

Another area for future research would be to investigate how emotional signals conveyed by different modality cues such as bodily actions, face or voice are integrated in order to evaluate behaviour of other people in complex social scenes. Studies investigating the multisensory aspect of emotion perception that have traditionally used faces and voices (see de Gelder & Van den Stock, 2011 for a review) have shown a strong bi-directional influence between vision and audition. Only a small number of studies thus far have examined how auditory information influences perception of emotion from bodily emotion expression. Two studies have shown that recognition of emotions from static body postures (Van den Stock, et al., 2007) and whole body actions (Van den Stock, et al., 2008) was influenced by affective vocalization. These studies, however, only used a limited number of emotional signals and did not manipulate any of the scene parameters. Future research could therefore investigate context-dependent integration of emotional signals by manipulating the emotional content of surrounding environment or manipulating the reliability of different cues by, e.g. presenting bodily stimuli over different viewing distances. Similar methodology can also be applied in investigating perception of other bodily socially meaningful signals such as trustworthiness or approachability.

In everyday life, we are also often required to interpret emotions and behaviour of other people in a multi-agent or crowded environment. As presented in Chapter 3, the presence of another individual within the same social scene can significantly influence our action perception. The question still remains, to what extent the perception and judgement of emotion and social traits is affected by the presence of multiple individuals and how such social context affects the integration of emotional signals from different modalities.

Individual differences in the sensitivity to contextual information in emotion and social trait perception

In Chapter 7, I presented data suggesting that male observers may be less sensitive to prior visual context when judging trustworthiness of other individuals. Studies examining action and emotion perception presented in this thesis, however, did not investigate the role of individual difference in the potential sensitivity to visual adaptation and its influence on subsequent perception. Previous studies have shown that individual differences in negative emotionality influence the overestimation of temporal duration of angry and fearful expression (Tipples, 2008). Future research is required to investigate whether individuals with high anxiety, distress or negative emotionality would show stronger biases in emotion perception following adaptation to negative emotions. Because of their flexibility, adaptation paradigms may therefore be employed in examining impairments in perceptual processing of social stimuli in clinical populations.

8.4 Conclusion

In summary, the work presented here demonstrated how prior visual experience can influence our judgement and understanding of the behaviour of other individuals. Merely observing one individual's actions can significantly distort our perception and interpretation of the emotional state of other individuals. This significant influence of temporal context on social perception should be accounted for in future investigations of emotion and social trait perception.

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