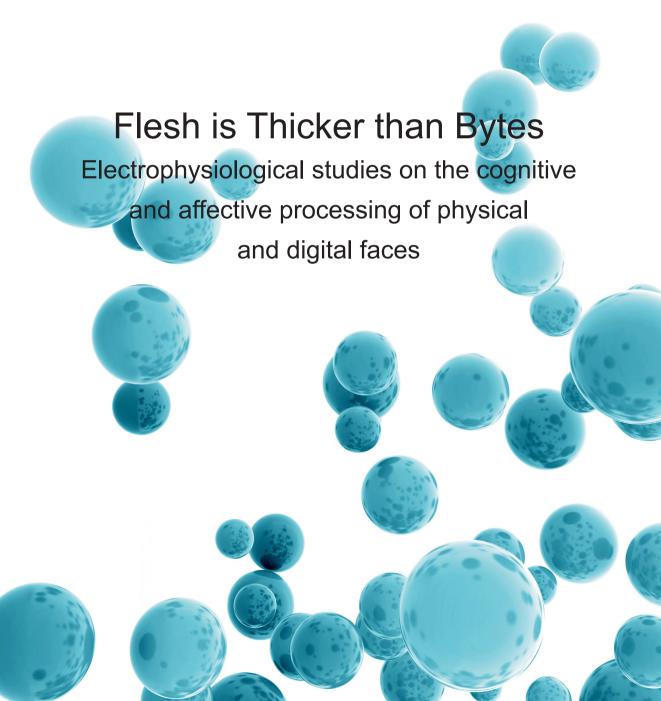
LAURA PÖNKÄNEN





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Flesh is Thicker than Bytes

Electrophysiological studies on the cognitive and affective processing of physical and digital faces

ACADEMIC DISSERTATION

To be presented, with the permission of the Faculty Council of Social Sciences of the University of Tampere, for public discussion in the Väinö Linna auditorium K104, Kalevantie 5, Tampere, on 1 December 2017, at 12 o'clock.

UNIVERSITY OF TAMPERE

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Acta Universitatis Tamperensis 2334 Tampere University Press Tampere 2017



ACADEMIC DISSERTATION University of Tampere Faculty of Social Sciences Finland

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Cover design by Mikko Reinikka

Acta Universitatis Tamperensis 2334 ISBN 978-952-03-0595-6 (print) ISSN-L 1455-1616 ISSN 1455-1616

Acta Electronica Universitatis Tamperensis 1839 ISBN 978-952-03-0596-3 (pdf) ISSN 1456-954X http://tampub.uta.fi

Suomen Yliopistopaino Oy – Juvenes Print Tampere 2017



ACKNOWLEDGEMENTS

I am grateful to my supervisors, Professor Jari Hietanen and Docent Jukka Leppänen. Jari, thank you for your dedication and enthusiasm in providing me all the invaluable support and knowledge during this thesis project. You have improved my academic thinking and writing skills enormously. It was a great opportunity to work under your supervision in the Social Brain project funded by the Academy of Finland. Jukka, I am grateful for the positive learning environment you provided me with. Your scientific curiosity and constructive commenting was inspiring and helpful. I am also grateful to Associate Professor Roxane Itier and Senior Lecturer Kaisa Tiippana for reviewing this thesis and giving me encouraging and helpful comments. Thank you, Professor Iiro Jääskeläinen, for accepting the invitation to be my opponent in the public defence.

A very special gratitude goes out to all the people at Human Information Processing Laboratory who I have collaborated with along the way. Mikko, thank you for being patient and helping me improve. I am grateful that you also taught me most of my technical skills in psychophysiology. For technical assistance and advice, I also thank Laboratory Engineer Pasi Kauppinen. For their unfailing support and assistance, I thank Terhi, Anneli, Stefanie, and Aki. I was also privileged to work with many talented students at the HIP lab. Ilkka, Annemari, Pauliina, Jenni, and Teemu, thank you for collaboration and assistance. Maija, thank you for compassion, insightful thinking and fun. Also, all the colleagues and fellow PhD students at the Psychology department in the University of Tampere, thank you for guidance and peer support.

I am also grateful to my family members and friends who have been there with me along the way. My mother Kirsti, my stepfather Jorma, and siblings Olli and Silja: you have given me endless support and helped me finding my strengths in life and taught me to never give up. I am also grateful to my late grandparents, who have given me encouragement and motivation for all my pursuits in academic life and life in general. To all my friends near and far I give my warmest thanks for inspiring conversations, kindness and support. Ransu, thank you for all the patience and warmth. In the darkest moments of academic brooding, you made me coffee. That, we agreed, should never be too dark. And finally, Anna, my partner in life. I would

not have made it this far without your loving support. Thank you for taking all those funny video clips of me Kermit-the-frogging around when trying to concentrate on finishing this thesis. I know you never stop laughing with me and trusting in me.

ABSTRACT

Engaging in face-to-face communication and being sensitive to others' gaze direction cues is an integral part of everyday social life of human beings. Effortless encoding of emotional and social signals embedded in faces is important in fluent social interaction. It has been studied that human beings have specialized brain structures and processes involved in social information processing. To date, most of the research on cognitive, affective, and motivational processing of faces has been conducted by studying how people process information embedded in pictures of faces. However, looking at pictures of faces differs from looking at of physically present real people. Looking at the eyes of physically present people differs from seeing these faces as pictures in many ways. People looking at each other face-toface are also being seen by each other, and thus having thoughts and feelings towards each other. Such meeting of minds is not possible when people are looking at faces of others presented as pictures. At present, it is unclear whether similar affective and social cognitive processes are in action when real faces instead of face pictures are being viewed. This thesis was aimed at studying whether cognitive, affective and motivational processes involved in face perception differ when the viewed face is a real human being, a dummy, or a picture. In four studies, various psychophysiological and behavioral responses to faces with differing potential (a 'live' human face, a dummy face, a picture of a face) and preparedness (direct gaze vs. averted gaze) for interaction were measured.

In Study I, the results showed enhanced early-stage visual processing in response to faces of real people compared to the perception of dummy faces. This difference was observed when the faces were presented live through a computer-controlled liquid crystal window, but not when presented as pictures on a computer screen. In Study II, gaze direction was shown to modulate the early face processing. Gaze that was directed to the perceiver enhanced visual processing more than an averted gaze, but again, only when the faces were physically present through the liquid crystal window. By measuring electroencephalographic alpha-power asymmetry from the left and right frontal brain regions, Study III showed that seeing a direct gaze was associated with a greater relative left-sided frontal activity, which implies motivation to approach. This pattern of activity was not shown for faces with an averted gaze.

This difference was found only when faces were physically present. Gaze contact with a physically present person also heightened the viewer's physiological arousal more than the averted gaze did. Finally, Study IV showed that a smile, in contrast to a neutral expression, enhanced arousal to direct gaze vs. averted gaze in the context of physically present faces.

Taken together, the results of Studies I–IV suggest that viewing another person live activates affective and cognitive processes differently than looking at pictures of faces does. The enhanced neurocognitive responses to live faces, especially when combined with a direct gaze, are likely to reflect action preparedness and self-awareness in response to being the target of someone's attention. Perhaps, to guide action adaptively in the presence of others, the brain systems dedicated to visual perception and processing of affective information allocate greater resources to reading and responding to physically present faces rather than to symbolic ones. Social cognitive neuroscience should thus begin to more clearly acknowledge the influence of physical presence and live social interaction while studying face processing.

TIIVISTELMÄ

Kasvoilla ja katseen suunnalla on keskeinen merkitys ihmisten välisessä sanattomassa viestinnässä. Kasvojen välittämien sosiaalisten ja emotionaalisten viestien nopea ja tarkka tunnistaminen helpottaa vuorovaikutusta arjessa, ja ihmisaivoissa onkin pitkälle erikoistuneet järjestelmänsä kasvojen välittämän tiedon käsittelyyn. Katseen suunta on yksi kasvojen tärkeimmistä sosiaalisista ja emotionaalisista sanattoman viestinnän välineistä, sillä katseesta voidaan päätellä, mihin toinen on suunnannut huomionsa. Erityisesti toisen ihmisen katseen kohteena oleminen herättää monenlaisia tunteita ja herkistää myös tunnistamaan toisen tunteita ja mielen sisältöjä. On olemassa paljon tutkimustietoa siitä, kuinka ihmisaivot käsittelevät kasvojen välittämiä sosiaalisia ja emotionaalisia viestejä. Näissä tutkimuksissa tutkittavat ovat yleensä katselleet kuvia kasvoista. Kasvokuvien katselu ei kuitenkaan vastaa sosiaaliselta ja emotionaaliselta sisällöltään tilannetta, jossa katsellaan toisen, fyysisesti läsnä olevan elävän ihmisen kasvoja. Tämän väitöskirjan tutkimuksissa I-IV selvitettiin aivojen sähköistä toimintaa, autonomisen hermoston reaktioita sekä itsearvioituja tunnetiloja mittaamalla, eroaako elävien, fyysisesti läsnä olevien kasvojen katselu kasvokuvien katselusta. Eläviä kasvoja katseltiin nestekidekalvoikkunan läpi, kun taas kasvokuvat esitettiin tietokoneen ruudulla. Lisäksi tarkasteltiin, oliko katseltavien kasvojen katseen suunnalla (tutkimukset II-IV) ja kasvojen ilmeellä (tutkimus IV) vaikutusta elävien kasvojen ja kasvokuvien havaitsemiseen.

Tutkimuksessa I osoitettiin, että nestekideikkunan läpi esitetyt, fyysisesti läsnä olevat ihmiskasvot tehostivat tiedonkäsittelyä aivoissa enemmän kuin ikkunan läpi esitetyn ihmisenkaltaisen mallinuken kasvot. Vastaavaa eroa ei kuitenkaan löytynyt, kun kasvot esitettiin kuvina. Tutkimuksessa II näytettiin, että suoraan kasvojen katselijaan suunnattu katse tehosti ihmiskasvoihin liittyvää tiedonkäsittelyä aivoissa, mutta jälleen vain tilanteessa, jossa elävät ihmiskasvot olivat fyysisesti läsnä. Tutkimuksen III tulokset osoittivat, että elävän ihmisen suoraan katsojaan suunnattu katse herätti voimakkaampaa lähestymismotivaatioon liittyvää otsalohkojen toimintaa ja suurempaa autonomisen hermoston aktiivisuutta kuin sivuun suunnattu katse, mutta vastaavaa katsesuunnan vaikutusta ei löytynyt kasvokuvia katseltaessa. Lopuksi tutkimuksessa IV näytettiin ainoastaan eläviä kasvoja ja osoitettiin, että

hymyilevät kasvot yhdistettynä katsojaan suuntautuneeseen katseeseen herättivät suurempaa autonomisen hermoston aktiivisuutta kuin suoraan katsojaan katsovat totiset kasvot. Kasvojen ilmeellä ei kuitenkaan ollut vaikutusta autonomiseen hermostoon, kun katseltavien kasvojen katse oli suuntautunut sivuun.

Näiden tutkimusten perusteella voidaan olettaa, että ihmisen keskushermosto käsittelee eläviin, fyysisesti läsnä oleviin kasvoihin liittyvää tietoa erityisellä herkkyydellä. Kasvokuvilla ei ole samaa vaikutusta sosiaaliseen vuorovaikutukseen ja tunteiden välittämiseen sekä vastaanottamiseen kuin elävillä, fyysisesti läsnä olevilla kasvoilla. Ihmisen fyysinen läsnäolo yhdistettynä toisen ihmisen katseen kohteena olemiseen on lisäksi voimakas tunteita ja kehollisia reaktioita herättävä tapahtuma, jota ei voi syntyä kasvokuvia katseltaessa. Kasvojen havaitsemista ja kasvokkain tapahtuvaa sosiaalista vuorovaikutusta tutkittaessa on siten tärkeää huomioida, että kasvojen vuorovaikutteisuudella, elävyydellä ja fyysisellä läsnäololla on merkitystä ihmisen tiedonkäsittelylle ja tunteille.

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LIST OF ORIGINAL PUBLICATIONS

The dissertation in based upon of the following four publications, which will be referred to in the text by their Roman numerals I – IV:

- I. Pönkänen, L. M., Hietanen, J. K., Peltola, M. J., Kauppinen, P. K., Haapalainen, A., & Leppänen, J. M. (2008). Facing a real person: An ERP study. *Neuroreport*, 19, 497-501.
- II. Pönkänen, L. M., Alhoniemi, A., Leppänen, J. M., & Hietanen, J. K. (2011). Does it make a difference if I have an eye contact with you or with your picture? An ERP study. *Social Cognitive and Affective Neuroscience*, 6, 486-494.
- III. Pönkänen, L. M., Peltola, M. J., & Hietanen, J. K. (2011). The observer observed: Frontal EEG asymmetry and autonomic responses differentiate between another person's direct and averted gaze when the face is seen live. International Journal of Psychophysiology, 82, 180-187.
- IV. Pönkänen, L. M., & Hietanen, J. K. (2012). Eye contact with neutral and smiling faces: effects on autonomic responses and frontal EEG asymmetry. *Frontiers in Human Neuroscience*, *6*, 122.

1 INTRODUCTION

Human beings are strongly motivated to form and manage emotional and social bonds with each other. Indeed, rather than primarily selfish or altruistic, people can be seen as profoundly "groupish" (Haidt, 2012). However, while it has become a common statement in neuroscience literature that humans have evolved to meet other minds (Cacioppo & Decety, 2011), substantially little is known of how the involvement of other people, or more precisely, the degree of perceived togetherness, actually makes a difference for people constantly perceiving, feeling and acting in the world. Pioneering social scientists such as Mead (1934) have proposed that one element that might lead to success in human social functioning is the fine-grained awareness of reactions that people observe in others. Recently, it has been suggested that virtually all emotions largely depend on the cognitive stance of the self, situated in real, imaginary, or symbolic relationships with the physical and social context (Paradiso & Rudrauf, 2012). In this view, self-awareness, as a sensitivity to "feel" others around, is at the core of social cognition and intersubjectivity. Cognitive, affective and motivational processes evoked by others' reactions, however, may likely have different functions depending on whether others meet our eye in person, or through a digital device, being thus present only symbolically.

Faces are rich sources of social and emotional information, and during the last few decades they have become common yardsticks in exploring how social signals observed in others guide emotion and cognition. Yet, despite the rapid technological evolution in the means of social interaction, research on social and emotional information processing has mainly focused on highly controlled situations, in which socially and emotionally rich stimuli, such as faces, have been presented in a digitally mediated form on a computer screen. These strictly controlled modes of presentation have the advantage of allowing researchers to distinguish separate phases and functions in the highly complex perceptual processes. Social and emotional processing of faces is, however, more than looking at digitally mediated faces, as vivid as they may be. In everyday life, looking at faces is social interaction itself. Not surprisingly, therefore, there has lately been a growing interest to study emotion-related phenomena with socially inspired paradigms (Kingstone, 2009).

Regarding the importance of realizing this boundary between actual and symbolic presence of humans, the effects that the perceived potential for real interaction might have on neural, perceptual, emotional, and behavioral processes could become a fruitful area of research.

This dissertation was designed to study whether seeing a face of an actual human being rather than seeing that same person as a picture on a computer screen has an influence on the neurocognitive responses evoked by the face being viewed. This introduction begins by exploring how socially tuned vision guides human behavior, followed by a short review of the functions of the human face and gaze in guiding social attention, evoking emotions, and fulfilling communicative goals. Finally, there will be a description of the specific aims of the studies in this dissertation.

1.1 Faces as social and emotional instruments

When we hand over a new object, say, a book we have recently read, to another person, where do we direct our attention? Most likely we spend the greatest amount of that time looking at the face, especially the eyes, of the person to whom the book is addressed. We want to know the receiver's immediate reaction. Does the receiver look surprised, or perhaps annoyed? Is the receiver prepared to say something? This everyday example illustrates how the sharing of visual information interweaves with the sharing of social information. Compared to other species, human beings have an astonishing ability to decode meanings embedded in the social world, and the human brain seems to have evolved socially adaptive networks to manage the challenges of social life (Barrett, Cosmides, & Tooby, 2010). In the last two decades, "social vision", i.e., how vision is guided and affected by the social nature of human beings (Nakayama, 2010), has begun to inspire researchers to study whether our visual perception and attention systems of the brain prioritize social over non-social objects. Through certain smiles, frowns, or gaze aversions, to begin with, people can establish, maintain, and end moments of mind sharing, even with strangers. To read messages in others' faces is not only to learn about them, but also with them.

The prioritization of social objects, such as faces, largely functions via emotions. Importantly, the face has been recognized as the main non-linguistic channel for communicating emotion (Argyle, 1988). Emotional states are the product of a variety of different response outputs, both physiological and behavioral, elicited by motivationally relevant external and internal events. To ensure that salient stimuli gain access to capacity-limited processes, emotion may enhance selective attention

in various stages of stimulus processing (Vuilleumier, 2005). Therefore, perhaps, emotional cues, such as facial expressions, are processed automatically (Vuilleumier, 2002). Faces are also detected and categorized faster than many other object categories, and a large body of evidence has shown that faces become prioritized during perceptual, recognition, and memory processes (Palermo & Rhodes, 2007). The primate brain's face perception network seems to be suitable for instant decisions based on clear-cut visual signals (Tsao & Livingstone, 2008). Face processing relies on a distributed cortical network in the occipital, temporal and frontal lobes, responding disproportionately to face stimuli (Atkinson & Adolphs, 2011; Nummenmaa & Calder, 2009). Other cortical regions, which are not primarily visual, such as the somatosensory cortices, and subcortical structures such as the amygdala, also participate in this process (Atkinson & Adolphs, 2011; Nummenmaa & Calder, 2009). Ample evidence has also shown that the brain may use emotionally salient information, such as faces carrying social information, to reshape high-level cognition and behavior (Bradley, 2009). High-level face-perception abilities seem to depend on the interplay of several anatomically and functionally distinct neural networks, and the nature of these interactions is task dependent (Atkinson & Adolphs, 2011). Rather than functioning in a purely hierarchical manner, face perception seems to involve a complex interplay of systems directing attention to different facial features based on task demands, environment, and social context (Nummenmaa & Calder, 2009).

Numerous findings from electrophysiological studies have suggested the existence of face-selective cortical processing mechanisms (for a review, see Eimer, 2011). Event-related potential (ERP) technique applied in the measurements of the electroencephalography (EEG) is a feasible method to measure perceptual processes allowing examining of visual processing in high temporal resolution. In face perception, ERPs can be applied in investigating the automaticity of perception by tracking down temporally dissociable processing stages. One widely studied ERP marker that has given insights into the time course and functional properties of face processing in the human brain is the N170 response (Eimer, 2011; Rossion & Jacques, 2011). It is a negative component peaking around 150-180ms poststimulus, and shown to be involved especially in the structural encoding of faces (Bötzel, Schulze, & Stodieck, 1995; Bentin et al., 1996). Visually evoked ERP components, such as N170, are elicited over posterior visual cortical areas, and their absolute size is tied on low-level visual stimulus factors such as luminance, spatial frequency, contrast, and symmetry (Eimer, 2011; Rossion & Jacques, 2011). The N170 is shown to be greater in response to faces than any other type of objects, and this amplitude difference between faces and non-face objects together with the characteristic scalp topography of N170 is thought to reflect the activation of face-selective brain areas (Eimer, 2011; Rossion & Jacques, 2011). The N170 is not only found to be larger but also earlier to faces than other objects (Itier & Taylor, 2004).

To some degree, the perception of facial emotion seems not to be entirely automatic but also susceptible to inner motives and goals (Holmes, Bradley, Kragh Nielsen, & Mogg, 2009; Schacht & Sommer, 2009; Schupp et al., 2007). Many studies have found the N170 response to be modulated by affective and motivational content of faces (Batty & Taylor, 2003; Blau, Maurer, Tottenham, & McCandliss 2007), yet N170 is not sensitive to face familiarity (Bentin & Deouell, 2000) suggesting that it rather relates to the formation of visual representation of a face prior to within-category identification. Besides N170, there are other early-stage ERP components that are thought to reflect affectively and motivationally guided face perception. The effects of explicit attention and emotional significance are suggested to operate additively during early perceptual encoding of visual stimuli (200-350 ms after stimulus onset), when stimuli are presumably selected for enhanced processing (Schupp et al., 2007). One such component, EPN (early posterior negativity), is a negative deflection over temporo-occipital regions peaking approximately 200 ms after stimulus presentation. It has shown to be sensitive to affective and motivational salience of objects, and to entangle with higher cognitive functions (Rellecke, Sommer, & Schacht, 2012). For instance, high-arousing pleasant and unpleasant images, as compared with their low-arousing counterparts, evoke greater EPN (Keil et al., 2002; Schupp, Junghofer, Weike, & Hamm, 2003).

1.2 Gaze direction in social communication

Being social creatures by nature, humans seem to be very interested in where others direct their attention. A most feasible means of communicating the direction of attention is human eye gaze. A passing stranger may glance at us, and as brief and unnoticeable this event may be, we may carry the impact of this brief engagements with us – for instance, making us feel happy, safe or threatened (see Marsh, Johnston, Richardson, & Smith, 2009). Essentially, following others' eyes may promote survival (Frischen, Bayliss, & Tipper, 2007; Ricciardelli, Bricolo, Aglioti, & Chelazzi, 2002). Natural selection has favored visual signals based on the chromatic opposition, i.e., white versus any other color of the spectrum, and white color ensures optimal reflectance even in reduced luminosity (Bouissac, 2010). Compared to other animal

species, humans have the largest ratio of exposed sclera in the eye outline, and the human sclera is distinctly paler than the facial skin and iris (Kobayashi & Kohshima, 2001). It is suggested that this unique morphology of the human eye is an adaptation to widen the visual field by increasing eye movements of humans in order to excel in visual information gathering, and on the other hand, to make the gaze direction an especially rich and effortless means of communicating one's current interests to others (Kobayashi & Kohshima, 2001). Human eye gaze thus plays a critical role in the development and maintenance of social exchange.

Despite the special advantage for gaze communication in humans, other primates can utilize the gaze direction of their conspecifics as a cue in coordinating their own actions (Tomasello, Call, & Hare, 1998). One recent study on social cognition in rhesus monkeys showed that when there was a video depicting a nonfamiliar conspecific gazing at the subject, it captured more visual attention and enhanced sympathetic arousal (pupil dilation) compared to a video with a monkey not gazing at the subject or a nonsocial stimulus (Machado, Bliss-Moreau, Platt, & Amaral, 2011). However, when nonhuman primates and members of many other animal species notice that their conspecific is gazing directly towards them, they tend take it as a sign of the other's dominance or potential aggressive behavior (for a review, see Emery, 2000). For some nonhuman animals, their eye coloration might be an adaptation to rather camouflage than reveal their direction of gaze to avoid aggressive confrontations (Perrett & Mistlin, 1990). For humans, instead, eye contact is thought to be one of the earliest signs of affiliation. An eye contact between two persons makes them emotionally glued, and hence socially attentive and sensitive to each other. The capacity and affectively guided motivation to shared attention is thought to contribute to the emergence of theory of mind, which refers to the ability to understand mental states of others (Baron-Cohen, 1995). Joint attention relies on the ability to follow other person's gaze; as an ostensive signal, gaze is a critical platform for later emotional and social development (Csibra & Gergely, 2009).

There is rich behavior and brain activity associated with mutual gaze and eye contact. Within the first years of life, human infants start treating the faces of other people as objects worthy of their limited attentional resources. As Senju and Johnson have presented in their review (2009), somehow the brain, possibly in concert with the growing amount of interaction with the environment, generates motor commands to look at the face, especially the eye region in it. The question of how the bias to detect and orient to faces with direct gaze develops in human ontogeny is still under debate and warranting more studying (Senju & Johnson, 2009). It is shown that newborns identify other people by hearing their voice and looking at

their faces (Guellai et al., 2011), and they spend more time looking at the eyes than at any other areas of the face (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000). The enhanced neurocognitive processing of direct gaze over averted gaze or closed eyes seems to emerge very early in development; during the first few months of life, faces with a direct gaze start to generate larger face sensitive electrophysiological responses than do faces with an averted gaze (Farroni, Csibra, Simion, & Johnson, 2002; Farroni, Johnson, & Csibra, 2004; Grossmann, Johnson, Farroni, & Csibra, 2007). Infants also tend to smile in eye contact but decrease smiling when the gaze of an interaction partner is directed away (Hains & Muir, 1996). In early human development, gaze direction perception, coordination created via gaze, facial expression, and affect attunement participate in the building of advanced forms of social-cognitive understanding (Reddy & Morris, 2004; Reddy, 2010; Rochat, 2009). Gaze among other communicative acts has also a crucial role in coordination of cooperation from early on (Warneken, Chen, & Tomasello, 2006). The early-emerging motivation to engage in eye contact may result from the general reward value of social stimuli.

In adulthood, gaze direction continues to carry essential information in nonverbal communication. Gaze direction aids in regulating turn taking in conversation (Kendon, 1967), and eye contact enhances mimicry of motor actions during social interaction (Wang, Newport & Hamilton, 2010). Humans also automatically direct their attention according to other people's gaze or head direction cues (e.g., Driver et al., 1999; Friesen & Kingstone, 1998; Hietanen, 1999, 2002). Indeed, a natural response to a gaze shift would be to follow it - when the gaze of another person is imitated, the imitator's gaze-shift is faster than without imitation (Ricciardelli et al., 2002; Terburg, Aarts, Putman, & van Honk, 2012). Perhaps this tendency to reflexively follow others' points of visual interest serves as a rapid means of information diffusion within a group in order to react on the possibly imminent resources or threats that have caught someone's attention. On the other hand, depending on the context, direct gaze may possess processing advantages relative to averted gaze. For instance, direct gaze is detected faster than averted gaze (Conty, Tijus, Hugueville, Coelho, & George, 2006; Senju, Hasegawa, & Tojo, 2005; Senju, Kikuchi, Hasegawa, Tojo, & Osanai, 2008) and direct gaze can facilitate the categorization and recognition of faces, memory for faces, and recognition of emotional expressions (Adams & Kleck 2003, 2005; Mason, Hood, & Macrae, 2004; Sander, Grandjean, Kaiser, Wehrle, & Scherer, 2007). Moreover, gaze that is directed to oneself can be read as a sign of interest to oneself, as an intention to share feelings and other types of information, and to monitor the whole interaction process.

Indeed, once information has been recognized as self-related, this information becomes more salient (Symons & Johnson, 1997). Senju and Johnson (2009) have labelled the various psychological and physiological effects that result from a perceived eye contact as "an eye-contact effect".

The human brain appears to be highly sensitive to facial and bodily cues that involve information about the direction of other people's attention (Frischen, Bayliss, & Tipper, 2007). Brain-imaging studies have explored several key components in the brain circuits for eye gaze perception (Nummenmaa & Calder, 2009). The specific brain regions involved in encoding of gaze direction include especially the posterior area of superior temporal sulcus (STS) (Hoffman & Haxby, 2000; Pelphrey, Morris, & McCarthy, 2004; Puce, Allison, Bentin, Gore, & McCarthy, 1998; Sato, Kochiyama, Uono, & Yoshikawa, 2008). Dynamic facial expressions and gaze shifts seem to contribute to the elevated response for dynamic faces in the posterior STS region, and the posterior STS seems to be most sensitive to dynamic changes in gaze or expression (Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011). Moreover, there are other areas such as the intraparietal sulcus (IPS) (Hoffman & Haxby, 2000), inferior parietal cortex (Calder et al., 2007), fusiform gyrus (FFG), and amygdala (George, Driver, & Dolan, 2001) that have been related to the processing of various cognitive and emotional aspects of human gaze. It is suggested that the amygdala participates in binding perceptual representations with memory and emotion, modulating ongoing cognition based on the emotional significance of the stimuli (Büchel, Morris, Dolan, & Friston, 1998; LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998; Oya, Kawasaki, Howard, & Adolphs, 2002; Phelps et al., 2001). Furthermore, ostensive gestures, such as gaze and calling one's name, have been shown to elicit activity in the dorsal medial prefrontal cortex (Calder et al., 2002; Kampe, Frith, & Frith, 2001; Schilbach et al., 2006), an area involved in a variety of mentalizing tasks (Amodio & Frith, 2006). The saliency assessment of gaze signals involves thus interplay between lower and higher-level visual and emotional processing structures.

It is suggested that the face expresses cognitive processes involved in orienting of attention and evaluation of emotion-eliciting events (Sander et al., 2007). In decoding these processes, the interplay between gaze direction and facial expression seems to be important. Facial expressions expand and modify the meaning of a particular gaze direction, thus facilitating the understanding of what is happening in the social and physical settings and in the minds of the people in there (for a review, see Itier & Batty, 2009). The brain seems to unite different sources of facial information at the early processing stages. This integration gives the perceiver a more

accurate picture of the immediate objectives of the others under observation. In 200 ms, information about the gaze direction, gesture, and facial emotion is bind together in the premotor cortex, likely to prepare the perceiver to react according to the nature of the integrated information, as demonstrated in a combined fMRI and EEG study (Conty, Dezecache, Hugueville, & Grezes, 2012). EEG studies have shown an integration of gaze and emotion processing at 200-300 ms (Klucharev & Sams, 2004; Rigato, Menon, Johnson, & Farroni, 2011). In brain imaging studies, this uniting of gaze direction with facial expression has been shown to engage the amygdala (Sato, Yoshikawa, Kochiyama, & Matsumura, 2004; Sato, Kochiyama, Uono, & Yoshikawa, 2010), a central area involved in social saliency detection (Boll, Gamer, Kalisch, & Büchel, 2011; Hadjikhani Hoge, Snyder, & de Gelder, 2008; N'Diaye, Sander, & Vuilleumier, 2009; Sato et al., 2004).

1.3 The feeling of being observed

Artists have long recognized the power of gaze, as a signal and source of emotions that make us feel human. When two persons hold their gaze in each other's eyes, they are sensitive to each other, simultaneously observing and being observed by another mind that is actively participating in the process of perception. Furthermore, at the point where two or more people are physically situated in a shared perceptual reality, it is not just two minds meeting, but two bodies alike. Recent theoretical viewpoints have addressed radical embodiment of cognition, referring to the fact that in a social reality, cognition is perhaps most strongly in the guidance of action: our own actions, and the possible actions of the other agent in shared space (e.g., Marsh, Johnston, Richardson, & Smith, 2009). Therefore, two persons facing each other are not just two isolated mindful agents, but rather there is another, socially embedded cognitive reality consisting of two perceivers who attract each other in synchronous action. Individuals, via mutual dependency, form together a "social unit ", which is relational in a way that cognitive processes in that unit resonate back and forth, and hence a state of an individual should be assessed in relation to the state of other's (Marsh et al., 2009).

Social encounters can be highly demanding decision-making situations, and thus being the object of someone's gaze may increase arousal in multiple ways. General arousal is the energetic component sensitizing the organism for action. This process of action readiness is guided by peripheral nervous system, and reflected in, for instance, cardiovascular, pupillary and electrodermal responses (Hamm, Schupp, &

Weike, 2003). Damasio (1994) has proposed in his "somatic marker hypothesis" that physiological arousal guides social cognitive, affective, and motivational processing of objects in various decision-making situations. The affiliative conflict theory suggests that there is an optimal level of intimacy in every dyad, driven towards equilibrium by forces of approach and avoidance, and regulated by the amount of mutual gazing (Argyle & Dean, 1965). Arousal level may alter with the subjective intimacy level in face-to-face situations. It is also possible that mutual attention shared by a dyad itself increases arousal (Lachat et al., 2012; see also Patterson, Jordan, Hogan, & Frerker, 1981). Eve contact has been observed to increase physiological arousal in adults when there has been a real human being face-to face with them (Gale, Spratt, Chapman, & Smallbone, 1975; Helminen Kaasinen, & Hietanen, 2011; Hietanen, Leppänen, Peltola, Linna-aho, & Ruuhiala, 2008; Kleinke & Pohlen, 1971; McBride, King, & James, 1965; Nichols & Champness, 1971). Despite the heterogeneity in the quality of the face-to-face contact in these studies (e.g., interaction quality, distance, and gaze duration), a plausible explanation for the arousal enhancement is the notion of being a target for another's attention and heightened sensitivity for the shared social space (see also Honma, Tanaka, Osada, & Kuriyama, 2012). The feeling of being observed may evoke thoughts related to how one is seen and judged in the eyes of the others.

The presence of others seems to demand substantial amount of attentional capacity from an individual. To function successfully in social situations, a human being must have capacity to experience oneself both as a subject and as an object at a same time. Wilms et al. (2010) proposed that the awareness of mental states follows when one becomes psychologically engaged with someone as an active participant of reciprocal interaction, thereby establishing a subject-subject ("Me-You") rather than a subject-object ("Me-She/He") relationship. This may be manifested as elevated physiological arousal in the person whom the presence of others concerns, perhaps also due to the evaluation of possible challenges and threats that the other's presence may induce (Blascovich, Mendes, Hunter, & Salomon, 1999). Depending on the context, either the challenges or the threats are weighted more over the others, sometimes even on the verge of maladaptive consequences (see George & Stopa, 2008; Silvia, & Gendolla, 2001). When people attribute minds to others, the mind is proposed to realize in terms of two dimensions: agency (capacity to "do") and experience (capacity to "feel"). In this way, mind is in the eye of the perceiver (Waytz, Gray, Epley, & Wegner, 2010). Furthermore, Waytz et al. (2010) discussed that perceiving mental states in another entity may intensify the perceiver's psychological experience of events. People are observed to behave more prosocially if they think

that they are under the scrutiny of another entity possessing a mind (Hoffman, McCabe, & Smith, 1996), likely because they intend to maintain a favorable impression to real or imagined others. Even relatively subtle cues, such as pictures of eyes, can increase prosocial behavior both in laboratory settings and in daily life (Haley & Fessler, 2005; Bateson, Nettle, & Roberts, 2006). Nevertheless, face-to-face meeting with another in person may increase these processes even more than a digitally mediated meeting.

In social interaction, human beings have intentions, and targets of their intentions. Likewise, people tend to rapidly evaluate whether objects in their vicinity have intentions of their own, even in minimalistic interactions (Auvray, Lenay, & Stewart, 2008). Evidently, virtually present humans can show attention and possess intentions similarly to human beings who are physically present. Interacting with a real vs. artificial partner via digital screen has indeed been shown to elicit differential processing patterns in the brain (Gallagher, Jack, Roepstorff, & Frith, 2002; McCabe et al., 2001; Rilling et al., 2004; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). However, as compared to physically present humans, symbolically present humans do not have similar possibilities to immediately act according their intentions towards the interaction partner; they can touch the mind but not the body. A considerable amount of evidence has also shown that the mere presence of other people can have an influence on the performance of an individual in a variety of tasks (Guerin, 1986), yet sometimes the mere presence does not influence individual performance per se, but the presence of spectators who have an opportunity to observe what the individual does (Cottrell, Wack, Sekerak, & Rittle, 1968). Indeed, rather than actual glaring on the observer's eyes, it seems to be the observer's subjective awareness of the other's eyes on the self that enhances physiological arousal in response to the observed face (Honma, et al. 2012). The arousal that results from being in the focus of someone's mind can be seen as adaptive action readiness to the possible immediate consequences when the other is almost within an arm's each from the self.

Importantly, the feeling of mutual regard is, perhaps, as often as not a positive one. Whether it is or not, may be influenced by various inter- and intrapersonal factors, such as gender, physical distance, dominance, and proneness to social anxiety (Moukheiber et al., 2010; Roelofs et al., 2010; Wieser, Pauli, Alpers, & Muehlberger, 2009). People can also differ in their attentiveness to mental states of others, for instance, in their general need to belong (Pickett, Gardner, & Knowles, 2004). It has been shown that anxiety can increase together with a degree of an observer perspective, i.e., the degree to which one feels looking oneself from an external point

of view rather than through one's own eyes (Coles, Turk, Heimberg, & Fresco, 2001). Furthermore, individuals with high or low anxiety alike are shown to report lower self-evaluation of performance when they have given a speech in an observer perspective, imagining that they look at themselves from a second-person point of view, vs. when they have imagined looking at themselves through their own eyes, form a first-person perspective (Spurr & Stopa, 2003). Indeed, being the target of other's gaze can draw a person's attention to oneself with a variety of consequences depending on the person and the acquired perspective. Duval and Wicklund (1972) propose that other people are a strong stimulus for awareness of the self as a social object. Engaging in a social task seems to increase public self-awareness and anxiety (Froming, Walker, & Lopyan, 1982; Kimble, Hirt, & Arnold, 1985). George and Stopa (2008) found that increasing self-focus of participants increased their public self-awareness. They suggested that if a person holds a negative self-image, it may become more salient with an increase in public self-awareness - thus it may be the interaction between public self-awareness and negative images or impressions of self that creates a problem. Some have also suggested that eye contact provokes anxiety in individuals with autism spectrum disorder (ASD) and thus reduces their motivation to engage in an eye contact (Dalton et al., 2007). However, the evidence supporting these claims is conflicting and not based on facing real people who are physically present.

It is often claimed that encounter with social stimuli evokes the sense of reciprocal involvement and normative evaluation of the situation. For instance, when we see someone's face, our reactions to that face are influenced by our feelings and all learned associations. Importantly, it has been questioned whether all social processing is fundamentally emotional (see Adolphs, 2010; Olsson & Ochsner, 2008). It is difficult to even imagine occasions in which social processing, beginning with perception of faces, for instance, is not more or less entangled with affective processing. Interestingly, most studies on social information processing at a neural level have utilized stimulus material other than corporeally present human beings. It is, however, not far-fetched to think that meeting one's boss, fiancée, or a favorite celebrity is different when taking place live than via digital means. Rich, dynamic social environments, such as live face-to-face interactions, require rapid online updating of information, and, more importantly, social interactions seem to be rewarding in a different way from nonsocial encounters (Sanfey et al., 2003). Therefore, the emotional impact of social stimuli should also be assessed with physically present social stimuli, meeting the criteria of potential reciprocity and

normative evaluation. Varying both the social nature of stimuli and processing demands is important in face processing studies.

1.4 Motivation to approach or avoid facial signals

Deeply rooted in the human evolutionary heritage lays the fundamental motivation to gain pleasure and avoid harm, by approaching or avoiding their ostensive sources. It has been widely discussed how these fundamental tendencies may have survival value, leading to the development of brain systems that implicitly guide human beings to approach beneficial events and avoid harmful ones (for a review, see Elliot & Covington, 2001). These two core motivations are referred to as approach and avoidance motivation and are both considered vital for survival (Elliot, & Covington, 2001). For example, avoidance manifests itself in the startle, salivary, and blink reflex, and has been examined even in single celled organisms that withdraw from intense light (Elliot & Covington, 2001; Lang & Bradley, 2010). The approach system is more closely related to hedonistic activities, such as gathering of food and gaining sexual pleasure (Elliot & Covington, 2001; Lang & Bradley, 2010). At its core, affect may be constituted by a constantly changing stream of alterations in the organism's neurophysiological state, which is translated into internal affective code that indicates whether an event is harmful or beneficial (Barrett, Mesquita, Ochsner, & Gross, 2007). Instant reactions to both appetitive and aversive emotional cues enhance perceptual processing and information gathering, and by elevating arousal, mobilize the organism for actions accordingly (Lang & Bradley, 2010). A large body of evidence supports the view that states of being prepared to approach or avoid targets are distinguishably represented in the human brain. The aversive and appetitive cues activate primitive circuitry in the limbic brain and primitive cortex areas. Higher activation of visual processing areas for emotional stimuli is attributable to re-entrant projections to the sensory system from the brain's motivational circuits (Lang & Bradley, 2010).

Studies measuring asymmetric EEG alpha-band activity in the frontal cortices have played a central role in the research on approach-avoidance responses to emotive stimuli, showing that transient emotional states can shift the balance of interhemispheric activity (Allen, Coan, & Nazarian, 2004; Davidson, 1995, 2004) Referring to studies of emotional states, Davidson (1983) proposed that frontal asymmetry was not related to the valence of an emotional stimulus but rather to the motivational system that is engaged by that stimulus. He suggested that the left PFC

is involved in a system facilitating approach behavior to appetitive stimuli, whereas the right PFC is involved in a system facilitating withdrawal behavior from aversive stimuli. To explain prefrontal asymmetries for emotional valence processing, this model assumes that processing related to emotional valence itself is not lateralized in PFC. Emotion-related lateralization is observed rather because emotions can have either approach or avoidance related dimensions. Somewhat similarly, a so-called motivational direction model has claimed that leftward frontal brain activity (based on alpha-band power) is involved in the experience and expression of approach-related emotions and motivation, whereas rightward activity is linked to avoidance-related emotions and motivation (Harmon-Jones, Gable, & Peterson, 2010; Sutton & Davidson, 1997). Therefore, emotion will be associated with a relative right or left asymmetry depending on the extent to which it is accompanied by approach or withdrawal tendencies (Davidson, 1983).

As any other objects, human beings can have more or less favorable impact on the person facing them. It is valuable to have dedicated brain mechanisms guiding individuals to approach or avoid others based on their nonverbally communicated signals, due to the possible survival value that lies within. Human beings commonly have a strong motivation to be accepted and included in social relations, and this desire may increase approach motivation towards acceptance cues. Gaze direction can be a powerful signal of both exclusion and inclusion. People commonly express liking of others by increasing mutual gaze (Maxwell, Cook, & Burr, 1985), and tend to feel ostracized even when strangers presented in pictures look away from them (Wirth, Sacco, Hugenberg, & Williams, 2010). Yet only with real people, a person can truly be acknowledged or ostracized. Wesselmann, Cardoso, Slater, & Williams (2012) showed that people felt more socially disconnected when a passerby did not have an eye contact with them as compared to when an eye contact was formed, and it did not even matter whether the confederate was smiling or having a neutral expression. Interestingly, the gaze direction effect became non-significant when those who did not recall being acknowledged by a stranger were excluded, underlining that the effect of awareness of being looked at by others affects the feelings the encounter evokes.

As noted by Wirth et al. (2010), even pictures of faces can be powerful inclusion or exclusion signals. They can also elicit approach-avoidance neural responses. Relative leftward EEG asymmetry in response to seeing pictures of happy faces and rightward asymmetry in response to pictures of angry faces (all with a direct gaze) has been observed in infants (Davidson & Fox, 1982). At a neural level, direct and averted gaze can also elicit motivational tendencies to approach or avoid (Hietanen

et al., 2008). Hietanen et al. (2008) showed that seeing another person's direct vs. averted gaze had an influence on the observer's neural approach-avoidance motivation related responses. It was found that another person's direct gaze elicited a relative left-sided frontal EEG-activation (approach tendency), whereas averted gaze activated right-sided asymmetry (avoidance tendency). In addition, faces with direct gaze elicited more intense activation in the autonomic nervous system than the averted gaze did. Importantly, all these effects were observed only when participants were facing a real person rather than a picture of a face. It thus seems that, there is mixed evidence on whether there are different neurocognitive processes guiding approach and avoidance responses to other people who are present in person rather than present as digital representations.

2 AIMS OF THE STUDY

2.1 Study I

The stimuli in face processing studies have commonly been pictures of faces, either photographic or schematic, or, more recently, off-line video clips. At a level of visual cognition, it is useful to carry research with highly controlled stimulus material, such as digitally manipulated face pictures. However, it seems that a lot of research claiming to cover social aspects of visual cognition has been conducted by applying nonsocial stimulus material. Although various types of pictures generally elicit the same pattern of early face-sensitive ERP responses (Sagiv & Bentin, 2001), they cannot act, or be acted upon socially, in the physical (embodied) space. We thus wanted to examine whether the perceived corporeal and social presence would have an influence already in the early-stage perceptual encoding of faces. The present study focuses on typical ERP components that have been of major interest in the face and emotion processing research. Considering earlier ERP research, the N170 and EPN responses might be enhanced according to the emotional and motivational saliency of stimulus content. The question arises whether embodied faces presented live have greater influence on the affective-motivational modulations on N170 and EPN responses than pictures of faces. In this study, we investigated whether ERPs to a face of another human differ when presented either live or as a picture.

In Study I, to examine the differences in responses to live and picture stimuli, we presented facial stimuli both as pictures on a computer screen and live through an electronic shutter. A voltage sensitive liquid crystal (LC) shutter can be made opaque or transparent within a millisecond range, thus it allows presentation of live stimuli with a strict control of timing. The participants were shown a human face, a dummy face, and a non-face object (a vase) live and as pictures. By including the dummy face, we controlled the possibility that the ERP difference between real faces and pictures could result from low-level visual differences instead of differences in their potential for social interaction. As compared to face pictures, live faces are three-dimensional (3D). However, because both the human and the dummy faces presented live were 3D, the effect of this factor could be ruled out. Although great care was taken to ensure that the stimuli were visually as similar as possible in live

and picture presentation modes, it was not possible to ignore certain low-level visual differences between the presentation modes. These include differences in the luminance and texture properties of the stimuli as well as possible minor facial movements in the live condition. The study design thus only involved comparison of the ERPs to a human face, dummy face, and a control object separately for live and picture conditions. The participants also evaluated their valence and arousal in response to the facial stimuli. This was done to investigate whether evaluative affective responses differed between the faces in the live and picture presentation modes and whether they were associated with the physiological measures. The main hypotheses were that (i) in both presentation conditions, the human and the dummy faces would elicit enhanced and shorter latency N170 than the non-face object, (ii) in the picture condition, the human and the dummy faces would elicit undifferentiated N170 and EPN responses (both stimuli being non-social stimuli), whereas (iii) in the live condition, the human face would elicit greater N170 and EPN amplitudes and shorter N170 latencies than the dummy face (only human face being a social stimulus.

2.2 Study II

In Study I, we aimed to show that something in the "humanness" or perceived potential for social interaction of a face would enhance early visual ERP responses. All faces in Study I displayed direct gaze, implicating that the persons posing as models for the live human faces actually saw and paid attention to the observers (experimental participants) of these faces. Based on these results we could not, however, conclude whether it was only the corporeal and social presence itself that enhanced the visual processing of these faces or whether it was the notion of being observed, via the gaze directed to the observer, that had the greatest contribution to this effect. As effective the influence of a seen gaze in a picture or in other nonsocial form of presentation may be, it does not capture the very essence of direct gaze as a means of gathering information about the person who is looked at, and in creating mutual contact and mind-sharing between two persons. Averted gaze, in turn, likely communicates interest to peripheral targets, or avoidance of mutual contact with an encountered person. It is therefore likely that the gaze direction makes a difference in terms of physiological responses to seeing a face, whether that face is presented live or as a picture. To clarify this issue, we decided to investigate the effect of social attention via gaze direction on the early perception of live faces.

We measured ERPs to faces with a direct gaze, averted gaze and closed eyes again in two modes of presentation: live and picture. Eyes averted and eyes closed are likely to evoke lower self-involvement and potential for interaction than the direct gaze. Moreover, like direct gaze, the eyes closed condition is visually symmetrical, offering a condition to control for a possible confounding effect of visual symmetry vs. asymmetry in the eye region between faces with a direct vs. an averted gaze. As in Study I, due to an impossibility to control all the low-level visual differences between the presentation conditions, direct comparisons between the conditions were not made. The participants had also a self-evaluation task during the ERP measurements. We studied whether the gaze direction had an influence on self-reported valence and arousal and whether they differed between presentation modes. The main hypotheses were that i) the direct gaze would elicit more negative-going (meaning greater) N170 and EPN amplitudes than both averted gaze and closed eyes and ii) these effects would be seen in the live condition only.

2.3 Study III

In this study, we measured skin conductance responses (SCRs) and relative hemispheric asymmetry in frontal EEG activity to investigate motivational and affective responses to another person's direct and averted gaze presented live vs. as pictures. SCRs have been related to general physiological arousal (Dawson, Schell, & Filion, 1990) and EEG frontal asymmetry to approach-withdrawal tendencies inherent in affective reactions (Davidson, 1993). Skin conductance is one form of electrodermal activity, which reflects the arousal of the sympathetic autonomic nervous system (Boucsein, 2012). Electrodermal activity is regarded as a sensitive and valid indicator for a lower arousal range, reflecting small, mostly cognitively determined, variations in arousal (Boucsein, 2012).

During physiological recordings, the participants were asked to perform two tasks: to discriminate the gaze direction of the stimulus faces and to evaluate how pleasant they felt immediately after seeing each face. We also studied whether the gaze direction would have an effect on the subjective ratings of self-awareness and, especially, on self-awareness related to how one is perceived in the eyes of the other people. We also wanted to investigate the possible effects of stimulus gender. Hietanen et al. (2008) had only female faces as stimuli, and pictures of female faces have shown to be rated as more approachable than pictures of male faces (Campbell Neuert, Friesen, & McKeen, 2010). This might apply to live faces as well. It is thus

possible that physiological approach-avoidance tendencies in response to real faces are sensitive to the sex of the gazing person. Here we decided to use both a female and a male face as stimuli. Because this was the first study in which we attempted to investigate the possible effects of stimulus face sex on neural approach-avoidance related responses, we recruited female participants only. Previous research has shown that females show greater physiological responses to emotion-related facial cues than males (Anokhin & Golosheykin, 2010), and females are behaviorally more sensitive to eye gaze as compared to males (Gueguen & Jacob, 2002). Four main hypotheses were tested: i) perceiving a direct gaze would elicit relative left-sided frontal EEG asymmetry indicative of a motivational tendency to approach and averted gaze would elicit smaller relative left-sided asymmetry or even relative rightsided asymmetry indicative of avoidance, ii) the SCRs would be greater for the direct vs. averted gaze, iii) public self-awareness would be heightened in response to a direct vs. averted gaze, and iv) to extend and corroborate the earlier findings (Hietanen et al., 2008), we expected to obtain all these effects in the live but not in the picture presentation mode, and with a concomitant behavioral task to ensure comparable attention allocation to live faces and pictures of faces.

2.4 Study IV

Hietanen et al. (2008) found that seeing another person with a direct, rather than an averted, gaze differently activated the neural systems participating in the regulation of basic approach-avoidance motivation. Moreover, in Study III, as well as in earlier studies with rather similar designs (Hietanen et al., 2008; Helminen et al., 2011), enhanced physiological arousal in response to eye contact with a "live" person was observed, and it was suggested that this effect relates to increased self-awareness evoked by the immediacy and attention of another, observing person. In these previous studies, however, the stimulus persons displayed a neutral expression on their faces, yet it has been observed that both the facial expression and the gaze direction are valuable determinants in inferring peoples' motivational tendencies (Adams et al., 2003; 2005).

Here we wanted to investigate the effect of facial expression on the psychophysiological responses to direct and averted gaze, and we focused on the effects of a smile, since in everyday social interactions, it is an expression closely related to approach motivation. A smile, accompanied by an eye contact, is commonly seen as a sign of acceptance and affiliation, and seeing a happy face elicits

positive feelings in the observer (e.g., Wild, Erb, & Bartels, 2001). There might also be normative expectations for people who seek eye contact to smile. Indeed, in many cultures, a smiling face is associated with the expression of happiness, and a face without a smile is inferred to communicate dominance (Keating et al., 1981). Smiling people also tend to be perceived as more sociable than people with neutral faces (Matsumoto & Kudoh, 1993). Not smiling, then, is a social signal in itself. It is possible that the use of neutral faces as stimuli in our previous studies exerted, in fact, a negative rather than neutral or positive effect on the observer. An unknown person maintaining a neutral face and an eye contact thus withholds a critical sign of benevolent intention that is usually communicated via smiling. This, in turn, may evoke the feeling that this person is indifferent, or even judgmental, towards others.

In Study IV we measured autonomic arousal and frontal EEG alpha asymmetry in response to real faces to examine whether affective and motivational neural responses to seeing a direct and an averted gaze would be modulated by facial expression (neutral/smiling). A smiling face might be a more rewarding target to look at (Lau, 1982), and hence a more approachable and salient stimulus than a neutral expression. It has been proposed that increased electrodermal activity reflects subjective salience of affective stimuli (Critchley, 2002), and autonomic arousal as measured by SCRs is shown to enhance both when experiencing happiness (see Kreibig, 2010 for a review), and when seeing a happy face (Dimberg & Thunberg, 2007). Martin and Gardner (1979) found greater arousal to a smiling than a neutral face in live interaction. They also varied the confederates' gaze direction but concluded that only facial expression had a significant effect on arousal. There were thus reasons to assume that a smile on a face of a person looking at the observer could enhance the observer's psychophysiological responses. Another question was whether a smile has similar effects when presented together with an averted gaze. The main hypotheses were that i) there would be greater autonomic arousal and greater relative left-sided frontal asymmetry to seeing a direct vs. an averted gaze, and ii) these effects would be enhanced when the gaze is accompanied by a smile rather than a neutral expression.

3 METHODS AND RESULTS

3.1 Overview of the methods

3.1.1 The participants

In Studies I-IV, the participants were right-handed undergraduates from the University of Tampere or Tampere Technical University. They gained either course credits or movie tickets for participation, had normal or corrected-to-normal vision, and pre-reportedly no history of neurological or psychiatric diagnoses. All participants gave their informed, written consent prior to the experiment.

3.1.2 Face presentation

The stimuli were faces of young adults, and in Study I, a head (and upper torso) of a realistic-looking dummy (a fashion mannequin) was also used as a stimulus. In all Studies, the faces were viewed through a 30 × 40 cm voltage-sensitive LC shutter (Figure 1), and in Studies I-III, the face were also presented as pictures on a computer screen. The face pictures were digital color photographs on a desktop computer screen, and the retinal size of the stimulus faces in both live and picture presentation modes were approximately 8.0° horizontally and 11° vertically. In Studies I-III, the LC shutter (LC-TEC Displays AB) was attached to a white frame between the stimulus and the participant. In Study IV, the shutter (NSG UMU Products Co., Ltd.) was attached to a black frame, in which the LC window size was adjusted to have the same measures as in the previous studies. The LC shutter switched between opaque and transparent states within an overall speed of 3 ms. The state of the LC shutter (transparent or opaque), as well as the presentation of the face pictures, was controlled by NeuroScan Stim software (NeuroScan, El Paso, Texas, USA). During the face viewing through the LC shutter, the stimulus persons were instructed to avoid all extra bodily movement and to look directly at the eyes of the participant. The eye level between the stimulus person and the participant was

always matched before the recordings started. In Studies II–IV, fixation marks were attached on the stimulus person's left and right sides on the LC shutter panel to control the stimulus person's angle of gaze aversion in the live presentation mode. The deviance from the direct gaze was 30°. During the inter-stimulus interval (ISI), the shutter remained opaque and the computer screen remained black.



Figure 1. The presentation of faces through the liquid crystal shutter.

3.1.3 Physiological measures

In Studies I-II, event-related potentials (ERPs) in the electroencephalography (EEG) were recorded in order to study early-stage neurocognitive processes. The analyses focused on relatively early components associated with face perception and attention/emotion/motivation. Continuous EEG was recorded using an electrode cap (Electro-Cap International, Eaton, OH). The recording was made with 22 tin electrodes positioned according to the 10–20 system, and referenced to the nose tip. Skin abrasion and electrode paste were used to reduce the electrode impedances below $5k\Omega$. Horizontal electro-oculography (HEOG) and vertical electro-oculography (VEOG) were recorded bipolarly from the sites beside the outer canthi of each eye (HEOG) and above and below the left eye (VEOG). The EEG signal was amplified with SynAmps amplifiers with a gain of 5000 and a 1–200 Hz band-

pass filter (50-Hz notch filter enabled). The continuous signal was digitized at 1000 Hz. The EEG-signal was segmented to 600-ms epochs starting 100 ms prior to stimulus presentation, and segments with eye movements and blinks were excluded from further analyses. For the accepted trials, the average waveforms for each participant within each of the experimental conditions were calculated.

In Studies III-IV, there were two physiological methods to investigate affectivemotivational reactions: skin conductance responses (SCR), and frontal alpha-power asymmetry in the EEG activity. The EEG was recorded with tin electrodes from the sites F3, F4, F7, F8, C3, Cz, C4, P3, and P4. The signal was also recorded from the left ear (A1), and referenced online to the right ear (A2). Off-line, the continuous EEG signal was corrected for blink artifact using a blink reduction algorithm (Semlitsch, Anderer, Schuster, & Presslich, 1986), and referred to both ears. Eye movements other than blinks and other visible artifacts were eliminated based on visual inspection. Artifact-free EEG during the 5-s stimulus period was segmented to eight 1.024-ms epochs with 75% overlap between adjacent epochs. Spectral power was calculated for each epoch using Fast Fourier Transform (FFT) with a 10% Hanning taper. The obtained power spectra were averaged over all artifact-free epochs within each trial and over separate trials within each experimental condition. Trials with less than 50% artifact-free epochs were excluded from averaging. For average power spectra within each condition, power density values (µV2) within the alpha band (8-13 Hz) were calculated and natural ln-transformed to normalize the distributions.

The EEG asymmetry scores were calculated for electrode pairs at frontal (F8/F7, F4/F3), central (C4/C3), and parietal (P4/P3) scalp regions by subtracting the Intransformed power density values for the left site from that for the right site (Allen et al., 2004). Alpha activity has been shown to inversely relate to cortical activity (Davidson, Marshall, Tomarken, & Henriques, 2000). The main data analysis was confined to the data measured from the electrode pair F4/F3, since the affective and motivational effects on the frontal EEG asymmetry are frequently detected from these recording sites (Davidson, 1995). The other recording sites were also analyzed to detect the relative asymmetry differences, but the investigated effects were significant from the mid-frontal electrode pair F4/F3 only.

For the SCRs, the electrodes (Ag/AgCl) were coated with isotonic electrode paste and attached to the palmar surface on the medial phalanxes of the index and middle fingers on the participant's non-dominant hand. The signal was acquired with a SCR amplifier supplying constant-voltage AC excitation (22 mV) (ADInstruments). The skin conductance coupler was calibrated prior to each session to detect activity in

the range of 0–40 Mho. The sampling rate was 100/s. An SCR lasts several seconds and usually follows a characteristic pattern of an initial, relatively steep rise, a short peak, and then a slower return to baseline (Boucsein, 2012). The SCR was defined as a maximum change from the baseline level (at the stimulus onset) during a 4-second time period starting after 1 s from the stimulus onset till the end of the stimulus presentation. Responses contaminated by participant's body movements or technical problems during the measurement were eliminated from subsequent analysis. For the statistical analyses, the data were averaged over the trials in each condition for each participant. The mean value of SCR was computed across all trials within the stimulus category including those without a measurable response as a zero response. This method of calculation, reflecting the peak amplitude of the SCR, results in the magnitude of the galvanic skin conductance responses (cf., Dawson et al., 1990). We also utilized data transformations which best normalized the SCR data in question. In Study III, we performed a log transformation [log (SCR + 1)], and in Study IV, a square root (SQ) transformation [SQ (SCR)].

3.1.4 Behavioral measures

To broaden the interpretation of the results from the physiological indicators, we collected subjective evaluations on the face stimuli. In particular, we wanted to study whether the subjective ratings would differ in live vs. picture presentation modes. In Studies I-II, the participants completed a Self-Assessment Manikin (SAM; Bradley & Lang, 1994) to assess their affective valence (positive/negative) and arousal (excited/calm) to the stimuli on a nine-point scale. Moreover, the participants moved a lever of a custom-built potentiometer to indicate how pleasant the participants felt after viewing each face (Study III) or how positive/negative the facial expression in each stimulus face appeared (Study IV). The output voltages from the potentiometer between -2 (extremely unpleasant/negative) and pleasant/positive), and the lever of the potentiometer moved approximately 4 cm forwards or backwards from the central position labeled as "neutral". The output of potentiometer was collected with the SCR measurement (ADInstruments). In Study III, we used a situational self-awareness scale (SSAS; Govern and Marsch, 2001). Three of the 9 items of SSAS measure public selfawareness (e.g., Right now, I am concerned about the way I present myself), another three of the items measure private self-awareness (e.g., Right now, I am conscious of my inner feelings), and the remaining three measure awareness of "immediate

surroundings" (e.g., Right now, I am keenly aware of everything in my environment). The items have a seven-point scale ranging from 1 (strongly disagree) to 7 (strongly agree).

In Study IV, we measured individual differences in behavioral approachavoidance tendencies, proneness to situational and trait anxiety, and feelings of social awareness in response to face stimuli. To study behavioral approach-avoidance tendencies, we administered behavioral activation vs. inhibition scales (BIS/BAS), developed to measure individual differences in the neurobiological motivational systems regulating approach-avoidance behavior (Carver & White, 1994). This method is based on Gray's (1994) theory on how behavior is regulated by behavioral inhibition (BIS) and behavioral activation (BAS) systems. The BIS is activated in a conflict situation, and serves to interrupt or inhibit ongoing goal-directed behavior. The BAS, in turn, mediates approach behavior and is engaged by stimuli signaling reward. (Carver and White, 1994). BIS/BAS scores are found to correlate with lateralized prefrontal cortex activity: right-sided activity has been related to increase in BIS, and left-sided activity to increase in BAS (Balconi & Mazza, 2009; Berkman & Lieberman, 2010; Gray, Braver, & Raichle, 2002; Wacker, Chavanon, Leue, & Stemmler, 2008). Situational and trait anxiety were investigated via a STAI-STATE anxiety inventory (Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983). Finally, to investigate social presence in relation to psychophysiological measures, we applied a custom version of Social presence scale, originally designed to measure feelings of social presence in human-computer online interactions settings (see Sallnäs, 2005).

3.2 Study I

3.2.1 Methods of Study I

In the final study sample, there were 19 participants (16 females; mean age 23.9 years, range 19–40). An additional three participants were tested, but excluded owing to excessive artifacts (N = 2) or technical problems (N = 1). Three types of stimuli were presented: the face of an adult male (one of the two experimenters) the face of a lifesized male dummy (Figure 2), and a control stimulus (a brown vase). The face displayed a neutral expression and a direct gaze. In the live presentation mode, the participants were seated at a distance of 110 cm from the frame and 70 cm from the computer screen. The stimulus person was seated at a distance of 53 cm from the

frame. In both live and picture presentation modes, the three different stimuli were presented in separate blocks. Within each block, the stimulus was repeated 70 times with a 500-ms presentation time and a 2000-ms inter-stimulus interval. After every 10th trial, there was a 20-s break. A short signal was given through the speakers 5 s before the start of the next 10-trial sequence to alert the participant and the stimulus person behind the shutter to remain as motionless as possible. The order of the stimulus blocks within the presentation modes was counterbalanced across participants. Immediately after each stimulus block, the participants evaluated their valence and arousal towards the stimuli with the Self-Assessment Manikin. Continuous EEG was recorded while the faces were viewed. For N170, the peak was defined as the minimum amplitude within a 108–180-ms time window for the temporal and occipital recording sites. For EPN, mean amplitudes were analyzed in each condition within a 180–300-ms time window at temporal sites. The peak amplitude and latency scores were analyzed separately for the live and picture conditions.

3.2.2 Results of Study I

In the picture presentation mode, there were greater N170 responses for human and dummy faces than for the vase on the left and right occipital sites. Furthermore, the dummy face elicited larger N170 than the vase at the left temporal site (T5), but the human face did not differ either from the dummy or from the vase (control object). Such differences were not observed at the right temporal site (T6). For the EPN, there were no amplitude differences in the picture presentation mode at the left and right temporal sites. In the live presentation mode, there were differences both in the N170 and EPN amplitudes depending on the stimulus type. At occipital and temporal measurement sites, there was larger N170 for the human and dummy faces than for the vase. Similarly, the EPN was greater for the human and dummy faces than for the vase. Importantly, however, the N170 amplitude did not differ between the human face and the dummy, whereas the EPN was larger for the human face than for the dummy. N170 latencies were shorter for the human and dummy faces than for the vase both in the picture and in the live presentation modes. However, the N170 latencies were not shorter for the human face than for the dummy in the picture presentation mode, and in the live presentation mode the N170 latency was shorter for the human vs. the dummy face only at the left occipital site (O1). The ERP grand means for the both stimulus presentation modes are shown in Figure 2.

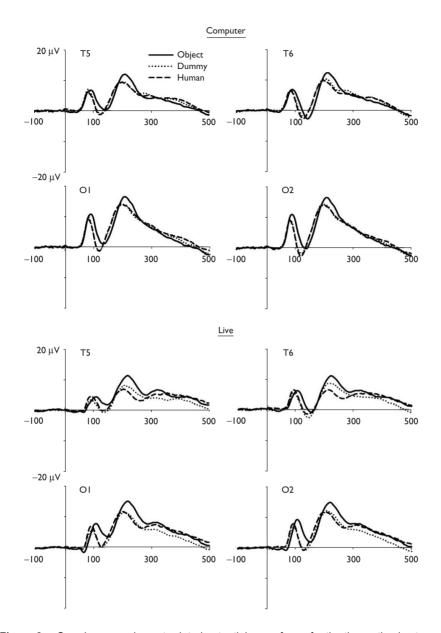


Figure 2. Grand-averaged event-related potential -waveforms for the three stimulus types at occipital (O1, O2) and temporal (T5, T6) channels in the computer (picture) and live presentation modes.

The results from self-reported valence and arousal (scale range: 1–9) are shown in Table 1. Valence ratings did not differ in the picture presentation mode. In the

live presentation mode, instead, the human face was evaluated as more pleasant than the dummy face, but neither of these ratings differed from those measured for the vase. The arousal ratings did not differ between the face types (human, dummy) or between the faces and the vase in either of the presentation modes.

Table 1. Self-rated arousal and valence as a function of stimulus type and presentation mode.

Presentation mode	Valence		Arousal	
	M	SD	М	SD
Picture				
Human	5.79	1.51	2.68	0.95
Dummy	5.58	1.61	2.58	1.26
Control	6.05	1.22	2.68	1.20
Live				
Human	6.68	1.34	2.84	1.30
Dummy	5.89	1.15	3.05	1.18
Control	6.11	1.45	2.74	1.10

3.3 Study II

3.3.1 Methods of Study II

The participants (16 females; mean age 24.1 years, range 20–43) were presented a female face (the experimenter displaying a neutral expression and gazing either straight forward, to the left or to the right, or having closed eyes. In the live presentation mode, the participants were seated at a distance of 110 cm from the frame and 70 cm from the computer screen. The stimulus person was seated at a distance of 53 cm from the frame. The participants were told that the experiment concerned face processing and they were instructed to look at the stimulus faces as naturally as possible. The live and picture stimuli were presented in separate blocks. In both blocks, 180 trials were presented (60 per stimulus type) with a 500-ms presentation time and a 2000-ms inter-stimulus interval. Within the blocks, the stimuli were presented in 10-trial sequences repeating the same stimulus. Within each block, there were six 10-trial sequences of direct, averted and closed eyes conditions.

The order of these sequences was randomized. After each 10-trial sequence, there was a 15-s break. A short signal was given 5 s before the start of the next 10-trial sequence to alert the participant, and, in the live condition, the person behind the shutter. Immediately after each 10-trial sequence, the participants completed the Self-Assessment Manikin to evaluate the stimuli. For N170, mean response amplitude was analyzed within a 110-150-ms time window in the picture condition and within a 125-165-ms time window in the live condition, because N170 occurred later in the live condition. For EPN, the mean response amplitude was analyzed within a 190-290-ms time window in both conditions. Since the peak of N170 was not clear in all participants, the analysis of the peak latencies was not reasonable. We also analyzed the mean P1 responses within a 70–110-ms time window in the picture condition and within an 80-120-ms time window in the live condition to investigate whether the gaze direction had an effect at a very early processing stage, as some studies have found the P1 being sensitive to facial cues, such as facial expressions (Batty and Taylor, 2003; Holmes et al., 2009; Holmes, Nielsen, & Green, 2008). The amplitude analyses of the components were based on ERPs recorded from selected occipital and temporal electrode sites.

3.3.2 Results of Study II

The early-stage P1 component was not sensitive to gaze direction of the stimulus faces in either live or picture presentation mode. Instead, at later processing stages, N170 and EPN were sensitive to gaze direction, but for the live faces only. The N170 and EPN amplitudes did not differ between the gaze stimuli when the faces were presented as pictures. In the live presentation mode, instead, the N170 for direct gaze was greater compared to averted gaze. There were no N170 amplitude differences between direct gaze and closed eyes and between the averted gaze and the closed eyes. Furthermore, for the live faces, the EPN was sensitive to gaze direction. There was greater EPN for direct vs. averted gaze, and, marginally, for direct gaze vs. closed eyes. Figure 3 shows the mean N170 and EPN amplitudes for the different gaze stimuli averaged across recording site and hemisphere.

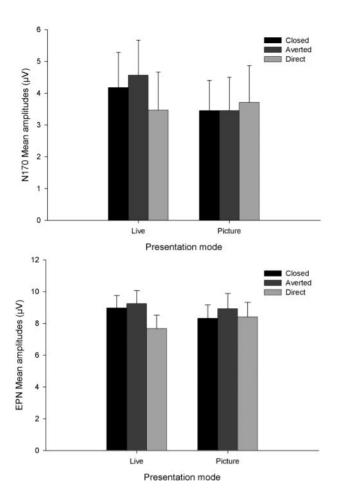


Figure 3. Mean amplitudes of the N170 and EPN components in the picture and live presentation modes for the three different gaze conditions.

In the behavioral results (see Table 2), gaze direction did not have an effect on valence and arousal ratings of the face pictures. However, in the live presentation mode, direct gaze resulted in less pleasant feelings than averted gaze and closed eyes. Averted gaze elicited somewhat less pleasant feelings than closed eyes. Similarly, direct gaze was evaluated as more arousing than averted gaze, and averted gaze, in turn, was evaluated as more arousing than closed eyes. Any associations between the amplitude of the ERP responses and the ratings of valence and arousal in either of the stimulus presentation modes were not found.

Table 2. Self-rated valence and arousal scores (1 = very unpleasant/low arousal; 9 = very pleasant/high arousal) as a function of stimulus type (eyes: direct, averted and closed) and presentation mode.

Presentation mode	Valence M (s.d.)	Arousal M (s.d.)
Picture		
Direct	6.47 (1.54)	1.66 (1.07)
Averted	6.39 (1.48)	1.97 (1.17)
Closed	6.63 (1.54)	1.41 (1.01)
Live		
Direct	5.93 (1.65)	2.57 (1.51)
Averted	6.50 (1.45)	1.90 (1.30)
Closed	7.00 (1.24)	1.22 (1.01)

3.4 Study III

3.4.1 Methods of Study III

The participants were 25 females (mean age = 21.3 years, range = 19–26 years). After some participants were excluded from the final data sample due to excessive artifacts or technical errors, the final data sample included 23 participants for the EEG, 21 participants for the SCR, and 24 participants for the SSAS analysis. The stimulus persons were the two experimenters (male and female; see Figure 4) collecting the data. In both presentation modes, each participant viewed faces of only one person, half of them viewing the female and the other half, the male. The experimenter serving as a stimulus person assisted the other experimenter in the preparation of the physiological recordings and had some small talk with the participant meanwhile, but they refrained from giving any instructions for the participants in order to diminish status difference between them as a stimulus person and the participant. During the face viewing study blocks, the stimulus person sat silent behind the LC panel. Each time the shutter opened, the stimulus person's gaze was directed either to the participant's eyes or averted to the left or to the right. During the openings, the stimulus persons also aimed at having a neutral expression on their faces. In the

live condition, the stimulus persons had a distance of 30 cm from the panel. The participants' distance from the panel and the computer screen was 70 cm. There were 16 trials within a block. On 8 trials, the gaze was direct and, on the remaining 8 trials, averted. The presentation order of the trials within a block was pseudorandom (no more than three consecutive trials of the same type). Each trial lasted for 5 s, and the ISI varied randomly from 25 to 30 s. A short audio signal was presented through the speakers 5 s before each trial to direct the participant's attention to the shutter/computer screen and, in the live condition, to prepare the stimulus person to the opening of the shutter.



Figure 4. The stimulus persons with direct and averted gaze.

Prior to the face viewing, the experimenter explained that the participant's physiological responses would be measured while they viewed another person's face. The participants were instructed to remain relatively motionless during the trials and to respond verbally immediately after each trial whether the gaze direction of the stimulus face they saw was direct or averted. Immediately after each gaze discrimination response, the participants were asked to consider how pleasant they felt during the stimulus presentation and slide a lever of the potentiometer accordingly. During the experiment, one experimenter sat near the participant in such a way that they were invisible to the participant, but able to observe and make

record of the participant's and stimulus person's possible body movements. After the physiological recordings, the SSAS ratings were collected for live and picture faces in separate blocks. In each block, there were a total of six trials: three with direct gaze and three with averted gaze. The participants were instructed to watch the stimulus and to complete a set of three questions after every trial. Responses contaminated by movement artifact or technical problems were eliminated from subsequent analysis. The number of eliminated trials did not differ between direct and averted gaze neither in the live or picture condition.

3.4.2 Results of Study III

In the gaze discrimination task, the overall response accuracy was very high, 99.6%, and the accuracy did not differ between direct and averted gaze neither in the live or picture condition. For the pleasantness ratings, the viewing of pictures was evaluated slightly more pleasant than viewing of the live faces. Gaze direction and stimulus person's sex did not modify these ratings. In the live presentation mode, there was no difference in the ratings between the female and male stimulus person. When the faces were presented as pictures, the female stimulus person obtained higher ratings than the male stimulus person, although this difference did not turn out to be statistically significant.

Due to an interaction effect of gaze direction, presentation mode, and stimulus sex, the effect of gaze direction was analyzed separately for both presentation modes and for female and male stimuli. For the live female stimulus, the mean EEG asymmetry score was significantly higher (greater relative left-sided asymmetry) for the direct vs. averted gaze, whereas there was no difference in the asymmetry scores between direct and averted gaze in the female picture presentation mode. For the male stimulus person, the gaze direction did not have any effect on the asymmetry scores in either presentation mode. Moreover, in the live presentation mode, the mean asymmetry score for the direct gaze was higher for the female than the male stimulus person, whereas this was not the case in the picture presentation mode. There was no difference between the female and male stimuli in the asymmetry scores for the averted gaze in either presentation mode. Figure 5 shows the mean asymmetry scores as a function of gaze direction and presentation mode.

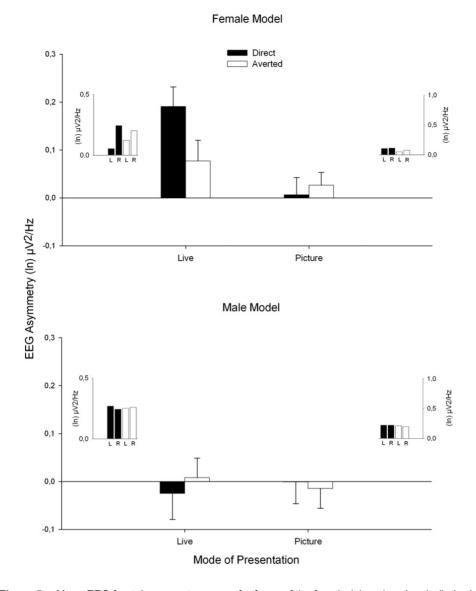


Figure 5. Mean EEG frontal asymmetry scores for faces of the female (above) and male (below) stimulus models as a function of gaze direction and presentation mode. The ordinates express the difference in the EEG alpha power (in In-transformed μV2/Hz) between electrodes F4 and F3. Positive values indicate relative left-sided asymmetry and negative values indicate relative right-sided asymmetry. The small insert graphs show the absolute values of the EEG alpha power recorded from the left hemisphere (L, electrode F3) and right hemisphere (R, electrode F4) electrodes in different stimulus conditions.

Since there was the effect of sex of the stimulus faces in some of the EEG alpha asymmetry results, and we had only one female and one male as stimuli, it was

possible that some facial attributes other than those related to sex evoked differential affective responses. These, in turn, might have interacted with the motivational reactions to gaze direction. To further examine this issue, we collected supplementary data by showing pictures of our stimulus persons (the same photographs which were used in the picture condition) together with corresponding face pictures of four other individuals (2 males and 2 females) to 12 additional female participants. Like in the experiment, each picture was shown for 5 s. Immediately after each picture, the face was rated on a 7-point scale for the following characteristics: fear, joy, anger, sadness, surprise, disgust, approachability, dominance, and likeability. The results showed that the original female model of the study was evaluated as expressing less anger and disgust but more sadness than the male model. In addition, the female model was evaluated as being more likeable than the male model.

For the SCRs, there was an interaction between gaze direction and presentation mode. As a result, the live and picture conditions were analyzed separately. In the live presentation mode, the SCR was larger for the direct vs. averted gaze. In the picture presentation mode, there was no difference between direct and averted gaze. Sex of the stimulus face did not have an effect on the SCR results. Figure 6 shows the mean SCRs as a function of gaze direction and presentation mode.

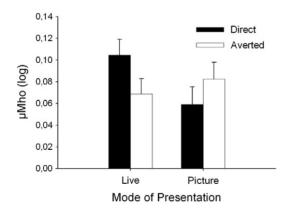


Figure 6. Mean skin conductance responses [in log-transformed (SCR + 1) μMho] for faces as a function of gaze direction and presentation mode.

The SSAS rating data were analyzed separately for each three subscales of self-awareness (public, private, and surroundings). For the public self-awareness, there was an interaction between gaze direction and presentation mode, thus the

presentation modes were analyzed separately. In the live presentation mode, the public self-awareness was marginally higher for direct vs. averted gaze. In the picture presentation mode, the gaze direction had no effect on public self-awareness. The public self-awareness was higher also for the direct gaze in the live than in the picture presentation mode. Importantly, the other types of self-awareness ratings (private and surroundings) did not differ in either presentation mode. For all three types of self-awareness ratings, it did not make a difference whether the participants viewed a male or a female face. Finally, we investigated whether the stimulus presentation order (the live faces presented before or after the face pictures) would have an effect on physiological or behavioral results. As anticipated, the order of the face presentation had no influence on the aforementioned results.

3.5 Study IV

3.5.1 Methods of Study IV

The participants were 22 females (mean age = 22.7 years, range = 19–39 years). Three participants were excluded from the final EEG and SCR analyses due to excessive artefacts, leaving 19 participants for the physiological data sample. The stimuli were the faces of two female students naïve to the purpose of the experiment and unknown to the participants. They were instructed to present a neutral and a smiling face with a direct and an averted gaze. In this experiment, only live faces were used as stimuli. In the smiling face condition, the stimulus persons were displayed nonenjoyment (or "social") smiles by aiming at restricting the smile to the mouth area, thus lacking the activity of m. orbicularis oculi involved in enjoyment (or "Duchenne") smiles (Ekman, Davidson, & Friesen, 1990; Frank et al., 1993). It was easier for the stimulus persons to generate nonenjoyment than enjoyment smiles repeatedly, and our objective was to have as little variability as possible in the smiles throughout the experiment.

The distance from the LC shutter was 30 cm for the stimulus person and 100 cm for the participant. Each participant saw the faces of both stimulus persons. The presentation order of the stimulus persons was counterbalanced across the participants. There were 32 trials: 16 smiling and 16 neutral faces. Half of the smiling and neutral faces were paired with a direct gaze, and the other half, with an averted gaze. The faces were presented in four blocks: two for one stimulus person and two

for the other. Within a block, there were a total of 8 trials. The presentation order of the stimulus types within a block was pseudo-random (no more than two consecutive trials of the same type). Between the blocks, there was a short break during which the stimulus persons changed places. The experimenter monitored the skin conductance level throughout the experiment and controlled the timing of stimulus presentation. After initiation of each trial, there was an audio signal presented via an earplug to the stimulus person to prepare her to the opening of the shutter. Four seconds after the audio signal, the LC shutter became transparent. Each face was presented for 5 seconds, and the inter-stimulus-interval (ISI) was varied manually in each trial so that the minimum ISI was fixed to 11 seconds.

3.5.2 Results of Study IV

The SCR results (see Figure 7) showed greater arousal for seeing the direct vs. averted gaze both in the neutral and in the smiling face, being even more pronounced in response to the smiling face. Overall, the SCRs did not correlate with the valence ratings. However, when analyzing the different gaze direction - facial expression combinations separately, we found a negative correlation between the SCRs and the valence ratings for the neutral expression with a direct gaze, implicating that those who tended to rate a neutral face with a direct gaze as being negative showed greater autonomic arousal toward those faces. None of the other behavioral measures did correlate with the SCRs.

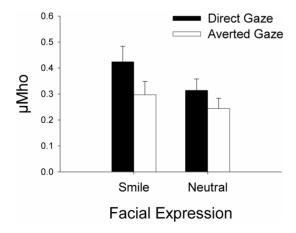


Figure 7. Mean skin conductance responses (square root-transformed SCRs in μMho) as a function facial expression and gaze direction.

The alpha-band power distribution in the EEG was not modulated by gaze direction or facial expression. However, there was substantial variation among the participants in their overall alpha-asymmetry scores. Some participants showed negative asymmetry scores (indicative of avoidance) in response to all types of stimuli, and their asymmetry scores were more negative for the direct vs. averted gaze. Others, in contrast, had positive asymmetry scores (indicative of approach) to all stimulus types, and their asymmetry scores were more positive for the direct vs. averted gaze. We thus calculated new asymmetry indices: 1) individual's asymmetry score averaged across all experimental conditions (asyscore overall) and 2) the difference in asymmetry scores for direct and averted gaze (asyscore_direct asyscore averted). For the latter index, increasing negative values would indicate increasingly stronger avoidance-related brain activity for direct vs. averted gaze, whereas increasing positive values would indicate increasingly stronger approachrelated brain activity for direct vs. averted gaze. When these indices were correlated, we found a marginally significant correlation between the overall asymmetry index and the gaze direction difference index (see Figure 8). The behavioral ratings did not correlate with the asymmetry scores.

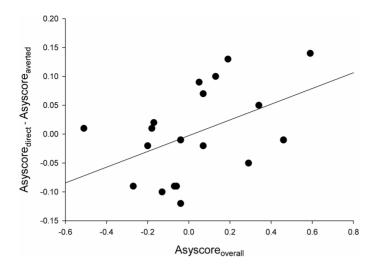


Figure 8. A scatter plot with a linear fit curve for the overall asymmetry score in the EEG alpha power (in In-transformed μV2/Hz between F4 and F3) averaged across all experimental conditions (X-axis; asyscoreoverall) vs. the difference in asymmetry scores for direct and averted gaze (Y-axis; asyscoredirect –asyscoreaverted). For X-axis scores, negative values indicate right-sided asymmetry and positive values indicate left-sided asymmetry. For Y-axis scores, negative values indicate stronger avoidance-related brain activity for direct vs. averted gaze, whereas positive values indicate stronger approach-related brain activity for direct vs. averted gaze.

The valence ratings of the faces showed that, in general, the smiling faces were rated as being positive, whereas the neutral faces were rated as being slightly negative. The smiling faces (M = 0.76, SD = 0.32) were rated as being more positive than the neutral faces (M = -0.41, SD = 0.21). The faces with a direct gaze (M = 0.29, SD = 0.19) were rated as being more positive than the faces with an averted gaze (M = 0.06, SD = 0.19), whether the faces were smiling or not. The valence ratings did not correlate with the other behavioral measures of this study.

4 DISCUSSION

4.1 Overview of the results: the live face effect

In this series of studies, event-related potentials (ERPs) and alpha band power analysed from the electroencephalographic (EEG) activity were applied in order to study the neurocognitive processes involved in perception of facial information. Furthermore, measures of psychophysiological arousal and subjective feelings in response to different types of facial stimuli were applied. Overall, looking at live faces of people present in person tuned the viewers' affective-motivational brain systems differently than a variety of faces looked at via picture presentation media.

Study I showed that early visual encoding of a faces was more intensive when the face being viewed was a real human being rather than a dummy. This enhancement was observed only when faces were presented live through a liquid crystal window, but not when presented as pictures on a computer screen. In Study II, the early enhancement in visual processing was greater for live faces with direct than averted gaze or closed eyes, yet again this difference was not found in response to the pictures of these very same faces. Study III continued investigating the effects of gaze direction in live faces vs. face pictures. Earlier evidence of greater approachrelated neural activity and autonomic arousal to live faces with direct than averted gaze (Hietanen et al., 2008) was elaborated by showing that when attention allocation to real faces and face pictures was coordinated by a gaze-related task, the direct and averted gaze still evoked differential neurocognitive processing only in response to the live faces. Furthermore, Study IV, employing live presentation of faces only, examined the combined effects of emotional expression and gaze direction. Autonomic arousal was greater for smiling than neutral faces in response to an eye contact, whereas there was no such difference between facial expressions in response to an averted gaze. However, the difference in frontal asymmetry for direct vs. averted gaze, observed in the earlier studies, was not replicated in Study IV, and the facial expression did not have an effect on this response either.

Taken together, the results of Studies I-IV indicate that presentation medium may have a substantial top-down influence on low-level visual processing as well as on affective-motivational processing at later processing stages. I will now discuss the results of these studies in more detail. Moreover, I will discuss the general methodology and future implications of these studies against recent research in affective-social neurosciences and related fields. Finally, I shall present concluding remarks based on this discussion.

4.2 Seeing a live face enhances visual perception

The results of Study I showed enhanced neural processing of a human face as compared to a dummy face when both were presented live, but not when they were presented as pictures. The results did not provide strong support for the hypothesis that the negative occipitotemporal potential N170, suggested to reflect the structural encoding of face, discriminates between the human face and the dummy in either presentation modes. Instead, at a later processing stage, the EPN reliably discriminated between the human and the dummy faces in the live condition, but not when they were presented as pictures. The live face perhaps attains special regard at the EPN stage in which affective and motivational factors may have a more prominent role than at the N170 stage in visual processing. There seems to be particular significance, perhaps affective and motivational by nature, in the physically present human face. Previous research has shown that affective-motivational factors, whether related to threat or reward, can intensify visual processing early in the visual processing stream (Balconi and Pozzoli, 2003; Werheid, Schacht, and Sommer, 2007).

A physically present real face has potential for interaction in the eyes of the viewer, hence attaining high affective and motivational significance. An organism's recognized potential for a variety of actions, the state of preparedness, might be an important signal for the human attention system; it is more adaptive to intensify processing resources toward a potentially reactive rather than an inactive object in sight. A non-mediated, potentially reactive human face enhances visual attention and thus summons extra resources to higher-level processing and action planning. For instance, during face perception, a variety of motor responses to faces (i.e., facial mimicry) are prepared before the interpretation of the facial signals has been finished (Freeman, Ambady, Rule, & Johnson, 2008), possibly because such preparatory actions improve understanding the immediate feelings and intentions of the other person in order to mediate social interaction accordingly. Recent evidence suggests that perceptual sensitivity and behavioral responsiveness to others' actions and mental states is based on low-level saliency mechanisms rather than higher-level

representational processing (Dolk et al., 2011; Vlainic, Liepelt, Colzato, Prinz, & Hommel, 2010). There are neurocognitive mechanisms that are possibly involved in action prediction and preparedness. Cortical areas such as STS are sensitive to how another person's motion is related to his or her intentions (Vander Wyk, Hudac, Carter, Sobel, & Pelphrey, 2009), therefore having a role in constraining the options for likely next actions.

Acting upon mutual understanding of intentions is, indeed, essential in smooth cooperation. Complexity of human social systems can be thought to formulate selection pressures for neural circuits that decode and assess social information efficiently (Dunbar, 1993; Dunbar & Shultz, 2007), and the decoding process might be driven by activity in neurocircuits related to the managing of affect and reward. Comprehensive and accurate analysis of the nature of environmental stimuli is essential in predicting what is about to happen next, and all the more important it becomes when the organism as a target of attention has a mind of its own. Indeed, besides the reactivity potential, perhaps more "mind", i.e., feelings, thoughts and intentions, is related to a real human being who is physically present, whereas this process might be less efficient in response to a lifeless dummy, or any type of inorganic presence. The dummy and the picture of a human being can be seen as organic only via the symbolic meaning given to them, as they are recognized as artificial representations of human being. This ability presumably develops in concert with the understanding of symbolic function in general. Therefore, one might argue that the perception of a real face, without translation or transformation according to its symbolic meaning, is in many ways more "direct" than the perception of a face picture, a symbol.

Acknowledging the contents of mind of another person can have profound influences on psychological processes emerging in the meeting of minds. The results of this study could potentially contribute to the designing of digital representations of others to evoke social presence. A live human could be a useful yardstick in studying the social presence effects of various types of virtual characters representing human beings. Nevertheless, it warrants further studying whether the physical presence of other human beings as subjective and objective targets of attention, simultaneously seeing and being seen, increases other mental activity besides visual processing. Early selective visual attention provides the building blocks for higher-order social cognition and action, but it remains unclear how the processing enhancement of live faces at the early perceptual state advances or intensifies the higher-order and top-down processes. For instance, executive functions might be influenced by social context, such as the degree of social responsiveness of a face to

be attended. Another important approach would be to investigate how the acknowledged presence of other people prepares for action (Marsh, Richardson, & Schmidt, 2009). Live interaction with others sharing the same space makes us more aware of the mobility and spatial representation of our own body, because we may have to react adaptively to other's bodily responses in our vicinity. People tend to anthropomorphize, i.e., to attribute minds to external entities, when their behavior is unpredictable, thus following no mechanical rules (Waytz et al., 2010). Perceived predictability of behavior in humans, in turn, may increase dehumanization in various degrees (Haslam, 2006). Acknowledging these results there seems to be a possibility that an offline video of a person's face, or a static picture, does not leave much room for unpredictability of action, being therefore less "human" than a physically present person, even when the viewer knows that the other person acts upon instructions. Physically present persons have different degrees of freedom in their actions than pictures or digital recordings of faces, and knowing this may lead, in part, to the enhanced attention to live faces. The higher the potential for unpredictable movement, the higher the demand for the interplay between the attention systems and executive functions might be.

4.3 Visual processing of gaze direction in real faces

In Study I, the faces being viewed all displayed a direct gaze only, yet it has been extensively studied how gaze direction can have an effect on early neurocognitive processing of faces. The purpose of Study II was therefore to examine whether gaze direction has an effect on face-sensitive ERPs and whether the effect differs depending on the presentation mode (live vs. picture). The amplitude of both the N170 and EPN was greater for direct gaze vs. averted gaze and closed eyes in response to live faces. No such gaze direction discrimination was observed for the face pictures. However, in Study I, the N170 did not differentiate between the real face and the dummy, but in Study II it made a difference whether the face was real or not, and looking at the viewer or not, already at the N170 stage. Some studies have suggested that early-stage ERPs are sensitive to physical properties of stimuli (Tobimatsu & Celesia, 2006), yet it appears that the sensitivity might be more than physical. It is observed that the N170 amplitude response elicited by faces is distinct from that elicited by non-face stimuli, regardless of whether the stimuli are linedrawn, contrast reversed, spatially filtered, or even imagined (Bentin & Carmel, 2002; Sagiv & Bentin, 2001). Based on the results of Study II, N170 not only differentiates

direct gaze from averted gaze but also does it only in the live presentation mode. This suggests that N170 indeed is somewhat sensitive to social and affective factors. However, the N170 sensitivity to different types of real and artificial faces needs further studying. Another question concerns the specific areas of the brain involved in directing greater attention to the visual processing of faces. In many cases, neural sources are difficult or impossible to identify with confidence from scalp EEG alone, hence studies applying source localization of ERPs would give more insight into the mechanisms that direct more attention resources to the processing of live faces against other types of faces.

In Study II, the findings of Study I were elucidated by showing that it is not only the face being "real" that intensifies visual processing. With real faces, direct gaze condition offered an opportunity to form social contact with the viewer, whereas averted gaze condition made such a contact more difficult. "Social contact" can, of course, refer to a variety of matters. People can interact socially with others through digital means: they can share both verbal and nonverbal information via a video call, for instance. But meeting another's gaze through a digital device is still different from meeting that gaze in person. Facing a live person with a direct gaze is not only a matter of letting someone to observe the self, but also a matter of letting someone who is near one's own personal space to observe the self. This sort of a meeting thus evokes intimacy and perhaps enhances the experienced self-relevance of the situation and awareness of how one is seen by others. Live eye contact with another person thus creates a momentary, shared togetherness, which cannot be formed with offline presentation of digital faces. This sort of social awareness that is emerged by an exposition to the gaze of real faces, as compared to viewing these faces as pictures, may evoke greater emotional sensitivity in the human neurocognitive system. The building blocks for such emotional sensitivity seem to emerge very early in the human development. For instance, infants are thought to have schemas for spontaneous facial imitation and emotional attuning (Meltzoff and Moore 1989; Meltzoff and Brooks 2001). Emotional sensitivity might thus mean greater alertness to feelings that emerge in the observer through spontaneous mimicry, and the observed real person may sensitize the perceptual and affective systems of the observer more than a person who is only symbolically present. Perhaps this early emotional resonance is greater when one feels that he or she is connected by gaze to the other person. This emotional resonance might also heighten when low-level brain systems devoted to the detection of intrinsically significant signals, such as others' imminent attention that is directed to self, are activated.

In Studies I, and II, self-reported pleasantness and arousal in response to the faces was examined in different presentation modes. In Study I, the human face was rated as more pleasant than the dummy face, yet only when seen live. Human face is, of course, simply more common object to look at than an artificial dummy face, and thus possibly more pleasant. However, this does not explain why there was no such difference in pleasantness for the human and dummy faces when presented as pictures. The live human face might be more pleasant than a dummy because of the potential reactivity it possesses, or because it has potential for meeting of minds, having immediate thoughts and feelings similarly as the person viewing the face. At a more general level, it is also possible that the pleasantness relates to the overall higher complexity or unpredictability of the human face as compared to the inanimate dummy or the face picture. On the other hand, in Study II, the direct gaze was rated as more arousing and less pleasant than the averted gaze and closed eyes for the live faces. There was no such difference in the picture presentation mode. It is interesting that in Study I, live faces were rated more pleasant than face pictures. However, in that study, we did not have averted gaze faces as a stimulus at all, and it remains open whether direct gaze would have been rated as less pleasant in comparison with an averted gaze. It is possible that direct gaze, presented even as briefly as in Study II, heightens self-awareness and evokes an uneasy feeling of being looked at, and even more so when contrasted with a viewing of faces with an averted gaze. The finding that facial pictures did not have any gaze-sensitive effects on the behavioral ratings may be related to lower social and personal relevance of facial pictures, which, again, are not capable for actual observation of others, nor action towards them.

4.4 Does seeing a direct gaze motivate to approach?

As a signal, gaze direction has many motivational functions. Studies III-IV continued examining the effects of gaze direction as an affective and motivational signal on the approach-avoidance system of the human brain. Relative leftward frontal EEG asymmetry has been assumed to represent motivational tendency to approach, whereas rightward asymmetry is related to avoidance (Davidson, 2004; Harmon-Jones, Lueck, Fearn, & Harmon-Jones 2006; Harmon-Jones et al., 2010; van Honk & Schutter, 2006). I will now discuss the effects of gaze direction on the frontal asymmetrical alpha-activity in response to faces shown, again, live through the LC

window and as pictures (Study III), or live only with different facial expressions (Study IV).

4.4.1 Meeting of minds motivates to approach

Earlier evidence (Hietanen et al., 2008) has shown greater relative left-sided frontal asymmetry to direct vs. an averted gaze, and, conversely, greater relative right-sided asymmetry in response to averted vs. direct gaze. The effect was shown with live presentation of faces but not with face pictures. These results are thought to reflect observers' greater motivational approach tendency to seeing another person with a direct vs. averted gaze. Study III replicated the main finding by Hietanen et al. (2008), showing greater leftward asymmetry in response to direct vs. averted gaze in the live condition but not in the picture condition. In the live condition, knowledge of the other person's capability to see the observer can influence social-cognitive processes. Attention direction adaptation (Teufel et al., 2009) and automatic attention shifts by head orientation cues (Teufel, Alexis, Clayton, & Davis, 2010) have been shown to be modulated depending on whether the participants were lead to believe that the other person can see them or not via a video-link. Compatible with previous evidence (Study I and II; Hietanen et al., 2008) implicating greater visual and motivational processing for live direct vs. averted gaze but not for the face pictures, Teufel, Fletcher, and Davis (2010) suggested that mental-state attributions could modulate even the basic perceptual processing of social stimuli. People tend to show increased motor resonance in response to human vs. computer partners, based on the belief of the nature of the agent rather than the actual behavior of the agent (Stanley, Gowen, & Miall, 2007). Although implying agency to non-human actors in computer-mediated games activates brain areas related to mentalizing, this activation tends to be greater in response to human game partners (Kircher et al., 2009; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004). With another person in the vicinity of an observing person there is always the possibility that the other reacts immediately to one's own alleged intentions. This tendency to read others' intentions may enhance neurally rooted motivational tendencies to approach or avoid the other person, particularly when the other is a real, physically present person whose intentions could have an imminent physical effect on the viewer. With pictures or other digital faces, acts such as mutual touching would not be possible.

In Hietanen et al. (2008), the participants viewed the faces without a concomitant task, while Study III employed two tasks concurrently with the face viewing: gaze

direction discrimination and self-evaluation of pleasantness. Therefore, it is unlikely that greater attention allocation to live vs. pictorial faces would explain the gaze direction effect that was observed only with the live faces. However, there were also a few differences between the results of Hietanen et al. (2008) study and Study III, some of which may relate to the task demands. In Hietanen et al. (2008) study, the averted gaze elicited relative right-sided frontal asymmetry, whereas in Study III, there was relative left-sided frontal asymmetry, indicative of approach tendency, in response to both direct and averted gaze. Although direct gaze was associated with greater leftward asymmetry than the averted gaze, both gaze directions showing leftward asymmetry is in line with the behavioral findings. In Study III, the participants' feelings of pleasantness were relatively high in both direct and averted gaze conditions. It is possible that the task demands may have contributed to the finding that both gaze directions showed leftward asymmetry. Contrary to Hietanen et al. (2008), in Study III, there were two tasks during the face viewing: rating of own feeling of pleasantness and discrimination of gaze direction. Watching a direct gaze presumably has high personal relevance, whether there is task or not, since direct gaze signals attention towards the self. This is not the case with an averted gaze. The averted-gaze faces may, instead, have gained higher personal relevance because of the task demands of Study III. Perhaps the tasks, then, increased the possible reward value of watching averted gaze faces. In fact, the level of engagement during taskrelated processing has been shown to affect frontal alpha activity, particularly when the task has been related to rewards (Miller & Tomarken, 2001). Nevertheless, Conty et al., 2010 have shown that face pictures with a direct gaze elicited greater arousal than those with an averted gaze (or closed eyes) when presented in the context of a demanding word-spelling task, but the effect was not observed in the context of a similar but easier task. In their study, however, the tasks were not related to the faces being viewed, as was the case in the present study. The effects of task difficulty and type need thus to be explored further in the experiments studying relative frontal asymmetries in response to social objects such as faces.

It is also important to note that all participants were females in Study III. Rather surprisingly, the greater relative leftward asymmetry to direct vs. averted gaze was shown only among the participants who viewed a same-sex face. The other half of the participants with an opposite-sex face to view tended to show a reverse pattern, indicating greater leftward asymmetry to an averted instead of a direct gaze. Since every participant was shown only either a female or a male face during the study, it was not possible to compare responses to own-sex vs. opposite-sex faces within the participants. In the study by Campbell et al. (2010), for instance, both the female and

male participants rated the own-sex faces more approachable than the opposite-sex faces, although the approachability ratings favoured female faces overall. There is also evidence showing differences in how men and women respond to eye contact with own-sex vs. opposite-sex persons, regardless of whether the persons are present live or via digital means (i.e., Schrammel, Pannasch, Graupner, Mojzisch, & Velichkovsky, 2009; Swaab & Swaab, 2009). Furthermore, in Study III, there was only one female and one male as face stimuli. It is possible that facial morphology cues may have an effect on the classification of neutral faces (Hess, Adams, & Kleck, 2007), and the gender effect may interplay with expression recognition; neutral expressions have been inferred to reflect dominance in men but not in women (Hareli, Shomrat, & Hess, 2009). The question of whether other facial attributes besides those related to gender might have contributed to the responses towards the stimulus faces was investigated further in Study III. The results of the complementary data showed that the female face was rated as expressing less anger and disgust, but more sadness than the male face. The female face was also evaluated as more likeable than the male face. The raters did not participate in the original study, and they were shown face pictures only, thus limiting the generalization of these results. Nevertheless, this supplementary data suggests that, at a neural level, tendencies to approach or avoid may be affected by a variety of factors other than those related to the gaze direction. Experimental designs aiming at investigation of the effects of these kinds of variables is warranted.

4.4.2 Facial expression modulates gaze direction processing of live faces

In Study IV, it was expected that a face, presented live and displaying a direct gaze with a smile, would enhance relative leftward frontal alpha asymmetry, indicative of motivational tendency to approach, more than a similar face with a neutral expression. We presumed that facial expression would not make such a difference with the averted gaze faces. However, the results showed that the frontal asymmetrical alpha-activity did not differentiate between smiling and neutral faces. Similarly, direct and averted gaze did not elicit differential relative alpha asymmetry, regardless of the facial expression. This is not in line with the results of Study III and Hietanen et al. (2008), in which gaze direction differentiation in frontal asymmetrical activity was found in response to the live faces with a neutral expression. There might be several reasons for these findings.

It has been said that the experience of emotion is socially rooted, representing interpersonal relationships (Barrett, Quigley, Bliss-Moreau, & Aronson, 2004). Comparably, perception of emotion can be affected by the relationship between the perceivers. What is common to Hietanen et al. (2008) study and Studies III and IV is that the participants looked at persons, not just faces in isolation. In the studies presented in this dissertation, we did not take account the feelings of the person acting as a face stimulus. The stimulus persons reported that it felt somewhat awkward to look at other people, and to be observed, through the LC window. The persons being viewed were also the experimenters of the study, who interacted, albeit limitedly, with the participants prior to the experiment. The level of interaction was probably greatest in Hietanen et al. (2008) study, in which the strongest evidence for direct gaze eliciting leftward (approach) asymmetry was observed. In Study III, verbal interaction between the participant and the stimulus person was intended to be rather minimal. The stimulus person had an assisting role in the EEG measurement preparations to minimize the status difference between the participant and the stimulus person. In Study IV, the stimulus persons stayed in another room until all the preparatory work done for the measurements, and the interaction between them and the participant was restricted to saying "hello" to the participants prior to the actual experiment. Previous evidence has shown that face familiarity can modulate neural responses to faces (Gobbini & Haxby, 2007), and people seem to make eye contact with closely familiar people more frequently and for longer durations than with strangers (Russo, 1975). It is not clear, of course, whether face familiarity via just a short acquaintance makes a difference in terms of neural markers of approach-avoidance motivation. There is but one study in which leftward asymmetry in response to happy faces and rightward asymmetry in response to angry faces (all with a direct gaze) has been observed (Davidson & Fox, 1982). Importantly, the participants were infants who were presented pictures of their caregivers (mothers), implying that the face familiarity itself, and perhaps emotions related to the caregivers, possibly had an effect on the frontal asymmetrical activity.

Furthermore, to clarify why the smiling and neutral faces did not elicit differential frontal alpha activity, we could speculate what these facial expressions might have signified for the viewers. It has been shown that happy faces are recognized as "happy" very efficiently, even when presented with low expression intensity (Hess, Blairy, & Kleck, 1997), and errors in smile classification are generally quite rare (Haidt & Keltner, 1999). Importantly, however, errors in interpretation of specific smiles are much more frequent (Bernstein, Young, Brown, Sacco, & Claypool, 2008). Niedenthal, Mermillod, Maringer, and Hess (2010) have discriminated

between smiles produced by positive emotion (enjoyment smiles), positive social motives (affiliative smiles), and smiles communicating and maintaining social status (dominance smiles). They argue that those smiles feel different, and may thus elicit distinctive responses in terms of reward, action, and somatosensory experience. In Study IV, the smiling face stimuli were intended to communicate social approach and acceptance, i.e., being affiliative smiles with a social motive. For the perceiver, however, genuine (enjoyment) smiles appear to have greater intrinsic reward value than polite (affiliative) smiles; it has been shown that game partners with an enjoyment smile have been preferred over politely smiling counterparts, even if this preference has caused smaller monetary reward (Shore & Heerey, 2011). Niedenthal et al. (2010) also speculate that smiles hiding negative intentions or feelings might be associated with the experience of negative rather than positive affect, as indicated by right-lateralized frontal alpha activation (Boksem, Smolders, & De Cremer, 2012; Davidson et al. 1990). In Study IV, however, the smiling faces were rated as being positive, whereas the neutral faces were evaluated as being slightly negative. Fairly precise exemplars of neutral facial expressions can be created digitally, meaning that there is no facial muscle activity on that face. This is not the case with live face stimuli. A neutral face may have been evaluated as expressing a variety of dispositions related, for instance, to gender role expectations, dominance, and emotional states. Both smiling and neutral faces with a direct gaze were rated more positively than those with an averted gaze. Despite these ratings, there was a great variation in the frontal asymmetry patterns: some participants showing, generally, leftward relative asymmetry, others, instead, rightward relative asymmetry, in response to the faces overall.

Another issue that deserves further attention is the fact that the face stimuli were presented without a clearly defined intent. Laidlaw, Foulsham, Kuhn, and Kingstone (2011), for instance, have addressed why mutual gazing does not automatically signal motivation to approach; it is the dynamics and social-normative context of the gaze that matters The valence of the expression does not necessarily correspond to the intention of the person bearing the expression (e.g., Ambadar, Cohn, & Reed, 2009). Non-Duchenne (affiliative) smiles are less often used as a signal of social intent than Duchenne (enjoyment) smiles (Hess & Bourgeois, 2010). The ambiguity of the facial expression may actually determine how relevant gaze direction is for evaluating the observed person's goals and emotions (Bindemann, Burton, & Langton, 2008). This is related to the question of possible interaction effects of gaze direction and facial expression on the frontal asymmetry patterns in response to faces. In Study IV, we found none. Yet, according to the results by Adams and Kleck (2003; 2005), a smile

and direct gaze should both potentiate approach motivation, and recent evidence has shown that it takes less time to initiate steps toward a smiling vs. an angry face, suggesting that a smile can facilitate approach behavior (Stins et al., 2011). The affiliative smiles in Study IV were not intense and, in terms of intention, unambiguous signals enough to enhance approach motivation, even when presented with a direct gaze. In fact, studies that have found frontal asymmetry related to approach motivation for positive stimuli have commonly included rather strong appetitive or aversive visual objects. For instance, strongly desired objects (such as desserts for hungry people) have been observed to evoke frontal asymmetry related to approach motivation (Gable & Harmon-Jones, 2008). If we consider the smiling faces presented in Study IV, it is not surprising that they were rated as being positive. However, less likely such smiling faces evoke a desire to approach, at least not substantially more than faces with neutral expression might.

4.4.3 Affective style in motivational tendency towards faces

There was large individual variance in the frontal asymmetry patterns in Study IV. Although there was no gaze direction effect on the frontal alpha-band EEG asymmetry at a general level, a closer look at the asymmetry scores showed surprising findings. The magnitude of the mean asymmetry score calculated across responses to all stimulus conditions exhibited a marginally significant positive correlation with the differential score expressing whether direct gaze evoked less (negative values) or more (positive values) left-sided brain activity (implying approach motivation) compared to averted gaze. In other words, the increase of the overall asymmetry score was associated with a tendency that direct gaze elicited greater approachrelated activity than the averted gaze did. This result could reflect differences in personal dispositions related to affective style. In previous research, left-sided trait asymmetry has been associated with positive affect and approach behavior, whereas right-sided trait asymmetry has been related to negative affect, anxiety, and behavioral avoidance (Allen & Kline, 2004; Coan, Allen, & Harmon-Jones, 2001; Davidson and Irwin, 1999; Heller & Nitschke, 1998; Mathersul, Williams, Hopkinson, & Kemp, 2008). One line of this research has compared individual differences in BIS-BAS (behavioral inhibition-behavioral activation) scales with relative frontal alpha asymmetry in resting (trait) EEG alpha activity. However, some studies have found no specific lateralization effect as function of BIS-BAS

dichotomy (Balconi, Brambilla, & Falbo, 2009; Wacker, Heldmann, & Stemmler, 2003).

In Study IV, we did measure whether affective style, measured as a function of the BIS-BAS system, was related to frontal EEG asymmetry scores in response to the faces, but we failed to find such a relation. It is noteworthy that we measured not trait but only stimulus-bind (state) alpha activity thus direct comparisons between trait and state anterior alpha asymmetries in relation to BIS-BAS system would not be fruitful. The roles of different frontal areas in disambiguating state and trait-like motivational tendencies need to be addressed in further studies. It is also plausible that the observed individual differences in asymmetry scores in response to the face stimuli in Study IV are related to other underlying differences that dispositional affective styles would not explain. It would be interesting to investigate whether relative asymmetrical activity to social stimuli would be related to individual differences in domains that are linked to personal dispositions in social behavior, such as to introversion or extroversion as personality characteristics. There is some recent evidence showing an association between neuroticism and avoidance-related, relative right-sided frontal asymmetry (Uusberg, Allik, & Hietanen, 2015).

Furthermore, based on the existing fMRI evidence, it seems that the viewpoints emphasizing asymmetrical frontal activity to reflect either direction or valence of affective motivation are not necessarily mutually exclusive. Therefore, the whole concept of approach and avoidance as motivational tendencies seems to warrant careful examination. In various situations, people end up engaging in motivational conflicts, and there are conflicting forces driving either to approach or avoid an event. Previous research has shown that motivational and emotional processing may overlap so that it becomes challenging to interpret frontal asymmetrical activity (see Elliot & Thrash, 2002; Spielberg, Stewart, Levin, Miller, & Heller, 2008; Wacker et al., 2008, 2003). Related to the problems in interpreting anterior alpha activity asymmetry patterns, Allen and Kline (2004) have concluded that EEG alone is perhaps not the most suitable means of registering hemispheric activity asymmetries because it is based on a relative voltage difference scores, meaning that the left- and right-side scores are not independent from each other. In the fMRI literature, the recent findings on frontal asymmetric activation have been heterogenic. Trait-level approach motivation has been associated with left-lateralized middle frontal gyrus activation, whereas trait-level withdrawal motivation has been associated with rightward activity in the same site (Spielberg et al., 2012). Approach motivation has also been associated with activation of the medial prefrontal cortex and the nucleus accumbens, whereas avoidance motivation seems to be linked with activation of the

amygdala and anterior cingulate cortex (Wager, Phan, Liberzon, & Taylor, 2003). Pizzagalli, Sherwood, Henriques, and Davidson, (2005), in turn, found left DLPFC activation in response to reward preference, and Berkman and Lieberman (2010) found relative left vs. right DLPFC activation to goal-directed approach action motivation. Some have suggested that BIS and BAS might also be indicators of individual capacity for cognitive control (see Coan & Allen, 2004). The specific relations between emotion, motivational intensity and motivational direction in explaining frontal asymmetry fluctuations need to be elucidated. It is also worth waiting that wider application of source localization algorithms would provide more specific information on the anterior asymmetry functions.

4.5 Autonomic arousal in response to faces

In addition to investigating whether presentation mode, gaze direction and facial expression have an effect on the frontal EEG asymmetry in Studies III and IV, these studies also explored the intensity of affective responses to the face stimuli. To study the intensity of affective responses, autonomic nervous system activation was investigated by measuring electrodermal activity. The results showed that, in terms of arousal, live faces feel different than pictures of faces. Both gaze direction and facial expression were found to have a role in this process.

4.5.1 The feeling of being observed

The results of Study III showed greater skin conductance response (SCR), implying greater sympathetic arousal, to direct vs. averted gaze. For the SCRs, there were no such gender differences in response to the face stimuli that were shown for the frontal EEG asymmetry results. As anticipated, the effect of gaze direction was shown in response to the live faces, but not for the face pictures. These results are therefore in line with the live face effect on the SCRs, being similarly greater for direct than averted gaze as in a passive viewing of faces in Hietanen et al. (2008) study. The results of Study III also showed that when the faces were looked at with a concomitant task, it was rather the attention directed to the observer than the mere presence of the eyes that evokes enhanced arousal in face-to-face encounter, corroborating evidence by Hietanen et al. (2008) and Helminen et al. (2011), which showed greater arousal to live faces with direct than averted gaze. The results are

also in line with other previous evidence showing enhanced autonomic responses to eye contact with a live partner vs. looking at a picture presentation of the same person (Bailey, Chorosevic, White, & White, 1981). Also, other studies employing live presentation of faces have shown enhanced SCRs (Nichols and Champness, 1971) and elevated blood pressure (Williams & Kleinke, 1993) to live direct vs. averted gaze.

Somehow, then, meeting the eyes of a person who is physically situated close to self creates a specific intimacy, that is, private, affective atmosphere, between the persons in face-to-face interaction. Increased intimacy, in turn, tends to elevate arousal (Patterson, Jordan, Hogan, & Frerker, 1981; Patterson, 1976). Yet there is a critical question concerning the conditions in which intimacy is created. It has been recently shown that an eye contact with another, physically present person evokes grater psychophysiological responses when the participants believed that the person facing them through an electronic shutter could see them through the shutter as compared to the situation when they believed that the other person could not see them (Myllyneva & Hietanen, 2015). Hence, the mere belief of the other's observation abilities could have increased self-awareness and intimacy. In addition, in an extensive review, Argyle (1988) has addressed how both the act and manner of looking matters in face-to-face communication. The distance and duration of the gaze, besides the person to look at being physically and mentally present, might play a critical role. The difference between a glance and a stare can be demonstrated by comparing the acts of shaking hands vs. holding hands. These acts are physically quite similar, yet in terms of intimacy, they have different implications. In Studies III and IV, the distance between the participant and the stimulus person was held approximately in one meter. This distance may have caused mild discomfort during the viewing of live faces. In Study III, viewing the pictures of faces was indeed rated as more pleasant than viewing the live faces.

Presentation media may also have an influence on distance effects on arousal in the face viewing; it seems that a picture of a face on a television screen needs to produce a much larger retinal image to obtain the same proximity effect as a live face (Stapley, 1972). This finding may apply to computer screens as well. Similarly to real face-to face encounters, virtual humans can have an influence on patterns of interpersonal distance and sense of social presence (Bailenson, Blascovich, Beall, & Loomis, 2001, 2003). With virtual humans, there is, however, no anticipation of a physical encounter. Gale, Spratt, Chapman and Smallbone (1975) observed that arousal diminished as a function of face-to-face distance, yet arousal for direct gaze was higher than for averted gaze at any distance tested. Physiological response

patterns tend to change systematically with proximity and probability of an encounter (Lang & Bradley, 2010). Recent theoretical viewpoints have, indeed, highlighted the self as an enactive being; perception and movement are closely intertwined, and people are continuously aware of their bodies in relation to external objects (McGann & De Jaegher, 2009; Zahavi, 2002), perhaps even more so when the object in sight is another person, giving the situation more personal relevance. Zahavi (2002) refers to Edmund Husserl's phenomenological views in stating that "hand cannot touch without being touched". Similarly, perhaps, the gaze cannot meet another without being met.

Self-awareness ratings for the facial stimuli in Study III support the notion that direct gaze enhances personal relevance of the situation when live, physically present faces are being looked at. The results showed that direct gaze elicited higher ratings of public self-awareness in the live than in the picture condition, replicating earlier evidence (Hietanen et al., 2008). Now, these previous findings were expanded by showing that, in the live condition only, the other person's gaze direction had an influence on the self-rated public self-awareness: direct gaze evoked marginally higher public self-awareness ratings as compared to averted gaze. This type of awareness possibly makes the person alert and sensitive to others' emotional and motivational signals, whether being positively tuned or not. Self-awareness, especially the "public" type of it, likely increases with the feeling of being observed by another person. This result also supports earlier findings showing elevated arousal in response to the feeling of being the target of the other's eyes (Honma et al., 2012). As suggested earlier in Study II and in Hietanen et al. (2008) study, being a target for another person's attention, not only via digital means but physically in a close distance, possibly increases attention towards the face being viewed and sensitizes the viewer to view the self in the second person perspective, i.e., as imagining how one would be seen in the eyes of the other. In live condition only the direct gaze of a real person had an actual, known, and potentially – if not likely – touchable target: the participant. In Study IV there were live faces only, so it can only be speculated whether subjectively determined social presence would have been as high as that with pictures of faces in question. However, in Study IV, the ratings of social presence in response to the stimulus faces showed that the participants felt moderate levels of social presence during the experiment. As social presence was measured only at the end of the experiment, and not separately for the different stimulus conditions, the implications of these results are rather limited and show only that, even though the face-viewing situation was quite passive, it was regarded as a social situation.

4.5.2 The effect of facial expression on arousal

Not only gaze direction, but also facial expression seems to have a critical role in elevating physiological arousal to real, live faces. In Study IV, in which only live faces through the LC window were presented as stimuli, it was shown that viewing of smiling faces evoked greater arousal than viewing of neutral faces, and, the effect of gaze direction was more pronounced in response to a smiling than a neutral face. The autonomic arousal was also greater to seeing a smiling vs. a neutral face with a direct gaze. These results reflect the emotional saliency of both the direct gaze and the smile, and shows that a combination of these signals results in a strong autonomic response. The results are in line with Schrammel et al. (2009) study, showing higher zygomaticus major (a facial muscle related to enjoyment smiles) activity in response to seeing happy vs. angry or neutral faces. In that study, eye contact also increased the intensity of the experienced emotion. Direct gaze may also emphasize the affective content of communicative messages. There is a substantial amount of behavioral and neurocognitive evidence showing how gaze direction and facial expression cues need to be combined to grasp the feelings of others in relation to the viewer (George & Conty, 2008). Direct gaze and smile can both be regarded as signals inviting to closer interaction. To conclude, live faces, in particular those with eyes directed to the viewer with a smile, enhanced arousal.

In Study IV, there was considerable variation in the valence ratings for the neutral faces; some participants rated them being slightly positive, whereas to others they appeared negative. Such a variation was not observed for the smiling faces, which were consistently evaluated as positive. Interestingly, those who were more inclined to evaluate a neutral, direct gazing face as being negative showed more pronounced autonomic arousal toward those faces. This suggests that, for those persons, the viewing of neutral faces with a direct gaze may have been a negative experience. One possibility for this result is that some individuals may emphasize arousal as an aspect of their emotional experience more than less sensitive individuals in that regard (Barrett, Quigey, Bliss-Moreau, & Aronson, 2004). Previous research has related the feeling of uneasiness under others' observation to social anxiety. Fear of eye contact is thought to be central in social anxiety disorder (SAD) (Baker, Heinrichs, Kim, & Hofmann, 2002; Safren et al., 1999; Stein, Kasper, Andersen, Nil, & Lader, 2004). One study showed that, in general, direct gaze did not induce differential electrodermal or cardiac activity than averted gaze, but socially anxious individuals showed greater cardiac acceleration, indicating perhaps greater fear-related arousal, in response to dynamic avatar faces with direct vs. averted gaze (Wieser et al., 2009).

It would be interesting to study the impact of different means of face presentation on the anxiety levels in persons with and without SAD. Although the participants in Study IV had reportedly no diagnosed psychiatric disorders, there might have been differences in their proneness to social anxiety. Furthermore, recent psychophysiological and behavioral evidence has shown that eye contact with a real face stimuli is aversive and negatively arousing for adolescents with social anxiety disorder (Myllyneva, Ranta, & Hietanen, 2015).

4.5.3 Arousal in relation to temporal SCR characteristics

In Studies III and IV, we measured the maximum value of the skin conductance amplitude in response to each face stimuli, and then averaged these peak amplitudes (occurring 1-5s after face presentation) across each stimulus condition. This method seems to serve as a fairly robust measure of stimulus-induced arousal, but it also leaves several arousal-related factors unattended. Skin conductance responses tend to habituate quickly, approximately after eight repetitions, even in the context of strong emotional content (Dawson, Schell, & Filion, 2007). In the present studies, the content of our stimulus material was rather mild. Not surprisingly, therefore, the habituation effect seemed to occur rapidly. However, our measurement devices did not allow us to measure the actual rate of habituation. The recordings were done with only one channel, and required manual separation of SCRs. This may create problems of response determination due to large tonic changes and overlapping SCRs, possibly leading to a skewed data set. In the future, methods such using a high-pass software filter and utilizing more than one channel in the recordings (Figner & Murphy, 2011), should be considered. It would be more useful to measure both the amplitude and temporal characteristics to gain a more valid indicator of the SCRs than those measured separately (Figner & Murphy, 2011). Furthermore, we had participants with extremely weak SCRs to all stimuli, but they were still included in the data samples of Studies III and IV. Considering that electrodermally labile persons might be more sensitive to environmental contingencies than stable ones (Boucsein, 2012), individual differences in electrodermal sensitivity should be taken account when SCRs are being measured.

4.6 General methodological evaluation and future directions

Throughout several sections above, I have addressed the importance of selecting socially meaningful stimulus material for studies in social cognition. Despite giving new insight into this matter, the results of the present studies left many questions of the live face effect unanswered. Here I will review the core of these and propose directions for studies in the future.

4.6.1 Static vs. dynamic faces

Social communication via facial expressions and body postures involves motion and a sequential exchange of information between individuals, neither of which is captured in the static pictures of faces presented in Studies I-III. However, live faces cannot stay entirely still even for short periods of time. There is always some involuntary facial movement, such as muscle contradictions, eye-lid movements, and pupil size changes. People are largely unaware of the fact that they imitate for instance their interaction partner's postures and facial gestures, and this automatic imitation can increase mutual bonding and liking (Wiltermuth & Heath, 2009). Facial movement is a two-way, ongoing process that is affected by streams of facial movements from others and it is subject to various "audience effects", i.e., those effects adjusted by the presence of others (Parkinson, 2005). When an observed action is perceived, it takes around 200 ms of the cortical areas involved in motor system functions to get activated (Catmur, Mars, Rushworth, & Heyes, 2011; Nishitani & Hari, 2002). Within this time range, the premotor cortex can integrate gaze, gesture, and emotion cues from the face and upper body, and at an earlier stage, emotion cues are processed independently in the amygdala (Conty et al., 2012). As automatic mimicry is very rapid, it is plausible that even the enhanced early-stage neural responses to real faces in Studies I-II were influenced by this automatic imitation that is suggested to result from basic perception-to-action mapping (see Wilson, 2002, for a review). Visual processing of faces is thus possibly modulated by action.

Niedenthal et al. (2010) suggest that eye contact triggers an embodied simulation of the perceived facial expression and its correspondent feeling for use in interpretation. It has also been found that dynamics enhances emotion recognition of facial expressions (Ambadar, Schooler, & Cohn, 2005). Weyers, Muhlberger, Hefele, & Pauli (2006) compared to facial expression recognition of static and

dynamic avatar faces and found that dynamic expressions led to better recognition rates and higher intensity and realism ratings. Others, in turn, have found that participants mimic expressions of pain most clearly when they are engaged in an eye contact with the person expressing pain (Bavelas, Black, Lemery, & Mullett, 1986). At a neural level, it is also shown that eye contact enhances the effects of mimicry and controls mimicry by modulating the strength of cortical connections between mPFC and STS (Wang, Ramsey, & de C. Hamilton, 2011). In addition, likeability of virtual reality faces has been reportedly better for direct than for averted gaze shift (Kuzmanovic et al., 2009). There is also evidence showing that pictures of faces with eyes shifting toward the participant are more likable than faces shifting their gaze in the opposite direction (Mason, Tatkow, & Macrae, 2005). Eyes shifting towards oneself may thus be considered as an active expression of interest, resulting in more positive evaluations than an averted gaze shift. Importantly, not only the eye movements of the faces to look at should be considered, but the eye movements of the dyad. Social presence may affect gazing patterns on both sides: people may, for instance, direct their attention differently to the eye region of the other person in real face-to-face contact as compared to face-to-face contact via digital means. Therefore, eye movement studies comparing physical and digital presentations of faces would be warranted in the future.

Movement is also important for the ecological validity of faces, since people look at moving instead of entirely static faces in ordinary social situations. Motion dynamics can thus be signals by which people reveal each other that they are agents, i.e., entities with autonomous, observant minds, in the first place (see Auvray, Lenay, & Steward, 2009; Di Paolo, Rohde, & Iizuka, 2008). In that sense, it is not surprising that arousal, as indexed by SCR amplitude, has been shown to be greater for moving vs. static videos depicting emotional stimuli (Simons, Detenber, Roedema, & Reiss, 1999). Parkinson (2005) suggests that, rather than arguing whether facial movement primarily functions as expressing emotions or communicating motives, it should be acknowledged that faces represent a range of different simultaneous functions during social interaction, and facial movement not only transmits, but also participates in, emotional action. Gaze, pointing gestures, bodily and facial emotion can be all considered as affiliative gestures that are worth mimicking to better cooperate with the sender. Interacting dyad's higher degree of imitating another person's speech inflections and physical expressions (chameleon effect) is suggested to be a sign of higher degree of mutual rapport, involvement and togetherness (Chartrand & Bargh, 1999; van Baaren, Holland, Kawakami, & van Knippenberg, 2004). It is therefore understandable that these cues are integrated at such an early

stage. Real faces are given a priority in the early perceptual processing, perhaps because of the strong, involuntary tendency to smoothly coordinate one's own reactions to the other and the other's reactions to self, such as to integrate subtle motor information with visual processing of other's face. This is one of the reasons why real, corporeal faces should be compared with online and offline video images presenting faces capable of imitation and of being imitated in determining whether the "live face effect" would happen independently of online or offline mimicry effects. At present, a consistent picture of the early stage couplings of motor and visual perceptual areas in face processing could not be formed, warranting, therefore, further research.

4.6.2 Body vs. mind

One explanation for the fact that the effects of gaze direction were observed only in the live presentation mode was that the live face had corporeal presence, potential for initiating interaction, mutual intimacy, and social awareness of other human beings. Indeed, one central issue that has largely been neglected in social and affective neuroscience is corporeality. It is rather surprising, since the medium of social interaction may deeply affect the way people behave towards each other. In recent years, however, promising steps have been made to explore "embodied cognition", which loosely refers to the idea that cognition is largely dependent and affected by the bodily sensations of the ever-altering physical and motor representations of self and others (Krueger, 2011). Yet an unanswered question is whether intercorporeality is equivalent with intersubjectivity in social interaction. When a person is observing another, and being observed, too, the presence of embodied mind could differ from the presence of (computer) mediated mind in terms of cognitive and emotional resources directed to the perceptual process. Artificial humans, embodied conversational agents and humanoid robots are assumed to facilitate human-computer interaction (HCI). According to Vogeley and Bente (2010), the new artificial intelligence (AI) development has begun to consider relational and emotional aspects of communication in nonverbal communication, and the goal is to equip machines with social and emotional intelligence, both in responding and interpreting social-emotional cues "naturally". There is already some evidence showing that seeing a robot's gaze direction in physical face-to-face setting can improve performance in a cooperative task similarly as seeing a human gaze direction (Boucher et al., 2012). Hence, humans are sensitive

to gaze cues of humanoid robot in physical interaction somewhat similarly as with real human beings. Moreover, viewing some types of avatar and robotic creatures tend to engage brain systems that are activated by viewing social signals (Chaminade & Cheng, 2009). When we look at faces of other people live or on a digital screen, we might have a chance to interact with them or not. For instance, faces in a digital screen during a video call may appear online or offline. However, opportunity for physical interaction is missing in all digitally mediated face viewing.

As Clark (1999) has pointed out, information can be relevant for action expectancies in various degrees. Would it make a difference if, for instance, the dummy that served as a stimulus model in Study I was capable of moving in its surroundings? More interestingly, would it make a difference if the person watching the dummy could predict how the dummy could move, versus not knowing and thus not being capable of predicting whether and how the dummy's movements could affect the self? There are also further questions on mental states in relation to action. Would it make a difference for the human visual system whether the viewer knew that a real person, who sees him/her, would be mentally present and alert but physically paralyzed? In the future, studies in cognitive science and neurosciences should closely investigate how the perceived mental states, actions and action predictions could alone and together modify the functioning of the human brain systems involved in visual information processing. These questions are closely related to the broader question of what is the human vision system for. According to Clark, "the central task of vision is to use visual information efficiently in the service of real-world, real-time action. Perception includes consultations of the outside world in service of action instead of rich and detailed "inner" representations of the world" (Clark, 1999). These repeated consultations of the surroundings should likely be faster and more effective in situations involving embodied others who can act inside and outside their heads; they can think, plan, and move online, and their actions may alter the physical space of the person who has faced them. Biological vision is, therefore, for making the most efficient use of the persisting external scene, to get a grip of the world – a thought that has been underlined by Maurice Merleau-Ponty in his studies on phenomenology of perception (2002). Indeed, we could think that a physically embodied entity that has a human, or human-like, mind has a capacity to govern, to rule and manipulate its immediate surroundings in its very physical and mindful presence. If human perceptual system has, as Merleau-Ponty (2002) has suggested, developed to function successfully in the situation at-hand, a potentially greater threat – as well as reward – is no other than another similar, intentional creature in our immediate physical surroundings, in the very same

temporal and spatial sphere. Even though any online or offline symbolic target of our visual processing could have immediate effects on our inner states, these targets could not get a true grip on the temporal and spatial sphere we currently existed as embodied persons. Therefore, our visual system should be prepared to be most sensitive and effective in situations including shared physical space with other intentional, and hence always somewhat unpredictable organisms who, especially when they are aware of our presence in the very same space, may rapidly manipulate objects or people around us.

4.6.3 Individualism vs. interactionalism

To be successful, social interaction requires both ongoing evaluation of the social signals sent by the interaction partner and monitoring of one's own feelings and thoughts. In social neuroscience and related fields, there has been discussion on the growing need to "go social", referring to the challenge to acknowledge the complexities of social world in study designs (De Jaegher, 2009; Zaki & Ochsner, 2009). It is common for neurocognitive studies of face processing that the faces are looked at, maybe accompanied by some face related tasks, but this process is not bidirectional: the face does not look back, nor respond to the actions of the viewer. In the studies presented in this dissertation, the live faces did look back. However, they did not give explicit feedback to the viewer, being therefore somewhat passive objects in sight. The experimental design may have represented more individual than interactive processes. Yet in this dissertation, on several occasions, the word "social interaction" has been used when making implications concerning the viewing of these faces. In general, the background assumptions guiding the research of social brain functions have, until recently, been fairly individualistic. Such research has focused on the mental processes of an individual who is thought to reconstruct a mental model of the signals sent by other people, and based on the reconstruction, to give meaning to these signals. When we meet other people live, or look at their faces as pictures or through other "off-line" devices, we tend to instantly decode the feelings, desires or thoughts their faces likely reflect. We thus seem to apply our mentalizing capabilities quite instinctively, whether the face is socially and bodily present or not. An interesting question is, however, whether mentalizing differs in the actual presence of a real person as compared to off-line social perception. Mentalizing abilities of individuals with different clinical disorders, including people with autism or schizophrenia, have mainly been studied by using static or animated

off-line face stimuli without possibility for social feedback (e.g., automatic imitation). Yet it would be essential to investigate to which degree the social dysfunctions in these disorders are related to problems in social interaction and social perception.

The level of involvement should, indeed, be taken seriously. There is a critical difference between "I-thinking" and "we-thinking". Oberman, Pineda, and Ramachandran (2007), for instance, showed that the more the participant was involved in virtual social interaction (i.e., received the ball from the on-screen players in a ball tossing game), the more activation there was in the participant's mirror neuron system, which is a system responsive to human actions and intentions (Gallese, 2001). There are also results showing greater activity in adult motor cortex when human actions were presented live than on videotape (Järveläinen, Schürmann, Avikainen, & Hari, 2001). In another study, when adults and 6- to 7-month-old infants viewed actions of other people presented online either live or on a television screen, the sensorimotor area in the brain was more activated when real vs. televised actions of adult humans were being viewed (Shimada & Hiraki, 2006). However, in Shimada and Hiraki (2006) study, the experimenter engaged the infant's attention by directly talking to the infant during the testing. It was not reported where the experimenters gazed at when their actions were being viewed. It is possible that active social communication with the infant made the real actions more meaningful, not the "realness" alone. When small children were trained to learn new words embedded in natural social interaction or, alternatively, via an educative video viewed either alone or with an adult, a significant enhancement in word learning was reached only by natural social interaction (DeLoache et al., 2010). However, the videos were off-line, not able to reciprocally react to the babies' own actions even unintentionally. In fact, there are studies in which dramatic effects have been shown when babies have been exposed to an adult that suddenly becomes nonresponsive in face-to-face interaction ("still face" studies; see Striano, Reid, & Hoehl, 2006). Indeed, a recent study (O'Doherty et al., 2011) demonstrated that it is not the medium of interaction per se, but the reciprocity of interaction, that matters most in the learning of communication skills. Also, it has been shown that infants show phonetic learning from live, but not prerecorded, exposure to a foreign language, and this suggests that foreign launguage learning process is enhanced by social interaction (Kuhl, Tsao, & Liu, 2003). It is thought that children learn to understand other minds by learning to share their visual social signals (Moll & Meltzoff, 2011). It is thus likely that real faceto-face encounters are a necessary condition for social cognitive abilities to evolve, but after these basic skills have been developed, people can understand other minds by engaging in social interaction with others who are socially responsive via digital

devices. The role of both intentional and unintentional reciprocity in the adults' responsiveness to different face presentation mediums deserves further examination in the future.

4.6.4 Individual differences in affective processing of faces

As discussed above, the studies of the present dissertation have provided evidence that emotional impact of live faces seems to be greater than that of face pictures. Furthermore, the results showed that neurocognitive responses to live faces had greater individual variation than responses to face pictures. It would be worth examining whether individuals with and without diagnosed neurological or psychiatric disorders characterized by atypical processing of social information differ in processing of live faces, and whether these results would be similar with digitally presented faces. There is also a question of how early the differentiation of responses to live faces form pictures emerges in human development. It would be interesting to investigate whether the risk for developing such clinical disorders would be tractable in early childhood through specific neurocognitive markers, such as ERPs. Individuals with ASD have shown to process faces differently than typically developed individuals, and these differences seem to emerge in early childhood (Kylliäinen & Hietanen, 2006; Kylliäinen et al., 2011; Joseph et al., 2008; Dalton et al., 2005). It has been suggested that the weak motivation of children with ASD to engage in eye contact may not result from the eyes being aversive stimuli for them, but, instead, is a consequence of hypo-activation in the amygdala-mediated arousal system (Senju & Johnson, 2009). As all the studies cited above had either dynamic or static digitally presented stimulus faces, it would be interesting to study arousal and motivational responses evoked by live faces in typically developed individuals and in individuals with ASD, by combining explicit and implicit measures of valence and arousal. There is already preliminary evidence that infants and small children who show atypical neurocognitive or behavioral attention to the eyes and gaze directions of adults have found to be in risk for having neurodevelopmental disorders, such as autism, later in life (Elsabbagh et al., 2012). Psychophysiological studies have also found atypical ERPs to direct gaze in infant siblings of individuals with the broad autism phenotype (Elsabbagh et al., 2009).

Mechanisms of social perception and self-awareness tend to be entangled in many psychiatric disorders (Paradiso & Rudrauf, 2012). Attention to the eyes seems to be atypical not only in anxiety disorder and in individuals with autism, but also in other

neurological and psychiatric disorders, such as in children with psychopathic traits (Dadds, Jambrak, Pasalich, Hawes, & Brennan, 2011). Considering the results of the present studies and the pioneering work of others who have studied symbolic and actual face-to-face interaction (e.g., DeLoache et al., 2010; Shimada & Hiraki, 2006), research on deficits in social information processing should consider developing methods rooted in interactionalist rather than individualistic models. These studies should also take the effects of mentalizing into account. Mentalizing abilities in different clinical disorder groups, including people with autism or schizophrenia, has mainly been studied by using static or animated off-line face stimuli without possibility for social feedback (e.g., automatic imitation). Likewise, the rehabilitation of social-cognitive functioning should seek methods that better approximate interactionalist aspects in information processing. As suggested above, it is far less engaging to attend and respond to a digital face vs. a real person. Not surprisingly, people who score high in social anxiety scales have reported feeling more anxious in corporeal social interaction than in computer-mediated online interaction (Yen et al., 2012). However, the possible anxiety-level variation in corporeal vs. mediated interaction should be examined also experimentally, with physiological measures of arousal in various interactive conditions. Furthermore, (Chiu et al., 2008; see also Frith et al., 2008) provided some preliminary evidence that individuals with autism may treat human and computer game partners similarly. Hence, as it has been proposed, objects which are not fundamentally social, i.e., interactive robots or game partners, may not offer the best solution for social deficit rehabilitation of children with autism, but instead, it would be important to learn how individuals with atypical theory of mind development respond to and get reward from engagements with real people. This should be tested especially in social situations without clear interaction outcome expectations.

4.6.5 Concluding remarks

People ordinarily look at faces to communicate with each other, and to fulfil a variety of social and emotional goals. In this dissertation, the medium of face presentation is shown to have an effect on the electrophysiological signature of face perception: the attention system of the human brain seems to be more sensitive to faces belonging to real, potentially responsive individuals as compared to pictures of faces. One might be tempted to ask whether it makes such a dramatic difference in ordinary social communication if our brains automatically respond slightly differently to real

vs. digitally mediated faces. To give insight into these questions in the future, social and affective neurosciences should broaden the line of research in designing studies that allow live and dynamic stimulus material, carefully specified social scenarios, reciprocity of social interaction, and the comparison of individual differences in social information processing. Some researchers have already called for the systematic comparison between stimuli that range in their approximation to a real social interaction (see Risko, Laidlaw, Freeth, Foulsham, & Kingstone, 2012). There are methodological challenges in stimulus controllability vs. "naturalness" to overcome in exploring neurocognitive mechanisms, but increasing interaction potential with real people acting as stimuli should be a goal for future studies in social and cognitive neurosciences and in related fields of study. Importantly, it has been reminded that currently no neural computation or neuronal network specifically dedicated to social stimuli or social cognition alone has been identified (Przyrembel, Smallwood, Pauen, & Singer, 2012). It is, therefore, an interesting question whether epistemic access to the mental states of others is completely identical depending on whether there is interaction. Acknowledging the evidence that social reward is processed differently from non-social reward (Zink et al., 2008), Adolphs (2012) has wondered whether a social stimulus is different because of greater saliency, unpredictability, or arousal – or because of some sort of combination effect. Some of these effects might be inaccessible to our conscious minds but tractable via brain research methods. The results presented in this dissertation give support to some sort of combination effect. The rapidly developing information society we live in would greatly benefit from studies on the subtle impacts of different means of social perception and interaction on human information processing. It is also essential to continue designing digital media devices that allow detailed social information sharing.

An equally essential question is whether the real vs. digitally mediated presence of others is beneficial or not to individual and inter-individual performance. Cumulating evidence shows it can be either way, depending on the objectives. Virtual presence tends to excel if the primary objective is information dissemination, while actual presence outperforms in the promotion of mutual understanding and trust (Rhoads, 2010). Most clinicians likely agree that it is invaluable to be sensitive to the reactions of the client and to the feelings the client evokes in oneself. These feelings emerge early in the information processing stream and might be mediated by social presence. On the other hand, despite reducing sensitivity to visual cues, videomediated communication may have beneficiary effects over live interaction in occasions when live interaction (such as a child witness interviewed in the court in

person vs. via a video-link) would likely evoke considerable amount of anxiety and motivation to compliance (Doherty-Sneddon & McAuley, 2000). Moreover, creative problem solving skills can actually be better when people communicate online via computer rather than face-to-face (see Furnham, 2000). Perhaps sensitivity, and even fear, of reactions among fellow humans in real face-to-face communication lead to enhanced arousal and draw cognitive resources away from creating original ideas. In reconstructing the classical group conformity study by Asch (1955), Berns et al. (2005) found that the social presence of others not only made people consciously change their judgments, but also modulated the perception of an external object itself. In the age of rising popularity for conducting education, clinical counseling, and group decision-making by virtual means, these questions warrant further multidisciplinary research.

To better envisage the subtle impacts of embodied social presence, research on automatic and controlled social information processing that dares to be "socially aware" will hopefully come to fruition. Sometimes, in cognitive and neurosciences, it seems to be too easily forgotten how profoundly bodily presence and bodily relations define human life. In the field of social perception and interaction studies, it is important to bear in mind that people are not only to look at but also to live with. At a first sight, we know nothing but we are affected; prepared for action. Perhaps, then, we see a trace of our ancestors peek out: always curious, always ready – to make war or peace, with just a single stare.

5 REFERENCES

- Adams Jr., R. B., & Kleck, R. E. (2003). Perceived gaze direction and the processing of facial displays of emotion. Psychological Science, 14, 644–647.
- Adams Jr., R. B., Kleck, R. E. (2005). Effects of direct and averted gaze on the perception of facially communicated emotion. Emotion, 5, 3–11, doi:10.1037/1528-3542.5.1.3.
- Adolphs R. (2010). Conceptual challenges and directions for social neuroscience. Neuron, 65, 752-767.
- Allen, J. J. B., Coan, J. A., & Nazarian, M. (2004). Issues and assumptions on the road from raw signals to metrics of frontal EEG asymmetry in emotion. Biological Psychology, 67(1), 183–218. https://doi.org/10.1016/j.biopsycho.2004.03.007
- Allen, J. J. B., & Kline, J. P. (2004). Frontal EEG asymmetry, emotion, and psychopathology: the first, and the next 25 years. Biological Psychology, 67(1–2), 1–5. https://doi.org/10.1016/j.biopsycho.2004.03.001
- Ambadar, Z., Cohn, J. F., & Reed, L. I. (2009). All Smiles are Not Created Equal: Morphology and Timing of Smiles Perceived as Amused, Polite, and Embarrassed/Nervous. Journal of Nonverbal Behavior, 33(1), 17–34. https://doi.org/10.1007/s10919-008-0059-5
- Ambadar, Z., Schooler, J. W., & Cohn, J. F. (2005). Deciphering the Enigmatic Face: The Importance of Facial Dynamics in Interpreting Subtle Facial Expressions. Psychological Science, 16(5), 403–410. https://doi.org/10.1111/j.0956-7976.2005.01548.x
- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: the medial frontal cortex and social cognition. Nature Reviews Neuroscience, 7(4), 268–277. https://doi.org/10.1038/nrn1884
- Anokhin, A. P., & Golosheykin, S. (2010). Startle modulation by affective faces. Biological Psychology, 83(1), 37–40. https://doi.org/10.1016/j.biopsycho.2009.10.001
- Argyle, M. (1988). Bodily communication. Methuen. Retrieved from https://books.google.fi/books/about/Bodily_Communication.html?id=crYOAAA AQAAJ&redir_esc=y
- Auvray, M., Lenay, C., & Stewart, J. (2008). Perceptual interactions in a minimalist virtual environment. New Ideas in Psychology, 27, 32–47. https://doi.org/10.1016/j.newideapsych.2007.12.002
- Bailenson, J. N., Blascovich, J., Beall, A. C., & Loomis, J. M. (2001). Equilibrium Theory Revisited: Mutual Gaze and Personal Space in Virtual Environments. Presence, 10(6), 583–598. Retrieved from https://vhil.stanford.edu/mm/2001/bailenson-equilibrium.pdf
- Bailenson, J. N., Blascovich, J., Beall, A. C., & Loomis, J. M. (2003). Interpersonal Distance in Immersive Virtual Environments. Pers Soc Psychol Bull at Eindhoven Univ of Technology on, 29(819). https://doi.org/10.1177/0146167203253270

- Bailey, R. C., Chorosevic, P., White, D., & White, H. (1981). Physiological Arousal and Perceptions of a Member of the Opposite Sex. The Journal of Social Psychology, 115(2), 271–276. https://doi.org/10.1080/00224545.1981.9711666
- Baker, S. L., Heinrichs, N., Kim, H.-J., & Hofmann, S. G. (2002). The Liebowitz social anxiety scale as a self-report instrument: a preliminary psychometric analysis. Behaviour Research and Therapy, 40(6), 701–715. https://doi.org/10.1016/S0005-7967(01)00060-2
- Balconi, M., Brambilla, E., & Falbo, L. (2009). Appetitive vs. defensive responses to emotional cues. Autonomic measures and brain oscillation modulation. Brain Research, 1296, 72–84. https://doi.org/10.1016/j.brainres.2009.08.056
- Barrett, L. F., Mesquita, B., Ochsner, K. N., & Gross, J. J. (2007). The Experience of Emotion. Annual Review of Psychology, 58(1), 373–403. https://doi.org/10.1146/annurev.psych.58.110405.085709
- Barrett, L. F., Quigley, K. S., Bliss-Moreau, E., & Aronson, K. R. (2004). Interoceptive sensitivity and self-reports of emotional experience. Journal of Personality and Social Psychology, 87(5), 684–97. https://doi.org/10.1037/0022-3514.87.5.684
- Batki, A., Baron-Cohen, S., Wheelwright, S., Connellan, J., & Ahluwalia, J. (2000). Is there an innate gaze module? Evidence from human neonates. Infant Behavior and Development, 23(2), 223–229. https://doi.org/10.1016/S0163-6383(01)00037-6
- Bavelas, J. B., Black, A., Lemery, C. R., & Mullett, J. (1986). "I show how you feel": Motor mimicry as a communicative act. Journal of Personality and Social Psychology, 50(2), 322–329. https://doi.org/10.1037/0022-3514.50.2.322
- Bentin, S., & Carmel, D. (2002). Accounts for the N170 face-effect: a reply to Rossion, Curran, & Gauthier. Cognition, 85(2), 197–202. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12127700
- Bentin, S., & Deouell, L. Y. (2000). STRUCTURAL ENCODING AND IDENTIFICATION IN FACE PROCESSING: ERP EVIDENCE FOR SEPARATE MECHANISMS. Cognitive Neuropsychology, 17(1–3), 35–55. https://doi.org/10.1080/026432900380472
- Bernstein, M. J., Young, S. G., Brown, C. M., Sacco, D. F., & Claypool, H. M. (2008). Adaptive Responses to Social Exclusion: Social Rejection Improves Detection of Real and Fake Smiles. Psychological Science, 19(10), 981–983. https://doi.org/10.1111/j.1467-9280.2008.02187.x
- Bindemann, M., Mike Burton, A., & Langton, S. R. H. (2008). How do eye gaze and facial expression interact? Visual Cognition, 16(6), 708–733. https://doi.org/10.1080/13506280701269318
- Boksem, M. A. S., Smolders, R., & De Cremer, D. (2012). Social power and approach-related neural activity. Social Cognitive and Affective Neuroscience, 7(5), 516–20. https://doi.org/10.1093/scan/nsp006
- Boll, S., Gamer, M., Kalisch, R., & Büchel, C. (2011). Processing of facial expressions and their significance for the observer in subregions of the human amygdala. NeuroImage, 56(1), 299–306. https://doi.org/10.1016/j.neuroimage.2011.02.021
- Bötzel, K., Schulze, S., & Stodieck, S. R. (1995). Scalp topography and analysis of intracranial sources of face-evoked potentials. Experimental Brain Research, 104(1), 135–43. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7621932
- Boucher, J.-D., Pattacini, U., Lelong, A., Bailly, G., Elisei, F., Fagel, S., ... Ventre-Dominey, J. (2012). I Reach Faster When I See You Look: Gaze Effects in Human–Human and

- Human–Robot Face-to-Face Cooperation. Frontiers in Neurorobotics, 6, 3. https://doi.org/10.3389/fnbot.2012.00003
- Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: the Self-Assessment Manikin and the Semantic Differential. Journal of Behavior Therapy and Experimental Psychiatry, 25(1), 49–59. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7962581
- Calder, A. J., Beaver, J. D., Davis, M. H., Van Ditzhuijzen, J., Keane, J., & Lawrence, A. D. (2007). Disgust sensitivity predicts the insula and pallidal response to pictures of disgusting foods. European Journal of Neuroscience, 25(11), 3422–3428. https://doi.org/10.1111/j.1460-9568.2007.05604.x
- Calder, A. J., Lawrence, A. D., Keane, J., Scott, S. K., Owen, A. M., Christoffels, I., & Young, A. W. (2002). Reading the mind from eye gaze. Neuropsychologia, 40(8), 1129–1138. https://doi.org/10.1016/S0028-3932(02)00008-8
- Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS Scales. Journal of Personality and Social Psychology, 67(2), 319–333. https://doi.org/10.1037/0022-3514.67.2.319
- Catmur, C., Mars, R. B., Rushworth, M. F., & Heyes, C. (2011). Making mirrors: premotor cortex stimulation enhances mirror and counter-mirror motor facilitation. Journal of Cognitive Neuroscience, 23(9), 2352–62. https://doi.org/10.1162/jocn.2010.21590
- Chaminade, T., & Cheng, G. (2009). Social cognitive neuroscience and humanoid robotics. Journal of Physiology-Paris, 103(3–5), 286–295. https://doi.org/10.1016/j.jphysparis.2009.08.011
- Chiu, P. H., Kayali, M. A., Kishida, K. T., Tomlin, D., Klinger, L. G., Klinger, M. R., ... Turner, R. (2008). Self responses along cingulate cortex reveal quantitative neural phenotype for high-functioning autism. Neuron, 57(3), 463–73. https://doi.org/10.1016/j.neuron.2007.12.020
- Coan, J. A., Allen, J. J., & Harmon-Jones, E. (2001). Voluntary facial expression and hemispheric asymmetry over the frontal cortex. Psychophysiology, 38(6), 912–25. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12240668
- Coles, M. E., Turk, C. L., Heimberg, R. G., & Fresco, D. M. (2001). Effects of varying levels of anxiety within social situations: relationship to memory perspective and attributions in social phobia. Behaviour Research and Therapy, 39(6), 651–665. https://doi.org/10.1016/S0005-7967(00)00035-8
- Conty, L., Russo, M., Loehr, V., Hugueville, L., Barbu, S., Huguet, P., ... George, N. (2010). The mere perception of eye contact increases arousal during a word-spelling task. Social Neuroscience, 5(2), 171–186. https://doi.org/10.1080/17470910903227507
- Cottrell, N. B., Wack, D. L., Sekerak, G. J., & Rittle, R. H. (1968). Social facilitation of dominant responses by the presence of an audicence and the mere presence of others. Journal of Personality and Social Psychology, 9(3), 245–50. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/5666972
- Critchley, H. D. (2002). Book Review: Electrodermal Responses: What Happens in the Brain. The Neuroscientist, 8(2), 132–142. https://doi.org/10.1177/107385840200800209
- Dalton, K. M., Nacewicz, B. M., Alexander, A. L., Davidson, R. J., Han, Q., Jiang, L., & al., et. (2007). Gaze-Fixation, Brain Activation, and Amygdala Volume in Unaffected Siblings of Individuals with Autism. Biological Psychiatry, 61(4), 512–520. https://doi.org/10.1016/j.biopsych.2006.05.019

- Davidson, R., & Fox, N. (1982). Asymmetrical brain activity discriminates between positive and negative affective stimuli in human infants. Science, 218(4578). Retrieved from http://science.sciencemag.org/content/218/4578/1235.long
- Davidson, R. J. (2004). What does the prefrontal cortex "do" in affect: perspectives on frontal EEG asymmetry research. Biological Psychology. https://doi.org/10.1016/j.biopsycho.2004.03.008
- De Jaegher, H. (2009). Social understanding through direct perception? Yes, by interacting. Consciousness and Cognition, 18(2), 535–542. https://doi.org/10.1016/j.concog.2008.10.007
- DeLoache, J. S., Chiong, C., Sherman, K., Islam, N., Vanderborght, M., Troseth, G. L., ... O'Doherty, K. (2010). Do Babies Learn From Baby Media? Psychological Science, 21(11), 1570–1574. https://doi.org/10.1177/0956797610384145
- Di Paolo, E. A., Rohde, M., & Iizuka, H. (2008). Sensitivity to social contingency or stability of interaction? Modelling the dynamics of perceptual crossing. New Ideas in Psychology, 26(2), 278–294. https://doi.org/10.1016/j.newideapsych.2007.07.006
- Dimberg, U., & Thunberg, M. (2007). Speech anxiety and rapid emotional reactions to angry and happy facial expressions. Scandinavian Journal of Psychology, 48(4), 321–8. https://doi.org/10.1111/j.1467-9450.2007.00586.x
- Dolk, T., Hommel, B., Colzato, L. S., Schütz-Bosbach, S., Prinz, W., & Liepelt, R. (2011). How "social" is the social Simon effect? Frontiers in Psychology, 2, 84. https://doi.org/10.3389/fpsyg.2011.00084
- Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-Cohen, S. (n.d.). Gaze Perception Triggers Reflexive Visuospatial Orienting. Retrieved from http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.212.3316&rep=rep1&ty pe=pdf
- Dunbar, R. I. M. (1993). Coevolution of neocortical size, group size and language in humans. Behavioral and Brain Sciences, 16(4), 681. https://doi.org/10.1017/S0140525X00032325
- Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the Social Brain. Science, 317(5843), 1344–1347. https://doi.org/10.1126/science.1145463
- Elliot, A. J., & Covington, M. V. (2001). Approach and Avoidance Motivation. Educational Psychology Review, 13(2), 73–92. https://doi.org/10.1023/A:1009009018235
- Elliot, A. J., & Thrash, T. M. (2002). Approach-avoidance motivation in personality: approach and avoidance temperaments and goals. Journal of Personality and Social Psychology, 82(5), 804–18. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12003479
- Elsabbagh, M., Volein, A., Csibra, G., Holmboe, K., Garwood, H., Tucker, L., ... Johnson, M. H. (2009). Neural Correlates of Eye Gaze Processing in the Infant Broader Autism Phenotype. Biological Psychiatry, 65(1), 31–38. https://doi.org/10.1016/j.biopsych.2008.09.034
- Emery, N. J. (2000). The eyes have it: the neuroethology, function and evolution of social gaze. Neuroscience and Biobehavioral Reviews, 24(6), 581–604. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10940436
- Farroni, T., Csibra, G., Simion, F., & Johnson, M. H. (2002). Eye contact detection in humans from birth. Proceedings of the National Academy of Sciences, 99(14), 9602–9605. https://doi.org/10.1073/pnas.152159999

- Farroni, T., Johnson, M. H., & Csibra, G. (2004). Mechanisms of eye gaze perception during infancy. Journal of Cognitive Neuroscience, 16(8), 1320–6. https://doi.org/10.1162/0898929042304787
- Figner, B. (2011). Using Skin Conductance in Judgment and Decision Making Research. Society for Judgment and Decision Making Series, 163–184. Retrieved from http://ecitations.ethbib.ethz.ch/view/pub:49933
- Freeman, J. B., Ambady, N., Rule, N. O., & Johnson, K. L. (2008). Will a category cue attract you? Motor output reveals dynamic competition across person construal. Journal of Experimental Psychology: General, 137(4), 673–690. https://doi.org/10.1037/a0013875
- Friesen, C. K., & Kingstone, A. (1998). The eyes have it! Reflexive orienting is triggered by nonpredictive gaze. Psychonomic Bulletin & Review, 5(3), 490–495. https://doi.org/10.3758/BF03208827
- Frith, C. D., Frith, U., King-Casas, B., Anen, C., Camerer, C. F., Quartz, S. R., & Montague, P. R. (2008). The self and its reputation in autism. Neuron, 57(3), 331–2. https://doi.org/10.1016/j.neuron.2008.01.014
- Gale, A., Spratt, G., Chapman, A. J., & Smallbone, A. (1975). EEG correlates of eye contact and interpersonal distance. Biological Psychology, 3(4), 237–45. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/1212482
- George, N., Driver, J., & Dolan, R. J. (n.d.). Seen Gaze-Direction Modulates Fusiform Activity and Its Coupling with Other Brain Areas during Face Processing. https://doi.org/10.1006/nimg.2001.0769
- Gobbini, M. I., & Haxby, J. V. (2007). Neural systems for recognition of familiar faces. Neuropsychologia, 45(1), 32–41. https://doi.org/10.1016/j.neuropsychologia.2006.04.015
- Grossmann, T., Johnson, M. H., Farroni, T., & Csibra, G. (2007). Social perception in the infant brain: gamma oscillatory activity in response to eye gaze. Social Cognitive and Affective Neuroscience, 2(4), 284–291. https://doi.org/10.1093/scan/nsm025
- Guellai, B., Streri, A., Vollmer-Conna, U., Martin, A., Ahluwalia, J., & Sebastián-Gallés, N. (2011). Cues for Early Social Skills: Direct Gaze Modulates Newborns' Recognition of Talking Faces. PLoS ONE, 6(4), e18610. https://doi.org/10.1371/journal.pone.0018610
- Guerin, B. (1986). Mere presence effects in humans: A review. Journal of Experimental Social Psychology, 22(1), 38–77. https://doi.org/10.1016/0022-1031(86)90040-5
- Haidt, J., & Keltner, D. (1999). Culture and Facial Expression: Open-ended Methods Find More Expressions and a Gradient of Recognition. Cognition & Emotion, 13(3), 225–266. https://doi.org/10.1080/026999399379267
- Haley, K. J., & Fessler, D. M. T. (2005). Nobody's watching? Evolution and Human Behavior, 26(3), 245–256. https://doi.org/10.1016/j.evolhumbehav.2005.01.002
- Hareli, S., Shomrat, N., & Hess, U. (2009). Emotional versus neutral expressions and perceptions of social dominance and submissiveness. Emotion, 9(3), 378–384. https://doi.org/10.1037/a0015958
- Harmon-Jones, E., Gable, P. A., & Peterson, C. K. (2010). The role of asymmetric frontal cortical activity in emotion-related phenomena: A review and update. Biological Psychology, 84(3), 451–462. https://doi.org/10.1016/j.biopsycho.2009.08.010
- Haslam, N. (2006). Dehumanization: An Integrative Review. Personality and Social Psychology Review, 10(3), 252–264. https://doi.org/10.1207/s15327957pspr1003_4

- Hess, U., Adams, R. B., & Kleck, R. E. (2007). Looking at You or Looking Elsewhere: The Influence of Head Orientation on the Signal Value of Emotional Facial Expressions. Motivation and Emotion, 31(2), 137–144. https://doi.org/10.1007/s11031-007-9057-x
- Hess, U., Blairy, S., & Kleck, R. E. (1997). The Intensity of Emotional Facial Expressions and Decoding Accuracy. Journal of Nonverbal Behavior, 21(4), 241–257. https://doi.org/10.1023/A:1024952730333
- Hess, U., & Bourgeois, P. (2010). You smile–I smile: Emotion expression in social interaction. Biological Psychology, 84(3), 514–520. https://doi.org/10.1016/j.biopsycho.2009.11.001
- Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributedhuman neural system for face perception. Nature Neuroscience, 3(1), 80–84. https://doi.org/10.1038/71152
- Holmes, A., Bradley, B. P., KRAGH Nielsen, M., & Mogg, K. (2009). Attentional selectivity for emotional faces: Evidence from human electrophysiology. Psychophysiology, 46(1), 62–68. https://doi.org/10.1111/j.1469-8986.2008.00750.x
- Holmes, A., Nielsen, M. K., & Green, S. (2008). Effects of anxiety on the processing of fearful and happy faces: An event-related potential study. Biological Psychology, 77(2), 159–173. https://doi.org/10.1016/j.biopsycho.2007.10.003
- Honk, J. van, & Schutter, D. J. L. G. (2006). From Affective Valence to Motivational Direction. Psychological Science, 17(11), 963–965. https://doi.org/10.1111/j.1467-9280.2006.01813.x
- Honma, M., Tanaka, Y., Osada, Y., & Kuriyama, K. (2012). Perceptual and not physical eye contact elicits pupillary dilation. Biological Psychology, 89(1), 112–116. https://doi.org/10.1016/j.biopsycho.2011.09.015
- Itier, R. J., & Taylor, M. J. (2004). N170 or N1? Spatiotemporal Differences between Object and Face Processing Using ERPs. Cerebral Cortex, 14(2), 132–142. https://doi.org/10.1093/cercor/bhg111
- Järveläinen, J., Schürmann, M., Avikainen, S., & Hari, R. (2001). Stronger reactivity of the human primary motor cortex during observation of live rather than video motor acts. Neuroreport, 12(16), 3493–3495. https://doi.org/10.1097/00001756-200111160-00024
- Kampe, K. K. W., Frith, C. D., & Frith, U. (n.d.). " Hey John ": Signals Conveying Communicative Intention toward the Self Activate Brain Regions Associated with " Mentalizing, " Regardless of Modality. Retrieved from http://discovery.ucl.ac.uk/6242/1/6242.pdf
- Keating, C. F., et al, A., Segall, M. H., Cysneiros, P. G., Kilbride, J. E., Leahy, P., ... Wirsing, R. (1981). Culture and the perception of social dominance from facial expression. Journal of Personality and Social Psychology, 40(4), 615–626. https://doi.org/10.1037/0022-3514.40.4.615
- Keil, A., Bradley, M. M., Hauk, O., Rockstroh, B., Elbert, T., & Lang, P. J. (2002). Large-scale neural correlates of affective picture processing. Psychophysiology, 39(5), 641–9. https://doi.org/10.1017.S0048577202394162
- Kimble, C. E., Hirt, E. R., & Arnold, E. M. (1985). Self-Consciousness, Public and Private Self-Awareness, and Memory in a Social Setting. The Journal of Psychology, 119(1), 59–69. https://doi.org/10.1080/00223980.1985.10542872

- Kircher, T., Blümel, I., Marjoram, D., Lataster, T., Krabbendam, L., Weber, J., ... Krach, S. (2009). Online mentalising investigated with functional MRI. Neuroscience Letters, 454(3), 176–181. https://doi.org/10.1016/j.neulet.2009.03.026
- Kleinke, C. L., & Pohlen, P. D. (1971). Affective and emotional responses as a function of other person's gaze and cooperativeness in a two-person game. Journal of Personality and Social Psychology, 17(3), 308–13. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/5546894
- Klucharev, V., & Sams, M. (2004). Interaction of gaze direction and facial expressions processing: ERP study. Neuroreport, 15(4), 621–5. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/15094464
- Kobayashi, H., & Kohshima, S. (2001). Unique morphology of the human eye and its adaptive meaning: comparative studies on external morphology of the primate eye. Journal of Human Evolution, 40(5), 419–435. https://doi.org/10.1006/jhev.2001.0468
- Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: A review. Biological Psychology, 84(3), 394–421. https://doi.org/10.1016/j.biopsycho.2010.03.010
- Krueger, J. (2011). Extended cognition and the space of social interaction. Consciousness and Cognition, 20(3), 643–657. https://doi.org/10.1016/j.concog.2010.09.022
- Kuhl, P. K., Tsao, F.-M., & Liu, H.-M. (2003). Foreign-language experience in infancy: effects of short-term exposure and social interaction on phonetic learning. Proceedings of the National Academy of Sciences of the United States of America, 100(15), 9096–101. https://doi.org/10.1073/pnas.1532872100
- Kuzmanovic, B., Georgescu, A. L., Eickhoff, S. B., Shah, N. J., Bente, G., Fink, G. R., & Vogeley, K. (2009). Duration matters: Dissociating neural correlates of detection and evaluation of social gaze. NeuroImage, 46(4), 1154–1163. https://doi.org/10.1016/j.neuroimage.2009.03.037
- Kylliäinen, A., & Hietanen, J. K. (2006). Skin Conductance Responses to Another Person's Gaze in Children with Autism. Journal of Autism and Developmental Disorders, 36(4), 517–525. https://doi.org/10.1007/s10803-006-0091-4
- LaBar, K. S., Gatenby, J. C., Gore, J. C., LeDoux, J. E., & Phelps, E. A. (1998). Human amygdala activation during conditioned fear acquisition and extinction: a mixed-trial fMRI study. Neuron, 20(5), 937–45. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9620698
- Laidlaw, K. E. W., Foulsham, T., Kuhn, G., & Kingstone, A. (2011). Potential social interactions are important to social attention. Proceedings of the National Academy of Sciences of the United States of America, 108(14), 5548–53. https://doi.org/10.1073/pnas.1017022108
- Lau, S. (1982). The Effect of Smiling on Person Perception. The Journal of Social Psychology, 117(1), 63–67. https://doi.org/10.1080/00224545.1982.9713408
- Martin, W. W., & Gardner, S. N. (1979). The Relative Effects of Eye-Gaze and Smiling on Arousal in Asocial Situations. The Journal of Psychology, 102(2), 253–259. https://doi.org/10.1080/00223980.1979.9923495
- Mason, M. F., Hood, B. M., & Macrae, C. N. (n.d.). Look into my eyes: Gaze direction and person memory. https://doi.org/10.1080/09658210344000152
- Mason, M. F., Tatkow, E. P., & Macrae, C. N. (2005). The Look of Love. Psychological Science, 16(3), 236–239. https://doi.org/10.1111/j.0956-7976.2005.00809.x

- Mathersul, D., Williams, L. M., Hopkinson, P. J., & Kemp, A. H. (2008). Investigating models of affect: Relationships among EEG alpha asymmetry, depression, and anxiety. Emotion, 8(4), 560–572. https://doi.org/10.1037/a0012811
- Matsumoto, D., & Kudoh, T. (1993). American-Japanese cultural differences in attributions of personality based on smiles. Journal of Nonverbal Behavior, 17(4), 231–243. https://doi.org/10.1007/BF00987239
- Maxwell, G. M., Cook, M. W., & Burr, R. (1985). The encoding and decoding of liking from behavioral cues in both auditory and visual channels. Journal of Nonverbal Behavior, 9(4), 239–263. https://doi.org/10.1007/BF00986883
- McBride, G., King, M. G., & James, J. W. (1965). Social proximity effects on galvanic skin responses in adult humans. The Journal of Psychology, 61(1), 153–7. https://doi.org/10.1080/00223980.1965.10544805
- McGann, M., & De Jaegher, H. (2009). Self–other contingencies: Enacting social perception. Phenomenology and the Cognitive Sciences, 8(4), 417–437. https://doi.org/10.1007/s11097-009-9141-7
- Merleau-Ponty, M. (2002). Phenomenology of perception. Routledge. Retrieved from https://books.google.fi/books/about/Phenomenology_of_Perception.html?id=q3 HwhfjRmswC&redir_esc=y
- Miller, A., & Tomarken, A. J. (2001). Task-dependent changes in frontal brain asymmetry: effects of incentive cues, outcome expectancies, and motor responses. Psychophysiology, 38(3), 500–11. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11352139
- Moll, H., & Meltzoff, A. N. (2011). How does it look? Level 2 perspective-taking at 36 months of age. Child Development, 82(2), 661–73. https://doi.org/10.1111/j.1467-8624.2010.01571.x
- Moukheiber, A., Rautureau, G., Perez-Diaz, F., Soussignan, R., Dubal, S., Jouvent, R., & Pelissolo, A. (2010). Gaze avoidance in social phobia: Objective measure and correlates. Behaviour Research and Therapy, 48(2), 147–151. https://doi.org/10.1016/j.brat.2009.09.012
- Myllyneva, A., Ranta, K., & Hietanen, J. K. (2015). Psychophysiological responses to eye contact in adolescents with social anxiety disorder. Biological Psychology, 109, 151–158. https://doi.org/10.1016/j.biopsycho.2015.05.005
- N'Diaye, K., Sander, D., & Vuilleumier, P. (2009). Self-relevance processing in the human amygdala: Gaze direction, facial expression, and emotion intensity. Emotion, 9(6), 798–806. https://doi.org/10.1037/a0017845
- Nichols, K. A., & Champness, B. G. (1971). Eye gaze and the GSR. Journal of Experimental Social Psychology, 7(6), 623–626. https://doi.org/10.1016/0022-1031(71)90024-2
- Nishitani, N., & Hari, R. (2002). Viewing lip forms: cortical dynamics. Neuron, 36(6), 1211–20. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12495633
- Nitschke, W. H. J. B. (1998). The Puzzle of Regional Brain Activity in and Anxiety: The Importance of Subtypes and Comorbidity. Cognition & Emotion, 12(3), 421–447. https://doi.org/10.1080/026999398379664
- Nummenmaa, L., & Calder, A. J. (2009). Neural mechanisms of social attention. Trends in Cognitive Sciences, 13(3), 135–143. https://doi.org/10.1016/j.tics.2008.12.006
- Oberman, L. M., Pineda, J. A., & Ramachandran, V. S. (2007). The human mirror neuron system: a link between action observation and social skills. Social Cognitive and Affective Neuroscience, 2(1), 62–6. https://doi.org/10.1093/scan/nsl022

- Oya, H., Kawasaki, H., Howard, M. A., & Adolphs, R. (2002). Electrophysiological responses in the human amygdala discriminate emotion categories of complex visual stimuli. The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 22(21), 9502–12. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12417674
- Paradiso, S., & Rudrauf, D. (2012). Struggle for life, struggle for love and recognition: the neglected self in social cognitive neuroscience. Dialogues in Clinical Neuroscience, 14(1), 65–75. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/22577306
- Parkinson, B. (2005). Do Facial Movements Express Emotions or Communicate Motives?

 Personality and Social Psychology Review, 9(4), 278–311.

 https://doi.org/10.1207/s15327957pspr0904_1
- Patterson, M. L., Jordan, A., Hogan, M. B., & Frerker, D. (1981a). Effects of nonverbal intimacy on arousal and behavioral adjustment. Journal of Nonverbal Behavior, 5(3), 184–198. https://doi.org/10.1007/BF00986135
- Patterson, M. L., Jordan, A., Hogan, M. B., & Frerker, D. (1981b). Effects of nonverbal intimacy on arousal and behavioral adjustment. Journal of Nonverbal Behavior, 5(3), 184–198. https://doi.org/10.1007/BF00986135
- Patterson, M. L., & L., M. (1976). An arousal model of interpersonal intimacy. Psychological Review, 83(3), 235–245. https://doi.org/10.1037/0033-295X.83.3.235
- Pelphrey, K. A., Morris, J. P., & McCarthy, G. (2004). Grasping the Intentions of Others: The Perceived Intentionality of an Action Influences Activity in the Superior Temporal Sulcus during Social Perception. Journal of Cognitive Neuroscience, 16(10), 1706–1716. https://doi.org/10.1162/0898929042947900
- Phelps, E. A., O'Connor, K. J., Gatenby, J. C., Gore, J. C., Grillon, C., & Davis, M. (2001). Activation of the left amygdala to a cognitive representation of fear. Nature Neuroscience, 4(4), 437–441. https://doi.org/10.1038/86110
- Pickett, C. L., Gardner, W. L., & Knowles, M. (2004). Getting a Cue: The Need to Belong and Enhanced Sensitivity to Social Cues. Personality and Social Psychology Bulletin, 30(9), 1095–1107. https://doi.org/10.1177/0146167203262085
- Pitcher, D., Dilks, D. D., Saxe, R. R., Triantafyllou, C., & Kanwisher, N. (2011). Differential selectivity for dynamic versus static information in face-selective cortical regions. NeuroImage, 56(4), 2356–2363. https://doi.org/10.1016/j.neuroimage.2011.03.067
- Pizzagalli, D. A., Sherwood, R. J., Henriques, J. B., & Davidson, R. J. (2005). Frontal Brain Asymmetry and Reward Responsiveness: A Source-Localization Study. Psychological Science, 16(10), 805–813. https://doi.org/10.1111/j.1467-9280.2005.01618.x
- Przyrembel, M., Smallwood, J., Pauen, M., & Singer, T. (2012). Illuminating the dark matter of social neuroscience: Considering the problem of social interaction from philosophical, psychological, and neuroscientific perspectives. Frontiers in Human Neuroscience, 6, 190. https://doi.org/10.3389/fnhum.2012.00190
- Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 18(6), 2188–99. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9482803
- Reddy, V. (2010). How infants know minds. Harvard University Press. Retrieved from http://www.hup.harvard.edu/catalog.php?isbn=9780674046078
- Reddy, V., & Morris, P. (2004). Participants Don't Need Theories: Knowing Minds in Engagement. Theory & Psychology, 14(5), 647–665. https://doi.org/10.1177/0959354304046177

- Rilling, J. K., Sanfey, A. G., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2004). The neural correlates of theory of mind within interpersonal interactions. NeuroImage, 22(4), 1694–1703. https://doi.org/10.1016/j.neuroimage.2004.04.015
- Safren, S. A., Heimberg, R. G., Horner, K. J., Juster, H. R., Schneier, F. R., & Liebowitz, M. R. (1999). Factor Structure of Social Fears: The Liebowitz Social Anxiety Scale. Journal of Anxiety Disorders, 13(3), 253–270. https://doi.org/10.1016/S0887-6185(99)00003-1
- Sallnäs, E.-L. (2005). Effects of Communication Mode on Social Presence, Virtual Presence, and Performance in Collaborative Virtual Environments. Presence: Teleoperators and Virtual Environments, 14(4), 434–449. https://doi.org/10.1162/105474605774785253
- Sander, D., Grandjean, D., Kaiser, S., Wehrle, T., & Scherer, K. R. (2007). Interaction effects of perceived gaze direction and dynamic facial expression: Evidence for appraisal theories of emotion. European Journal of Cognitive Psychology, 19(3), 470–480. https://doi.org/10.1080/09541440600757426
- Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The Neural Basis of Economic Decision-Making in the Ultimatum Game. Science, 300(5626). Retrieved from http://science.sciencemag.org/content/300/5626/1755.long
- Sato, W., Kochiyama, T., Uono, S., & Yoshikawa, S. (2008). Time course of superior temporal sulcus activity in response to eye gaze: a combined fMRI and MEG study. Social Cognitive and Affective Neuroscience, 3(3), 224–32. https://doi.org/10.1093/scan/nsn016
- Schacht, A., & Sommer, W. (2009). Emotions in word and face processing: Early and late cortical responses. Brain and Cognition, 69(3), 538–550. https://doi.org/10.1016/j.bandc.2008.11.005
- Schrammel, F., Pannasch, S., Graupner, S.-T., Mojzisch, A., & Velichkovsky, B. M. (2009). Virtual friend or threat? The effects of facial expression and gaze interaction on psychophysiological responses and emotional experience. Psychophysiology, 46(5), 922–931. https://doi.org/10.1111/j.1469-8986.2009.00831.x
- Schupp, H. T., Junghofer, M., Weike, A. I., & Hamm, A. O. (2003). Attention and emotion: an ERP analysis of facilitated emotional stimulus processing. Neuroreport, 14. https://doi.org/10.1097/00001756-200306110-00002
- Schupp, H. T., Stockburger, J., Codispoti, M., Junghofer, M., Weike, A. I., & Hamm, A. O. (2007). Selective Visual Attention to Emotion. Journal of Neuroscience, 27(5), 1082–1089. https://doi.org/10.1523/JNEUROSCI.3223-06.2007
- Semlitsch, H. V., Anderer, P., Schuster, P., & Presslich, O. (1986). A Solution for Reliable and Valid Reduction of Ocular Artifacts, Applied to the P300 ERP. Psychophysiology, 23(6), 695–703. https://doi.org/10.1111/j.1469-8986.1986.tb00696.x
- Senju, A., Hasegawa, T., & Tojo, Y. (2005). Does perceived direct gaze boost detection in adults and children with and without autism? The stare-in-the-crowd effect revisited. Visual Cognition, 12(8), 1474–1496. https://doi.org/10.1080/13506280444000797
- Shimada, S., & Hiraki, K. (2006). Infant's brain responses to live and televised action. NeuroImage, 32(2), 930–939. https://doi.org/10.1016/j.neuroimage.2006.03.044
- Shore, D. M., & Heerey, E. A. (2011). The value of genuine and polite smiles. Emotion (Washington, D.C.), 11(1), 169–74. https://doi.org/10.1037/a0022601

- Silvia, J., Silvia, J., & Gendolla, G. H. E. (2001). On introspection and self-perception: Does selffocused attention enable accurate self-knowledge. REVIEW OF GENERAL PSYCHOLOGY, 241--269. Retrieved from http://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.470.5208
- Simons, R. F., Detenber, B. H., Roedema, T. M., & Reiss, J. E. (1999). Emotion processing in three systems: The medium and the message. Psychophysiology, 36(5), 619–627. https://doi.org/10.1111/1469-8986.3650619
- Spielberg, J. M., Miller, G. A., Warren, S. L., Engels, A. S., Crocker, L. D., Banich, M. T., ... Heller, W. (2012). A brain network instantiating approach and avoidance motivation. Psychophysiology, 49(9), 1200–1214. https://doi.org/10.1111/j.1469-8986.2012.01443.x
- Spielberg, J. M., Stewart, J. L., Levin, R. L., Miller, G. A., & Heller, W. (2008). Prefrontal Cortex, Emotion, and Approach/Withdrawal Motivation. Social and Personality Psychology Compass, 2(1), 135–153. https://doi.org/10.1111/j.1751-9004.2007.00064.x
- Spurr, J. M., & Stopa, L. (2003). The observer perspective: effects on social anxiety and performance. Behaviour Research and Therapy, 41(9), 1009–1028. https://doi.org/10.1016/S0005-7967(02)00177-8
- Stanley, J., Gowen, E., & Miall, R. C. (2007). Effects of agency on movement interference during observation of a moving dot stimulus. Journal of Experimental Psychology: Human Perception and Performance, 33(4), 915–926. https://doi.org/10.1037/0096-1523.33.4.915
- Stein, D. J., Kasper, S., Andersen, E. W., Nil, R., & Lader, M. (2004). Escitalopram in the treatment of social anxiety disorder: Analysis of efficacy for different clinical subgroups and symptom dimensions. Depression and Anxiety, 20(4), 175–181. https://doi.org/10.1002/da.20043
- Stins, J. F., Roelofs, K., Villan, J., Kooijman, K., Hagenaars, M. A., & Beek, P. J. (2011). Walk to me when I smile, step back when I'm angry: emotional faces modulate whole-body approach—avoidance behaviors. Experimental Brain Research, 212(4), 603–611. https://doi.org/10.1007/s00221-011-2767-z
- Swaab, R. I., & Swaab, D. F. (2009). Sex differences in the effects of visual contact and eye contact in negotiations. Journal of Experimental Social Psychology, 45(1), 129–136. https://doi.org/10.1016/j.jesp.2008.06.009
- Teufel, C., Alexis, D. M., Clayton, N. S., & Davis, G. (2010). Mental-state attribution drives rapid, reflexive gaze following. Attention, Perception, & Psychophysics, 72(3), 695–705. https://doi.org/10.3758/APP.72.3.695
- Teufel, C., Alexis, D. M., Todd, H., Lawrance-Owen, A. J., Clayton, N. S., & Davis, G. (2009). Social Cognition Modulates the Sensory Coding of Observed Gaze Direction. Current Biology, 19(15), 1274–1277. https://doi.org/10.1016/j.cub.2009.05.069
- Teufel, C., Fletcher, P. C., & Davis, G. (2010). Seeing other minds: attributed mental states influence perception. Trends in Cognitive Sciences, 14(8), 376–382. https://doi.org/10.1016/j.tics.2010.05.005
- Tobimatsu, S., & Celesia, G. G. (2006). Studies of human visual pathophysiology with visual evoked potentials. Clinical Neurophysiology, 117(7), 1414–1433. https://doi.org/10.1016/j.clinph.2006.01.004
- TOMASELLO, M., CALL, J., & HARE, B. (1998). Five primate species follow the visual gaze of conspecifics. Animal Behaviour, 55(4), 1063–1069. https://doi.org/10.1006/anbe.1997.0636

- Tsao, D. Y., & Livingstone, M. S. (2008). Mechanisms of face perception. Annual Review of Neuroscience, 31, 411–37. https://doi.org/10.1146/annurev.neuro.30.051606.094238
- Uusberg, H., Allik, J., & Hietanen, J. K. (2015). Eye contact reveals a relationship between Neuroticism and anterior EEG asymmetry. Neuropsychologia, 73, 161–168. https://doi.org/10.1016/j.neuropsychologia.2015.05.008
- Vlainic, E., Liepelt, R., Colzato, L. S., Prinz, W., & Hommel, B. (2010). The Virtual Co-Actor: The Social Simon Effect does not Rely on Online Feedback from the Other. Frontiers in Psychology, 1, 208. https://doi.org/10.3389/fpsyg.2010.00208
- Vogeley, K., & Bente, G. (2010). "Artificial humans": Psychology and neuroscience perspectives on embodiment and nonverbal communication. Neural Networks, 23(8), 1077–1090. https://doi.org/10.1016/j.neunet.2010.06.003
- Wacker, J., Chavanon, M.-L., Leue, A., & Stemmler, G. (2008). Is running away right? The behavioral activation-behavioral inhibition model of anterior asymmetry. Emotion, 8(2), 232–249. https://doi.org/10.1037/1528-3542.8.2.232
- Wacker, J., Heldmann, M., & Stemmler, G. (2003). Separating emotion and motivational direction in fear and anger: effects on frontal asymmetry. Emotion (Washington, D.C.), 3(2), 167–93. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12899417
- Wager, T. D., Phan, K. L., Liberzon, I., & Taylor, S. F. (2003). Valence, gender, and lateralization of functional brain anatomy in emotion: a meta-analysis of findings from neuroimaging. NeuroImage, 19(3), 513–31. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12880784
- Wang, Y., Ramsey, R., & de C. Hamilton, A. F. (2011). The Control of Mimicry by Eye Contact Is Mediated by Medial Prefrontal Cortex. Journal of Neuroscience, 31(33), 12001–12010. https://doi.org/10.1523/JNEUROSCI.0845-11.2011
- Warneken, F., Chen, F., & Tomasello, M. (2006). Cooperative Activities in Young Children and Chimpanzees. Child Development, 77(3), 640–663. https://doi.org/10.1111/j.1467-8624.2006.00895.x
- Waytz, A., Gray, K., Epley, N., & Wegner, D. M. (2010). Causes and consequences of mind perception. Trends in Cognitive Sciences, 14(8), 383–388. https://doi.org/10.1016/j.tics.2010.05.006
- Wesselmann, E. D., Cardoso, F. D., Slater, S., & Williams, K. D. (2012). To Be Looked at as Though Air: Civil Attention Matters. Psychological Science, 23(2), 166–168. https://doi.org/10.1177/0956797611427921
- Weyers, P., Muhlberger, A., Hefele, C., & Pauli, P. (2006). Electromyographic responses to static and dynamic avatar emotional facial expressions. Psychophysiology, 43(5), 450–453. https://doi.org/10.1111/j.1469-8986.2006.00451.x
- Wild, B., Erb, M., & Bartels, M. (2001). Are emotions contagious? Evoked emotions while viewing emotionally expressive faces: quality, quantity, time course and gender differences. Psychiatry Research, 102(2), 109–124. https://doi.org/10.1016/S0165-1781(01)00225-6
- Williams, G. P., & Kleinke, C. L. (1993). Effects of Mutual Gaze and Touch on Attraction, Mood, and Cardiovascular Reactivity. Journal of Research in Personality, 27(2), 170– 183. https://doi.org/10.1006/jrpe.1993.1012
- Wilms, M., Schilbach, L., Pfeiffer, U., Bente, G., Fink, G. R., & Vogeley, K. (2010). It's in your eyes--using gaze-contingent stimuli to create truly interactive paradigms for

- social cognitive and affective neuroscience. Social Cognitive and Affective Neuroscience, 5(1), 98–107. https://doi.org/10.1093/scan/nsq024
- Wilson, M. (2002). Six views of embodied cognition. Psychonomic Bulletin & Review, 9(4), 625–636. https://doi.org/10.3758/BF03196322
- Wiltermuth, S. S., & Heath, C. (2009). Synchrony and Cooperation. Psychological Science, 20(1), 1–5. https://doi.org/10.1111/j.1467-9280.2008.02253.x
- Wirth, J. H., Sacco, D. F., Hugenberg, K., & Williams, K. D. (2010). Eye Gaze as Relational Evaluation: Averted Eye Gaze Leads to Feelings of Ostracism and Relational Devaluation. Personality and Social Psychology Bulletin, 36(7), 869–882. https://doi.org/10.1177/0146167210370032
- Yen, J.-Y., Yen, C.-F., Chen, C.-S., Wang, P.-W., Chang, Y.-H., & Ko, C.-H. (2012). Social anxiety in online and real-life interaction and their associated factors. Cyberpsychology, Behavior and Social Networking, 15(1), 7–12. https://doi.org/10.1089/cyber.2011.0015
- Zahavi, D. (2002). First-person thoughts and embodied self-awareness: Some reflections on the relation between recent analytical philosophy and phenomenology. Phenomenology and the Cognitive Sciences, 1(1), 7–26. https://doi.org/10.1023/A:1015568518276
- Zaki, J., & Ochsner, K. (2009). The Need for a Cognitive Neuroscience of Naturalistic Social Cognition. Annals of the New York Academy of Sciences, 1167(1), 16–30. https://doi.org/10.1111/j.1749-6632.2009.04601.x
- Zink, C. F., Tong, Y., Chen, Q., Bassett, D. S., Stein, J. L., Meyer-Lindenberg, A., ... Grodd, W. (2008). Know your place: neural processing of social hierarchy in humans. Neuron, 58(2), 273–83. https://doi.org/10.1016/j.neuron.2008.01.025

6 ORIGINAL PUBLICATIONS (STUDIES I-IV)

VISION, CENTRAL NEUROREPORT

Facing a real person: an event-related potential study

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Received I8 December 2007; accepted I0 January 2008

Although faces are typically perceived in the context of human interaction, face processing is commonly studied by displaying faces on a computer screen. This study on event-related potential examined whether the processing of faces differs depending on whether participants are viewing faces live or on a computer screen. In both the conditions, the participants were shown a real face, a dummy face, and a control object. NI70 and early posterior negativity

discriminated between faces and control object in both the conditions. Interestingly, early posterior negativity differentiated between the real face and the dummy face only in the live condition. The results indicate that a live face, as a potentially interacting stimulus, is processed differently than an inanimate face already at the early processing stages. NeuroReport 19:497–501 © 2008 Wolters Kluwer Health | Lippincott Williams & Wilkins.

Keywords: event-related potentials, face processing, motivation, social communication

Introduction

Several behavioral, neurophysiological, and neuroimaging studies [1–3] have shown that the visual processing of facial information is specialized compared with the processing of other objects. Studies on event-related potential (ERP) have revealed that N170, a negative component peaking at approximately 170 ms after stimulus onset in occipitotemporal regions, is enhanced in amplitude and reduced in latency in faces compared with other objects [4,5]. Although N170 has been linked to the structural encoding stage of face processing [6], recent studies have shown that it is modulated by cognitive and affective factors, such as emotional expression [7,8], semantic context [9], and spatial attention [10].

Studies investigating the visual processing of motivationally salient stimuli other than faces have shown that the early posterior negativity (EPN) [11] is enhanced to motivationally significant stimuli [12,13] and to attended stimuli [14]. The EPN is a negative-going occipitotemporal potential occurring approximately 150–350 ms after stimulus onset and has been related to the perceptual encoding and early selection of visual stimuli [11]. The processing intensification reflected in EPN possibly serves the basic motivational approach-avoidance system guiding stimulus evaluation at later processing stages [15,16].

The N170 and EPN responses may be especially modulated by affective-motivational factors when socially meaningful stimuli are involved. The stimuli in face processing studies have commonly been pictures of faces, either real or schematic. Although both types of pictures generally elicit the same pattern of face-sensitive ERP responses [6], neither of them holds the potential for interpersonal communication. Rapid evaluation of affective-motivational significance

is, however, crucial in a real face-to-face interaction. The question arises whether the presentation mode (live vs. picture) has an influence on the affective-motivational modulations on N170 and EPN responses.

In this study, we investigated whether ERPs to facial stimuli differ when presented either live or as pictures. The participants were shown a human face, a dummy face, and a control object either live through an electronic shutter or as pictures on a computer screen. By including the dummy face, we controlled the possibility that the ERP differences between real faces and pictures of real faces might reflect the fact that live faces are three-dimensional. In the live condition, both the human and the dummy faces were three-dimensional, but only the human face had a potential for social interaction. Although great care was taken to ensure that the stimuli were visually as similar as possible in both presentation modes, the design involved comparison of the ERPs only within each mode of stimulus presentation. The hypotheses were that (i) in both presentation conditions, the human and the dummy faces would elicit enhanced and shorter latency N170 responses than the control object, (ii) in the picture condition, the human and the dummy faces would elicit undifferentiated N170 and EPN responses, whereas (iii) in the live condition, the human face would elicit stronger N170 and EPN amplitudes and shorter N170 latencies than the dummy face.

Methods

Participants

The participants were 19 adults (16 females, mean age 23.9 years, range: 19–40) who gained a course credit for

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participation. An additional three participants were tested, but excluded owing to excessive artefacts (two participants) or technical problems (one participant). Informed and written consent was obtained from each participant.

Stimuli and procedure

Three different stimuli were presented to the participants: the face of an adult male, the face of a dummy life-sized male, and a control stimulus (a brown vase). The faces displayed a neutral expression and a direct gaze. All stimuli extended 7.7° vertically and 5.6° horizontally. The stimuli were presented in two conditions: live condition and picture condition.

In the live condition, the stimuli were presented through a $40 \times 30\,\mathrm{cm}$ liquid crystal (LC) shutter attached to a white frame between the stimulus and the participant (Fig. 1). The participants were seated at a distance of 110 cm from the frame. In the picture condition, the stimuli were digital photographs presented on a computer screen. The participants were seated 70 cm away from the screen. In both conditions, the three different stimuli were presented in separate blocks. Within each block, the stimulus was repeated 70 times with a 500 ms presentation time and a 2000 ms interstimulus interval. After every 10th trial, there was a 20-s break. A short signal was given through the speakers 5 s before the start of the next 10-trial sequence to alert the participant and the live model behind the shutter to remain motionless.

Stimulus presentation was controlled in both conditions by Neuroscan Stim software (NeuroScan, El Paso, Texas, USA) running on a desktop computer. The voltage-sensitive LC shutter (LC-TEC Displays AB, Borlänge, Sweden) switched between opaque and transparent states within an overall speed of 3 ms, exceeding the refresh rates of conventional displays. The order of the presentation conditions and the order of the stimulus blocks within the conditions were counterbalanced across participants. Immediately after each stimulus block, the participants

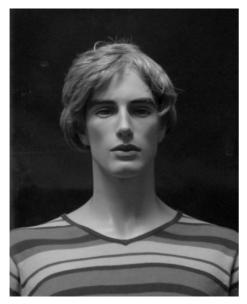


Fig. I The dummy face behind the liquid crystal shutter.

completed a Self-Assessment Manikin [17] to assess their affective responses (valence and arousal) to the stimuli.

Electrophysiological recording and data analysis

Continuous electroencephalography was recorded using an electrode cap (Electro-Cap, Eaton, Ohio, USA) with 21 tin electrodes positioned according to the 10-20 system and referenced to the nose tip. Horizontal electrooculography (HEOG) and vertical electrooculography (VEOG) eye movements were bipolarly monitored from the sites beside the outer canthi of each eye (HEOG) and above and below the left eye (VEOG). Skin was abraded to reduce the electrode impedances below $5 \,\mathrm{k}\Omega$. The electrical signal was amplified with a 0.1-100 Hz band-pass filter (NeuroScan/SynAmps, El Paso, Texas, USA), digitized at 500 Hz, and stored on a computer disk. Off-line, the continuous electroencephalography signal was digitally filtered using a 30 Hz lowpass filter and segmented to 600-ms epochs starting 100 ms before presentation of the stimulus. The segments were baseline-corrected against the mean voltage during the 100ms prestimulus period. Segments with eye movements and blinks were excluded from further analyses using $\pm 50 \,\mu\text{V}$ thresholds for the HEOG and VEOG. In light of the accepted trials (on average, 58±11 trials/stimulus condition), the average waveforms for each individual participant within each of the six experimental conditions were calculated.

For N170, the peak was defined as the minimum amplitude within a 108–180-ms time window for waveforms at sites O1, O2, T5, and T6. The peak amplitude and peak latency scores were analyzed separately for the live and picture conditions by a 3 (stimulus: real person, dummy face, control) × 2 (channel: temporal, occipital) × 2 (hemisphere: left, right) repeated measures analysis of variance (ANOVA). For EPN, mean amplitudes were analyzed in each condition within a 180–300-ms time window at sites T5 and T6 and these data were analyzed by a 3 (stimulus) × 2 (hemisphere) repeated measures ANOVA. A Greenhouse–Geisser correction procedure was applied when appropriate.

Results

N170 amplitudes

The ERP grand means are illustrated in Fig. 2. For the pictures, the stimulus × channel × hemisphere ANOVA revealed interactions for stimulus \times channel, F(2,36)=6.61, P < 0.01, $\eta^2 = 0.27$ and for stimulus × hemisphere, F(2,36) = 3.35, P < 0.05, $\eta^2 = 0.16$. Owing to these interactions, the effect of stimulus was analyzed separately for temporal and occipital sites in the left and right hemispheres. At occipital channels, a main effect of stimulus was found for O1, F(2,36)=6.67, P<0.01, $\eta^2=0.27$ and O2, F(2,36)=6.53, P < 0.01, $\eta^2 = 0.27$, resulting from larger negative amplitudes for the human and dummy faces than for the control object, Ps<0.01. A main effect of stimulus emerged at T5, F(2,36)=3.92, P=0.03, $\eta^2=0.18$. The dummy face elicited larger N170 response than the control object, P=0.01, but the human face did not differ either from the dummy face or from the control object. No significant main effects were observed at T6.

In the live condition, ANOVA indicated a stimulus \times channel interaction, F(2,36)=5.80, P < 0.01, $\eta^2 = 0.24$. A main effect of stimulus was found at occipital channels, F(2,36)=24.03, P < 0.001, $\eta^2 = 0.57$. Pairwise comparisons

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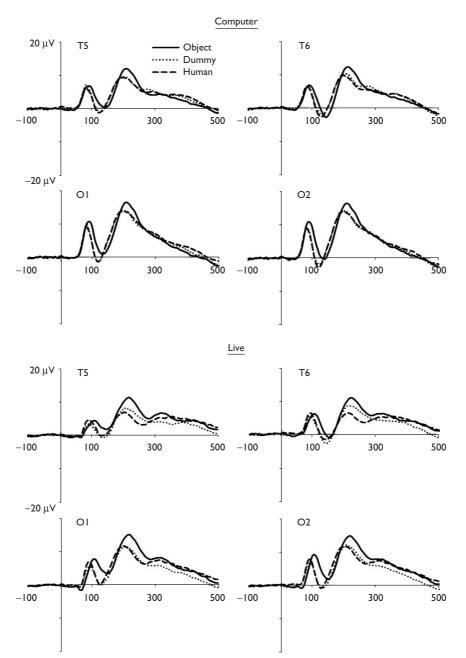


Fig. 2 Grand-averaged event-related potential-waveforms for the three stimulus types at occipital (OI, O2) and temporal (T5, T6) channels in the picture and live presentation modes.

revealed stronger N170 responses for human and dummy faces than for the control object, Ps < 0.001. A similar main effect of stimulus emerged at temporal channels, F(2,36)=7.83, P=0.002, $\eta^2=0.30$. The human face and the dummy face elicited larger N170 responses than the control object, Ps < 0.01.

N170 latencies

In the picture condition, ANOVA indicated a main effect of stimulus at temporal channels, F(2,36)=33.3, P<0.001, η^2 =0.65 and at occipital channels, F(2,36)=19.97, P<0.001,

 η^2 =0.53. Pairwise comparisons at temporal and occipital channel sites indicated shorter latencies for the human and dummy faces than for the control object, Ps<0.01. Other effects were not significant.

In the live condition, ANOVA revealed stimulus \times channel interaction, F(1.1,21.7)=4.59, P < 0.05, $\eta^2 = 0.20$ and stimulus \times hemisphere interaction, F(2,36)=3.26, P < 0.05, $\eta^2 = 0.15$. In occipital channels, a main effect of stimulus emerged at O1, F(1.2,22.2)=10.70, P < 0.001, $\eta^2 = 0.37$ and at O2, F(1,25)=18.11, P < 0.001, $\eta^2 = 50$. Further analyses indicated shorter latencies for the human and dummy faces than for the control object at O1 and O2, Ps < 0.05.

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 Table I
 Self-rated valence and arousal scores as a function of stimulus type and presentation mode

	Valence		Arousal	
Presentation mode	М	SD	М	SD
Picture				
Human	5.79	1.51	2.68	0.95
Dummy	5.58	1.61	2.58	1.26
Control	6.05	1.22	2.68	1.20
Live				
Human	6.68	1.34	2.84	1.30
Dummy	5.89	1.15	3.05	1.18
Control	6.11	1.45	2.74	1.10

Additionally, the human face resulted in shorter latencies than the dummy face at O1, P<0.01. The T6 showed a main effect of stimulus, F(2,36)=4.01, P<0.05, η^2 =0.18. Pairwise comparisons indicated shorter latencies for the dummy face than for the control object, P<0.05. No significant latency effects were observed at T5.

Early posterior negativity amplitudes

In the picture condition, a stimulus × hemisphere ANOVA showed no significant amplitude differences. In the live condition, a significant main effect of stimulus was found, F(2,38)=10.43, P<0.001, $\eta^2=0.37$. Further comparisons indicated smaller positive amplitudes for the human face, P<0.001 and for the dummy face, P<0.05 than for the control object. Importantly, in the live condition, there was also a significant difference between the human face and the dummy face; there was more negative shift in EPN amplitudes for the human face than for the dummy face, P<0.05.

Behavioral data

The results from self-reported valence and arousal (scale range: 1–9) are shown in Table 1. In the picture condition, there were no significant main effects in valence evaluations. In the live condition, a one-way ANOVA showed a main effect of stimulus F(2,38)=4.75, P<0.01, $\eta^2=0.20$. Further analyses indicated that the human face was evaluated as more pleasant than the dummy face, P<0.01, but neither of these ratings differed from those measured for the control object. The arousal evaluations did not differ significantly between stimulus conditions.

Discussion

The results showed that the negative occipitotemporal potential N170, suggested to reflect the structural encoding of face, discriminated the human and the dummy faces from the control object in both presentation conditions. Although some differences in responses to the live face versus dummy face were observed (most notably the N170 latency in live condition at O1 was shorter for the human face than for the dummy face), our results did not provide strong support for the hypothesis that N170 discriminates between the human face and the dummy face either in the live condition or in the picture condition. As a result, we argue that the potential of a face for interaction may not have an influence on neural face processing at the stage reflected in N170 responses.

Instead, the EPN reliably discriminated between the human and the dummy faces in the live condition, but not when they were presented as pictures on a computer screen. The human face was also subjectively rated more pleasant than the dummy face, but only when seen live. We suggest that the present results reflect an intensified, possibly affective-motivational, visual processing that facing a live person elicits. The evidence from several studies support this view by showing that affective-motivational factors can intensify visual processing reflected already in the early stage of stimulus encoding and selection regardless of the valence (i.e. threat or reward) of the stimulus [18,19]. The live human face could be considered to be a reactive stimulus that, in principle, is capable of initiating interaction. None of the other stimuli presented in this study possessed this capability. We suggest that it is more adaptive to intensify processing resources toward a reactive rather than an inactive stimulus. This facilitates preparing appropriate action plans at later information processing stages.

The studies concerning the neural substrates of emotional visual perception have suggested that the amygdala is involved in both early and late processing of emotionally salient stimuli [20,21]. The modulation in the EPN amplitudes found in this study may reflect the affective-motivational influence of the amygdala on early visual processing of socially salient stimuli. Interestingly, it was recently reported that a patient with bilateral amygdala damage fixated more on the mouth area of a face during a real face-to-face conversation than on the mouth area of a face in a photograph [22]. This result may reflect the role of the amygdala in modulating the later stages of visual processing and, indeed, that the influence is different depending on whether live faces or pictures of faces are viewed.

Conclusion

This study proposes that a live human face elicits affective processes and intensifies early visual processing more than a picture of a face, thus possibly preparing the organism for successful planning of appropriate reactions to social stimuli. Further research is needed to explore more in detail the specific neurocognitive mechanisms involved in looking at a living face versus looking at a picture of a face. As action-readiness is always an essential element of social interaction, it should be taken into account when studying neural mechanisms of social perception.

Acknowledgements

This research was supported by the Academy of Finland (Project 1111850) and the Finnish Cultural Foundation.

References

- Carmel D, Bentin S. Domain specificity versus expertise: factors influencing distinct processing of faces. Cognition 2002; 83:1–29.
- Haxby JV, Hoffman E, Gobbini MI. Human neural systems for face recognition and social communication. Biol Psychiatry 2002; 51:59–67.
- 3. Itier RJ, Latinus M, Taylor M. Face, eye and object early processing: what is the face specificity? *Neuroimage* 2006; **29**:667–676.
- Bentin S, Allison T, Puce A, Perez A, McCarthy G. Electrophysiological studies of face perception in humans. J Cogn Neurosci 1996; 8:551–565.
- Itier RJ, Taylor M. N170 or N1? Spatiotemporal differences between object and face processing using ERPs. Cereb Cortex 2004; 14:132–142.

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- Sagiv N, Bentin S. Structural encoding of human and schematic faces: holistic and part-based processing. J Cogn Neurosci 2001; 13:937–951.
- 7. Batty M, Taylor MJ. Early processing of the six basic facial emotional expressions. *Brain Res Cogn Brain Res* 2003; **17**:613–620.
- Guillaume T, Tiberghien G. An event-related potential study of contextual modifications in a face recognition task. *NeuroReport* 2001; 12:1209–1216
- Galli G, Feurra M, Viggiano MP. 'Did you see him in the newspaper?'
 Electrophysiological correlates of context and valence in face processing.
 Brain Res 2006; 1119:190–202.
- Holmes A, Vuilleumier P, Eimer M. The processing of emotional facial expression is gated by spatial attention: evidence from event-related potentials. Cogn Brain Res 2003; 16:174–184.
- Schupp HT, Stockburger J, Codispoti M, Junghöfer M, Weike AM, Hamm AO. Selective visual attention to emotion. J Neurosci 2007; 27: 1082–1089.
- Codispoti M, Ferrari V, Junghöfer M, Schupp HT. The categorization of natural scenes: brain attention networks revealed by dense sensor ERPs. *Neuroimage* 2006; 32:583–591.
- Delorme A, Rousselet GA, Mace MJ, Fabre-Thorpe M. Interaction of topdown and bottom-up processing in the fast visual analysis of natural scenes. Cogn Brain Res 2004; 19:103–113.

- Hillyard SA, Annlo-Vento L. Event-related brain potentials in the study of visual selective attention. Proc Natl Acad Sci U S A 1998; 95:781–787.
- Bradley MM, Codispoti M, Cuthbert BN, Lang PJ. Emotion and motivation I: defensive and appetitive reactions in picture processing. *Emotion* 2001; 1:276–299.
- Schupp HT, Junghöfer M, Weike AI, Hamm AO. Emotional facilitation of sensory processing in the visual cortex. Psycol Sci 2003; 14:7–13.
- Bradley MM, Lang PJ. Measuring emotion: the Self-Assessment Manikin and the semantic differential. J Behav Ther Exp Psychiatry 1994; 25:49–59.
- Balconi M, Pozzoli U. Face-selective processing and the effect of pleasant and unpleasant emotional expressions on ERP correlates. Int J Psychophysiol 2003; 49:67–74.
- Werheid K, Schacht A, Sommer W. Facial attractiveness modulates early and late event-related potentials. Biol Psychol 2007; 76:100–108.
- Anderson AK, Phelps EA. Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature* 2001; 411:305–309.
- Oya H, Kawasaki H, Howard MA, Adolphs R. Electrophysiological responses in the human amygdala discriminate emotion categories of complex visual stimuli. J Neurosci 2002; 22:9502–9521.
- Spezio ML, Huang PS, Castelli F, Adolphs R. Amygdala damage impairs eye contact during conversations with real people. J Neurosci 2007; 11:3994–3997.

doi:10.1093/scan/nsq068 SCAN (2011) 6, 486–494

Does it make a difference if I have an eye contact with you or with your picture? An ERP study

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Several recent studies have begun to examine the neurocognitive mechanisms involved in perceiving and responding to eye contact, a salient social signal of interest and readiness for interaction. Laboratory experiments measuring observers' responses to pictorial instead of live eye gaze cues may, however, only vaguely approximate the real-life affective significance of gaze direction cues. To take this into account, we measured event-related brain potentials and subjective affective responses in healthy adults while viewing live faces with a neutral expression through an electronic shutter and faces as pictures on a computer screen. Direct gaze elicited greater face-sensitive N170 amplitudes and early posterior negativity potentials than averted gaze or closed eyes, but only in the live condition. The results show that early-stage processing of facial information is enhanced by another person's direct gaze when the person is faced live. We propose that seeing a live face with a direct gaze is processed more intensely than a face with averted gaze or closed eyes, as the direct gaze is capable of intensifying the feeling of being the target of the other's interest and intentions. These results may have implications for the use of pictorial stimuli in the social cognition studies.

Keywords: gaze direction; face perception; visual attention; event-related potentials; social cognition

INTRODUCTION

When two people happen to make eye contact, especially if not acquainted, they probably promptly start thinking whether the other person wants something from them, and how they look in the eyes of that person. It has been suggested that looking at the eyes of another person elicits a host of social cognitive and affective processes, such as heightened self-awareness and sense of intimacy (Argyle, 1981; Kleinke, 1986). In a live face-to-face situation, it is essential for a viewer to imagine him/herself in the eyes of the other, whose reactions may have a profound impact on the immediate interaction outcomes. However, looking at the eyes of a picture, for example, in networking communities, is not self-relevant in an immediate sense. A face picture, although capable of eliciting a variety of processes related to the mental state, cannot affect the perceiver physically. Another difference between seeing others' faces live vs in a virtual/pictorial form relates to perspective taking. When faced with a picture or a virtual equivalent of another person, the viewer does not need to evaluate the impressions given to these characters as much as when faced with another person live. Hitherto, however, in face processing studies, the face stimuli have usually been presented as pictures or animations on a computer screen. In the present study, we

Received 11 December 2009; Accepted 16 June 2010 Advance Access publication 22 July 2010

In this study, participant consent was obtained according to the Declaration of Helsinki, and the ethical committee in the University of Tampere approved the study. We thank Mikko Peltola for his help in the data analysis and preparation of stimulus materials. This work was supported by the NEURO-Programme of The Academy of Finland [Grant number 1111850 (to J.K.H.)].

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investigate the impact of direct gaze on the brain responses to another person's face depending on whether the face is seen live or as a picture.

Several studies in the field of cognitive neuroscience have shown that face processing is specialized in adult human brain and that a large, distributed network of areas is involved in the processing of facial information (see Haxby et al., 2000 for a review). A feasible tool for studying the neurocognitive bases of face processing has been to measure event-related changes in electroencephalography (EEG) and magnetoencephalography (MEG) (i.e. Rossion and Jacques, 2008). Studies using these methods have shown that a negative occipitotemporal component N170 and its magnetic counterpart M170, peaking at 140-170 ms after stimulus presentation, is more sensitive to faces and isolated eyes than to other objects (Bentin et al., 1996; Sams et al., 1997; Itier and Taylor, 2004). The N170 is likely to reflect 'the concept of a face' (structural encoding of holistic face configuration). Realistic and schematic pictures of faces elicit generally the same pattern of N170 responses (Sagiv and Bentin, 2001), but, to the best of our knowledge, there is only one published study reporting N170 responses to facial stimuli other than pictures (Pönkänen et al., 2008).

Recently, we examined the effect of presentation mode on ERP responses to faces by presenting human faces and realistic dummy faces as pictures on a computer screen and live through a computer-controlled liquid crystal (LC) shutter (Pönkänen *et al.*, 2008). The study demonstrated that the N170 responses to a human face and a dummy face were indistinguishable in both viewing conditions. Instead, the human face elicited stronger middle-latency early posterior

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negativity (EPN) than the dummy, but only when presented live. In the picture condition no such difference was observed. The EPN is a negative-going occipitotemporal potential occurring ~150-350 ms after stimulus onset and it has been associated with the perceptual encoding and early selection of visual stimuli carrying affective and motivational significance (Junghöfer et al., 2001; Schupp et al., 2007; Kissler et al., 2009). EPN has also been shown to be sensitive to faces classified as attractive (Werheid et al., 2007) and threatening (Schupp et al., 2004). We suggested that as a live human face has potential for social interaction, it is a motivationally significant stimulus and capable of eliciting greater EPN than a dummy face. Other recent results have also shown differential brain responses to live faces vs pictures. In a frontal EEG-asymmetry study (Hietanen et al., 2008), seeing another person with a direct gaze elicited a left-sided asymmetry associated with a motivational tendency to approach, whereas seeing an averted gaze elicited a right-sided asymmetry indicative of a motivational tendency of avoidance. Again, this pattern of results was observed only when the stimulus faces were seen live.

In the present study, we continued investigating whether the potentiality for interaction is reflected in the face-sensitive ERPs. Here, we examined the effects of gaze direction. Direction of gaze conveys valuable information about other peoples' focus of interest. A direct gaze informs the observer that another person is looking at him or her and is probably willing to interact. Depending on the context, direct gaze can be seen as a sign of attraction (Mason *et al.*, 2005), social control or threat (Kleinke, 1986; Emery, 2000). An averted gaze, in turn, signals diversion of interest towards targets in the nearby environment.

The eye region attracts attention from early on in human development, and it has been reported that typically developing infants (Taylor et al., 2001a; Farroni et al., 2002, 2004) and children (Senju et al., 2005) show greater ERPs to pictures of faces with a direct compared to averted gaze, reflecting enhanced perceptual processing of these faces. The gaze sensitive ERP results are less consistent in adults. Taylor et al. (2001b) reported no ERP differences between pictures of faces with direct and averted gaze. Instead, Watanabe et al. (2002) reported greater N170 for static faces with averted vs direct gaze, although only to a gaze averted to right. Similarly, in a combined MEG and fMRI study, responses around 170 ms after stimulus onset were more negative to averted vs direct gaze (Sato et al., 2008). Itier et al. (2007) showed greater N170 to an averted vs direct gaze with front-view faces only. Puce et al. (2000) also reported greater N170 when the eyes moved from direct to averted position compared to opposite gaze shifts. In contrast to these studies, Conty et al. (2007) reported larger ERPs to direct vs averted gaze. They showed that N170 was greater to eyes moving from an intermediate gaze direction to a direct position than to the opposite movement. The authors suggested that because they used a common baseline

for both gaze directions, i.e. the intermediate eye position, the design was more appropriate for comparisons between direct and averted gaze. The greater amplitudes for the direct gaze were suggested to reflect an intensified early processing of direct gaze. They also showed that direct gaze resulted in increased P3 amplitudes, which presumably reflected stronger attention capture and intensified emotional processing.

In the present study, we investigated whether a model's direct gaze enhances ERP responses to faces and whether this enhancement depends on the mode of stimulus presentation. Thus, we measured ERPs to faces with a direct gaze, averted gaze and closed eyes in two modes of presentation: live and picture. Although great care was taken to ensure that the stimuli were visually as similar as possible in both presentation modes, we cannot rule out certain low-level visual differences between the presentation modes. These include differences in the luminance and texture properties of the stimuli as well as possible minor facial movements in the live condition. Importantly also, live faces were 3D whereas pictures were 2D. Therefore, in our data analysis, we took a conservative approach and refrained from comparisons between the presentation conditions. To make the design more robust, we also included two 'non-direct-gaze' conditions. Eyes averted and eyes closed conditions are likely to evoke lower self-involvement and potentiality for interaction than the direct gaze condition. Moreover, like direct gaze, the eyes closed condition is visually symmetrical, offering a condition to control for a possible confounding effect of visual symmetry vs asymmetry in the eye region between faces with a direct vs an averted gaze. The participants also evaluated their affective responses during the ERP measurements. This was done to investigate whether the gaze direction had an influence on self-reported valence and arousal and whether they differed between presentation modes. In our earlier studies, both type of face (real vs dummy; Pönkänen et al., 2008), and gaze direction (Hietanen et al., 2008) affected the valence and arousal ratings only in the live condition. The main hypotheses were that i) the direct gaze would elicit more negative-going N170 and EPN amplitudes than both averted gaze and closed eyes and ii) these effects would be seen in the live condition only.

METHODS

Participants

The participants were 20 university undergraduates (16 females, right handed, mean age = 24.1 years, range 20–43) who gained a course credit for participation. All participants had normal or corrected-to-normal vision. Informed, written consent was obtained from each participant prior to the experiment.

Stimuli and procedure

The stimuli were static faces of an adult female displaying a neutral emotion and gazing either straight forward (direct), gazing 30° to the left or to the right (averted), or having the

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eyes closed (closed). All stimuli were presented in two conditions: picture and live. In the picture condition, a digital photograph of the same person as in the live condition was presented on a computer screen. The participants were seated $70\,\mathrm{cm}$ away from the computer screen. The faces extended $\sim 7.7^\circ$ vertically and 5.3° horizontally. In the live condition, the stimuli were presented through a $40\times 30\,\mathrm{cm}$ voltage-sensitive LC shutter (LC-TEC Displays AB, Borlänge, Sweden) attached to a white frame between the stimulus person and the participant (Figure 1). The LC shutter switched between opaque and transparent states within an overall speed of 3 ms. The participants were seated at a distance of 110 cm from the frame and the model was seated at a distance of 53 cm from the frame. The retinal size of the faces was similar to that in the picture condition.

After the participants arrived to the laboratory the general EEG procedures were explained. The participants were told that the experiment concerned face processing and they were instructed to look at the stimulus faces as naturally as possible, and to remain relatively motionless during the trials. The live and picture stimuli were presented in separate blocks. In both blocks, 180 trials were presented (60 per stimulus type) with a 500-ms presentation time and a 2000-ms inter-stimulus interval. Within the blocks, the stimuli were presented in 10-trial sequences repeating the same stimulus. Within each block, there were six 10-trial sequences of direct, averted and closed eves conditions. The order of these sequences was randomized. After each 10-trial sequence, there was a 15-s break. A short signal was given through the speakers 5 s before the start of the next 10-trial sequence to alert the participant, and, in the live condition, also the model behind the shutter. The presentation order of the stimulus blocks (picture vs live) was counterbalanced



Fig. 1 The live model behind the LC shutter.

across participants. Immediately after each 10-trial sequence, the participants completed a paper-and-pencil Self-Assessment Manikin (Bradley and Lang, 1994) to assess their affective responses to the stimuli. Stimulus presentation was controlled in both conditions by NeuroScan Stim2 software running on a desktop computer.

Electrophysiological recordings and data analysis

Continuous EEG was recorded using an electrode cap (Electro-Cap) with 22 tin electrodes positioned according to the 10-20 system, and referenced to the nose tip. Horizontal (HEOG) and vertical (VEOG) eye movements were bipolarly monitored from the sites beside the outer canthi of each eye (HEOG) and above and below the left eye (VEOG). Skin was abraded to reduce the electrode impedances below $5 k\Omega$. The electrical signal was amplified with a 0.1-100 Hz band-pass filter (Neuroscan/SynAmps), digitized at 500 Hz, and stored on a computer disk. Off-line, the continuous EEG signal was digitally filtered using a 30 Hz low-pass filter, and segmented to 600 ms epochs starting 100 ms prior to stimulus presentation. The segments were baseline-corrected against the mean voltage during the 100 ms pre-stimulus period. Segments with eye movements and blinks were excluded from further analyses using $\pm 75 \,\mu\text{V}$ thresholds for the HEOG and VEOG. Average waveforms for each participant within each of the six experimental conditions were calculated from the accepted trials.

For N170, mean response amplitude was analysed within a 110–150 time window in the picture condition and within a 125–165 in the live condition, since N170 occurred later in the live condition. For EPN, the mean response amplitude was analyzed within a 190–290 ms time window in both conditions. Since the peak ofN170 was not clear in all participants, the analysis of the peak latencies was not reasonable. The amplitude analyses were based on ERPs recorded from electrodes O1, O2, T5 and T6. In all cases, the analysis was a 3 (stimulus: direct gaze, averted gaze, eyes closed) × 2 (channel: temporal, occipital) × 2 (hemisphere: left, right) repeated measures analysis of variance (ANOVA). A Greenhouse-Geisser correction procedure was applied when necessary.

RESULTS

N170 amplitudes

The grand-averaged ERPs are illustrated in Figure 2. In the picture condition, a three-way ANOVA indicated a main effect of channel, F(1,19)=11.27, mean square error (MSE) = 34.37, P < 0.01, reflecting that the N170 amplitudes were more negative for temporal than for occipital channels, and a main effect of hemisphere, F(1,19)=11.52, MSE=16.41, P < 0.01, reflecting more negative N170 responses in the right than in the left hemisphere. None of the other effects were significant. In the live condition, there were main effects of channel, F(1,19)=27.31, MSE=45.68, P < 0.001, and hemisphere, F(1,19)=11.72, MSE=12.11,

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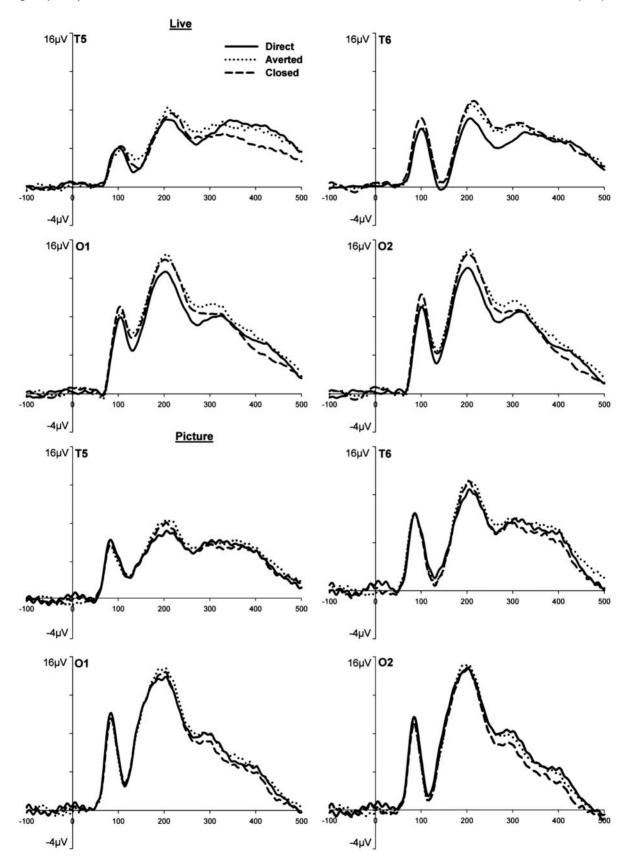


Fig. 2 Grand-averaged ERP waveforms at the temporal T5 and T6 and occipital O1 and O2 channels for the three stimulus types (direct gaze, averted gaze and closed eyes) in the picture and live conditions.

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P < 0.01, reflecting more negative N170 amplitudes for temporal than occipital channels, and more negative responses in the right than left hemisphere. There was also a main effect of gaze, F(2,38) = 3.92, MSE = 6.30, P < 0.05, but no interaction effects. Pairwise comparisons (LSD) indicated that, for direct gaze ($M = 3.47 \,\mu\text{V}$), the N170 was shifted in the negative direction compared to responses for averted gaze $(M = 4.57 \,\mu\text{V})$, P < 0.05. The differences between direct gaze and closed eyes ($M = 4.18 \,\mu\text{V}$) and between averted gaze and closed eyes were not significant, both P's > 0.05. Figure 3 shows the mean N170 responses for the gaze stimuli in both conditions averaged across recording channels and hemispheres. Inspection of the grand-averaged responses in Figure 2 also shows prominent P1 responses. Therefore, we analyzed the mean P1 responses within a 70-110 time window in the picture condition and within an 80-120 time window in the live condition to ascertain whether the gaze direction already had an effect at a very elementary processing stage. However, three-way ANOVAs did not show a main effect of gaze either in the picture condition, F(2,38) = 0.75, MSE = 4.46, P > 0.05, or in the live condition, F(2,38) = 3.17, MSE = 5.28, P > 0.05. Nor were there any interactions.

EPN amplitudes

In the picture condition, a three-way ANOVA showed a main effect of channel, F(1,19)=54.56, MSE=17.44, P<0.001, indicating larger EPN for temporal channels. Other main effects and interactions were not significant, all P's > 0.05. The main effect of channel was also significant in the live condition, F(1,19)=72.81, MSE=16.38, P<0.001. However, in the live condition, there was also a main effect of gaze, F(1.4,27.0)=5.88, MSE=13.34, P<0.05. Pairwise comparisons indicated more negative EPN for direct ($M=7.68\,\mu\text{V}$) vs averted gaze ($M=9.24\,\mu\text{V}$), P<0.01, and, marginally, for direct gaze vs closed eyes ($M=8.97\,\mu\text{V}$), P=0.05. Other main effects and interactions were not significant, all P's > 0.05. Figure 3 shows the mean EPN amplitudes for the different gaze stimuli in both conditions averaged across recording channel and hemisphere.

Valence and arousal ratings

The results from valence and arousal ratings (scale range: 1-9) are shown in Table 1. In the picture condition there were no significant effects for these ratings, P's > 0.05. In the live condition a one-way ANOVA showed a main effect of gaze for the valence ratings, F(2,38) = 9.09, MSE = 0.64, P = 0.001, indicating that direct gaze was evaluated to elicit less pleasant feelings than averted gaze, P < 0.05 and closed eyes, P < 0.01. Averted gaze elicited marginally less pleasant feelings than did closed eyes, P = 0.06. Similarly, for the arousal ratings, there was a main effect of gaze, F(2,38) = 15.02, MSE = 0.61, P < 0.01, indicating that direct gaze was evaluated as more arousing than averted gaze, P < 0.01 and closed eyes, P < 0.001. Furthermore, averted

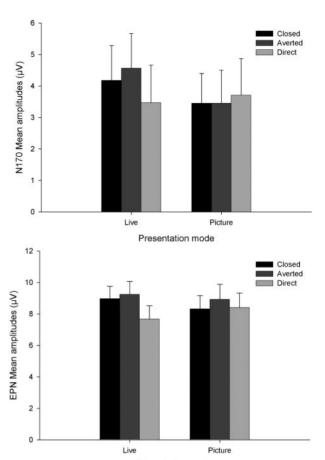


Fig. 3 Mean amplitudes of the N170 and EPN components in the picture and live conditions for the three different gaze conditions.

Presentation mode

gaze was evaluated as more arousing than closed eyes, P < 0.05. In order to analyze whether the ERP responses were associated with the subjective evaluations we also correlated the mean ERP responses with the valence and arousal ratings. There were no significant correlations in either of the stimulus conditions, P's > 0.05.

DISCUSSION

The aim of the present study was to examine whether gaze direction has an effect on face-sensitive ERPs and whether the effect differs depending on the presentation mode of the stimulus (live *vs* picture). As we hypothesized, the N170 and EPN were greater for direct *vs* averted gaze and closed eyes in the live condition only. Our behavioural data showed that the valence and arousal ratings for direct gaze also differed from those for averted and closed eyes, again, only in the live condition.

A critical question is why we observed the discrimination between gaze directions only in the live condition. The intensified ERPs to direct gaze could possibly be attributed to the heightened social relevance of live faces, which, unlike facial pictures, are actually capable of action. Although a ERPs in gaze perception SCAN (2011) 491

Table 1 Self-rated valence and arousal scores (1 = very unpleasant/low arousal; 9 = very pleasant/high arousal) as a function of stimulus type (eyes: direct, averted and closed) and presentation mode

Presentation mode	Valence M (s.d.)	Arousal M (s.d.)
Picture		
Direct	6.47 (1.54)	1.66 (1.07)
Averted	6.39 (1.48)	1.97 (1.17)
Closed	6.63 (1.54)	1.41 (1.01)
Live		
Direct	5.93 (1.65)	2.57 (1.51)
Averted	6.50 (1.45)	1.90 (1.30)
Closed	7.00 (1.24)	1.22 (1.01)

picture of a face may elicit a variety of cognitive and affective reactions, as numerous behavioural and physiological experiments show, the observer realizes that it cannot communicate physically. Moreover, seeing a live face triggers pondering of the thoughts and intentions of the other person and likely prepares the observer for any actions to come. A facial picture or virtual character does not need to be treated with the same pattern of outcome predictions in mind. Bearing some resemblance to the present study, Shimada and Hiraki (2006) showed in a brain imaging study that infants' sensory motor activity was greater in response to human actions vs an object movement only when both stimulus types were presented in a live setting, not when presented on a TV screen. Adults' reactions to person-performed actions were also more prominent in response to live than video-taped actions. The authors suggested that others' live movements are more salient in attracting observers' attention, perhaps due to the assumed possibility of social interaction.

Perhaps the live presentation of a face, more than a picture or an animated face, also enhances the self-relevance of the stimulus by heightening the observer's feeling of being personally involved, and possibly being someone's target of interest. In our earlier study (Hietanen et al., 2008), we found that a direct gaze presented live resulted in increased ratings of experienced 'public' self-awareness, that is, awareness of how one is perceived by others compared to a direct gaze in a picture. The mode of presentation had no effect on the self-awareness related to one's surroundings or inner feelings. Recently, enhanced EPN to own-face pictures vs other-face pictures was reported (Gunji et al., 2009). Interestingly, this effect was lacking in participants with pervasive developmental disorders characterized by many difficulties, especially in theory of mind skills. It was suggested that the EPN enhancement of one's own face may have indicated elevated self-awareness. Our results showing enhanced EPN to live direct gaze could also indicate elevated self-awareness in the observer. Further studies are required to investigate whether the level of self-awareness is influenced by another person's gaze direction. Heron (1970)

argues that intimacy between two individuals is fully realized only by mutual gazing (or touching): 'What I thus meet is the mental glance or the consciousness of the other directed through his eyes' (pp. 260). This 'meeting of gaze' cannot occur with a facial picture or animation. In other words, we can look at but not into that gaze.

However, we want to note that, in certain conditions, virtual humans and human-like characters may also be self-relevant in terms of social interaction and intimacy (Mojzisch et al., 2006; Schilbach et al., 2006); virtual humans can influence, for instance, the patterns of interpersonal distance and the sense of social presence (Bailenson et al., 2001, 2003). Recently, there have been promising ways to study social interaction in conditions enabling 'online' social interaction between a human partner and a virtual character whose gaze is responsive to the viewer's own gaze (Schilbach et al., 2010; Wilms et al., 2010). Contrary to the above-mentioned studies, in the present study, we employed a paradigm in which the participant was not actively engaged in the interaction process. Thus, although our study design enabled eye contact between the viewers, we cannot ascertain the level to which the participants engaged themselves with the other's gaze. More generally, an interesting question relates to the discussion about the nature of 'social interaction' itself: does social interaction require active guiding of the interaction process itself or can mere presence between two persons looking at each other be considered as social interaction (cf. Rizzolatti and Sinigaglia, 2010; Schilbach, 2010; Sinigaglia, 2010). It is evident that more studies examining the experienced presence and the neural correlates of seeing and interacting with a live person vs a responsive virtual human partner are warranted.

At the neural level, the amygdala seems to play a prominent role in facilitating the early encoding and selection of behaviourally relevant social and emotional information (Fitzgerald et al., 2006; Kleinhans et al., 2007; Ousdal et al., 2008), and the amygdala has been shown to be activated more by direct than averted gaze (Kawashima et al., 1999; Calder et al., 2002). It is possible that the enhanced deployment of cortical encoding resources to direct gaze reflects the amygdalar input to posterior perceptual representation areas generating the N170 response. The EPN, in turn, reflects middle-latency stimulus discrimination and action selection processing (Di Russo et al., 2006), enhanced by motivationally and emotionally significant stimuli, such as facial expressions (Schupp et al., 2004). Again, as the amygdala is supposed to have a significant role in emotional face processing (Adolphs, 2003; Fizgerald et al., 2006), the enhanced EPN to emotional stimuli and, in general, to stimuli carrying motivational significance possibly also reflects the fast and involuntary amygdalar input in cortical networks (Schupp et al., 2004). Both the N170 and EPN intensifications to direct gaze in our study possibly relate to the motivational and emotional significance of a 492 SCAN (2011) L. M. Pönkänen et al.

'live' person with direct gaze, a stimulus that should be given a processing advantage in order to effectively decode its meaning.

An interesting question is, of course, why, in a recent study, Conty et al. (2007) did indeed obtain gaze-sensitive ERP results by showing facial pictures, but we did not. A possible explanation may be related to the fact that they utilized face stimuli with dynamic gaze, whereas we presented faces with a static gaze. At a neural level, source localization studies have suggested that the STS region is the main source of N170 response (i.e. Batty and Taylor, 2003; see Rossion and Jaqcues, 2008 for the other putative sources), and the STS region seems to be activated by socially meaningful motion (Senior et al., 2000; Grossman and Blake, 2002; Proverbio et al., 2009). Also, the source reconstruction of ERPs by Conty et al. (2007) themselves implied that the STS was more active during the direct than averted gaze condition. Moreover, in a neuroimaging study by Pelphrey et al. (2004) using virtual, dynamic gaze stimuli, there was greater activation in the STS to direct vs averted gaze. Thus it is possible that the differential N170 responses to pictorial direct vs averted gaze stimuli in Conty et al. (2007) study reflected the additional effect that the motion processing exerted on N170 responses and, possibly, on experienced social relevance of the pictorial stimuli. Instead, the present results show that, although motion is important in understanding facial cues (Ambadar et al., 2005), even static gaze direction stimuli, when presented live, may have an effect on ERPs. In the future, it would obviously be useful to compare ERPs to pictorial vs live faces, both with dynamic gaze, and to investigate whether both viewing conditions show similar patterns of activation in the STS and other parts of the social brain network.

Regarding the gaze direction effects, our ERP results are consistent with those of Conty et al. (2007), as they found more sensitive N170 amplitudes to faces with direct than averted gaze. Thus, our results support the view that the direct gaze is, perhaps, motivationally such a meaningful stimulus that it is processed more intensely than other gaze directions at a very early face processing stage (cf. Conty et al., 2007). Although our results showed a significant difference between N170 responses to direct and averted gaze, the N170 to closed eyes did not differ significantly from N170 to either; N170 amplitude to closed eyes was between those to direct and averted gaze. We expected greater N170 to direct gaze than both to averted and closed eyes, both representing lower potentiality for interaction and less self-relevance than direct gaze. However, perhaps, closed eyes represent an intermediate condition between direct and averted gaze, also from the point of view of potentiality for interaction. Closed eyes signal neither intention for interaction nor active avoidance of it. Instead, closed eyes may be interpreted as signalling attention towards one's inner sensations. Earlier ERP/MEG studies involving a closed eyes condition are few and the results remain inconclusive

(Watanabe et al. 1999; Taylor et al. 2001b, 2001c). We anticipate forthcoming studies to clarify these issues.

Our behavioural results showed that the direct gaze was rated as more arousing and less pleasant than the averted gaze and closed eyes in the live condition only. We reported a similar finding (direct vs averted gaze) in our earlier study (Hietanen et al., 2008), in which the gaze stimuli were shown for 5 s. We suggested that the less positive evaluations of direct than averted gaze may have reflected the long eye contact experienced as somewhat unnatural or intrusive. Now we found a similar result with a stimulus duration (500 ms) corresponding to a sudden glance from a stranger in everyday life. In regular conversation, the normal duration for mutual glance is even longer, around 1.5 s (Argyle, 1981). Thus, in the present type of an experiment, the gaze duration does not seem to affect the valence evaluations. The finding that facial pictures did not have any gaze-sensitive effects on the behavioural ratings may reflect a lack of social and personal relevance in facial pictures. It is noteworthy that in our earlier study (Hietanen et al., 2008) as well as in the present study the participants did not evaluate the characteristics of the stimulus faces, but their own feelings evoked by viewing these. In studies in which the stimulus faces were evaluated, pictures of faces with eyes shifting toward the participant (in 2 s) were rated as more likable than faces shifting their gaze in the opposite direction (Mason et al., 2005), and likeability of virtual reality faces has been reportedly better for direct than for averted gaze shift (Kuzmanovic et al., 2009). These likeability ratings also increased with the duration of direct gaze (1-4s). Eyes shifting towards a participant may be considered to be an active expression of interest, resulting in more positive evaluations than an averted gaze shift. Also, the fMRI results of Kuzmanovic et al. (2009) suggested that the longer the gaze duration, the more sophisticated mentalizing abilities were required. Hence, the longer the gaze the more profound the experienced self-involvement. However, in light of our present behavioural results we suggest that when the direct gaze is presented live, even briefly, the level of self-involvement may be high without an uneasy feeling of being stared at.

In the present study, we used faces of females only, yet gender, and more specifically sexual preference, seems to affect face perception. It has been shown that women, in general, are behaviourally more sensitive to eye contact than men (Gueguen and Jacob, 2002), and that in the reward areas of the brain (ventral striatum), the effect of gaze direction is dependent on the sexual relevance (Kranz and Ishai, 2006) and attractiveness (Kampe *et al.*, 2001) of the faces. Gaze direction has also been shown already to interact with facial expression (Adams and Kleck, 2003, 2005; Lobmaier *et al.*, 2008; Doi and Shinohara, 2009), in the early visual processing stages (Klucharev and Sams, 2007). Perceiving another person's intentions from the face relies heavily on combining information from both the facial expressions and gaze direction. It is possible that a

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threatening or otherwise particularly significant facial expression with a direct gaze enhances the self-relevance of the face.

To summarize, the present study showed that a face with a direct gaze elicited stronger early-stage ERP responses than a face with an averted gaze, but only when the face was seen live. The enhanced early response to a direct gaze may facilitate the processing of facial information and subsequent processing of affective and motivational signals sent by the person observed, which, in turn, will facilitate further planning of behaviour. Facing a live person with a direct gaze is likely to create sensations of intimacy and enhance the experienced self-relevance and awareness of how one is seen by others. Our study could potentially contribute to the designing of computerized representations of others to evoke social presence. According to Biocca (2003), this is an intensively pursued design goal in areas such as high-speed teleconferencing systems, social robots and embodied agents. The experimental approach of the present study could possibly help researchers in designing virtual human presentation by suggesting that using a live human as a yardstick is a fairly precise way to test the social presence and 'humanness' of the virtual characters evoked. Evidently, in the field of social neuroscience, there is a growing need for studies comparing intra- and inter-personal processes when interacting with physical and virtual others.

Conflict of Interest

None declared.

REFERENCES

- Adams, R.B., Kleck, R.E. (2003). Perceived gaze direction and the processing of facial displays of emotion. *Psychological Science*, 14(6), 644–7.
- Adams, R.B., Kleck, R.E. (2005). Effects of direct and averted gaze on the perception of facially communicated emotion. *Emotion*, 5(1), 3–11.
- Adolphs, R. (2003). Is the human amygdala specialized for processing social information? *Annals of the New York Academy of Sciences*, 985, 326–40.
- Ambadar, Z., Schooler, J.W., Cohn, J.F. (2005). Deciphering the enigmatic face: The importance of facial dynamics in interpreting subtle facial expressions. *Psychological Science*, 16(5), 403–10.
- Argyle, M. (1981). Bodily Communication. London, England: Methuen.
- Bailenson, J.N., Blascovich, J., Beall, A.C., Loomis, J.M. (2001). Equilibrium theory revisited: Mutual gaze and personal space in virtual environments. *Presence*, 10(6), 583–98.
- Bailenson, J.N., Blascovich, J., Beall, A.C., Loomis, J.M. (2003). Interpersonal distance in immersive virtual environments. *Personality and Social Psychology Bulletin*, 29(7), 819–33.
- Batty, M., Taylor, M.J. (2003). Early processing of the six basic facial emotional expressions. *Brain Research*, 17(3), 613–20.
- Bentin, S., Allison, T., Puce, A., Perez, A., McCarthy, G. (1996).
 Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8(6), 551–65.
- Biocca, F., Harms, C., Burgoon, J.K. (2003). Toward a more robust theory and measure of social presence: Review and suggested criteria. *Presence*, 12(5), 456–80.
- Bradley, M.M., Lang, P.J. (1994). Measuring emotion: The Self-Assessment Manikin and the semantic differential. *Journal of Behavioral Therapy and Experimental Psychiatry*, 25(1), 49–59.
- Calder, A.J., Lawrence, A.D., Keane, J., et al. (2002). Reading the mind from eye gaze. *Neuropsychologia*, 40(8), 1129–38.

Conty, L., N'Diaye, K., Tijus, C., George, N. (2007). When eyes create the contact! ERP evidence for early dissociation between direct and averted gaze motion processing. *Neuropsychologia*, 45(13), 3024–37.

- Di Russo, F., Taddei, F., Apnile, T., Spinelli, D. (2006). Neural correlates of fast stimulus discrimination and response selection in top-level fencers. *Neuroscience letters*, 408(2), 113–8.
- Doi, H., Shinohara, K. (2009). The perceived duration of emotional face is influenced by the gaze direction. *Neuroscience Letters*, 457(2), 97–100.
- Emery, N.J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience & Biobehavioral Reviews*, 24(6), 581–604
- Farroni, T., Johnson, M.J., Csibra, G. (2004). Mechanisms of eye gaze perception during infancy. *Journal of Cognitive Neuroscience*, 16(8), 1320–6.
- Farroni, T., Csibra, G., Simion, F., Johnson, M.J. (2002). Eye contact detection in humans from birth. Proceedings of the National Academy of Sciences of the United States of America, 99(14), 9602–5.
- Fitzgerald, D.A., Angstadt, M., Jelsone, L.M., Nathan, P.J., Phan, K.L. (2006). Beyond threat: amygdala reactivity across multiple expressions of facial affect. *Neuroimage*, 30(4), 1441–8.
- Grossman, E.D., Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron*, 35(6), 1167–75.
- Gueguen, N., Jacob, C. (2002). Direct look versus evasive glance and compliance with request. The Journal of Social Psychology, 142(3), 393–6.
- Gunji, A., Inagaki, M., Inoue, Y., Takeshima, Y., Kaga, M. (2009). Event-related potentials of self-face recognition in children with pervasive developmental disorders. *Brain & Development*, 31(2), 139–47.
- Haxby, J., Hoffman, E., Gobbini, I.M. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4(6), 223–33.
- Heron, J. (1970). The phenomenology of social encounter: The gaze. *Philosophy and Phenomenological Research*, 31(2), 243-64.
- Hietanen, J.K., Leppänen, J.M., Peltola, M.J., Linna-aho, K., Ruuhiala, H.J. (2008). Seeing direct and averted gaze activates the approach-avoidance motivational brain systems. *Neuropsychologia*, 46(9), 2423–30.
- Itier, R.J., Taylor, M. (2004). N170 or N1? Spatiotemporal differences between object and face processing using ERPs. Cerebral Cortex, 14(2), 132–42.
- Itier, R.J., Alain, C., Kovacevic, N., McIntosh, A.R. (2007). Explicit versus implicit gaze processing assessed by ERPs. Brain Research, 1177, 79–89.
- Junghöfer, M., Bradley, M.M., Elbert, T.R., Lang, P.J. (2001). Fleeting images: A new look at early emotion discrimination. *Psychophysiology*, 38(2), 175–8.
- Kampe, K.K., Frith, C.D., Dolan, R.J., Frith, U. (2001). Reward value of attractiveness and gaze. *Nature*, 413(6856), 589.
- Kawashima, R., Sugiura, M., Kato, T., et al. (1999). The human amygdala plays an important role in gaze monitoring: A PET study. *Brain*, 122(4), 779–83.
- Kissler, J., Herbert, C., Winkler, I., Junghöfer, M. (2009). Emotion and attention in visual word processing: An ERP study. *Biological Psychology*, 80(1), 75–83.
- Kleinhans, N.M., Johnson, L.C., Mahurin, R., et al. (2007). Increased amygdala activation to neutral faces is associated with better face memory performance. *Neuroreport*, 18(10), 987–91.
- Kleinke, C.L. (1986). Gaze and eye contact: A research review. Psychological Bulletin, 100(1), 78–100.
- Klucharev, V., Sams, M. (2004). Interaction of gaze direction and facial expression processing: ERP study. Neuroreport, 15(4), 621–5.
- Kranz, F., Ishai, A. (2006). Face perception is modulated by sexual preference. Current Biology, 16(1), 63–8.
- Kuzmanovic, B., Georgescu, A.L., Eickhoff, S.B., et al. (2009). Duration matters: Dissociating neural correlates of detection and evaluation of social gaze. *Neuroimage*, 46(4), 1154–63.
- Lobmaier, J.S., Tiddeman, B.P., Perrett, D.I. (2008). Emotional expression modulates perceived gaze direction. *Emotion*, 8(4), 573–7.
- Mason, M.F., Tatkow, E.P., Macrae, C.N. (2005). The look of love: Gaze shifts and person perception. *Psychological Science*, 16(3), 236–9.

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Mojzisch, A., Schilbach, L., Helmert, J.R., Pannasch, S., Velichkovsky, B.M., Vogeley, K. (2006). The effects of self-involvement on attention, arousal, and facial expression during social interaction with virtual others: a psychophysiological study. Social Neuroscience, 1(3–4), 184–95.

- Ousdal, O.T., Jensen, J., Server, A., Hariri, A.R., Nakstad, P.H., Andreassen, O.A. (2008). The human amygdala is involved in general behavioral relevance detection: evidence from an event-related functional magnetic resonance imaging Go-NoGo task. *Neuroscience*, 156(3), 450–5.
- Pelphrey, K.A., Viola, R.J., McCarthy, G. (2004). When strangers pass: Processing of mutual and averted social gaze in the superior temporal sulcus. *Psychological Science*, 15(9), 598–603.
- Pönkänen, L.M., Hietanen, J.K., Peltola, M.J., Kauppinen, P.K., Haapalainen, A., Leppänen, J.M. (2008). Facing a real person: An event-related potential study. *Neuroreport*, 19(4), 497–501.
- Proverbio, A.M., Riva, F., Zani, A. (2009). Observation of static pictures of dynamic actions enhances the activity of movement-related brain areas. *PLoS ONE*, 4(5), e5389.
- Puce, A., Smith, A., Allison, T. (2000). ERPs evoked by viewing facial movements. *Cognitive Neuropsychology*, 17(1–3), 221–40.
- Rizzolatti, G., Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, 11(4), 264–74.
- Rossion, B., Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage*, 39(4), 1959–79.
- Sagiv, N., Bentin, S. (2001). Structural encoding of human and schematic faces: Holistic and part-based processing. *Journal of Cognitive Neuroscience*, 13(7), 937–51.
- Sams, M., Hietanen, J.K., Hari, R., Ilmoniemi, R.J., Lounasmaa, O.V. (1997). Face-specific responses from the human inferior occipito-temporal cortex. *Neuroscience*, 77(1), 49–55.
- Sato, W., Kochiyama, T., Uono, S., Yoshikawa, S. (2008). Time course of superior temporal sulcus activity in response to eye gaze: a combined fMRI and MEG study. Social Cognitive and Affective Neuroscience, 3(3), 224–32
- Schilbach, L. (2010). A second-person approach to other minds. *Nature Reviews Neuroscience*, 11(6), 449.
- Schilbach, L., Wilms, M., Eickhoff, S.B., et al. (2010). Minds made for sharing: initiating joint attention recruits reward-related neurocircuitry. *Journal of Cognitive Neuroscience*, 22(12), 2702–15.

- Schilbach, L., Wohlschlaeger, A.M., Kraemer, N.C., et al. (2006). Being with virtual others: Neural correlates of social interaction. *Neuropsychologia*, 44(5), 718–30.
- Schupp, H.T., Öhman, A., Junghöfer, M., Weike, A.I., Stockburger, J., Hamm, A.O. (2004). The facilitated processing of threatening faces: an ERP analysis. *Emotion*, 4(2), 189–200.
- Schupp, H.T., Stockburger, J., Codispoti, M., Junghöfer, M., Weike, A.M., Hamm, A.O. (2007). Selective visual attention to emotion. *Journal of Neuroscience*, 27(5), 1082–9.
- Senior, C., Barnes, J., Giampietroc, V., et al. (2000). The functional neuroanatomy of implicit-motion perception or representational momentum. *Current Biology*, 10(1), 16–22.
- Senju, A., Tojo, Y., Yaguchi, K., Hasegawa, T. (2005). Deviant gaze processing in children with autism: an ERP study. *Neuropsychologia*, 43(9), 1297–306.
- Shimada, S., Hiraki, K. (2006). Infant's brain responses to live and televised action. *Neuroimage*, 32(2), 930–9.
- Sinigaglia, C. (2010). Mirroring and making sense of others. Nature Reviews Neuroscience, 11(6), 449.
- Taylor, M.J., George, N., Ducorps, A. (2001c). Magnetoencephalographic evidence of early processing of direction of gaze in humans. *Neuroscience Letters*, 316(3), 173–7.
- Taylor, M.J., Edmonds, G.E., McCarthy, G., Allison, T. (2001a). Eyes first! Eye processing develops before face processing in children. *Neuroreport*, *12*(8), 1671–6.
- Taylor, M.J., Itier, R.J., Allison, T., Edmonds, G.E. (2001b). Direction of gaze effects on early face processing: eyes-only versus full faces. *Cognitive Brain Research*, 10, 333–40.
- Watanabe, S., Miki, K., Kakigi, R. (2002). Gaze direction affects face perception in humans. *Neuroscience Letters*, 325(3), 163–6.
- Watanabe, S., Kakigi, R., Koyama, S., Kirino, E. (1999). It takes longer to recognize the eyes than the whole face in humans. *Neuroreport*, 10(10), 2193–8.
- Werheid, K., Schacht, A., Sommer, W. (2007). Facial attractiveness modulates early and late event-related potentials. *Biological Psychology*, 76(1–2), 100–8
- Wilms, M., Schilbach, L., Pfeiffer, U., Bente, G., Fink, G.R., Vogeley, K. (2010). It's in your eyes: using gaze-contingent stimuli to create truly interactive paradigms for social cognitive and affective neuroscience. Social Cognitive and Affective Neuroscience, 5(1), 98–107.



Contents lists available at SciVerse ScienceDirect

International Journal of Psychophysiology

journal homepage: www.elsevier.com/locate/ijpsycho



The observer observed: Frontal EEG asymmetry and autonomic responses differentiate between another person's direct and averted gaze when the face is seen live

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ARTICLE INFO

Article history:
Received 13 March 2011
Received in revised form 11 August 2011
Accepted 18 August 2011
Available online 3 September 2011

Keywords: Motivation Gaze direction Face perception Electroencephalography Social cognition

ABSTRACT

Recently, we showed that another person's gaze direction influenced the perceiver's frontal EEG asymmetry and autonomic arousal in response to freely viewed real faces, but not in response to face pictures. However, the lack of a task during the viewing may have resulted in less attention allocation to face pictures vs. live faces. In the present study, the participants performed two online tasks while viewing the faces presented live through an electronic shutter and as pictures on a computer screen. The results replicated those from our previous experiment showing that direct gaze elicited greater relative left-sided frontal EEG asymmetry and autonomic arousal than averted gaze but, again, only in the live condition. However, the results also showed that two live stimulus faces (male and female) elicited differential EEG asymmetry responses in our participants (all females), and the effects of gaze direction were observed only for the (live) female faces. The results suggest that the discriminative responses to live faces vs. pictures are likely to reflect the participants' enhanced mental-state attributions and self-awareness when looking at and being looked by live faces. Thus, the motivation- and affect-related psychophysiological responses to gaze direction are most discriminative in the presence of another person, regardless of whether the face/gaze is actively monitored or not.

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1. Introduction

The vast development of computer- and video-mediated communication devices has allowed two people to effortlessly engage in face-to-face interaction without being physically near each other. Current research also shows that impressions given through computermediated communication approximate those given in live interaction (Weisbuch et al., 2009). How can it be explained, then, that only a minority of significant decisions related to other people, for instance, whom one is going to hire or marry, are currently based on interaction conducted by virtual means? Apparently, something is lost in transfer when people do not share the same physical space when communicating with each other. Smooth and efficient interaction between people requires accurate perception of a host of different types of nonverbal cues. Gaze direction seems to have an important role in gathering socially relevant information from other people (George and Conty, 2008; Kleinke, 1986). Monitoring of others' gaze is needed especially in the initiation of interaction, as it aids in defining the nature of dyadic relations (Exline et al., 1965) and motor plans (Nummenmaa et al.,

2009) in the first place. If the other person's gaze is turned away, it is likely to be seen as an act of aversion, whereas seeking of an eye contact is usually seen as a gesture of approach. Although these action tendencies can be communicated to some extent in virtual interaction, meeting the eyes of a person present in the same space is likely to elevate the anticipation of the other person's likely next actions and the urge to evaluate the consequences of these actions, and heighten the sense of reciprocal involvement.

In recent experiments, we have measured brain responses and autonomic responses to facial stimuli differing in preparedness for social interaction. These stimuli have been presented in two conditions, as pictures on a computer monitor and "live", referring here to a condition in which the stimulus person has been physically present and has shown his/her face through a computer-controlled liquid crystal (LC) window (e.g., Hietanen et al., 2008). The results have shown greater visual event-related potentials (ERPs) to a human face vs. a dummy face (Pönkänen et al., 2008) and to a direct vs. an averted gaze (Pönkänen et al., 2011), but only when the faces have been presented live through the LC window. In addition to these early-stage neurocognitive responses, Hietanen et al. (2008) showed that seeing another person's direct and averted gaze activates the motivational approachavoidance brain systems, respectively, indicated by asymmetrical alpha power distribution in the frontal electroencephalography (EEG). There is a growing body of evidence showing that approach motivation

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enhances relative left prefrontal cortex activity and that avoidance motivation enhances relative right prefrontal cortex activity, regardless of stimulus valence (for a review, see Harmon-Jones et al., 2010). Hietanen et al. (2008) also measured sympathetic arousal (skin conductance responses), considered to be a good index of the general energetic level (arousal) of behaviour (Andreassi, 2000), and showed greater arousal for direct gaze than averted gaze. Again, all these effects of gaze direction were observed only when the stimulus faces were presented live though the LC window. Thus, we suggested that when facing a live person, gaze direction is likely to play a greater role in influencing sensations of intimacy, experienced self-relevance, and awareness of how one is seen by another person who is physically present, as compared to seeing a picture of a face on a computer screen (Hietanen et al., 2008; Pönkänen et al., 2011).

However, there are several, different types of behavioral and neurophysiological studies showing gaze direction effects also when pictures or animations of faces are used as stimuli. Notably, in many of these studies (i.e., Conty et al., 2007; Mason et al., 2005; Sato et al., 2008; Schilbach et al., 2006) discrimination of gaze direction or some other explicit task related to face categorization was employed. In our aforementioned studies, instead, the faces were observed without a concomitant task (Hietanen et al., 2008; Pönkänen et al., 2011; Pönkänen et al., 2008). Thus, the question arises, whether the lack of a task, related to the gaze direction or not, might have contributed to the lack of gaze direction effects in the picture presentation mode in these studies.

There are several ways in which the presence of a concomitant task may contribute to the differing neurocognitive and motivational responses to gaze direction when faces are presented live vs. as pictures. With even a simple task, the participants' focus is directed according to the task requirements, whereas in free viewing of the face stimuli the participants' allocation of attention has more degrees of freedom. For example, when participants are asked to perform discrimination based on some facial attributes (e.g., expression, gender, gaze direction etc.) the participants have to pay attention to faces independent of whether they are presented live or as pictures. Instead, it is possible that participants allocate considerably less attention to faces without than with a face-related task and, moreover, that there is also a discrepancy in attention allocation between live faces and pictures of faces. A live face is potentially capable for changes (e.g., expression, gaze direction, mouth area movements) and the changes are likely to be somewhat intentional. A live face is "present", whereas the face pictures lack the charm of immediate presence. Moreover, there may be greater spontaneous attention to the eyes presented live vs. as pictures due to social learning: when facing another person for the first time, at least in western cultures it is common to catch the eyes of the other when initiating social interaction (Argyle, 1981). Hence, as suggested also in our previous studies (Hietanen et al., 2008; Pönkänen et al., 2011), free viewing of face pictures is likely to be less motivating and less attention-demanding than free viewing of live faces. Therefore, in the present study, we continued investigating the effects of seeing another person's direct vs. averted gaze on functioning of the approach-avoidance brain systems (frontal EEG asymmetry and autonomic responses) by comparing the effects of gaze direction between live vs. picture presentation modes, but this time in a condition where the participants were performing face-related tasks during the stimulus presentation. In the present study, we used two "online" tasks: discrimination of another's gaze direction and evaluation of one's own feelings of pleasantness in response to this stimulus. By including these two tasks we aimed at explicit simulation of other- and self-related mental attributions which are suggested to interplay in social cognitive processing (Legrand and Ruby, 2009; Mitchell, 2009).

In our previous study (Hietanen et al., 2008), we suggested that the differential physiological responses between live and picture conditions could be related to differences in experienced self-awareness when facing a live person vs. a picture, i.e., differences due to the fact that, in the

live condition, the perceiver knows that the other person can really see him/her, whereas in the picture condition the perceiver knows that this is not the case. In the present study, we were interested in expanding our previous results by investigating whether the gaze direction can modulate the self-awareness evaluations. In Hietanen et al. (2008) study, we compared self-awareness ratings during viewing of live vs. picture faces with a direct gaze. The results showed that subjective ratings of "public self-awareness", related to the feelings of how one is perceived in the eyes of others (Govern and Marsch, 2001), were higher when the faces were presented live vs. as pictures. Interestingly, evaluations of the other two types of self-awareness, directed to one's inner feelings or relations to external surroundings, were not affected by the presence of a live vs. picture face. In the present study, we wanted to investigate whether public self-awareness ratings are also influenced by the gaze direction, and whether the possible influence is restricted only to live faces.

In sum, in the present study, we measured relative hemispheric asymmetry in the frontal EEG and skin conductance responses (SCRs) to another person's direct and averted gaze presented live through an LC window vs. as pictures on a computer screen. During physiological recordings, the participants were performing two tasks: gaze direction discrimination and evaluation of one's own feelings of pleasantness towards the stimulus face. We also studied whether the gaze direction has an effect on the subjective ratings of self-awareness and, especially, on self-awareness related to how one is perceived in the eyes of the other people. This was investigated by employing the Situational Self-Awareness Scale questionnaire (SSAS; Govern and Marsch, 2001). Finally, we also wanted to investigate if the sex of the stimulus face would modulate the results. In our previous study (Hietanen et al., 2008), participants were shown only female faces. However, females have been reported being more approachable than males when rating facial pictures (Campbell et al., 2010). It is thus possible that the motivation- and affect-related psychophysiological responses could be sensitive to the sex of the gazing person. In the present study, therefore, we decided to use both a female and a male model as stimuli. Because this was the first study in which we attempted to investigate the possible effects of stimulus face sex on neural approach-avoidance -related responses, we recruited female participants only. Previous research has shown that females show greater physiological responses to emotion-related facial cues than males (e.g., Anokhin and Golosheykin, 2010), and females are behaviourally more sensitive to eye gaze as compared to males (Gueguen and Jacob, 2002). Four main hypotheses were tested: i) perceiving a direct gaze would elicit relative left-sided frontal EEG asymmetry indicative of a motivational tendency to approach and averted gaze would elicit smaller relative left-sided asymmetry or even relative right-sided asymmetry indicative of avoidance, ii) the SCR would be greater for the direct vs. averted gaze, iii) public selfawareness would be heightened in response to a direct vs. averted gaze, and iv) to extend and corroborate the earlier findings (Hietanen et al., 2008), we expected to obtain all these effects in the live but not in the picture presentation mode also when we apply a concomitant behavioural task to ensure comparable attention allocation to faces in both stimulus presentation modes.

2. Materials and methods

2.1. Participants

The participants were 25 right-handed female undergraduates (mean age = 21.3 years, range = 19–26 years) who gained course credits for participation. All participants had normal or corrected-to-normal vision. Informed, written consent was obtained from each participant prior to the experiment in accordance with the declaration of Helsinki. Two participants were removed from the final EEG analysis due to excessive artefacts. In addition, four participants were excluded

from the final SCR analysis due to a technical error (N=1), or excessive artefacts (N=3). In one participant, collection of the SSAS data (see below) was not successful due to a technical error. Hence, the final data sample included 23 participants for the EEG, 21 participants for the SCR, and 24 participants for the SSAS. In the final EEG sample, 11 of the participants saw the female stimulus person and 12 of them saw the male stimulus person (see below). In the SCR sample, these figures were 11 (female stimulus) and 10 (male stimulus), and in the SSAS sample, 12 and 12, respectively.

2.2. Stimuli and experimental procedure

The stimuli were faces gazing either straight forward or gazing 30° to the left or to the right. The stimulus persons aimed at having a neutral expression on their face. The stimulus persons were the two experimenters collecting the data: a female (L.M.P.) and a male (M.J.P.), presented in Fig. 1. The experimenter who was serving as a stimulus person did not give the instructions to the participant although she/he assisted in the preparation of the physiological recordings. The faces were presented in two conditions: live and picture. In the picture condition, a digital photograph of the model's face was presented on a computer screen. In the live condition, the faces were presented through a 30×40 cm LC shutter (LC-TEC Displays AB), attached to a white frame between the stimulus person and the participant. The LC-shutter switched between opaque and transparent states within an overall speed of 3 milliseconds. In both the picture and live condition, the participants were seated at a distance of 70 cm from the computer screen/ panel, and in the live condition the model was sitting at a distance of 30 cm from the panel. The retinal size of the faces was similar in both conditions: approximately 8.0° horizontally and 11° vertically.

The stimuli were presented in two separate blocks: one for the live faces and the other for the pictures. The order of the presentation mode (live/picture) was counterbalanced across the participants. For each participant, the same person was presented as a live and a picture stimulus. Half of the participants saw the female model and



Fig. 1. The faces of the female (above) and the male (below) stimulus models with direct and averted gaze.

the other half the male model. Within a block, there were a total of 16 trials. On 8 trials, the gaze was direct and, on the remaining 8 trials, the gaze was averted (left and right). The presentation order of the trials within a block was pseudo-random (no more than three consecutive trials of the same type). Each trial lasted for 5 s, and the interstimulus-interval (ISI) varied randomly from 25 to 30 s. This ISI range was employed due to the relatively long recovery period of the SCR. During the ISI, the shutter remained opaque and the computer screen had a black background. A short audio signal was presented through the speakers 5 s before the start of the next trial to direct the participant's attention to the shutter/computer screen and, in the live condition, to prepare the stimulus person to the opening of the shutter. Stimulus presentation was controlled in both presentation conditions by Neuroscan Stim software running on a desktop computer.

After arriving to the laboratory, the experimenter described the general procedure and explained that the participant's physiological responses would be measured while she viewed another person's face. The participants were instructed to remain relatively motionless during the trials and to respond verbally immediately after each trial whether the gaze direction of the stimulus face they saw was direct or averted. Immediately after each gaze discrimination response, the participants were asked to consider how they felt during the stimulus presentation and slide a lever accordingly. The lever of the potentiometer moved approximately 4 cm forwards or backwards from the central position labelled as "neutral". The end that was closer to the subject was labelled "pleasant" and the other end was labelled "unpleasant". The participants were able to use the device with slight finger movements of their dominant hand. The output voltage of the potentiometer was registered with the same equipment that was used to measure SCR. During the experiment, one experimenter sat near the participant in such a way that he/she was invisible to the participant, but was able to observe and make record of the participant's possible body movements and also, in the live face condition, the model's possible movements, eye-blinks, and facial actions. These records verified that the models remained as motionless as possible, and they did not blink during the stimulus presentation. The experimenter also recorded the participant's answers regarding the model's gaze direction.

After the physiological recordings, there was a short pause. After the pause, the participants were introduced to the SSAS questionnaire (Govern and Marsch, 2001). Three of the 9 items of SSAS questionnaire measure public self-awareness (e.g., Right now, I am concerned about the way I present myself), three of the items measure private selfawareness (e.g., Right now, I am conscious of my inner feelings), and three of the items measure awareness of "immediate surroundings" (e.g., Right now, I am keenly aware of everything in my environment). The items have a seven-point scale from 1 (strongly disagree) to 7 (strongly agree). SSAS ratings were collected in two blocks: for live and picture faces. For the participants, the order of these blocks was the same as during physiological recordings. In each block, there were a total of six trials: three with direct gaze and three with averted gaze. The presentation of the items of the SSAS questionnaire was arranged in such a way that for both gaze directions, ratings to all 9 items were collected. The participants were instructed to watch the stimulus and to complete a set of three questions after every trial. After answering to each set of questions, the participants were asked to inform the experimenter when they were ready to look at the next stimulus face (and to complete the next three questions). When the whole experiment was completed, the participants were debriefed and thanked for their contribution.

2.3. Acquisition of the physiological data

Continuous EEG was recorded with tin electrodes mounted in a stretch lycra electrode cap (Electro-Cap International, Eaton, OH) from F3, F4, F7, F8, C3, Cz, C4, P3, and P4. The signal was also recorded from the left ear (A1), and referenced online to the right ear (A2).

Horizontal (HEOG) and vertical (VEOG) eye movements were monitored bipolarly from the sites beside the outer canthi of each eye (HEOG) and above and below the left eye (VEOG). Skin abrasion and electrode paste were used to reduce the electrode impedances below 5 k Ω . The EEG signal was amplified with SynAmps amplifiers with a gain of 5000 and a 1-200 Hz band-pass filter (50-Hz notch filter enabled). The continuous signal was digitized at 1000 Hz and stored on a computer disk for off-line analyses. For the skin conductance measurements, the electrodes (Ag/AgCl) were coated with electrode paste and attached to the palmar surface on the medial phalanxes of the index and middle fingers on the participant's non-dominant hand. The signal was acquired with a SCR amplifier supplying constant-voltage AC excitation (22 mV) (ADInstruments). Power Lab 400 equipment was used to measure the skin conductance. Data collection was controlled by Power Lab Chart v3.6 computer programme running on a Power Macintosh 7100/80 computer. The skin conductance coupler was calibrated prior to each session to detect activity in the range of 0-40 µMho. The sampling rate was 100/s.

2.3.1. Data analysis

Off-line, the continuous EEG signal was corrected for blink artifact using a regression-based blink reduction algorithm (Semlitsch et al., 1986), and referred to both ears. Eye movements other than blinks and other visible artifacts were eliminated on the basis of visual inspection. Artifact-free EEG during the 5-s stimulus period was segmented to eight 1.024-ms epochs with 75% overlap between adjacent epochs. Spectral power was calculated for each epoch using Fast Fourier Transform (FFT) with a 10% Hanning taper. The obtained power spectra were averaged over all artifact-free epochs within each trial and over separate trials within each experimental condition. Trials with less than 50% artifact-free epochs were excluded from averaging. Based on this criterion, 5% of the trials were eliminated. For average power spectra within each condition, power density values (μV^2) within the alpha band (8–13 Hz) were calculated and natural In-transformed to normalize the distributions. Asymmetry scores were calculated for electrode pairs at frontal (F8/F7, F4/F3), central (C4/C3), and parietal (P4/P3) scalp regions by subtracting the In-transformed power density values for the left site from that for the right site (Allen et al., 2004). Alpha activity has been shown to be inversely related to cortical activity (Davidson et al., 2000). The main data analysis was confined to the data measured from the electrode pair F4/F3. The affective and motivational effects on the frontal EEG asymmetry are frequently detected from these recording sites (Davidson, 1995). However, the other recording sites were also analyzed to detect the relative asymmetry differences. Analysis of the data from the other recording sites revealed that also in the present study the investigated effects were significant from the mid-frontal electrode pair F4/F3 only. The SCR was defined as a maximum change from the baseline level (at the stimulus onset) during a 4-second time period starting after 1 s from the stimulus onset till the end of the stimulus presentation. Responses contaminated by participant's body movements or technical problems during the measurement were eliminated from subsequent analysis. Based on these criteria, 19% of the trials were eliminated. A Wilcoxon signed-ranks test indicated that the number of eliminated trials did not differ between direct and averted gaze neither in the live, Z = -.93, p = .35, or picture, Z =-1.27, p = .21, condition. For the statistical analyses, the data were averaged over the eight trials in each condition for each participant. The mean value of SCR was computed across all trials within the stimulus category including those without a measurable response as a zero response. This method of calculation results in the magnitude of the galvanic skin conductance responses (cf., Dawson et al., 1990). A log transformation $[\log (SCR+1)]$ was performed to normalize the data. The output voltages from the potentiometer used for pleasantness ratings were transformed to range between -2 (extremely unpleasant) and 2 (extremely pleasant).

3. Results

In the gaze discrimination task, the overall response accuracy was very high, 99.6%. A Wilcoxon signed-ranks test showed that the accuracy did not differ between direct and averted gaze neither in the live, Z=-.45, p=.66, or picture, Z=0, p=1, condition. For the pleasantness ratings, a three-way ANOVA (with Gaze and Presentation Mode as within-subject factors and Stimulus Sex as a between-subject factor) showed a significant main effect of Presentation Mode, F(1,23) = 6.99, p = .014, $\eta_p^2 = .23$, indicating that, overall, the picture condition (M=0.52, SD=0.61) was evaluated as slightly more pleasant than the live condition (M = 0.32, SD = 0.59). The main effects of Gaze or Stimulus Sex were not significant, ps>.4. There were no significant interaction effects, all ps>.05, but the interaction between Presentation Mode and Stimulus Sex approached significance, F(1,23) = 3.40, p = .078, $\eta_p^2 = .13$. In the live condition, there was no difference in the ratings between the female and male model (M = 0.31, SD = 0.59 vs. M = 0.32, SD = 0.62). In the picture condition, the female model obtained higher ratings than the male model (M = 0.65, SD = 0.53 vs. M = 0.38, SD = 0.66), although this difference did not turn out to be statistically significant, p > .2.

A three-way ANOVA on the frontal EEG asymmetry scores indicated a Gaze \times Presentation Mode \times Stimulus Sex interaction, F(1,21) = 7.35, p = .013, $\eta_p^2 = .26$. As a consequence, the effect of gaze was analysed separately for both presentation modes and for female and male stimuli (Fig. 2). For the live female stimulus, the mean asymmetry score was significantly higher (greater relative left-sided asymmetry) for the direct vs. averted gaze, t(10) = 3.42, p = .007, whereas there was no difference in the asymmetry scores between direct and averted gaze in the female picture presentation mode, t < 1. For the male stimulus, the gaze direction did not have any effect on the asymmetry scores in the live or in the picture condition, ts<1. Moreover, in the live condition, the mean asymmetry score for the direct gaze was significantly higher for the female than the male stimulus person, t(21) = 3.11, p = .005, whereas this was not the case in the picture presentation mode. There was no difference between the female and male stimuli in the asymmetry scores for the averted gaze in either presentation mode, both *t*s<.1.

For the SCRs, a three-way ANOVA with Gaze and Presentation Mode as within-subject factors and Stimulus Sex as a between-subject factor showed no significant main effects. However, there was a Gaze × Presentation mode interaction, F(1,19) = 6.24, p = .022, $\eta_p^2 = .25$. Stimulus Sex was not interacting with any of the other factors, all ps>.05. As a result, the live and picture conditions were analysed separately. A paired samples t-test showed that, in the live condition, the SCR was larger for the direct vs. averted gaze, t(20) = 3.12, p = .005. In the picture condition, there was no significant difference between direct and averted gaze, t<.1. Fig. 3 shows the mean SCRs as a function of gaze direction and presentation mode.

The SSAS rating data were analyzed separately for each three subscales of self-awareness (public, private, and surroundings; see Table 1). Each subscale was analyzed with a three-way ANOVA, Gaze and Presentation Mode as within-subject factors and Stimulus Sex as a between-subject factor. For the public self-awareness, there was an interaction between gaze direction and presentation mode, F(1,22) = 5.79, p = .025, $\eta_p^2 = .21$, but no significant main effects or other interactions. In the live condition, the public self-awareness was marginally higher for direct (M=3.38, SD) vs. averted gaze (M = 2.85), t(23) = 1.92, p = .067. In the picture condition, the gaze direction had no effect on public self-awareness, t < 1. The public selfawareness was higher also for the direct gaze in the live (M=3.38)than in the picture (M=2.86) presentation mode, t(23)=2.59, p = .016. Importantly, the other types of self-awareness ratings (private and surroundings) did not show any significant main effects or interactions in either presentation mode. For all three types of selfawareness ratings, the Stimulus Sex did not have any significant effects either.

Female Model

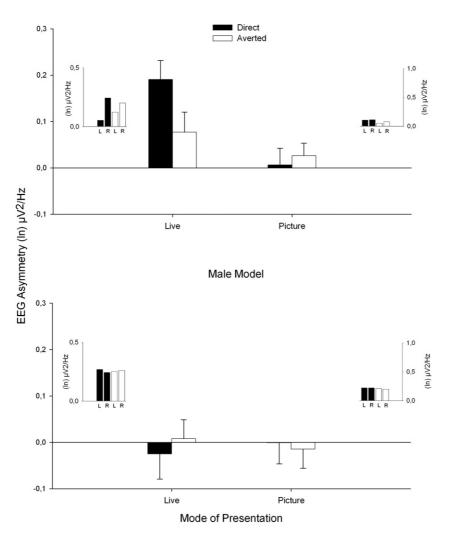


Fig. 2. Mean EEG frontal asymmetry scores for faces of the female (above) and male (below) stimulus models as a function of gaze direction and presentation mode. The ordinates express the difference in the EEG alpha power (in In-transformed $\mu V^2/Hz$) between electrodes F4 and F3. Positive values indicate relative left-sided asymmetry and negative values indicate relative right-sided asymmetry. The small insert graphs show the absolute values of the EEG alpha power recorded from the left hemisphere (L, electrode F3) and right hemisphere (R, electrode F4) electrodes in different stimulus conditions.

Finally, we investigated with a four-way ANOVA (with Gaze and Presentation Mode as within-subject factors and Stimulus Sex and Presentation Order as between-subject factors) whether the stimulus presentation order (the live faces presented before or after the face pictures) had any influence on the present physiological and

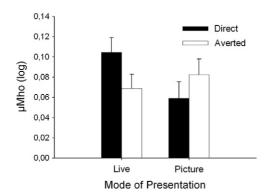


Fig. 3. Mean skin conductance responses [in log-transformed (SCR + 1) μ Mho] for faces as a function of gaze direction and presentation mode.

behavioural results. The Presentation Order showed no main or interaction effects, all *ps*>.1.

4. Discussion

The results of the present study showed that seeing another person's direct vs. averted gaze elicited differential affective and motivational physiological responses, and that these differences were observed only when the participants (all females) were viewing a live female

Table 1Self-rated SSAS scores for three types of self-awareness (public, private, surroundings; scale range 1–7) as a function of stimulus type (eyes: direct, averted) and presentation mode.

Presentation mode	Public		Private		Surroundings	
	M	SD	M	SD	M	SD
Live						
Direct	3.38	1.26	3.36	1.03	3.46	1.32
Averted	2.85	1.22	3.38	1.18	3.68	1.18
Picture						
Direct	2.86	1.26	3.31	0.97	4.00	0.99
Averted	2.93	1.14	3.31	1.13	3.90	1.20

stimulus face, but not when viewing a live male face or when the face stimuli were shown as pictures on a computer monitor. The results corroborate the findings of our previous study (Hietanen et al., 2008) in that looking at a live face with a direct gaze resulted in greater relative left-sided frontal EEG asymmetry and heightened skin conductance responses as compared to a face with an averted gaze. Given that the frontal EEG asymmetry has been suggested to be related to the motivational approach-avoidance tendencies (Davidson, 2004; Harmon-Jones, 2003; Harmon-Jones et al., 2006, 2010; Van Honk and Schutter, 2006), we propose that our present results may reflect the observers' greater motivational approach tendency to seeing another person with a direct vs. averted gaze. In this study we showed that the observed differences in physiological responses between live and picture conditions remained also when the participants actively engaged themselves with the faces by performing concurrent face-related tasks. Our present SCR results showed that a direct gaze was more arousing than averted gaze, again, only when faced live. The sex of the stimulus face had no influence on the SCRs. Other studies employing live presentation of faces are in line with these findings by showing enhanced autonomic arousal to live direct vs. averted gaze as indexed by increased SCRs (Nichols and Champness, 1971), and elevated blood pressure (Williams and Kleinke, 1993). Our SCR results also corroborate our present EEG findings showing that the gaze direction effect was limited to the live presentation mode. These results are also compatible with previous studies showing enhanced autonomic responses to eye contact with a live partner vs. looking at a picture presentation of the same person (Bailey et al., 1981). The systems regulating basic affective and motivational responses have been suggested to be comprised of sets of neural networks regulating the direction of the responses, i.e., the motivational tendency to approach or avoid the source of stimulation, and the energy used for these responses, i.e., the intensity of the motivational tendency (Lang et al., 1990). Thus, our results show that another person's gaze direction has an effect on the functioning of the two neural systems involved in the regulation of motivational tendencies. This effect, however, was limited to viewing female but not male faces in female participants.

It was a surprising result that the effect of gaze direction on the frontal EEG asymmetry was observed for the female stimulus person, but not for the male stimulus person. Moreover, the mean asymmetry score for the direct gaze presented live was higher (indicating relative left-sided asymmetry) for the female than the male stimulus person (for the male stimulus person, the mean asymmetry score was negative, indicating relative right-sided asymmetry), whereas there was no difference in the asymmetry scores for the live averted gaze between the female and male stimulus persons. We admit readily that we have no obvious explanation for these findings and, therefore, in the following, we can provide only some speculation upon this issue. There are previous results showing that, for females, eye contact with opposite-sex avatar faces is not as pleasant as eye contact with same-sex avatars (Schrammel et al., 2009). In negotiating situations, females have been found to cooperate better when in eye contact with another female than when not, but this preference was not observed when females negotiated with males (Swaab and Swaab, 2009). There are also perceived differences in power distribution between female-female and female-male dyads. In general, females have been shown to view male targets as more dominant than female targets in trait attribution tasks (see Feingold, 1998, for a meta-analysis). Interestingly, previous findings have indeed shown that the frontal EEG asymmetry is sensitive to power expectancies. In one study, participants primed with feelings of being high in power over another individual were observed to exhibit pronounced relative left-sided frontal asymmetry, whereas participants primed with low power expectancies showed relative right-sided frontal asymmetry (Boksem et al., 2009). Thus, one possibility is that, for our female participants, perceiving the male stimulus model's direct gaze evoked experiences of lower power status and a shift towards a relative right-sided frontal asymmetry, and this, in turn, resulted in no difference in the asymmetry scores for the male model's direct vs. averted gaze. Since we had only one female and one male as stimuli, another possibility is that some facial attributes in the stimulus persons, irrespective of their sex, evoked differential affective reactions. These, in turn, might have interacted with the motivational reactions to gaze direction.

In fact, we collected supplementary data by showing face photographs of both of our stimulus persons (the same photographs which were used in the picture condition) together with corresponding pictures from faces of four other individuals (2 males and 2 females) to 12 additional female participants. Like in the experiment, each picture was shown for 5 s. Immediately after each picture, the face was rated on a 7-point scale for the following characteristics: fear, joy, anger, sadness, surprise, disgust, approachability, dominance, and likeability. The results showed that the female model was evaluated as expressing less anger t(11) = -2.86, p = .015, and disgust, t(11) = -2.38, p = .036, but more sadness, t(11) = 2.24, p = .047, than the male model. In addition, the female model was evaluated as being more likeable than the male model, t(11) = 2.55, p = .027. The differences in other evaluation domains were not significant. The value of these additional data is limited as the raters did not participate in the original study and they looked at the face pictures only. Nevertheless, these results suggest that the faces of our two models indeed may have evoked differential evaluative responses. Except for sadness, the female model gained more favorable evaluations. Interestingly, although sadness can be regarded as a negative emotion, it has been shown to activate automatic approach motivation (Seidel et al., 2010). The gender role expectations might also have interacted with the impressions given by the stimulus faces: for instance, neutral expressions have been inferred to reflect dominance in men but not in women (Hareli et al., 2009).

It is apparent that the effects of both the participant's and the model's sex (as well as the effects of perceived facial affects) on gaze-related frontal asymmetry responses should be addressed in future studies. Although re-analysis of the results from our previous study (Hietanen et al., 2008) showed no effects of participant's sex (12 females, 8 males) on the responses to direct vs. averted gaze of the female models, it is obvious that now, after finding a significant effect of the model's sex, this issue should be investigated by employing a fully factorial (participant's sex × the model's sex) experimental design. In a recent study where the approachability of female and male faces was rated, the results showed that, although the female faces were rated overall as more approachable, both the female and male participants rated the own-sex faces more approachable than the opposite-sex faces (Campbell et al., 2010).

Even though the asymmetry scores were higher for the direct than averted gaze for the live female face, both gaze directions resulted in relative left-sided frontal asymmetry. In our previous study with female stimulus faces (Hietanen et al., 2008), however, averted gaze elicited relative right-sided asymmetry. These differences may relate to the processing strategy. In our previous experiment, the participants were viewing the faces freely, without a concomitant task, whereas in the present experiment they were actively engaged by the two tasks. The level of engagement during task-related processing has been shown to affect frontal alpha activity, particularly when the task has been related to rewards (Miller and Tomarken, 2001). It is possible that an active discrimination of gaze direction and especially the pleasantness evaluations rendered viewing of an averted gaze also a goal-directed process with high personal relevance. In the present study, however, the tasks were completed rather effortlessly. For instance, a recent study showed that face pictures having a direct gaze elicited greater arousal than those with an averted gaze (or closed eyes) when presented in the context of a demanding word-spelling task, but the effect was not observed in the context of a similar but easier task (Conty et al., 2010). In their study, however, the tasks were not related to the face stimuli, as was the case in the present study. It would be warranted to study the effects of the task type and difficulty also with faces presented live.

In the present study, direct gaze elicited higher ratings of public self-awareness in the live than in the picture condition, replicating the finding by Hietanen et al. (2008). Moreover, we expanded these previous findings by showing that, in the live condition only, the other person's gaze direction had an influence on the self-rated public self-awareness: direct gaze evoked marginally higher ratings as compared to averted gaze. This type of awareness possibly makes the person alert and sensitive to others' motivational signals, whether being positively tuned or not. In concordance with our earlier studies comparing live vs. picture presentation of faces (Hietanen et al., 2008; Pönkänen et al., 2011), we suggest that being looked at, or not, by a real person activates self-directed reflective processes differently than when looking at a picture of another person's face. Self-awareness, especially the "public" type of it, may relate to the feeling of being observed by another person. A picture cannot observe the intentions of the perceiver, but a sentient other can. In the present study, mental state attribution was more relevant in the live than in the picture condition. In live condition only the observed direct gaze had an actual, known target: the participant.

More recently, others have shown that knowledge of the other person's capability to see the observer can influence social-cognitive processes. Attention direction adaptation (Teufel et al., 2009) and automatic attention shifts by head orientation cues (Teufel et al., 2010a) has shown to be modulated depending on whether the participants were lead to believe that the other person was capable of seeing them or not via a video-link. Compatible with our previous propositions (Hietanen et al., 2008: Pönkänen et al., 2008), Teufel et al. (2010b) proposed that mental-state attributions could modulate even the basic perceptual processing of social stimuli. Thus, the lack of the measured affective and motivational physiological responses to face pictures in the present as well as in our previous study (Hietanen et al., 2008) may reflect the effects of mental-state attributions already at the early stage perceptual processing. This possibility is, in fact, supported by our previous results showing that the early, face sensitive N170 ERP response discriminated between direct and averted gaze in the live, but not in the picture condition (Pönkänen et al., 2011). However, it is also possible that the effects of mental-state attributions on social cognitive processes are augmented as one proceeds from basic perceptual processes to more complex socio-behavioral responses, to motivational responses and to preparation of overt actions. This possibility is supported by findings from studies investigating mentalizing-related brain activity to non-human vs. human actors. Although implying agency to non-human actors in computer-mediated games is capable of activating brain areas related to mentalizing, the activation has been shown to be greater in response to human game partners (Kircher et al., 2009; Rilling et al., 2004). Apparently, more studies are needed to clarify the role of mental-state attribution and self-awareness in affective and motivational processing of non-responsive vs. responsive faces. We suggest that behind all successful social engagement is the feeling of being together, being regarded as a mindful creature by another mindful creature. Whether it functions regardless of the media that aims at connecting people warrants further studying.

The behavioural results of the present study showed that the gaze direction did not have an effect on pleasantness ratings. Regardless of gaze direction, however, viewing the pictures was rated as more pleasant than viewing the live faces. It is possible that looking at and evaluating a silent, live face behind the LC window for an unusually long time (5 s) elicited feelings of being under the other person's control, and this resulted in slightly lower pleasantness ratings compared to observing pictures of faces. The participants did not know the purpose of the study, but they presumably thought that the stimulus person facing them knew better, the fact that we had the experimenters of this study as stimulus persons even reinforcing this notion. The lack of control over the interaction process likely relates to the inability to

affect the other person's behaviour (for instance, if the participant smiles, the stimulus person does not smile back), which might have caused feelings of powerlessness, and even exclusion. Thus, the lower overall ratings of pleasantness in the live vs. picture condition might have reflected perceived differences in the control of the situation between the participant herself and the stimulus person in the live condition. This possibility should be investigated in further studies controlling for the power differences.

In order to be successful, social interaction requires both ongoing evaluation of the social signals sent by the interaction partner and monitoring of one's own feelings and thoughts. In social neuroscience and related fields, there has been discussion on the growing need to define the "social" in social perception and interaction more precisely (De Jaegher, 2009; Kingstone et al., 2008; Teufel et al., 2010a, 2010b; Zaki and Ochsner, 2009) and to take into account the complexities of real-world situations (Kingstone et al., 2008). For instance, one might ask whether the social processes are similar when investigating reciprocal, face-to-face engagement in a computer-mediated context (i.e., Wilms et al., 2010) as opposed to situations when two persons are mutually present, situated physically close to each other. Recent theoretical viewpoints have highlighted the self as an enactive being; perception and movement are closely intertwined, and people are continuously aware of their bodies in relation to external objects (McGann and De Jaegher, 2009; Zahavi, 2002). For visual perception, this can be especially meaningful with other people being those objects in sight. It is possible that live interaction with others sharing the same space makes us more aware of the mobility and spatial representation of our own body, in order to react adaptively to others' bodily responses in our vicinity. Zahavi (2002) refers to Edmund Husserl's phenomenological views in stating that "hand cannot touch without being touched". Similarly, perhaps, the gaze cannot meet without being met.

Acknowledgements

This research was supported by the Academy of Finland (project n:o #130272 to J.K.H.), the Finnish Graduate School of Psychology, and the Emil Aaltonen Foundation.

References

Allen, J.J.B., Coan, J.A., Nazarian, M., 2004. Issues and assumptions on the road from raw signals to metrics of frontal EEG asymmetry in emotion. Biological Psychology 67, 183–218.

Andreassi, J.L., 2000. Psychophysiology: human behavior & physiological response, 4th edn. Lawrence Erlbaum Associate, New Jersey.

Anokhin, A.P., Golosheykin, S., 2010. Startle modulation by affective faces. Biological Psychology 83, 37–40.

Argyle, M., 1981. Bodily Communication. Methuen, London.

Bailey, R.C., Chorosevic, P., White, D., White, H., 1981. Physiological arousal and perceptions of a member of the opposite sex. The Journal of Social Psychology 115, 271–276.

Boksem, M.A.S., Smolders, R., De Cremer, D., 2009. Social power and approach-related neural activity. Soc. Cogn. Affect. Neurosci. doi:10.1093/scan/nsp006.

Campbell, D.W., Neuert, D., Friesen, K.B., McKeen, N.A., 2010. Assessing social approachability: individual differences, in-group biases, and experimental control. Canadian Journal of Behavioural Science 42, 254–263.

Conty, L., N'Diaye, K., Tijus, C., George, N., 2007. When eye creates the contact! ERP evidence for early dissociation between direct and averted gaze motion processing. Neuropsychologia 45, 3024–3037.

Conty, L., Russo, M., Loehr, V., Hugueville, L., Barbu, S., Huguet, P., Tijus, C., George, N., 2010. The mere perception of eye contact increases arousal during a word-spelling task. Social Neuroscience 5, 171–186.

Davidson, R.J., 1995. Cerebral asymmetry, emotion, and affective style. In: Davidson, R.J., Hugdahl, K. (Eds.), Brain Asymmetry. MIT Press, Cambridge, MA, pp. 361–387.

Davidson, R.J., 2004. What does the prefrontal cortex "do" in affect: perspectives on frontal EEG asymmetry research. Biological Psychology 67, 219–233.

Davidson, R.J., Jackson, D.C., Larson, C.L., 2000. Human electroencephalography. In: Cacioppo, T.J., Tassinary, L.G., Bernston, G.G. (Eds.), Handbook of Psychophysiology. Cambridge University Press, New York, pp. 27–52.

Dawson, M., Schell, A., Fillon, D., 1990. The electrodermal system. In: Cacioppo, J.T., Tassinary, L.G. (Eds.), Principles of psychophysiology. Cambridge University Press, New York, pp. 295–324.

- De Jaegher, H., 2009. Social understanding through direct perception? Yes, by interacting. Consciousness and Cognition 18, 535–542.
- Exline, R., Gray, D., Schuette, D., 1965. Visual behavior in a dyad as affected by interview content and sex of respondent. Journal of Personality and Social Psychology 1, 201–209.
- Feingold, A., 1998. Gender stereotyping for sociability, dominance, character, and mental health: a meta-analysis of findings from the bogus stranger paradigm. Genetic, Social, and General Psychology Monographs 124, 253–270.
- George, N., Conty, L., 2008. Facing the gaze of others. Clinical Neurophysiology 38, 197–207.
- Govern, J.M., Marsch, L.A., 2001. Development and validation of the situational selfawareness scale. Consciousness and Cognition 10, 366–378.
- Gueguen, N., Jacob, C., 2002. Direct look versus evasive glance and compliance with request. The Journal of Social Psychology 142, 393–396.
- Hareli, S., Shomrat, M., Hess, U., 2009. Emotional versus neutral expressions and perceptions of social dominance and submissiveness. Emotion 9, 378–384.
- Harmon-Jones, E., 2003. Clarifying the emotive functions of asymmetrical frontal cortical activity. Psychophysiology 40, 838–848.
- Harmon-Jones, E., Lueck, L., Fearn, M., Harmon-Jones, C., 2006. The effect of personal relevance and approach-related action expectation on relative left frontal cortical activity. Psychological Science 17, 434–440.
- Harmon-Jones, E., Gable, P.A., Peterson, C.K., 2010. The role of asymmetric frontal cortical activity in emotion-related phenomena: a review and update. Biol. Psychol. 84, 451–462.
- Hietanen, J.K., Leppänen, J.M., Peltola, M.J., Linna-aho, K., Ruuhiala, H.J., 2008. Seeing direct and averted gaze activates the approach—avoidance motivational brain systems. Neuropsychologia 46, 2423–2430.
- Kingstone, A., Smilek, D., Eastwood, J.D., 2008. Cognitive ethology: a new approach for studying human cognition. British Journal of Psychology 99, 317–340.
- Kircher, T., Blumel, I., Marjoram, D., Lataster, T., Krabbendam, L., Weber, J., et al., 2009. Online mentalising investigated with functional MRI. Neuroscience Letters 454, 176–181.
- Kleinke, C.L., 1986. Gaze and eye contact: a research review. Psychological Bulletin 100, 78–100.
- Lang, P.J., Bradley, M.M., Cuthbert, B.N., 1990. Emotion, attention, and the startle reflex. Psychological Review 97, 377–395.
- Legrand, D., Ruby, P., 2009. What is self-specific? Theoretical investigation and critical review of neuroimaging results. Psychological Review 166, 252–282.
- Mason, M.F., Tatkow, E.P., Macrae, C.N., 2005. The look of love: gaze shifts and person percention. Psychological Science 16, 236–239.
- McGann, M., De Jaegher, H., 2009. Self-other contingencies: enacting social perception. Phenomenology and the Cognitive Sciences 8, 417–437.
- Miller, A., Tomarken, A.J., 2001. Task-dependent changes in frontal brain asymmetry: effects of incentive cues, outcome expectancies, and motor responses. Psychophysiology 38, 500–511.
- Mitchell, J.P., 2009. Social psychology as a natural kind. Trends in Cognitive Sciences 13, 246–251.
- Nichols, K.A., Champness, B.G., 1971. Eye-gaze and the GSR. Journal of Experimental Social Psychology 7, 623–626.
- Nummenmaa, L., Hyönä, J., Hietanen, J.K., 2009. I'll walk this way: eyes reveal the direction of locomotion and mark passersby look and go the other way. Psychological Science 20. 1454–1458.

- Pönkänen, L.M., Hietanen, J.K., Peltola, M.J., Kauppinen, P.K., Haapalainen, A., Leppänen, J.M., 2008. Facing a real person: an event-related potential study. Neuroreport 19, 497–501
- Pönkänen, L.M., Alhoniemi, A., Leppänen, J.M., Hietanen, J.K., 2011. Does it make a difference if I have an eye contact with you or with your picture? An ERP study. Soc. Cogn. Affect. Neurosci. 6, 486–494.
- Rilling, J.K., Sanfey, A.G., Aronson, J.A., Nystrom, L.E., Cohen, J.C., 2004. The neural correlates of theory of mind within interpersonal interactions. NeuroImage 22, 1694–1703.
- Sato, W., Kochiyama, T., Uono, S., Yoshikawa, S., 2008. Time course of superior temporal sulcus activity in response to eye gaze: a combined fMRI and MEG study. Social Cognitive and Affective Neuroscience 3, 224–232.
- Schilbach, L., Wohlschlaeger, A.M., Kraemer, N.C., Newen, A., Shah, N.J., Fink, G.R., et al., 2006. Being with virtual others: neural correlates of social interaction. Neuropsychologia 44, 718–730.
- Schrammel, F., Pannasch, S., Graupner, S.-T., Mojzisch, A., Velichovsky, B., 2009. Virtual friend or threat? The effects of facial expression and gaze interaction on psychophysiological responses and emotional experience. Psychophysiology 46, 922–931.
- Seidel, E.-M., Habel, U., Kirschner, M., Gur, R.C., Derntl, B., 2010. The impact of facial emotional expressions on behavioral tendencies in women and men. Journal of Experimental Psychology. Human Perception and Performance 36, 500–507.
- Experimental Psychology. Human Perception and Performance 36, 500–507. Semlitsch, H.V., Anderer, P., Schuster, P., Presslisch, O.A., 1986. Solution for reliable and valid reduction of ocular artifacts, applied to the P300 ERP. Psychophysiology 23, 605–703
- Swaab, R.I., Swaab, D.F., 2009. Sex differences in the effects of visual contact and eye contact in negotiations. Journal of Experimental Social Psychology 45, 129–136.
- Teufel, C., Alexis, D.M., Todd, H., Lawrence-Owen, A.J., Calyton, N.S., Davis, G., 2009. Social cognition modulates the sensory coding of observed gaze direction. Current Biology 19, 1274–1277.
- Teufel, C., Alexis, D.M., Todd, H., Calyton, N.S., Davis, G., 2010a. Mental state attribution drives rapid, reflexive gaze following. Attention, Perception, & Psychophysics 72, 695–705.
- Teufel, C., Fletcher, P.C., Davis, G., 2010b. Seeing other minds: attributed mental states influence perception. Trends in Cognitive Sciences 14, 376–382.
- Van Honk, J., Schutter, D.J.L.G., 2006. From affective valence to motivational direction: the frontal asymmetry of emotion revised. Psychological Science 17, 963–965.
- Weisbuch, M., Ivcevic, Z., Ambady, N., 2009. On being liked on the web and in the "real world": consistency in first impressions across personal webpages and spontaneous behavior. Journal of Experimental Social Psychology 45, 573–576.
- Williams, G.P., Kleinke, C.L., 1993. Effects of mutual gaze and touch on attraction, mood, and cardiovascular reactivity. Journal of Research in Personality 27, 170–183.
- Wilms, M., Schilbach, L., Pfeiffer, U., Bente, G., Fink, G.R., Vogeley, K., 2010. It's in your eyes using gaze-contingent stimuli to create truly interactive paradigms for social cognitive and affective neuroscience. Social Cognitive and Affective Neuroscience 5, 98–107.
- Zahavi, D., 2002. First-person thoughts and embodied self-awareness: some reflections on the relation between recent analytical philosophy and phenomenology. Phenomenology and the Cognitive Sciences 1, 7–26.
- Zaki, J., Ochsner, K., 2009. The need for a cognitive neuroscience of naturalistic social cognition. Annals of the New York Academy of Sciences 1167, 16–30.

Eye contact with neutral and smiling faces: effects on autonomic responses and frontal EEG asymmetry

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In our previous studies we have shown that seeing another person "live" with a direct vs. averted gaze results in enhanced skin conductance responses (SCRs) indicating autonomic arousal and in greater relative left-sided frontal activity in the electroencephalography (asymmetry in the alpha-band power), associated with approach motivation. In our studies, however, the stimulus persons had a neutral expression. In real-life social interaction, eye contact is often associated with a smile, which is another signal of the sender's approach-related motivation. A smile could, therefore, enhance the affective-motivational responses to eye contact. In the present study, we investigated whether the facial expression (neutral vs. social smile) would modulate autonomic arousal and frontal EEG alpha-band asymmetry to seeing a direct vs. an averted gaze in faces presented "live" through a liquid crystal (LC) shutter. The results showed that the SCRs were greater for the direct than the averted gaze and that the effect of gaze direction was more pronounced for a smiling than a neutral face. However, in this study, gaze direction and facial expression did not affect the frontal EEG asymmetry, although, for gaze direction, we found a marginally significant correlation between the degree of an overall bias for asymmetric frontal activity and the degree to which direct gaze elicited stronger left-sided frontal activity than did averted gaze.

Keywords: motivation, facial expression, gaze direction, skin conductance response, electroencephalography, social cognition

INTRODUCTION

Gaze targeted toward an object can be seen as an expression of interest, either positive or negative. When someone turns his or her gaze to me, I may decide to approach or avoid this person. In making the final decision, it is useful to look at the gazer's facial expression. If the face expresses, for example, contempt while seeking eye contact, I may feel anxious and walk away, but if the face is happy, I am possibly inclined to approach the person looking at me. Facial expressions together with gaze direction thus convey information about the sender's emotions and personal goals. The perceptions of eye gaze and facial expression are partly processed by overlapping neural systems (Engell and Haxby, 2007), being independent at the early stages of neurocognitive processing but becoming integrated at the later stages (Rigato et al., 2010). However, the evidence concerning how gaze direction and facial expression interact during face processing is somewhat mixed.

When engaged in an eye contact with another person, we may end up thinking not only the impressions we get from the other ("What does he/she look like?"), but also the impressions given to the other ("What do I look like?"), implying that mutual gaze perhaps sensitizes us to the feelings of the encountered person and makes us more aware of ourselves. There is evidence that viewing another person with a direct gaze elicits greater autonomic arousal than viewing a person with an averted gaze (Nichols and Champness, 1971; Gale et al., 1975; Williams and Kleinke, 1993), even when the face is presented as an irrelevant stimulus during

a demanding cognitive task (Conty et al., 2010). We have found enhanced skin conductance responses (SCRs), indicative of autonomic arousal, in response to eye contact with a "live" person and we have suggested that this effect may relate to increased selfawareness in the proximity of another person (Hietanen et al., 2008; Helminen et al., 2011; Pönkänen et al., 2011). But would a smile on a face of a person looking at the observer exert an additional effect on his or her autonomic responses? Looking at a smiling face has been shown to elicit feelings of warmth in an observer (Lau, 1982), and owing to this possible reward value of a smile, a smiling face might be a more salient stimulus than a neutral expression. It has been proposed that increased electrodermal activity reflects subjective salience of affective stimuli (Critchley, 2002). SCRs are shown to be intensified both when experiencing happiness (see Kreibig, 2010 for a review) and when seeing a happy face (Dimberg and Thunberg, 2007). Also, Martin and Gardner (1979) found greater arousal to a smiling than a neutral face in live interaction. They also varied the confederates' gaze direction but concluded that only facial expression had a significant effect on arousal.

It has been proposed that both facial expression and gaze direction can signal the sender's motivational tendencies of approach and avoidance, and if the motivational tendency signaled by gaze direction and facial expression match (e.g., both signal approach), face perception is enhanced (shared signal hypothesis, Adams and Kleck, 2003, 2005). For example, Adams and Kleck (2003) showed that facial expressions signaling approach (expressions of joy and

anger) are perceived faster with direct than averted gaze, the pattern being reversed for expressions signaling avoidance (such as fearful and sad faces). However, Bindemann et al. (2008) have shown that these effects are task and stimulus bound. They provided, instead, evidence suggesting general impairments in facial expression recognition for faces with an averted gaze (Bindemann et al., 2008). Gaze direction has also an effect on perceived valence and intensity of facial expressions, and neutral expressions are interpreted as expressing approach-related emotions (such as joy) when combined with a direct gaze and avoidance-related emotions (such as fear) when combined with an averted gaze (Adams and Kleck, 2005). Sander et al. (2007) have interpreted these results within a framework of the appraisal theory. According to this theory, all facial cues are used to evaluate the meaning of these cues to one's own needs, intentions, and well-being. Because gaze is a critical cue for inferring the target of visual attention, it has a powerful influence on the appraisal of facial expressions and the self-relevance of the underlying emotion and motivation. According to the appraisal theory, the detection advantage of happy faces with a direct vs. an averted gaze is observed because a happy expression combined with a direct gaze implies a possible reward for the observer. In the context of happy faces, slightly averted gaze and face angles are prone to be misjudged to be looking at the observer (Lobmaier et al., 2008; Lobmaier and Perrett, 2011). The authors suggested that people prefer to think that they are the source of somebody else's happiness in order to improve their self-esteem.

In previous studies (Hietanen et al., 2008; Pönkänen et al., 2011), we provided psychophysiological evidence that seeing another person with a direct vs. an averted gaze differently activated the neural systems participating in the regulation of the approach-avoidance motivation. A large body of evidence supports the view that states of being prepared to approach or avoid targets are distinguishably represented in the brain and behavior. Studies of asymmetric EEG alpha-band activity measured over frontal scalp regions have played a central role in this research (Davidson, 1995, 2004; Allen et al., 2004). The alpha activity relates inversely to cortical activity (Davidson et al., 2000), and therefore, decrease in alpha power implicates increase in brain activity. A so-called motivational direction model has claimed that leftward frontal brain activity (based on the asymmetry in alpha-band power distribution; less alpha power on the left vs. right side) is involved in the experience and expression of approach-related emotions and motivation, whereas rightward activity is linked to avoidance-related emotions and motivation (Sutton and Davidson, 1997; van Honk and Schutter, 2006; Harmon-Jones et al., 2010). Compatibly with this theory, we reported enhanced relative left-sided frontal activity to seeing a direct rather than an averted gaze on a face of another person presented through a computer-controlled liquid crystal (LC) window (Hietanen et al., 2008; Pönkänen et al., 2011). Now, considering that in our previous studies the stimulus persons were having a neutral expression on their faces and, as noted above, that both the facial expression and gaze direction are used to infer the other person's motivational tendency, in this study, we wanted to investigate the effect of facial expression on the psychophysiological responses to direct and averted gaze. In the present study, we confined our investigation to the effects of a smile. There might be normative expectations for people who seek eye contact to smile. For instance, smiling people tend to be perceived as more sociable than people with neutral faces (Matsumoto and Kudoh, 1993). From this point of view, not smiling is an act in itself. One could ask whether the use of neutral faces in our previous studies exerted, in fact, a negative rather than neutral effect on the study participants. Eye contact with a person carrying a neutral expression may have resulted in the feeling that the person observed is indifferent, or even judgmental, toward the observer.

In the present study, we were also interested in investigating whether individual differences would modulate participants' responses to direct and averted gaze. There are individual differences in how people process facial information (see Calder et al., 2011), and, in general, social perception can differ depending on personal dispositions in approach-avoidance motivation (Elliot and Thrash, 2002; Strachman and Gable, 2006). Social anxiety, in particular, may alter ways of looking at faces and the motivation to approach or avoid them. Socially anxious individuals have been shown to avoid direct gaze, a result that was suggested to reflect the direct gaze being experienced as threatening (Horley et al., 2003; Wieser et al., 2009). Social anxiousness has been related to fear of social evaluation (Kocovski and Endler, 2000), also when the observed social signals appear positive (Weeks et al., 2008; Roelofs et al., 2010). Studies measuring the power in the alpha band EEG activity have shown that anxious arousal, characterized by somatic tension and physiological hyperarousal, is also associated with rightward brain activity (indicative of avoidance tendency) for both frontal and posterior regions (Engels et al., 2007). Carver and White (1994) introduced a self-report method (BIS/BAS scales) to measure the dispositional sensitivity of the neurobiologically based motivational systems regulating approach-avoidance behavior. This method is based on Gray's theory (see 1994, for review) about behavioral inhibition (BIS) and behavioral activation (BAS) systems. The BAS mediates approach behavior and is engaged by stimuli signaling reward. The BIS, in turn, is activated in a conflict situation, and serves to interrupt or inhibit ongoing goal-directed behavior (Carver and White, 1994). Recent brain imaging studies have found correlation between BIS/BAS activity and lateralized prefrontal cortex activity: right-sided activity was related to increases in BIS, whereas left-sided activity was associated to increases in BAS (Gray et al., 2002; Wacker et al., 2008, 2010; Balconi and Mazza, 2009; Berkman and Lieberman, 2010).

In this study, we measured SCRs and hemispheric asymmetry in the frontal EEG alpha-activity to seeing another person's live face. Both the gaze direction (direct and averted) and the facial expression (neutral and smiling) of the stimulus face were varied. Four main hypotheses were tested: (1) the SCR would be greater for a direct vs. an averted gaze, (2) perceiving a direct gaze would elicit relative left-sided frontal EEG asymmetry indicative of approach motivation, and (3) perceiving an averted gaze would elicit smaller relative left-sided asymmetry or even relative right-sided asymmetry indicative of avoidance, and (4) a smile in the stimulus face would enhance the differences in the SCR and frontal EEG asymmetry in response to a direct vs. an averted gaze. During physiological recordings, the participants evaluated

the affective valence of the stimuli. This was done to ensure that the participants paid attention to the faces and also to investigate the effects of gaze direction and facial expressions on explicit face evaluations. We were also interested in examining whether individual differences in anxiety and BIS/BAS activity would modulate the pattern of physiological and behavioral responses to faces. Furthermore, previously we have suggested that a direct gaze elicits greater approach motivation than an averted gaze in response to real faces but not to face pictures because real faces are socially present and capable of interaction (Hietanen et al., 2008; Pönkänen et al., 2011). Now, we wanted to measure whether social presence, defined as a sense of awareness of the presence of an interaction partner (Sallnäs, 2005), would be related to the psychophysiological responses to real faces. In the present study, we decided to investigate only female dyads (participant and model). Recently, we showed that female participants exhibited differential motivational responses to male and female faces (Pönkänen et al., 2011), and therefore, in the current study, we did not want to confound the effects of gaze and expression by those of gender.

MATERIALS AND METHODS

PARTICIPANTS

The participants were 22 right-handed female undergraduates (mean age = 22.7 years, range = 19–39 years, SD = 5.1) who gained either course credits or two movie tickets for participation. All had normal or corrected-to-normal vision. Informed, written consent was obtained from each participant prior to the experiment in accordance with the declaration of Helsinki. Three participants were excluded from the final EEG and SCR analyses due to excessive artifacts, leaving 19 participants for the physiological data sample.

STIMULI AND EXPERIMENTAL PROCEDURE

The stimuli were the faces of two young females blind to the purpose of the experiment and unknown to the participants. They were instructed to present a neutral and a smiling face with a direct and an averted gaze (Figure 1). In the smiling face condition, the stimulus persons were trained to display non-enjoyment (or "social") smiles by aiming at restricting the smile to the mouth area, thus lacking the activity of M. orbicularis oculi involved in enjoyment (or "Duchenne") smiles (Ekman et al., 1990; Frank et al., 1993). It was considerably easier for the models to generate non-enjoyment than enjoyment smiles repeatedly, and our objective was to have as little variability as possible in the smiles throughout the experiment. The faces were presented through a 30 × 40 cm custom-built electronic shutter with a voltage sensitive LC window (NSG UMU Products Co., Ltd.) switching from the opaque to transparent state within less than 1 ms. The LC shutter was attached to a black frame between the stimulus person and the participant, the distance from the LC shutter being 30 cm for the stimulus person and 100 cm for the participant. The retinal size of the stimulus face was approximately 8.0° horizontally and 11° vertically. The averted gaze directions of the stimulus person were controlled by attaching fixation marks on the stimulus person's side of the LC shutter panel, one to the right side and another to the left side. The deviance from the direct gaze was 30°. The state of the LC shutter (transparent or opaque)



FIGURE 1 | A stimulus model with direct and averted gaze having a smiling (above) and a neutral expression (below).

was controlled by Neuroscan Stim software running on a desktop computer.

Each participant saw the faces of both stimulus persons. The faces were presented in four separate blocks: two for one stimulus person and two for the other. Within a block, there were a total of eight trials. After every block, there was a short break during which the stimulus person was changed. The presentation order of the stimulus persons was counterbalanced across the participants. There were 32 trials altogether: 16 smiling and 16 neutral faces. A half of the smiling and neutral faces were paired with a direct gaze and the other half with an averted gaze (half of them to the left, and the other half to the right). The presentation order of the stimulus types within a block was pseudo-random (no more than two consecutive trials of the same type). Each face was presented for 5 s, and the inter-stimulus-interval (ISI) was varied manually in each trial. The minimum ISI was fixed to 11 s (range of the mean intervals across participants: 17-24s; grand mean: 19 s; maximum interval: 36 s). The experimenter was monitoring the skin conductance (SC) level on a computer screen throughout the experiment, and when the SC level seemed to have stabilized after the previous trial the experimenter initiated the next trial by pressing a start button. After pressing the button, there was a short audio signal intended to prepare the stimulus person to the opening of the shutter. The audio signal was presented via an earplug to the stimulus person. The earplug was not visible nor the signal audible to the participant. Four seconds after the audio signal, the LC shutter became transparent. During the ISIs and the breaks between the blocks, the shutter remained opaque. The mean duration of one block was 3.5 min.

After arriving to the laboratory, the participants were told that the experiment concerned face processing. They were instructed to assess the expression of the stimulus face on the positive negative dimension immediately after each trial. The participants gave their response by sliding a lever with their dominant hand accordingly. Slight finger movements were enough to slide the lever that moved approximately 4 cm to the left or to the right from the central position, labeled as "neutral." The left-end side of the potentiometer was labeled "extremely positive" and the rightend side was labeled "extremely negative." The output voltage of the potentiometer was registered with the same equipment that was used to measure SC levels. The output voltages could vary between 2 (extremely positive) and -2 (extremely negative). The participants were told that the shutter would be opened several times for short periods of time, and that after a few openings there would be a short break. They were instructed to sit as motionless as possible, hold their gaze in the center of the LC shutter, and to view the face stimulus each time the shutter was open. During the experiment, one experimenter sat in the laboratory in such a way that she was invisible to the participant, but able to observe the monitor showing the SC levels. There was a digital video camera to record the stimulus person's facial expressions, eye-blinks, and other facial or bodily actions.

Immediately after the physiological recordings, the participants filled in the following questionnaires: a state-trait anxiety inventory (STAI) (Spielberger et al., 1983), a modified version of a social presence questionnaire (see Sallnäs, 2005), and a 20-item BIS/BAS questionnaire (Carver and White, 1994). The social presence questionnaire was used to measure the participants' feelings of social presence during the experiment. Our modified version of the questionnaire consisted of seven adjective pairs or statements that could be used to describe the face viewing condition (e.g., personal-impersonal) on a bipolar seven-point scale.

ACQUISITION OF THE PHYSIOLOGICAL DATA

For the SC measurements, the electrodes (Ag/AgCl) were coated with electrode paste and attached to the palmar surface of the index and middle fingers on the participant's non-dominant hand. The signal was acquired with a SCR amplifier supplying constant-voltage AC excitation (22 mv) (ADInstruments). Power Lab 400 equipment was used to measure the SC. Data collection was controlled by LabChart Pro 7.1 programme running on a Dell Optiplex 760 computer. The sampling rate was 100/s. Continuous EEG was recorded with tin electrodes mounted in a stretch lycra electrode cap (Electro-Cap International, Eaton, OH) from F3, F4, F7, F8, C3, C4, P3, P4, and from both ears (A1, A2), all referenced online to Cz. Horizontal (HEOG) and vertical (VEOG) eye movements were monitored bipolarly from the sites beside the outer canthi of each eye (HEOG) and above and below the left eye (VEOG). Skin abrasion and electrode paste were used to reduce the electrode impedances below $5 \,\mathrm{k}\Omega$. The EEG signal was amplified with SynAmps amplifiers with a gain of 5000 and a 1-200 Hz band-pass filter (50 Hz notch filter enabled). The continuous signal was digitized at 1000 Hz and stored for off-line analyses.

DATA ANALYSIS

The face stimuli were videotaped and viewed off-line by two independent raters. They verified whether the models behaved according to the instructions in each trial and labeled each face having either a neutral expression or a polite smile. The raters agreed upon the facial expressions in 98.7% of the cases. The trials in which the facial expressions were not classified reliably were excluded from the final data analysis. Moreover, the records confirmed that the stimulus persons remained relatively motionless during the stimulus presentation. There were no observable differences between stimulus conditions in the stimulus persons' facial movements. The raters also detected the stimulus persons' blinks. On average, there were two blinks per one experimental session, and there were no differences in the number of blinks between the stimulus conditions. Trials containing stimulus person's blinks were excluded from the final data analyses.

The SCR was defined as a maximum change from the baseline level (at the stimulus onset) during a 4 s time period starting after 1 s from the stimulus onset till the end of the stimulus presentation. Responses contaminated by participant's body movements or technical problems during the measurement (16.9% of the trials) were eliminated from subsequent analysis. The statistical analyses were based on the mean values of SCRs computed for each participant across all trials within each stimulus category including those trials with maximum amplitude below 0.01 μ S. This method of calculation results in the *magnitude* of the galvanic SCRs (cf., Dawson et al., 1990). A square root transformation [Sqrt (SCR)] was performed to normalize the data.

The continuous EEG signal was corrected off-line for the participants' blink artifact using a regression-based blink reduction algorithm (Semlitsch et al., 1986), and referred to both ears. Eye movements other than blinks and other visible artifacts were eliminated on the basis of visual inspection. Artifact-free EEG during the 5s stimulus period was segmented to eight 1.024 ms epochs with 75% overlap between adjacent epochs. Spectral power was calculated for each epoch using Fast Fourier Transform (FFT) with a 10% Hanning taper. In epoching and overlapping the data segments, we followed the guidelines by Allen et al. (2004). According to these guidelines, short epochs are better to approximate the assumptions of the Fourier transform and they contain highly repeatable features throughout the waveform. Overlapping, in turn, diminishes the bias caused by the weighting functions in the windowing process which would result in the middle parts of each epoch receiving the most weight, and distal parts receiving negligible weight. The obtained power spectra were averaged over all artifact-free epochs within each trial and over separate trials within each experimental condition. Trials with less than 50% artifact-free epochs were excluded from averaging. Based on these criteria, 2.8% of the trials were eliminated. For average power spectra within each condition, power density values (μV^2) within the alpha band (8-13 Hz) were calculated and natural In-transformed to normalize the distributions. Asymmetry scores were calculated for electrode pairs at frontal (F8/F7, F4/F3), central (C4/C3), and parietal (P4/P3) scalp regions by subtracting the In-transformed power density values for the left site from that for the right site (Allen et al., 2004). The main data analysis was confined to the data measured from the electrode pair F4/F3, since the affective and motivational effects on the frontal EEG asymmetry are frequently detected from these recording sites (Davidson, 1995). The other recording sites were also analyzed to detect the relative asymmetry in EEG activity. The effects were significant only for the frontal electrode pair F4/F3, and approached significance for electrode pair F8/F7.

RESULTS

SKIN CONDUCTANCE RESPONSE

For the SCRs, an ANOVA with Gaze (direct, averted) and Expression (smiling, neutral) as within-subject factors resulted in the main effects of Gaze, $F_{(1, 18)} = 20.06$, p < 0.001, $\eta_p^2 = 0.53$, and Expression, $F_{(1, 18)} = 15.60$, p = 0.001, $\eta_p^2 = 0.46$, and a Gaze × Expression interaction, $F_{(1, 18)} = 5.26$, p = 0.034, $\eta_p^2 = 0.23$. Follow-up paired-samples t-tests indicated larger SCRs for the direct vs. averted gaze both in the neutral, $t_{(18)} = 3.04$, p = 0.007, and in the smiling face, $t_{(18)} = 4.66$, p < 0.001. Furthermore, SCRs were significantly greater for the direct gaze in the smiling vs. neutral face $t_{(18)} = 4.88$, p < 0.001, but for the averted gaze, this difference was only marginally significant, $t_{(18)} = 2.08$, p = 0.052. **Figure 2** shows the mean SCRs as a function of gaze direction and facial expression.

Overall, the SCRs did not correlate with the valence ratings. However, when analyzing the different Gaze \times Expression combinations separately, we found a significant negative correlation between the SCRs and the valence ratings for the neutral expression with a direct gaze, r = -0.53, p = 0.02. None of the other behavioral measures did correlate significantly with the SCRs.

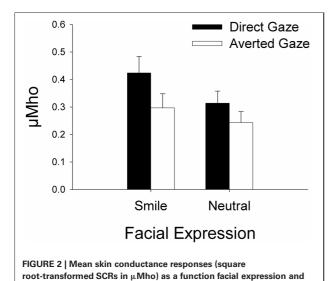


Table 1 | Means and standard deviations for STAI, BIS-BAS, and social presence questionnaire scores.

Measure	М	SD	
STAI Total	67.19	11.26	
STAI State	30.72	5.32	
STAI Trait	36.47	8.52	
BIS Total	24.25	5.80	
BAS Total	47.05	6.48	
BAS Reward	19.43	2.76	
BAS Drive	14.00	2.54	
BAS Fun	13.62	2.81	
Social Presence	4.48	0.91	

The mean values and standard deviations of the STAI, BIS/BAS, and social presence scale scores are presented in **Table 1**.

FRONTAL EEG ASYMMETRY

A Two-Way ANOVA with Gaze (direct, averted) and Expression (smiling, neutral) as within-subject factors showed no significant main effects or interactions on the EEG asymmetry scores calculated for the frontal F4/F3 electrode pair, all Fs < 1. A similar ANOVA for the F8/F7 electrode pair showed no main effects or interactions either, Fs < 1.

However, we noticed that there was substantial variation among the participants in their overall asymmetry scores. Some participants showed negative asymmetry scores (indicative of avoidance) in response to all types of stimuli, and their asymmetry scores were more negative for the direct vs. averted gaze. Others, in contrast, had positive asymmetry scores (indicative of approach) to all stimulus types, and their asymmetry scores were more positive for the direct vs. averted gaze. We calculated two new asymmetry indices: (1) participant's asymmetry score averaged across all experimental conditions (asyscore_{overall}) and (2) the difference in asymmetry scores for direct and averted gaze (asyscore_{direct} - asyscore_{averted}). For the latter index, increasing negative values would indicate increasingly stronger avoidance-related brain activity for direct vs. averted gaze, whereas increasing positive values would indicate increasingly stronger approach-related brain activity for direct vs. averted gaze. When these indices were correlated, we found a marginally significant correlation between the overall asymmetry index and the gaze direction difference index, r = 0.45, p = 0.05(see Figure 3). The results of the behavioral measures did not correlate with the asymmetry scores.

VALENCE EVALUATION

A similar ANOVA as above was run for the valence ratings. This analysis revealed the main effects of Gaze, $F_{(1, 21)} = 36.97$, p < 0.001, $\eta_p^2 = 0.64$, and Expression, $F_{(1, 21)} = 113.62$, p < 0.001, $\eta_p^2 = 0.84$, but not a significant interaction effect. The smiling faces (M = 0.76, SD = 0.32) were rated as being more positive than the neutral faces (M = -0.41, SD = 0.21), and the faces with a direct gaze (M = 0.29, SD = 0.19) were rated as being more positive than the faces with an averted gaze (M = 0.06, SD = 0.19).

gaze direction

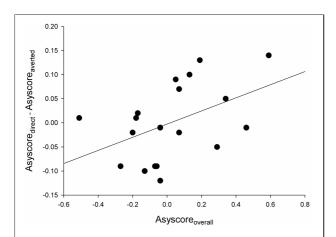


FIGURE 3 | A scatter plot with a linear fit curve for the participant's overall asymmetry score in the EEG alpha power (in In-transformed μ.V²/Hz between electrodes F4 and F3) averaged across all experimental conditions (*X*-axis; asyscore_{overall},) vs. the difference in asymmetry scores for direct and averted gaze (*Y*-axis; asyscore_{direct} – asyscore_{averted}). For *X*-axis scores, negative values indicate right-sided asymmetry (associated with avoidance) and positive values indicate left-sided asymmetry (associated with approach). For *Y*-axis scores, negative values indicate stronger avoidance-related brain activity for direct vs. averted gaze, whereas positive values indicate stronger approach-related brain activity for direct vs. averted gaze.

DISCUSSION

In this study, we measured autonomic arousal and frontal EEG asymmetry to faces presented "live" through an electronic shutter. Our main goal was to examine whether affective and motivational neural responses to seeing a direct vs. an averted gaze would be modulated by the expression (neutral/smiling) on the gazing face. We expected to observe greater arousal and greater relative left-sided frontal asymmetry to seeing a direct vs. an averted gaze, and we proposed that when a stimulus person was smiling instead of having a neutral expression, these effects would be enhanced.

We replicated our earlier findings (Hietanen et al., 2008; Helminen et al., 2011; Pönkänen et al., 2011) by showing greater SCRs to live faces with a direct vs. averted gaze. Here we also manipulated the facial expression of the stimuli and found that viewing of smiling faces elicited overall greater arousal than viewing of neutral faces, and, interestingly, that the effect of gaze direction was more pronounced in response to a smiling than a neutral face. The autonomic arousal was also greater to a smiling vs. a neutral face with an eye contact. This result reflects the emotional saliency of both the direct gaze and the smile, and shows that a combination of these signals results in a strong autonomic response. Indeed, both direct gaze and smiling face can be regarded as signals inviting to closer interaction. Increased intimacy, in turn, has been shown to elevate arousal (Patterson, 1976; Patterson et al., 1981).

Brain-imaging studies have shown that the amygdala is involved in the integration of emotional facial expressions and gaze direction (Sato et al., 2004, 2010). Sato et al. (2004) found greater amygdala activation to faces looking toward vs. away from the subject when the face was emotionally expressive rather than

neutral. The amygdala response also increased together with selfreported arousal. As the amygdala is known to play a central role in regulating affective arousal (Mangina and Beuzeron-Mangina, 1996; LeDoux, 2000; Williams et al., 2005; Laine et al., 2009), these results are highly compatible with the present ones. However, it must be noted that the results from the brain imaging studies regarding the effects of gaze direction and facial expression on amygdala activation are not consistent (Adams et al., 2003; Hadjikhani et al., 2008; Straube et al., 2009). It is possible that these discrepant findings reflect differences in the functions of face processing. For instance, Adams et al. (in press) studied amygdala activity in response to direct and averted gaze on faces expressing fear as a function of stimulus presentation time. Subregions of the amygdala were distinctively tuned to short and long stimulus durations. The authors proposed that the shorter presentation time (300 ms) triggers reflexive attention to the faces, whereas the longer time (1000 ms) allows reflective processing of stimulus significance. Possibly relating to the reflective processing mode, previous research has suggested that stimulus ambiguity and unpredictability can modify amygdala activation (Hsu et al., 2005; Herry et al., 2007; Whalen, 2007). Recent research has suggested greater amygdala activity in response to highly self-relevant stimuli (Sato et al., 2004; Hadjikhani et al., 2008; N'Diaye et al., 2009; Boll et al., 2011). The differences in the relative relevance between direct vs. averted gaze may depend, perhaps, on the social context, personals dispositions, and task demands. In the present study, the relatively long stimulus duration (5 s) allowed a reflective processing mode. Perhaps it was more self-relevant and, hence, more arousing to reflect upon the meaning of an emotional vs. a neutral face. Looking at a smiling rather than a neutral face may have triggered the viewers to mentalize more effectively the observed person's emotional and cognitive state.

Interestingly, there is one previous study that investigated the SCRs to smiling and neutral faces with a direct vs. averted gaze. Martin and Gardner (1979) also used "live stimuli" by having the participant and a confederate sitting face-to face while the confederate presented combinations of direct/averted gaze directions and smiling/neutral expressions during 20 s trial periods. Similar to the present results, that study also reported higher autonomic arousal to a smiling than a neutral face. However, they did not find any effect of gaze direction. We can only speculate on the possible reasons for this discrepancy. In Martin and Gardner (1979) study, only male dyads were used, whereas there were only female dyads in our study. Compared to men, women tend to be more sensitive to facial communicative gestures (Gueguen and Jacob, 2002), and, especially, to feel more observed when interacting face-to-face with another person (Argyle and Williams, 1969). Furthermore, we employed a valence-rating task during viewing of the faces, but, in Martin and Gardner (1979) study, the other person was passively observed. It is possible that, in the present study, the evaluation of the faces enhanced the effect of gaze direction on autonomic arousal.

The current results showed that the smiling faces were rated as being positive, whereas the neutral faces were evaluated as being slightly negative. Moreover, faces with a direct gaze were rated as being more positive than faces with an averted gaze, regardless of whether the face was smiling or not. Interestingly, in our

earlier studies in which the participants viewed neutral faces only (Hietanen et al., 2008; Pönkänen et al., 2011), looking at faces with averted gaze were rated to evoke higher level of pleasantness than faces with direct gaze. These overtly discrepant findings are likely to be explained by the fact that, in the current study, the participants evaluated how positive/negative the facial expression appeared, whereas in the previous studies they evaluated their own feelings in response to the faces. Now, we found that the participants made a clear distinction in the evaluations of smiling and neutral faces, and it was also relevant whether the stimulus person was looking at the participant or not. This is in line with the autonomic arousal results. Our results also showed a negative correlation between the SCRs and the valence ratings, but only for the neutral faces having a direct gaze. Those who were more inclined to evaluate a neutral, direct gazing face as being negative showed more pronounced autonomic arousal toward those faces. There was considerable variation in the valence ratings for the neutral faces; some participants rated them being slightly positive, whereas to others they appeared negative. Such a variation was not observed for the smiling faces which were consistently evaluated as positive. It can be speculated that a smiling face represents a salient communicative signal triggering autonomic arousal and positive evaluation in most individuals. A neutral face, instead, is a less salient signal, leaving more space for personal dispositions to influence the affective evaluations. A neutral face looking directly back to the viewer may be an especially effective signal in revealing individual differences in affective evaluations and in their association with autonomic responses. It is also important to note that the valence of the expression does not necessarily correspond to the intention of the person bearing the expression (e.g., Ambadar et al., 2009). Thus, a social smile can imply a sender's social motive to hide negative emotions, and, indeed, non-Duchenne smiles are less often used as a signal of social intent than Duchenne smiles (Hess and Bourgeois, 2010). Bindemann et al. (2008) have suggested that when information from gaze direction and facial expression is combined, the ambiguity of the expression might determine how important gaze direction is for determining the observed person's goals and emotions. In our study, the overall intensity of the smiles was low, and this expression was held still on a face for 5 s. If these smiles were regarded as contrived or otherwise ambiguous, it is possible that the elevated arousal to the smiling faces reflected these factors rather than the positivity or approachability of the expression itself. Apparently, this question warrants further studying to disambiguate the source of arousal in response to direct vs. averted gaze in expressive faces.

The results of the frontal alpha-band EEG asymmetry measures did not show effects of gaze direction or facial expression. This was contrary to our expectations. Particularly, the nonsignificant effect of gaze direction on frontal asymmetry was unpredicted since in our earlier studies with rather similar study designs we have observed greater relative left-sided activity for a direct vs. an averted gaze (Hietanen et al., 2008; Pönkänen et al., 2011). In these studies, the stimulus persons' identities have varied from experiment to experiment, and we cannot rule out the possibility that some factors related to their personal qualities could have had an effect on the results. However, one difference

between the experimental settings of the present and the previous studies was that, in the present study, the stimulus persons were students who did not interact with the participants prior to the experiment at all, whereas in the previous studies the stimulus persons were also the experimenters of these studies (welcoming the participants, shaking hands with them, assisting in the preparation of the physiological recordings, etc.). It is an interesting possibility that some sort of social connectedness, or dominance factor due to the experimenter status, would have such a dramatic effect on the results. This is clearly an important question and needs further studying.

Although we did not find a gaze direction effect on the frontal alpha-band EEG asymmetry, the magnitude of the mean asymmetry score calculated across responses to all stimulus conditions exhibited a marginally significant positive correlation with the differential score expressing whether direct gaze evoked less (negative values) or more (positive values) left-sided brain activity (implying approach motivation) compared to averted gaze. In other words, the increase of the overall asymmetry scores was associated with a tendency that direct gaze elicited stronger approach-related activity than did the averted gaze. One interesting possibility is that this result could reflect differences in personal dispositions affecting the approach-avoidance-motivation and reactions to gaze directions. On the other hand, our behavioral data failed to give support to this possibility. Unfortunately, we did not measure baseline EEG alpha-band activity, which could have revealed some trait-based effects in the responses to gaze direction. It has been shown that there are trait-level individual differences in affective styles. Left-sided trait asymmetry has been associated with positive affect and approach behavior, whereas right-sided trait asymmetry has been related to negative affect, anxiety, and behavioral avoidance (Heller and Nitschke, 1998; Davidson and Irwin, 1999; Allen and Kline, 2004; Mathersul et al., 2008).

It also stands out that the facial expression had an effect on autonomic responses, but not on the neural activity related to approach-avoidance tendencies. According to the shared signal hypothesis (Adams and Kleck, 2003, 2005), a smile and direct gaze should both potentiate approach motivation, and Stins et al. (2011) recently found that it takes less time to initiate steps toward a smiling vs. an angry face, suggesting that a smile prompts approach behavior. Furthermore, by recording alpha-band EEG activity Davidson and Fox (1982) have shown that infants show leftward frontal activity in response to happy faces and rightward activity in response to angry faces. Our present results did not show an effect of gaze or facial expression on the frontal EEG asymmetry. Given that we had only faces presenting neutral and low-intensity smile expressions in this study, it remains an open question whether a face that communicates strong appeal or danger might play a more dominant role in influencing the frontal EEG asymmetry.

In the current study, we also investigated whether anxiety, the activation of the behavioral motivation systems BIS/BAS, and the felt social presence would correlate with the autonomic arousal and frontal EEG asymmetry scores in response to the face stimuli. We found that none of these measures were related to the psychophysiological responses. In future studies, it would be useful to measure individual differences in resting (baseline) frontal

alpha-band EEG asymmetries, anxiety, and self-esteem when studying affective and motivational responses to eye gaze. These may be critical factors, especially when responses to faces with direct gaze (signaling social approval) and averted gaze (signaling rejection) are being studied. Since we tested only female dyads, the question of whether the observed results would be similar had we recruited also male or mixed dyads, remains. The ratings of social presence in response to the stimulus faces showed that the participants felt moderate levels of social presence during the experiment. However, we measured social presence only once, at the end of the experiment, and not separately for the different stimulus conditions. In the future, it would be worth studying how different types of evaluation tasks or active interaction between the participant and the stimulus person influence social presence and psychophysiological responses.

REFERENCES

- Adams, R. B. Jr., Franklin, R. G. Jr., Kveraga, K., Ambady, N., Kleck, R. E., Whalen, P. J., Hadjikhani, N., and Nelson, A. J. (in press). Amygdala responses to averted vs direct gaze fear vary as a function of presentation speed. Soc. Cogn. Affect. Neurosci. doi: 10.1093/scan/nsr038
- Adams, R. B. Jr., Gordon, H. L., Baird, A. A., Ambady, N., and Kleck, R. E. (2003). Effects of gaze on amygdala sensitivity to anger and fear faces. *Science* 300, 1536.
- Adams, R. B. Jr., and Kleck, R. E. (2003). Perceived gaze direction and the processing of facial displays of emotion. *Psychol. Sci.* 14, 644–647.
- Adams, R. B. Jr., and Kleck, R. E. (2005). Effects of direct and averted gaze on the perception of facially communicated emotion. *Emotion*
- Allen, J. J. B., Coan, J. A., and Nazarian, M. (2004). Issues and assumptions on the road from raw signals to metrics of frontal EEG asymmetry in emotion. *Biol. Psychol.* 67, 183–218.
- Allen, J. J., and Kline, J. P. (2004). Frontal EEG asymmetry, emotion, and psychopathology: the first, and the next 25 years. *Biol. Psychol.* 67, 1–5.
- Ambadar, Z., Cohn, J. F., and Reed, L. I. (2009). All smiles are not created equal: morphology and timing of smiles perceived as amused, polite, and embarrassed/nervous. I Nonverbal Behav 33, 17–34
- Argyle, M., and Williams, M. (1969).
 Observer or observed? Revisible perspective in person perception.
 Sociometry 32, 396–412.
- Balconi, M., and Mazza, G. (2009).

 Brain oscillations and BIS/BAS (behavioral inhibition/activation system) effects on processing masked emotional cues: ERS/ERD and coherence measures of alpha

- band. Int. J. Psychophysiol. 74, 158–165.
- Berkman, E. T., and Lieberman, M. D. (2010). Approaching the bad and avoiding the good: lateral prefrontal cortical asymmetry distinguishes between action and valence. *J. Cogn. Neurosci.* 22, 1970–1979.
- Bindemann, M., Burton, A. M., and Langton, S. R. H. (2008). How do eye gaze and facial expression interact? Vis. Cogn. 16, 708–733.
- Boll, S., Gamer, M., Kalisch, R., and Büchel, C. (2011). Processing of facial expressions and their significance for the observer in subregions of the human amygdala. *Neuroimage* 56, 299–306.
- Calder, A. J., Ewbank, M., and Passamonti, L. (2011). Personality influences the neural responses to viewing facial expressions of emotion. *Phil. Trans. R. Soc. B Biol.* Sci. 366, 1684–1701.
- Carver, C. S., and White, T. L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: the BIS/BAS scales. *J. Pers.* Soc. Psychol. 67, 319–333.
- Conty, L., Russo, M., Loehr, V., Hugueville, L., Huguet, P., Tijus, C., and George, N. (2010). The mere perception of eye contact increases arousal during a word spelling task. *Soc. Neurosci.* 5, 171–186.
- Critchley, H. D. (2002). Electrodermal responses: what happens in the brain *Neuroscientist* 8, 132–142
- Davidson, R. J. (1995). "Cerebral asymmetry, emotion, and affective style," in *Brain Asymmetry*, eds R. J. Davidson and K. Hugdahl (Cambridge, MA: MIT Press), 361–387.
- Davidson, R. J. (2004). What does the prefrontal cortex "do" in affect: perspectives on frontal EEG asymmetry research. *Biol. Psychol.* 67, 219–233.

To sum up, the results of the current study showed that facial expression modified autonomic arousal elicited by sustained eye contact with another person. Being in an eye contact with another individual had an arousal-enhancing effect that was greater to seeing a smiling rather than a neutral face. We suggest that an eye contact has a function of "tuning" two persons to each other, and a positive facial expression, perhaps, boosts to greater sharing of affective information.

ACKNOWLEDGMENTS

This research was supported by the Academy of Finland (Projects no: #130272 and #131786 to Jari K. Hietanen), the Finnish Graduate School of Psychology, and the Emil Aaltonen Foundation. We thank Pauliina Frilander, Stefanie Scheid, and Jenni Tepponen for their help in data collection.

- Davidson, R. J., and Fox, N. A. (1982). Asymmetrical brain activity discriminates between positive and negative affective stimuli in human infants. *Science* 218, 1235–1237.
- Davidson, R. J., and Irwin, W. (1999). The functional neuroanatomy of emotion and affective style. *Trends Cogn. Sci.* 1, 1–21.
- Davidson, R. J., Jackson, D. C., and Larson, C. L. (2000). "Human electroencephalography," in *Handbook* of *Psychophysiology*, eds T. J. Cacioppo, L. G. Tassinary, and G. G. Bernston (New York, NY: Cambridge University Press), 27–52.
- Dawson, M., Schell, A., and Fillon, D. (1990). "The electrodermal system," in *Principles of Psychophysiology*, eds J. T. Cacioppo and L. G. Tassinary (New York, NY: Cambridge University Press), 295–324.
- Dimberg, U., and Thunberg, M. (2007). Speech anxiety and rapid emotional reactions to angry and happy facial expressions. *Scand. J. Psychol.* 48, 321–328.
- Ekman, P., Davidson, R. J., and Friesen, W. V. (1990). Duchenne's smile: emotional expression and brain physiology, II. J. Pers. Soc. Psychol. 58, 343–353.
- Elliot, A. J., and Thrash, T. M. (2002). Approach-avoidance motivation in personality: approach and avoidance temperaments and goals. *I. Pers. Soc. Psychol.* 82, 804–818.
- Engell, A. D., and Haxby, J. V. (2007). Facial expression and gaze-direction in human superior temporal sulcus. *Neuropsychologia* 45, 3234–3241.
- Engels, A. S., Heller, W., Mohanty, A., Herrington, J. D., Banich, M. T., Webb, A. G., and Miller, G. A. (2007). Specificity of regional brain activity in anxiety types during emotion processing. *Psychophysiology* 44, 352–363.

- Frank, M. G., Ekman, P., and Friesen, W. V. (1993). Behavioral markers and recognizability of the smile of enjoyment. J. Pers. Soc. Psychol. 64, 83–93.
- Gale, A., Spratt, G., Chapman, A. J., and Smallbone, A. (1975). EEG correlates of eye contact and interpersonal distance. Biol. Psychol. 3, 237–245.
- Gray, J. R. (1994). "Three fundamental emotion systems," in *The Nature of Emotion. Fundamental Questions*, eds P. Ekman and R. J. Davidson (New York, NY: Oxford University Press), 243–247.
- Gray, J. R., Braver, T. S., and Raichle, M. E. (2002). Integration of emotion and cognition in the lateral prefrontal cortex. *Proc. Natl. Acad. Sci.* U.S.A. 99, 4115–4120.
- Gueguen, N., and Jacob, C. (2002).
 Direct look versus evasive glance and compliance with request. J. Soc. Psychol. 142, 393–396.
- Hadjikhani, N., Hoge, R., Snyder, J., and de Gelder, B. (2008). Pointing with the eyes: the role of gaze in communicating danger. *Brain Cogn*. 68, 1–8.
- Harmon-Jones, E., Gable, P. A., and Peterson, C. K. (2010). The role of asymmetric frontal cortical activity in emotion-related phenomena: a review and update. *Biol. Psychol.* 84, 451–462.
- Heller, W., and Nitschke, J. B. (1998).
 The puzzle of regional brain activity in depression and anxiety: the importance of subtypes and comorbidity. Cogn. Emot. 12, 421, 447.
- Helminen, T. M., Kaasinen, S. M., and Hietanen, J. K. (2011). Eye contact and arousal: the effects of stimulus duration. *Biol. Psychol.* 88, 124–130.
- Herry, C., Bach, D. R., Esposito, F., Di Salle, F., Perrig, W. J.,

- Scheffler, K., Lüthi, A., and Seifritz, E. (2007). Processing of temporal unpredictability in human and animal amygdala. *J. Neurosci.* 27, 5958–5966
- Hess, U., and Bourgeois, B. (2010). You smile-I smile: emotion expression in social interaction. *Biol. Psychol.* 84, 514–520.
- Hietanen, J. K., Leppänen, J. M., Peltola, M. J., Linna-aho, K., and Ruuhiala, H. J. (2008). Seeing direct and averted gaze activates the approach-avoidance motivational brain systems. Neuropsychologia 46, 2423–2430.
- Horley, K., Williams, L. M., Gonsalvez, C., and Gordon, E. (2003). Social phobics do not see eye to eye: a visual scanpath study of emotional expression processing. *J. Anxiety Disord.* 17, 33–44.
- Hsu, M., Bhatt, M., Adolphs, R., Tranel, D., and Camerer, C. F. (2005). Neural systems responding to degrees of uncertainty in human decision-making. *Science* 310, 1680–1683.
- Kocovski, N. L., and Endler, N. S. (2000). Social anxiety, self-regulation, and fear of negative evaluation. Eur. J. Pers. 14, 347–358.
- Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: a review. *Biol. Psychol.* 84, 394–421.
- Laine, C. M., Spitler, K. M., Mosher, C. P., and Gothard, K. M. (2009). Behavioral triggers of skin conductance responses and their neural correlates in the primate amygdala. J. Neurophysiol. 101, 1749–1754.
- Lau, S. (1982). The effect of smiling on person perception. J. Soc. Psychol. 117, 63.
- LeDoux, J. E. (2000). Emotion circuits in the brain. *Annu. Rev. Neurosci.* 23, 155–184
- Lobmaier, J. S., and Perrett, D. I. (2011). The world smiles at me: self-referential positivity bias when interpreting direction of attention. *Corn. Emot.* 25, 334–341.
- Lobmaier, J. S., Tiddeman, B., and Perrett, D. I. (2008). Emotional expression modulates perceived gaze direction. *Emotion* 8, 573–577.
- Mangina, C. A., and Beuzeron-Mangina, J. H. (1996). Direct electrical stimulation of specific human brain structures and bilateral electrodermal activity. *Int. J. Psychophysiol.* 22, 1–8.

- Martin, W. W., and Gardner, S. N. (1979). The relative effects of eye-gaze and smiling on arousal in asocial situations. *J. Psychol.* 102, 253–259
- Mathersul, D., Williams, L. M., Hopkinson, P. J., and Kemp, A. H. (2008). Investigating models of affect: relationships among EEG alpha asymmetry, depression, and anxiety. Emotion 8, 560–572.
- Matsumoto, D., and Kudoh, T. (1993).
 American-Japanese cultural differences in attributions of personality based on smiles. J. Nonverbal Behav.
 17, 231–243.
- N'Diaye, K., Sander, D., and Vuilleumier, P. (2009). Selfrelevance processing in the human amygdala: gaze direction, facial expression, and emotion intensity. *Emotion* 9, 798–806.
- Nichols, K. A., and Champness, B. G. (1971). Eye-gaze and the GSR. *J. Exp. Soc. Psychol.* 7, 623–626.
- Patterson, M. L. (1976). An arousal model of interpersonal intimacy. *Psychol. Rev.* 83, 235–245.
- Patterson, M. L., Jordan, A., Hogan, M. B., and Frerker, D. (1981). Effects of nonverbal intimacy on arousal and behavioral adjustment. J. Nonverbal Behav. 5, 184–198.
- Pönkänen, L. M., Peltola, M. J., and Hietanen, J. K. (2011). The observer observed: frontal EEG asymmetry and autonomic responses differentiate between another person's direct and averted gaze when the face is seen live. *Int. J. Psychophysiol.* 82, 180–187.
- Rigato, S., Farroni, T., and Johnson, M. H. (2010). The shared signal hypothesis and neural responses to expressions and gaze in infants and adults. Soc. Cogn. Affect. Neurosci. 5, 88–97.
- Roelofs, K., Putman, P., Schouten, S., Lange, W., Volman, I., and Rinck, M. (2010). Gaze direction differentially affects avoidance tendencies to happy and angry faces in socially anxious individuals. *Behav. Res. Ther.* 48, 290–294.
- Sallnäs, E.-L. (2005). Effects of communication mode on social presence, virtual presence, and performance in collaborative virtual environments. Presence-Teleop. Virt. 14, 434–449.
- Sander, D., Grandjean, D., Kaiser, S., Wehrle, T., and Scherer, K.

- R. (2007). Interaction effects of perceived gaze direction and dynamic facial expression: evidence for appraisal theories of emotion. *Eur. J. Cogn. Psychol.* 19, 470–480.
- Sato, W., Kochiyama, T., Uono, S., and Yoshikawa, S. (2010). Amygdala integrates emotional expression and gaze direction in response to dynamic facial expressions. *Neuroimage* 50, 1658–1665.
- Sato, W., Yoshikawa, S., Kochiyama, T., and Matsumura, M. (2004). The amygdala processes the emotional significance of facial expressions: an fMRI investigation using the interaction between expression and face direction. *Neuroimage* 22, 1006–1013.
- Semlitsch, H. V., Anderer, P., Schuster, P., and Presslisch, O. A. (1986). Solution for reliable and valid reduction of ocular artifacts, applied to the P300 ERP. Psychophysiology 23, 695–703.
- Spielberger, C. D., Gorsuch, R. L., Lushene, R., Vagg, P. R., and Jacobs, G. A. (1983). Manual for the State-Trait Anxiety Inventory. Palo Alto, CA: Consulting Psychologists Press.
- Stins, J. F., Roelofs, K., Villan, J., Kooijman, K. M., Hagenaars, A., and Beek, P. J. (2011). Walk to me when I smile, step back when I'm angry: emotional faces modulate whole-body approach—avoidance behaviors. Exp. Brain Res. 212, 603–611.
- Strachman, A., and Gable, S. L. (2006). What you want (and do not want) affects what you see (and do not see): avoidance social goals and social events. Pers. Soc. Psychol. Bull. 32, 1446–1458.
- Straube, T., Langohr, B., Schmidt, S., Mentzel, H.-J., and Miltner, W. H. R. (2009). Increased amygdala activation to averted versus direct gaze in humans is independent of valence of facial expression. *Neuroimage* 49, 2680–2686.
- Sutton, S. K., and Davidson, R. J. (1997). Prefrontal brain asymmetry: a biological substrate of the behavioral approach and inhibition systems. Psychol. Sci. 8, 204–210.
- van Honk, J., and Schutter, D. J. L. G. (2006). From affective valence to motivational direction: the frontal asymmetry of emotion revised. *Psychol. Sci.* 17, 963–965.

- Wacker, J., Chavanon, M.-L., Leue, A., and Stemmler, G. (2008). Is running away right? The behavioral activation-behavioral inhibition model of anterior asymmetry. *Emotion* 8, 232–249.
- Wacker, J., Chavanon, M.-L., Leue, A., and Stemmler, G. (2010). Trait BIS predicts alpha asymmetry and P300 in a Go/No-Go Task. Eur. J. Pers. 24, 85–105
- Weeks, J. W., Heimberg, R. G., Rodebaugh, T. L., and Norton, P. J. (2008). Exploring the relationship between fear of positive evaluation and social anxiety. J. Anxiety Disord. 22, 386–400.
- Whalen, P. J. (2007). The uncertainty of it all. *Trends Cogn. Sci.* 11, 499–500.
- Wieser, M. J., Pauli, P., Alpers, G. W., and Muhlberger, A. (2009). Is eye to eye contact really threatening and avoided in social anxiety? An eye-tracking and psychophysiology study. J. Anxiety Disord. 23, 93–103.
- Williams, G. P., and Kleinke, C. L. (1993). Effects of mutual gaze and touch on attraction, mood, and cardiovascular reactivity. J. Res. Pers. 27, 170–183.
- Williams, L. M., Barton, M. J., Kemp, A. H., Liddel, B. J., Peduto, A., Gordon, E., and Bryant, R. A. (2005). Distinct amygdala—autonomic arousal profiles in response to fear signals in healthy males and females. Neuroimage 28, 618–626.
- Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships with a potential conflict of interest.
- Received: 30 December 2011; accepted: 17 April 2012; published online: 04 May 2012
- Citation: Pönkänen LM and Hietanen JK (2012) Eye contact with neutral and smiling faces: effects on autonomic responses and frontal EEG asymmetry. Front. Hum. Neurosci. 6:122. doi: 10.3389/fnhum.2012.00122
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