

Body perception in social environments

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Body Perception in Social Environments

Juanzhi Lu



Maastricht University

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Body perception in social environments

**The neural basis of body expression perception
in social threat, social interaction and self-
identity**

DISSERTATION

to obtain the degree of Doctor at Maastricht University,
on the authority of the Rector Magnificus, Prof.Dr. Pamela Habibović
in accordance with the decision of the Board of Deans,
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by

Juanzhi Lu

Supervisor

Prof. Dr. Beatrice de Gelder

Maastricht University

Co-supervisor

Dr. Lars Riecke

Maastricht University

Assessment Committee

Prof. Dr. Milene Bonte (Chair)

Maastricht University

Prof. Dr. Alan Pegna

University of Queensland

Prof. Dr. Jan van den Stock

KU Leuven

Dr. Lars Hausfeld

Maastricht University

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Chapter 1

General introduction

1.1 Whole body expression and its contribution to social interactions

For human beings, detecting and perceiving others' emotions and reacting to these with adaptive behaviors is crucial to deal with potential threats in the social environment (Darwin, 1872). In daily life, two kinds of channels of communication convey emotions: verbal communication and non-verbal communication. In verbal communication, we can easily gather, for example, another person's anger through the person's increased tone of voice, faster speech, and aggressive words. In non-verbal communication, we understand people's emotions from their facial expressions (e.g., crying when they are sad) and body language (e.g. angry body expressions, with both hands tightly clenched into fists).

Both face and body convey similar information, especially affective signals. In the past years, many studies investigated the link between face expressions and emotion perception. Emotion recognition studies have investigated whole-face expressions, as well as parts of the face including eye gaze, mouth, and eyebrows by using various facial stimuli (Adolphs et al., 1999; Calder, 1996; Chakraborty et al., 2009; Dimberg & Petterson, 2000; Ilbeygi & Shah-Hosseini, 2012; Maglogiannis et al., 2009). More recently, researchers have also investigated expressions of the whole body and have emphasized that it provides another important emotional signal during social interaction (de Gelder, 2009; de Meijer, 1989; Ekman, 1965). Different from these detailed internal features of the face, emotional body expressions consist of whole body postures, gestures and large-scale movements (de Gelder, 2009; de Gelder & Poyo Solanas, 2021).

Many studies on body expressions show that the face and body may share some information and neural mechanisms. However, due to

the distinct features of body expressions compared to facial expressions, body expressions may allow for certain advantages over facial expressions. While both the face and body can express emotions, whole-body stimuli can convey more than just emotion, such as action intentions (de Gelder et al., 2023; Solanas, 2023). For instance, a functional magnetic resonance imaging (fMRI) study found that motor, prefrontal, and visual areas responded more strongly when faces were presented together with bodies rather than in isolation (Poyo Solanas et al., 2018). This suggests that bodies not only provide emotional and social information but also communicate emotion-related action intentions. Given the advantages of conveying action intentions and the larger scale of body gestures, body expressions can more directly communicate social threat signals (e.g., an angry body gesture indicating potential physical harm) compared to facial expressions in social interactions (de Gelder et al., 2010). Additionally, recognizing facial identity and expressions requires being in close range, whereas body identity and gestures are easily perceived from a distance. This highlights the potential for body language to be a more effective form of non-verbal communication, especially when facial cues are less discernible due to distance (de Gelder, 2009; Solanas, 2023). For example, people can greet each other from a distance by waving their hands, recognize friends by their body shape or walking pattern without seeing their faces, and catch someone's attention without being seen, such as by touching their shoulder from behind.

Starting from the importance of whole-body expression, this thesis aims to broaden the understanding of body expression across three novel key topics: social threat, the effects of prediction in social interactions, and self-identity. In the following sections of this introduction, I will first review EEG markers related to the neural

processing of body expression, and then discuss the current state of knowledge and progress in each of these three areas.

1.2 Neural processing of body and face expression

Electroencephalography (EEG) is an electrophysiological technique known for its high temporal resolution, capable of capturing neural activity within milliseconds (ms). The three experiments described in Chapters 2 through 4 utilize EEG, focusing mainly on event-related potential (ERP) features extracted from EEG data. In this section, I will introduce ERP and oscillatory features related to body expression processing.

Over the past few decades, researchers have identified that the N170 component is associated with encoding faces or face-related stimuli, while it is absent in response to houses and other objects (Bentin et al., 1996; Eimer, 1998; Puce et al., 1998). The N170 is a negative component that peaks 170ms in the occipital-temporal regions (Bentin et al., 1996). A related positive component, the vertex positive potential (VPP), peaks in the frontal-central region between 140 and 180ms and is also associated with face processing (Bötzel & Grüsser, 1989; Jeffreys, 1989; Jeffreys, 1996). Researchers suggest that the N170 and VPP derive from a common neural source, as their peaks are temporally coincident and exhibit identical functional properties (Joyce & Rossion, 2005). Most studies report on the N170 component without also discussing the VPP, even though these two components share similar functions and patterns during the neural processing stage, despite being located at different electrode sites. Therefore, in the following text, I will focus primarily on how the N170 is related to the

processing of faces and other stimuli, rather than discussing both the N170 and VPP.

Recent studies have found that the N170 is involved in the encoding of not only face stimuli but also body stimuli or face-body compound stimuli (He et al., 2018; Hietanen & Nummenmaa, 2011; Meeren et al., 2005; Stekelenburg & de Gelder, 2004; Tanaka & Jiang, 2024; van Heijnsbergen et al., 2007; Wang et al., 2017). A review involving 1,645 healthy adults found that the N170 is sensitive to facial expressions, with emotional faces (anger, fear, and happiness) eliciting larger N170 amplitudes than neutral faces (Hinojosa et al., 2015), suggesting that the N170 is not only sensitive to faces but also to the emotional expression. A previous study used face-body compound stimuli depicting winners and losers from "tennis," "table tennis," or "badminton" matches (Wang et al., 2017). The winner's whole body expression refers to a "winning body", which conveys a sense of victory and dominance. In contrast, the loser's whole body expression, known as a "losing body", is associated with perceptions of defeat and submissiveness. This study found that N170 amplitudes were enhanced in response to whole body expressions showing winning bodies compared to losing ones. Similarly, another ERP study reported that nude bodies elicited larger N170 amplitudes than clothed bodies (Hietanen & Nummenmaa, 2011). These findings suggest that emotional content influences body expression processing. However, other studies using fearful and neutral body stimuli did not observe a significant emotional effect on N170 (Stekelenburg & de Gelder, 2004; van Heijnsbergen et al., 2007). Given that the N170 is an early component in brain processing, previous studies have suggested that it reflects the processing of body expressions (van Heijnsbergen et al., 2007).

There are other ERP components evoked by body stimuli which may in part depend on different experimental designs. I will mainly introduce the P1 and N2 components, which have been frequently reported in body expression studies. First, the P1 component is an early visual component that occurs around 65-130ms in the occipital region (Meeren et al., 2005). Previous body expression studies have found that the P1 component is modulated by emotional body expressions, the congruence of emotional face-body compound stimuli, and body-face categories (Meeren et al., 2005; van Heijnsbergen et al., 2007; Wang et al., 2017). For example, Van Heijnsbergen et al. used realistic fearful and neutral body stimuli and found that the P1 latency for fearful bodies (111ms) reached its peak earlier compared to neutral bodies (114ms) (van Heijnsbergen et al., 2007). A similar emotion effect on the P1 component was observed, with P1 being larger in response to losing compared to winning bodies (see above) (Wang et al., 2017). Additionally, studies using emotionally congruent and incongruent face-body compound stimuli found a larger P1 amplitude for the incongruent condition compared to the congruent condition (Meeren et al., 2005; Wang et al., 2017). Moreover, Meeren et al. found a congruency effect on P1, in which isolated angry and fearful faces elicited a larger but slower response than isolated angry and fearful bodies (Meeren et al., 2005).

Second, the N2 component has also been shown to be affected by body emotion. For example, Wang et al. found enhanced N2 amplitudes in response to stimuli featuring losing compared to winning bodies (Wang et al., 2017). However, this emotion effect on N2 was not replicated in other body expression studies (Stekelenburg & de Gelder, 2004). A similar negative ERP component N250 appears nearly 250ms after human face presentation and reflects self-face identification, particularly distinguishing between familiar and unknown persons

(Abreu et al., 2023; Alzueta et al., 2019; Miyakoshi et al., 2008). A recent ERP study used face and body stimuli and presented two images in sequence in one trial. These two images either showed the same person's facial/ body expressions or different person's facial/ body expressions. They found that the same-person condition elicited significantly larger N250 responses than the different-person condition, suggesting that around 220–250ms, this negative component is related to person identity across both face and body categories (Tanaka & Jiang, 2024).

Another important feature extracted from EEG is oscillatory activity. Among the various oscillations in brain activity, theta band oscillations (4-7 Hz) have been linked to processing social stimuli (Knyazev, 2007; Maratos et al., 2009; Symons et al., 2016), including body parts (e.g., hands) (Moreau et al., 2020; Moreau et al., 2018) and whole body expressions (Bossi et al., 2020; Chesley et al., 2024).

These findings indicate that EEG signals serve as a valuable tool for detecting the neural dynamics of body and face perception, particularly in processing emotional body effects. In conclusion, the ERP components N170, P1, and N2, along with theta oscillations, are involved in the processing of body expressions. Previous studies have demonstrated an emotional body effect on N170 amplitudes when comparing winning and losing bodies, as well as nude and clothed bodies, though no significant difference was found between fearful and neutral bodies. Both fearful and angry body expressions are considered threat signals (de Gelder et al., 2023). However, it remains unclear whether this emotional body effect extends to the comparison between angry and neutral body expressions in the context of social threat perception. In the next section, I will review different types of (social) threat signals, as well as the neural markers involved in processing them.

1.3 Social threat perception

Rapid detection of threats in the social environment is critical for species survival (Green & Phillips, 2004). Previous research suggests that biologically salient threats are prioritized in human perception and that we have perceptual biases that enable us to respond to them very rapidly (LoBue & DeLoache, 2010). Various stimuli can elicit threat perception, and based on these stimuli's social attributions, we can categorize them as general threats or social threats. For example, general threat stimuli include animal stimuli, such as snakes and spiders, as well as modern stimuli like guns and knives. Social threat stimuli primarily consist of facial and body expressions.

First, snakes and spiders are among the most common threat-related stimuli. Participants respond faster to these threatening stimuli (e.g., snakes and spiders) than to non-threatening stimuli (e.g., flowers and mushrooms) (Blanchette, 2006). An ERP study found significantly larger P1 amplitudes for spiders and snakes compared to birds (Soares et al., 2017). These studies provide evidence that threat-related stimuli have an advantage in the perceptual system, being processed more efficiently and detected more rapidly.

Second, this threat advantage effect is also observed with evolutionary more recent threat stimuli. Participants respond faster to guns compared to pens and other neutral stimuli (Abado et al., 2023; Damjanovic et al., 2020). Another interesting ERP study found that snakes elicited larger N1 amplitudes than guns and neutral stimuli, while both snakes and guns elicited larger P2 and P3 amplitudes than neutral stimuli. This indicates that threatening stimuli obtain perceptual advantages and result in neural processing biases (Wang et al., 2023).

Third, regarding social threat, people respond more quickly to angry and fearful faces than to neutral and happy faces (Calvo et al., 2006; Fox et al., 2000; Hansen & Hansen, 1988; LoBue & DeLoache, 2010; Lundqvist & Ohman, 2005). More recently, researchers have found that threatening body stimuli also provide the same advantage in response time as threatening facial and animal stimuli. Specifically, participants reacted faster to angry stimuli compared to neutral stimuli in both facial and bodily conditions (de Valk et al., 2015). In more realistic, virtual reality environments, researchers have found a more pronounced freezing response to angry avatars (with full-body expressions) compared to neutral avatars. Specifically, angry body expressions elicited a lower heart rate and reduced body sway than neutral body expressions (Mello et al., 2022).

In summary, social threat stimuli have a perceptual advantage, resulting in processing biases reflected in both behavioral and neural evidence. These threat stimuli are detected more quickly, as indicated by shorter response times, and they elicit larger ERP amplitudes across multiple stages of neural processing, such as P1, P2, and P3 components. Additionally, social threat stimuli can trigger a freezing response. However, it remains unclear how angry body expressions specifically influence the neural processing of social threat in the brain. In Chapter 2, we will address this question using EEG combined with virtual reality (VR) technology to create an immersive 3D environment, in which avatars with angry or neutral body expressions are shown.

Most studies on social threat in body and face expressions focus on observing a single agent, leaving open the question of how people perceive emotional signals between two agents (dyads) during social interactions. Furthermore, it is unclear how knowledge, expectations, and predictions in the brain affect the perception of emotional body expressions when we perceive interactions between two agents. In the

next section, I will explore the perception of body expressions in social interactions and discuss the neural markers related to prediction effects.

1.4 Body expression and prediction in social interaction

1.4.1 Body expression perception in social interaction

People sitting in cafes facing the street often watch passersby, indicating a natural interest in observing social interactions from a third-person perspective. Social interaction studies can be categorized into two types: second-person and third-person studies. Second-person studies involve participants engaging directly in social interactions, such as experiencing social rejection, judgment, or feedback. Third-person studies involve participants passively observing social interactions (McMahon & Isik, 2023; Redcay & Schilbach, 2019).

A previous study found that emotion perception depends not only on the single individual but also on the dyads during social interaction (Abramson et al., 2021; Hareli et al., 2018). This implies that when observing a social interaction, the observer is likely able to perceive the interactive dimension of exchanges between two agents and process them as more than (and different from) the sum of two individuals' expressions. In this context, it has recently been argued that the human perceptual system uses specialized mechanisms for processing body dyads, similar to face processing (Abassi & Papeo, 2022). For example, a behavioral study found that fear recognition was facilitated more by an interacting angry emotion than by an interacting fearful emotion, and this effect occurred when participants viewed body or body-face compound stimuli, but not when they viewed faces alone (Abramson et al., 2021). Previous studies using still images to explore

social interactions from a third-person perspective found that dynamic stimuli result in better recognition rates than static stimuli, especially when body expressions are involved (Atkinson et al., 2012; de Gelder & Poyo Solanas, 2021; de Meijer, 1989). These studies indicate that body gestures and movements play an important role in emotion perception during social interaction.

1.4.2 The role of prediction in social interaction

In non-verbal communication, the ability to perceive and predict others' thoughts, emotions, and behaviors allows for better adaptation in social environments (Barrick et al., 2024). In many sports, successfully predicting what will happen in the next moment can improve athletes' performance (Huesmann & Loffing, 2024), and these predictions may be based on observing others' whole-body gestures. Imagine a situation where you are walking down a street and you see person A behind person B, touching B's shoulder. If person A is gentle and wants to catch B's attention, perhaps to inform them that they dropped something, you might predict that B will react with a happy expression (e.g., a happy facial or body expression). Conversely, if person A pushes B aggressively, you might predict that B will react with anger (e.g., an angry facial or body expression).

Prediction and expectancy effects on higher-order aspects of visual perception have been studied with a theoretical focus on perceptual priors, which represent knowledge about the probabilistic structure of objects and the world (Rao & Ballard, 1999). For example, an EEG study on visual expectancy effects found that incongruent combinations of objects and visual scenes elicit larger N300 and N400 event-related potentials than congruent scene-object combinations (Chen et al., 2022). Similarly, Kumar et al. (2021) found that the N300 is sensitive to the representativeness of items from natural scene

categories: less representative items (statistically irregular exemplars) were found to elicit larger N300 amplitudes than representative items (statistically regular exemplars) (Kumar et al., 2021). Another EEG study found that the visual perception of two consecutive emotional expressions elicits a stronger N400 when these two expressions are incongruent rather than congruent (Calbi et al., 2017). This effect was observed regardless of whether the expression was conveyed by images of the face or the body, hinting at a prediction-violation response.

In conclusion, prediction plays an essential role in social interactions, with the N300 and N400 ERP components serving as neural markers of violations of higher-order visual predictions. However, it remains unclear how such predictions affect the perception of emotional body expressions in social interactions. In Chapter 3, I introduce a novel paradigm to investigate this question. We induced emotional predictions in participants by showing them a video clip of a social interaction, in which one person approached and touched another either angrily or neutrally. Afterwards, a still image was presented, showing the emotional reaction of the touched person's whole body, which either matched or mismatched the emotional tone of the touch (angry or neutral). To vary the strength of the induced predictions, we parametrically reduced the saliency of emotional cues in the video. To assess the impact of these predictions on emotional body expression processing, we measured participants' behavioral and neural responses to the still image that resolved the interaction.

In the previous sections, we discussed the perception and prediction of others' emotions in both single-agent body expressions and dyadic interactions. As individuals in social contexts, perceiving ourselves is also crucial to our health and well-being. While most studies have explored self-identity through facial expressions, only a few studies have examined self-body identity or the integration of self-

identity across both face and body. In the next section, I will review relevant studies on self-identity and self-relevance in both behavioral and neural processes.

1.5 Body and face perception of self-identity

The concept of the self has been a subject of exploration in both psychology and philosophy for a long time (Woźniak et al., 2018). However, there is still no general agreement on the definition of the term "self" or "self-identity." Based on current research in psychology and neuroscience, "self-identity" refers to self-relevant stimuli containing social attributes about the self ("Me" or "My"), such as name, objects, face, and body.

Previous studies have found that response times are shorter when participants identify their own names compared to other names (Shi, 2016; Tacikowski & Nowicka, 2010). Besides names, there is other social information highly relevant to us. For example, when observers face a mirror, their physical appearance shows their faces and bodies. Even though observers may not examine their facial and body features every day, they can easily recognize themselves. A meta-analysis based on 54 studies found that individuals identify their own faces more quickly than others' faces (Bortolon & Raffard, 2018), which indicates that self-identity in face perception benefits from a reaction time advantage.

A review reported that the N2 ERP component, occurring in the frontal-central region around 200ms after stimulus onset, is linked to the processing of self-relevant stimuli (Knyazev, 2013), especially facial expressions of the self (Sui et al., 2013). Several studies found

that self-faces elicited smaller N2 amplitudes than other-faces, indicating that seeing one's own face is less familiar than seeing others' faces (Bola et al., 2021; Guan et al., 2014; Keyes et al., 2010; Scott et al., 2005; Sui et al., 2006). Other studies found that familiar faces and objects also elicit smaller N2 amplitudes than less familiar faces and objects (Carver et al., 2006; Muñoz et al., 2020). Taken together, the decreased N2 amplitude in self-face perception may indicate that people are more familiar with their own faces than with others' faces (Woźniak et al., 2018).

To date, only a few studies have explored the perception of self-identity from bodies or used personalized body images. In a fMRI study, researchers utilized full-body photos of participants clad in dark bathing suits and found that photos conveying self-identity triggered responses in the extrastriate, parietal regions, and middle frontal gyrus in the right hemisphere (Hodzic et al., 2009). An ERP study employed participant photos, presenting naturalistic, enlarged, and reduced body images to investigate the perception of self-body versus other-body under various attention tasks (Uusberg et al., 2018). Their findings indicate that the distinction between self-body and other-body influences the N170 component, known for its role in the initial stages of face and body perception (Stekelenburg & de Gelder, 2004).

In summary, self-body and self-face may have advantages in behavioral performance (e.g., quicker response times), as well as in consuming fewer brain resources, as reflected in lower N2 responses to self-face and self-body.

However, we still do not fully understand how the self-body contributes to self-identity perception. In Chapter 4, we used EEG and personalized avatars to investigate the neural mechanisms underlying personal identity perception. We created compound avatar images by

combining participants' own faces and bodies with those of others. Participants then underwent embodiment training for each avatar type in a VR environment, where they controlled the avatar's actions during physical exercise tasks. In the subsequent EEG task, participants viewed 2D images of the same avatars used in the VR environment, presented on a computer screen while their EEG was recorded. To evaluate self-identity perception, we measured participants' behavioral and neural responses to these avatar images.

1.6 Purpose and outline of the thesis

The work reported in this thesis aims to expand the theoretical understanding of body expression perception in the field of behavioral neuroscience. From the section above, we can infer that: 1) Body expression plays an essential role in social interactions. 2) N170 is a major ERP component that encodes body expression; other ERP components, such as P1 and N2, can also be elicited by body expressions according to various experimental paradigms. 3) Body expression can contribute to social threat perception and can elicit a freezing response. Social threat-related stimuli can have an advantage in shorter response times and greater ERP amplitudes (e.g., P1, P2, and P3). 4) Body expression conveys movement, action understanding, and emotional signals, allowing us to explore emotion prediction generated from social interactions between two individuals. The prediction error can elicit larger N300 and N400 amplitudes. 5) The decreased N2 amplitude in self-face perception may indicate that people are more familiar with their own faces than with others' faces. This thesis investigated research questions pertaining to the neural basis of body expression perception in three empirical chapters (Chapters 2 to 4):

Chapter 2. Most social threat studies focus on face stimuli, and few have reported on body expression in social threat perception, especially angry body expression. A previous study found that angry body expressions eliciting social threats can induce freezing responses, but we do not know how they impact our neural activities over time. In Chapter 2, we address this question using EEG combined with VR technology to create an immersive 3D environment. In this experiment, we primarily use the emotional information conveyed by body expressions and manipulate angry and neutral avatars to induce participants' feelings of social threat and non-threat. Additionally, with this VR scenario, we explore if the ability to control the threat impacts social threat perception by offering participants a controllable cue to stop the angry or neutral avatar approaching them. Participants' behavioral, EEG, and ECG signals were recorded to assess neural and cardiac responses to social threats and whether they were impacted by the ability to effectively control the threat.

Chapter 3. Previous studies on body-emotion expression mainly used a single agent's whole-body expression, while less is known about how people perceive emotional information from social interactions involving two agents interacting with whole-body expressions. Additionally, prediction plays an essential role in social interactions, and it remains unclear how such predictions affect the perception of emotional body expressions in social interactions. In Chapter 3, we induced emotional predictions in participants by showing them a video clip of a social interaction in which one person approached and touched another either angrily or neutrally. Afterwards, a still image was presented, showing the emotional reaction of the touched person's whole body, which either matched or mismatched the emotional tone of the touch (angry or neutral). To vary the strength of the induced predictions, we parametrically reduced the saliency of

emotional cues in the video. To assess the impact of these predictions on emotional body expression processing, we measured participants' behavioral and neural responses to the still image that followed the interaction.

Chapter 4. Most self-identity perception studies focused on the self-face, while only a few have explored the perception of self-identity from bodies or used personalized body images. It is still unclear how body expressions contribute to self-identity. In Chapter 4, we used individual body shape information conveyed by body expressions. We created personalized avatars for each participant to induce a strong identification with avatars representing their own identity, as well as another avatar whose face and body were completely different from the participants' to induce other-identity feelings. Participants' subjective ratings and EEG signals were recorded while they were presented with those avatars to assess their behavioral and neural responses to the avatar images.

Finally, chapter 5 summarizes the main findings of this thesis and discusses their implications and significance for behavioral neuroscience.

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Chapter 2

Early threat perception is independent of later cognitive and behavioral control. A virtual reality-EEG-ECG study

Based on:

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2.1 Abstract

Research on social threat has shown the influences of various factors, such as agent characteristics, proximity and social interaction on social threat perception. An important, yet understudied aspect of threat exposure concerns the ability to exert control over the threat and its implications for threat perception. In this study, we used a Virtual Reality (VR) environment showing an approaching avatar that was either angry (threatening body expression) or neutral (neutral body expression) and informed participants to stop avatars from coming closer under five levels of control success (0, 25, 50, 75, or 100%) when they felt uncomfortable. Behavioral results revealed that social threat triggered faster reactions at a greater virtual distance from the participant than the neutral avatar. Event-related potentials (ERPs) revealed that the angry avatar elicited a larger N170/vertex positive potential (VPP) and a smaller N3 than the neutral avatar. The 100% control condition elicited a larger late positive potential (LPP) than the 75% control condition. In addition, we observed enhanced theta power and accelerated heart rate for the angry avatar vs. neutral avatar, suggesting that these measures index threat perception. Our results indicate that perception of social threat takes place in early to middle cortical processing stages, and control ability is associated with cognitive evaluation in middle to late stages.

2.2 Introduction

The ability to detect threat and react adaptively is a major evolutionary endowment of many species (LeDoux & Daw, 2018). Human and non-human studies of defensive behavior have documented different kinds of behavior in the face of threat, mainly freezing and fleeing (Eilam, 2005). Freezing has been defined as a threat-anticipatory state whereby an individual is hyperattentive to an environmental, potentially threatening signal, presumably also enhancing its processing (Blanchard et al., 1986; Livermore et al., 2021; Mobbs & Kim, 2015; Terburg et al., 2018). Previous work has investigated freezing-like reactivity using threat-related social stimuli, such as facial expressions and affective films (Hagenaars et al., 2014; Roelofs et al., 2010; Stins et al., 2011), as well as computer-based tasks (e.g., a gun shooting task) (Gladwin et al., 2016) and most recently whole body expression (de Borst & de Gelder, 2022; de Gelder et al., 2010; Mello et al., 2022). Bradycardia, a reduction in one's heart rate, and reduced postural mobility are two principal physiological components of the freezing state in the face of threats (Roelofs et al., 2010). This pattern of physiological and behavioral activation is especially coordinated by the subcortical connections between amygdala nuclei - the basolateral nucleus receiving multisensory information and the central nucleus sending the main projections out - and the periaqueductal gray, the hypothalamus, and the rostral ventrolateral medulla (George et al., 2019). Stimulation of this circuit activates the sympathetic and parasympathetic nervous systems, which in turn coordinate switches from passive defensive states (e.g., freezing) to active defensive behavior (e.g., flight or fight) (Livermore et al., 2021; Terburg et al., 2018).

A critical factor for freezing-like reactions in humans is the

proximity of the threat. Studies on peripersonal space (PPS), the proximate space surrounding the body where interactions with environmental stimuli occur (Bufacchi & Iannetti, 2018; Di Pellegrino & Làdavas, 2015; Serino, 2019), have shown that personal distance is an important determinant of defensive behavior in social interactions (Bogdanova et al., 2021; Brozzoli et al., 2013; Cléry et al., 2015; Graziano & Cooke, 2006; Pellencin et al., 2018). The defensive reactivity to potentially threatening stimuli near the PPS is associated with reduced motor cortex excitability (Avenanti et al., 2012), increased physiological reactivity (Ruggiero et al., 2021), and enhanced neural processing of the target stimulus in brain regions involved in defensive behavior (Vieira et al., 2020). Moreover, the neural network underlying PPS has been shown to respond also to indicators of social threat, specifically in nearby space (de Borst et al., 2020; Ellena et al., 2021). A threatening character invading one's personal space is associated with increased activity in ventral premotor cortex and intraparietal sulcus (areas that are part of the brain network coding PPS) as well as amygdala and anterior insula (de Borst & de Gelder, 2022). Another line of research using electroencephalography (EEG) has shown that threatening body expression impact early event-related potentials (ERPs), such as N170 and vertex positive potential (VPP) (Stekelenburg & de Gelder, 2004; Van Heijnsbergen et al., 2007). These electrophysiological measures of threat also interact with PPS. A behavioral ERP study used a modified version of a paper-and-pencil validated measure of comfortable interpersonal distance (CID) to explore how participants react to the threat of interpersonal distance invasion (Perry et al., 2013). Participants were instructed to imagine they were in the center of the room, and as a friend or stranger approached, they could press a key to show that they wanted to stop the person from coming closer. It was observed that the potential threat (approaching person) elicited larger N1 for strangers compared to

friends, whereas friends/strangers had no significant effect on P1 and LPP components. These ERP responses occurred from 50 to 800ms. Besides distance, another critical factor for adaptive threat response is related to control over the threat. Threat experience may be reduced when, for example, threat escape or another behavioral control is possible (Terburg et al., 2018). Active control behavior refers to a sense of control that can reduce or stop the approaching threat (Iachini et al., 2016; Wendt et al., 2017).

A major obstacle in research on human behavior in the face of social threat is the difficulty of rendering threatening situations in a realistic manner and obtaining valid measures of human behavior and physiology. The use of virtual reality (VR) opens unique chances for this important research field (Monti & Aglioti, 2018; Parsons et al., 2017) as it allows participants to experience a threatening event in a controlled laboratory environment "as if" it was actually happening to them (de Borst & de Gelder, 2022; de Borst et al., 2020; Fusaro et al., 2016; Mello et al., 2022; Tieri et al., 2017). VR-based designs implementing social threat from avatars have successfully been used in behavioral, fMRI and EEG studies (de Borst & de Gelder, 2022; Mello et al., 2022; Stolz et al., 2019). Here, we combined VR with behavioral measures and measures of neural and cardiac activity to assess with millisecond temporal resolution the impact of the avatar emotion (angry/neutral) and various levels of threat-control success (0%, 25%, 50%, 75%, or 100%). Our goal was to measure how social threat is perceived under naturalistic conditions implemented in VR and whether the ability to effectively control the threat affects how the source of the threat is processed at behavioral, neural, and cardiac levels.

2.3 Methods

2.3.1 Participants

Thirty healthy right-handed participants were recruited for this study. All participants had normal or corrected-to-normal vision without brain injury, history of psychiatric disorder, or current psychotropic medication. Participants provided written consent at the beginning of the experiment. They earned 7.5EUR or received one credit point per hour of participation. Four participants' data were rejected because they did not press a button in more than 50% of the trials. Twenty-six participants' data were included in the analysis (13 females, 13 males; age range 18-29 years, mean = 24.65; standard deviation (SD) = 3.60). The Ethical Committee of Maastricht University approved the study, and all procedures conformed to the Declaration of Helsinki.

2.3.2 Design and procedures

VR scenario

The VR scenario consisted of a dark and narrow urban street, in which an avatar expressing an angry or neutral emotion, appeared and subsequently approached the participant. The VR scenario was programmed in Unity 3D (Unity Technologies, US). The basic design of the angry (raised arms) and neutral (arms down) body expressions were similar to a previous study (Mello et al., 2022), while the VR environment and the task settings were new for the present study. Before EEG data collection started, participants put on the VR headset (HTC VIVE) and freely explored the 3D VR world by physically moving their head and walking in the lab. This allowed them to walk along streets in the VR scenario and visually explore the surroundings. This served to make participants immersed in the VR environment.

Experimental design

The VR environment and task were explained to the participants. Participants were told that an angry or emotionally neutral avatar would appear in a dark, urban environment and approach them. They were

informed that pressing a control button (space bar) could stop the avatar from coming closer, and they were encouraged to do so as soon as they felt uncomfortable. At the beginning of each trial, a cue appeared indicating the likelihood that pressing the space bar would effectively stop the avatar. There were five different controllable cue conditions (Fig1A). In the 0% condition, the button press never stopped the approaching avatar, while in the 100% condition pressing the space bar always stopped the avatar. In the intermediate conditions, the bar press stopped the avatar from approaching with 25%, 50% and 75% probability. A sketch of a trial is shown in Fig1B. All trials were preceded by a cue presented 1s before the avatar's appearance. After a 1 ± 0.1 s interval, the avatar was first standing still for 1 ± 0.1 s at a virtual distance from the participant of 5m. The avatar then started moving towards the participant at a speed of 1.43 m/s. The trial procedure in Figure 1B shows two screenshots corresponding to the participants' view during the VR experiment. The first screenshot (left) shows the static avatar and the second screenshot (right) shows the approaching avatar. The approach of the avatar was simulated by increasing the size of the avatar over time, covering an increasing portion of the participants' field of view (videos of the approaching avatar can be found in the supplementary material). Participants were instructed to press the button as soon as they felt uncomfortable after the avatar approaching. In some trials, the avatar stopped as participants pressed the button, while at other trials (those with control success <100%), the button press did not always stop the avatar from approaching. If participants stopped the avatar successfully, the avatar remained still at its position until the next trial. The duration from the advent of the avatar until its disappearance was 3.5s.

The study used a 5×2 within-subject design with five controllable cue conditions and two avatar emotions (angry, neutral)

conditions. There were 40 trials per condition, and the total number of 400 trials was presented randomly in five runs, lasting in total 1h.

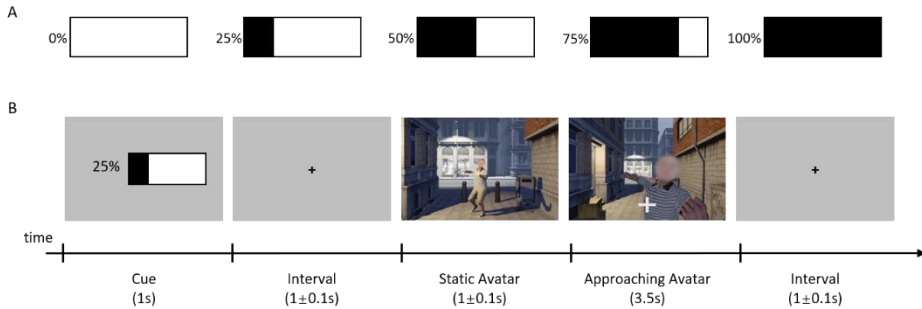


Fig. 1. (A) Five kinds of controllable cues. (B) A trial procedure.

2.3.3 EEG acquisition

EEG data were recorded using an international 10-20 system, a scalp cap with 63 electrodes, and a sampling frequency of 250Hz (BrainVison Products, Munich, Germany). The electrode positioned on Cz was used as the reference during recording, and the forehead electrode positioned on FP1 was used as a ground electrode. Four electrodes were used to measure the electrooculogram (EOG). Two of them were used as vertical electrooculograms (VEOG). One was placed above the right eye, and another was placed below the right eye. The other two electrodes were used as a horizontal electrooculogram (HEOG), with one placed at the outer canthus of the left eye, and the other at the outer canthus of the right eye. Three electrodes were used for Electrocardiography (ECG). Two ECG electrodes were put one centimeter below the center of the left and right collarbones separately. The third ECG electrode was put on the right waist. The remaining 56 electrodes covered the whole scalp, including locations FPz, AFz, Fz, FCz, CPz, Pz, POz, Oz, AF7, AF8, AF3, AF4, F7, F8, F5, F6, F3, F4, F1, F2, FC5, FC6, FC3, FC4, FC1, FC2, T7, T8, C5, C6, C3, C4, C1, C2, TP7, TP8, CP5, CP6, CP3, CP4, CP1, CP2, P7, P8, P5, P6, P3, P4,

P1, P2, PO7, PO8, PO3, PO4, O1, and O2. Impedances for reference and ground were maintained below 5kOhm and all other electrodes below 10kOhm. After lowering impedance, the VR headset was carefully placed on the chin rest. The participants were standing against a height-adjustable bar chair in front of a high desk with the VR headset-Chin rest setup (Fig2).

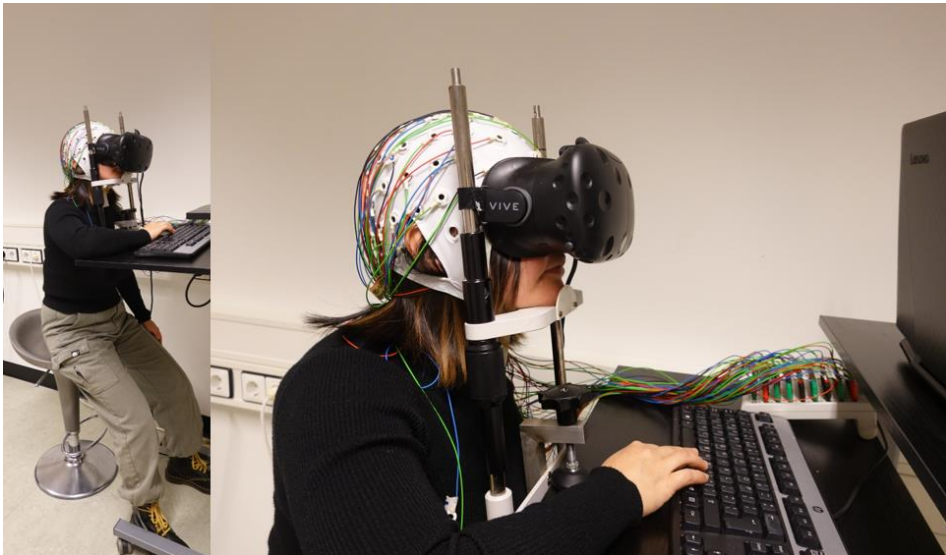


Fig. 2. VR-Chin rest-EEG setup shows a participant standing against the height-adjustable bar chair.

The heavy VR headset could potentially influence the EEG signal and cause head movement during the EEG data collection. To reduce these risks, we combined VR with a chin rest in our EEG experiment. The reason for this choice was that EEG is highly sensitive to stimulus phase-locked neural activity and muscle activity. More specifically, we focused the analysis on ERPs to the static avatar instead of the dynamic avatar because of the higher difficulty of obtaining clean and stable ERPs to dynamic stimuli. We refrained from investigating movements in the VR environment because it would have induced large

motor-related activity. While this would have further added to the external validity of the study, it would have confounded the ERPs to the emotional stimuli that were the focus of the study. Therefore, we think that limiting the investigation to static 3D representations helped us to obtain cleaner and more reliable neural measures of emotional processing, which we considered as most important.

2.3.4 EEG data preprocessing

EEG data were preprocessed and analyzed using FieldTrip version 20220104 (Oostenveld et al., 2011) in Matlab R2021b (MathWorks, U.S.). The signal was first segmented into epochs from 1000ms pre-stimulus (the static avatar) to 2000ms post-stimulus and then filtered with a 0.1–30 Hz band-pass filter. EEG data at each electrode were re-referenced to the average of all electrodes. Artifact rejection was done using independent component analysis (ICA, logistic infomax ICA algorithm; Bell & Sejnowski, 1995); on average, 1.88 ± 0.33 (mean \pm SD) components were removed per participant. Finally, single trials during which the peak amplitude exceeded 3 SD above/below the mean amplitude were rejected. On average, $75.36\% \pm 5.27\%$ (mean \pm SD) trials were preserved and statistically analyzed per participant.

2.3.5 Event-related potential analyses

The ERP analyses performed were time locked to the presentation of the static avatar to derive clean ERPs in response to the still image. Here, a time window from 200ms before the onset of static avatar until 1000ms after the onset was extracted from each trial of the preprocessed data. A baseline correction was applied by subtracting the average amplitude during the interval (-200 ~ 0ms) before the onset of the static avatar. The segmented EEG for each participant was averaged for each experimental condition, resulting in ERPs used for further statistical analyses, which were performed using IBM SPSS Statistics 27 (IBM Corp., Armonk, NY, USA). In the ERP analysis, we focused on the

ERPs elicited by social threatening/non-threatening body expressions (as represented by angry/neutral avatars) and their sensitivity to the level of threat control (controllable cues). We separated the EEG channels into five spatial clusters and identified for each region a prominent ERP component and centered a time window on its peak based on visual inspection of the overall ERP waveform, topographical distribution of grand-averaged ERP and previous studies (Chai et al., 2022; Cunningham et al., 2005; de Gelder et al., 2004; He et al., 2011; Luo et al., 2010; Stekelenburg & de Gelder, 2004; Van Heijnsbergen et al., 2007). The resulting ERP components and associated time windows are shown for each region in table 1. The mean amplitude was computed as the average of all electrodes within the cluster within the specific time window.

A repeated-measures 5×2 ANOVA (Controllable cue: 0% / 25% / 50% / 75% / 100% \times Avatar emotion: angry/neutral) was applied to the mean amplitudes; this was done for each ERP component separately. Degrees of freedom for F-ratios were corrected with the Greenhouse-Geisser method. Statistical differences were considered as significant given a $p < .05$. To control for type I errors, a Bonferroni correction was applied to the p -values associated with the main effects and interaction effects of every ERP component. Only corrected p -values were reported.

Table 1. Brain regions and electrodes of ERP components and associated time windows.

ERPs	Brain regions	Electrodes	Time windows
N170	Temporal	P7, P8, TP7, TP8, CP5, CP6, P5, P6	180-230ms
VPP	Central-occipital midline	Cz, CPz, Pz, POz, Oz	200-250ms
P3	Parietal	P5, P6, P7, P8, PO7, PO8	280-350ms
N3	Frontal-central (with midline)	FCz, Cz, FC1, FC2, C1, C2	300-350ms
LPP	Frontal-central (without midline)	FC5, FC6, F5, F6, F7, F8, C5, C6	500-800ms

2.3.6 Time-frequency analyses

To assess temporal variations in oscillatory EEG power within the range from 1-30Hz, we decomposed each trial using the complex Morlet wavelet transform (frequency-bin size: 1 Hz, three cycles per time window, time-bin size: 50ms). To reduce edge effects, we applied the time-frequency analysis to epochs of longer duration (corresponding to the duration of the preprocessed epochs before ERP computation; see above) and used a longer and earlier baseline in the interval (-500 ~ -100ms) before the onset of the static avatar. We focused the statistical analysis on oscillatory power in the theta (4-7Hz) band, based on literature showing that theta activity is related to the processing of threat and control, especially at frontal and central scalp regions (DeLaRosa et al., 2014; Lange et al., 2022; Ma et al., 2016). Thus electrodes positioned at Fz, FCz, Cz, F1, F2, FC1, FC2, C1, and C2 were selected for this analysis. Inspection of theta power revealed a peak between 100ms and 200ms after the onset time in the frontal central region consistently across conditions. Based on this observation, we extracted mean theta power during the time window (100 - 200ms) at the selected

electrodes and statistically analyzed it using the same repeated measures ANOVAs as for the ERP analysis; see above.

2.3.7 ECG analyses

A time window from 500ms before static avatar onset to 4500ms after the onset was extracted from the continuous ECG data. The ECGdeli toolbox (Pilia et al., 2021) was used for analyzing heart rate. One participant's ECG data was not recorded; thus, 25 participants' ECG data were included in the analysis. The electrode that was placed under the left collarbone was selected for this analysis as it was positioned closest to the heart, giving the strongest signal. Statistical analyses were the same as for ERP and theta power; see above.

2.3.8 Behavioral analyses

We instructed participants to press the button as soon as they felt uncomfortable with the approaching avatar. In some trials, participants pressed the button once (4.81% trials), while in other trials, participants did not press the button or pressed it more than once (16.42% trials). Two behavioral indicators were recorded. First, the virtual distance between the participant and avatar at the time when participants first pressed the button. For this, the time at which the participants pressed the response button was multiplied by the speed by which the avatar was approaching and this was subsequently subtracted by the distance at which the avatar initially appeared ($\text{Distance} = 3.5 - \text{Response Time} * \text{Speed}$). Second, the number of button presses was recorded. Like the physiological measures above, each behavioral indicator was subjected to a 5 (Controllable cue: 0% / 25% / 50% / 75% / 100%) \times 2 (Avatar emotion: angry/neutral) repeated-measures ANOVA.

2.3.9 VR questionnaire

Information about the participants' subjective experience during the VR scenario was obtained with a questionnaire, which participants filled in

after the experiment (Seinfeld et al., 2016; Seinfeld et al., 2021). The individual questionnaire items are shown in Table 2.

Table 2. The items and mean \pm SD rating scores in the VR questionnaire are shown. Ratings were made on a 7-point scale (1=not at all, 7=completely).

<i>Item</i>	<i>Question</i>	<i>Mean \pm SD</i>
<i>Realism</i>	To what extent have you experienced the situation as if it was real?	4.69 \pm 1.29
<i>Vulnerable</i>	Did you feel at any time that you were vulnerable?	3.96 \pm 1.61
<i>Violent</i>	How violent do you find this scene is?	3.69 \pm 1.38
<i>Assaulted</i>	Did you think that you could be physically assaulted during the scene?	3.19 \pm 1.77
<i>Attention to cue</i>	How much attention did you pay to the probability cues during the experience?	5.08 \pm 1.52
<i>Fear of static angry avatar</i>	How fearful did you feel when facing the static angry avatar?	3.23 \pm 1.67
<i>Fear of an approaching angry avatar</i>	The sense of uncomfortable increased when the avatar got closer to me.	5.38 \pm 1.55
<i>Fear of static neutral avatar</i>	How fearful did you feel when facing the static neutral avatar?	1.96 \pm 1.34
<i>Fear of an approaching neutral avatar</i>	The sense of uncomfortable increased when the avatar got closer to me.	4.69 \pm 1.44

2.4 Results

2.4.1 VR questionnaire results

The items of the VR questionnaire and the mean \pm SD of each item scores are shown in Table 2. We used a 7-point scale to test subjective feelings during the experiment, taking the median value "4" (the neutral subjective experience) as a reference to which we compared participants' scores on each item. One-sample t-test results showed that realism ($t(25) = 2.74, p = .011$), attention to cue ($t(25) = 3.61, p = .001$), fear of approaching angry avatar ($t(25) = 4.55, p < .001$) and fear of approaching neutral avatar ($t(25) = 2.46, p < .021$) were significantly larger than the reference value of 4, while fear of possible assault ($t(25) = -2.33, p = .028$), fear of static angry avatar ($t(25) = -2.36, p = .026$), and fear of static neutral avatar ($t(25) = -7.75, p < .001$) were significantly smaller than the reference value. Furthermore, subjective experience of vulnerability ($t(25) = -1.12, p = .904$) and violence ($t(25) = -1.14, p = .266$) were not significant. Paired t-test results revealed that fear of a static angry avatar was significantly larger than fear of a static neutral avatar ($t(25) = 4.44, p < .001$), and fear of an approaching angry avatar was significantly larger than fear of an approaching neutral avatar ($t(25) = 3.99, p < .001$).

2.4.2 Behavioral results

For the first behavioral indicator (distance), the main effect of emotion was significant ($F(1, 25) = 14.33, p < .001, \eta_p^2 = 0.36$) such that the distance between participants and the avatar was bigger when they saw the angry (2.24 ± 0.23) than neutral avatar (1.82 ± 0.21). The main effect of controllable cue was significant too ($F(4, 100) = 4.56, p = .029, \eta_p^2 = 0.15$). A paired T-test between each controllable cue condition revealed no significant results after Bonferroni correction. The linear effect of controllable cue was significant ($F(1, 25) = 5.07, p = .033, \eta_p^2 = 0.17$), showing that as the probability of the controllable cue increased, the tolerated distance decreased. The interaction effect between

emotion and controllable cue was non-significant ($F(4, 100) = 2.28, p = .096, \eta_p^2 = 0.08$) (Fig3A).

Applying the same analyses to the second behavioral indicator (number of button presses) yielded qualitatively identical results, showing more button responses to the angry vs neutral avatar and to low vs. high probabilities of control success (main effect of avatar emotion: $F(1, 25) = 4.43, p = .045, \eta_p^2 = 0.15$, angry: 1.61 ± 0.25 , neutral avatar: 1.40 ± 0.18 ; main effect of controllable cue: ($F(4, 100) = 6.15, p = .016, \eta_p^2 = 0.20$); linear effect of the controllable cue: $F(1, 25) = 6.58, p = .017, \eta_p^2 = 0.21$; interaction effect (not significant): $F(4, 100) = 1.83, p = .178, \eta_p^2 = 0.07$) (Fig3B).

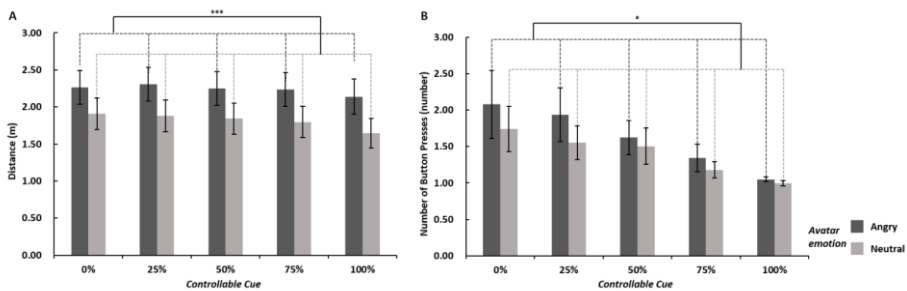


Fig. 3. (A) Means and standard error (SE) of distance per condition. (B) Means and S.E. of the number of button presses per condition. *** $p < .001$, * $p < .05$

2.4.3 ERPs

N170

The main effect of avatar emotion on the N170 amplitude was significant ($F(1, 25) = 9.77, p = .017, \eta_p^2 = 0.28$) such that the angry avatar elicited larger N170 amplitudes ($-2.04 \pm 0.48 \mu\text{V}$) than the neutral avatar ($-1.68 \pm 0.44 \mu\text{V}$). The main effect of controllable cue ($F(4, 100) = 0.34, p = 1, \eta_p^2 = 0.01$) and the interaction of the two factors were not significant ($F(4, 100) = 1.23, p = 1, \eta_p^2 = 0.05$) (Fig4).

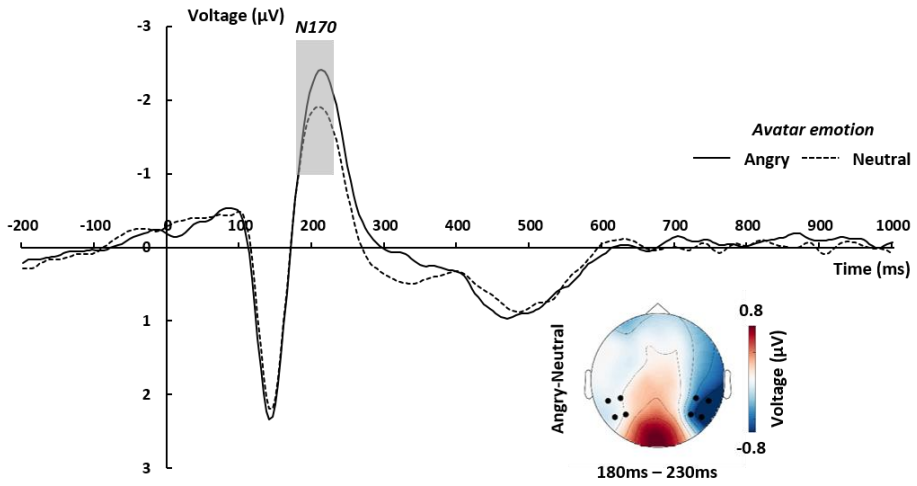


Fig. 4. Grand-averaged ERP waveforms of N170 per avatar emotion condition. Waveforms were calculated by averaging the data at the electrodes P7, P8, TP7, TP8, CP5, CP6, P5, and P6, and across the controllable cue conditions. The "angry" minus "neutral" topographic map was calculated by averaging the data within a time window of 180 to 230ms after the onset of the static avatar. The black dots highlight the electrodes that were used to calculate grand-averaged ERPs.

VPP

The main effect of avatar emotion on VPP was significant ($F(1, 25) = 12.63, p = .006, \eta_p^2 = 0.34$) such that the angry avatar elicited larger VPP amplitudes ($3.50 \pm 0.53 \mu\text{V}$) than the neutral avatar ($2.93 \pm 0.51 \mu\text{V}$). The main effect of the controllable cue ($F(4, 100) = 1.06, p = 1, \eta_p^2 = 0.04$) and the interaction of the two factors were not significant ($F(4, 100) = 0.12, p = 1, \eta_p^2 = 0.01$) (Fig5).

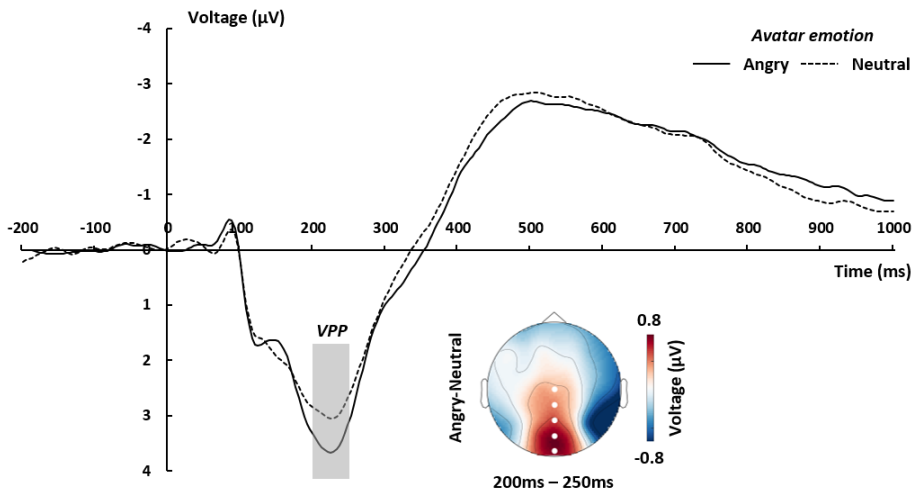


Fig. 5. Grand-averaged ERP waveforms of VPP per avatar emotion condition. Waveforms were calculated by averaging the data at the electrodes Cz, CPz, Pz, POz, and Oz, and averaged across controllable cue conditions. The "angry" minus "neutral" topographic map was calculated by averaging the data within a time window of 200 to 250ms after the onset of the static avatar. The white dots highlight the electrodes that were used to calculate grand-averaged ERPs.

N3

The main effect of avatar emotion on N3 was significant ($F(1, 25) = 9.28, p = .021, \eta_p^2 = 0.27$), such that the angry avatar elicited smaller amplitudes ($-1.83 \pm 0.25 \mu\text{V}$) than the neutral ($-2.12 \pm 0.26 \mu\text{V}$) avatar. The main effect of the controllable cue ($F(4, 100) = 2.37, p = .300, \eta_p^2 = 0.09$) and the interaction of the two factors were not significant ($F(4, 100) = 0.99, p = 1, \eta_p^2 = 0.04$) (Fig6).

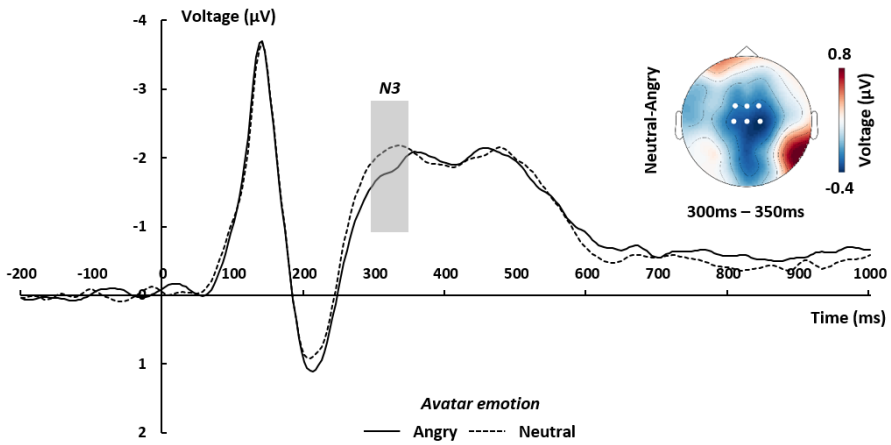


Fig. 6. Grand-averaged ERP waveforms of frontal-central N3 per avatar emotion condition. Waveforms were calculated by averaging the data at the electrodes FCz, Cz, FC1, FC2, C1, and C2, and averaged across controllable cue conditions. The "neutral" minus "angry" topographic map was calculated by averaging the data within a time window of 300 to 350ms after the onset of the static avatar. The white dots highlight the electrodes which were used to calculate grand-averaged ERPs.

P3

The main effect of avatar emotion on P3 was not significant ($F(1, 25) = 4.81, p = .150, \eta_p^2 = 0.16$). The main effect of controllable cue ($F(4, 100) = 1.36, p = 1, \eta_p^2 = 0.05$) and the interaction of the two factors were not significant ($F(4, 100) = 0.33, p = 1, \eta_p^2 = 0.01$).

LPP

The main effect of controllable cue on LPP was significant ($F(4, 100) = 4.24, p = .034, \eta_p^2 = 0.15$), such that the 100% cue elicited larger amplitudes ($0.18 \pm 0.25 \mu\text{V}$) than the 75% cue ($-2.56 \pm 0.26 \mu\text{V}$). The main effect of avatar emotion was not significant ($F(1, 25) = 1.47, p = .950, \eta_p^2 = 0.05$). The interaction of controllable cue and avatar emotion was not significant ($F(4, 100) = 2.68, p = .171, \eta_p^2 = 0.10$).

(Fig7).

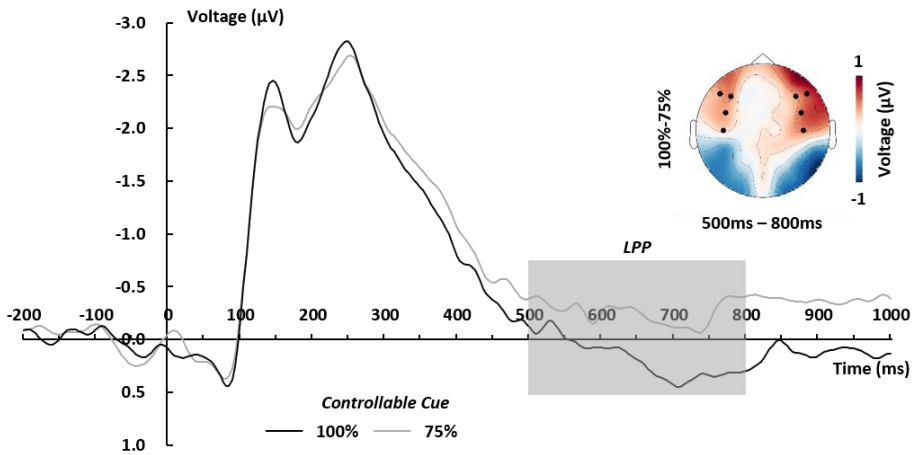


Fig. 7. Grand-averaged ERP waveforms of frontal-center LPP under the 100% and 75% controllable cue conditions. Waveforms were calculated by averaging the data at the electrodes FC5, FC6, F5, F6, F7, F8, C5, and C6. The 100% controllable cue condition minus 75% controllable cue condition topographic map was calculated by averaging the data within a time window of 500 to 800ms after the onset of the static avatar. The black dots are highlighted electrodes which were used to calculate grand-averaged ERPs.

2.4.4 Time-frequency results

The main effect of avatar emotion on frontocentral theta power was significant ($F(1, 25) = 7.87, p = .010, \eta_p^2 = 0.24$): theta power under the angry avatar condition (159.48 ± 20.68) was increased compared to neutral avatar condition (140.24 ± 20.85). The main effect of controllable cue ($F(4, 100) = 0.84, p = .501, \eta_p^2 = 0.03$) and the interaction of the two factors were not significant ($F(4, 100) = 0.74, p = .544, \eta_p^2 = 0.03$) (Fig8).

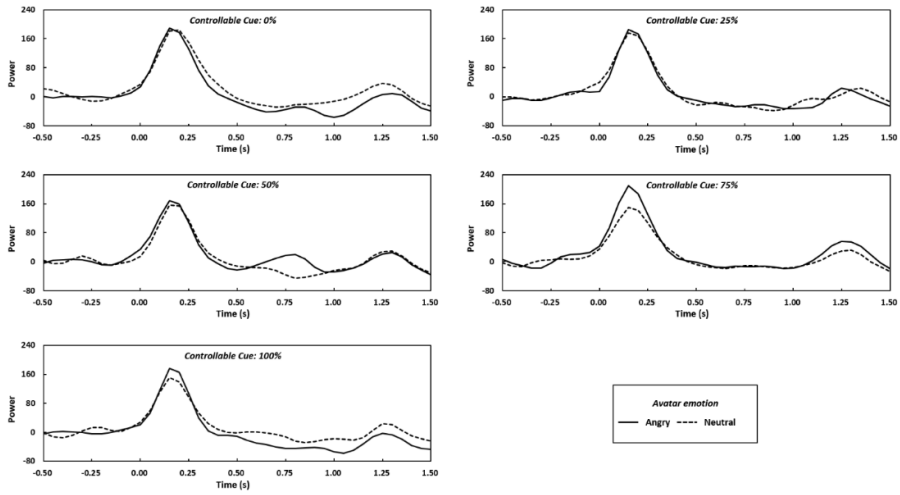


Fig. 8. Theta power was calculated by averaging the theta band (4-7Hz) at the electrodes Fz, FCz, Cz, F1, F2, FC1, FC2, C1, and C2 per condition.

2.4.5 ECG results

Avatar emotion had a significant main effect on ECG ($F(1, 24) = 7.482$, $p = .012$, $\eta_p^2 = 0.24$) such that the angry avatar elicited a higher heart rate (77.84 ± 2.49 beats per minute, BPM) than the neutral avatar (77.55 ± 2.45 BPM) did. The main effect of controllable cue ($F(4, 96) = 1.24$, $p = .301$, $\eta_p^2 = 0.05$) and the interaction of the two factors were not significant ($F(4, 96) = 0.45$, $p = .744$, $\eta_p^2 = 0.02$) (Fig9).

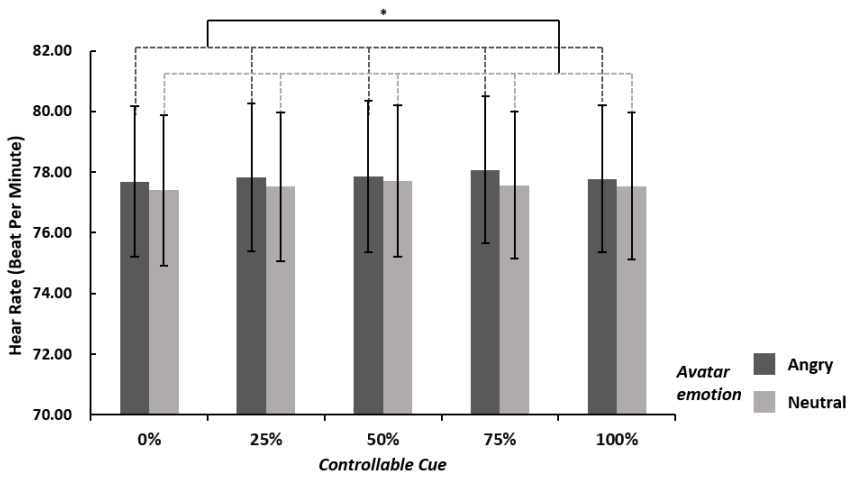


Fig. 9. Means and SE of heart rate per condition. $*p < .05$

2.5 Discussion

In this study, we investigated the behavioral, EEG, and cardiac responses of human participants that were facing angry and neutral avatars in a VR environment in which they had control various degrees of control over the interaction with the avatar. Behaviorally, we observed a difference in the time/distance at which participants felt uncomfortable with the approaching avatar depending on the presence of threat. This is in line with the literature showing that threat imminence triggers defensive behavior (Blanchard & Blanchard, 1990; de Haan et al., 2016; Qi et al., 2018; Riem et al., 2019; Terburg et al., 2018). The impact of personal distance for social threat experience was first shown with full body expression of avatars in a study using VR and fMRI (de Borst et al., 2020). Combining VR with EEG in the present study now allows a detailed picture of the time courses. The questionnaire results also suggested that participants felt more

threatened when facing an angry than a neutral avatar. Concerning the impact of controllability, we found a significant effect of the controllable cue condition for each of the two behavioral indicators. First, as the probability of successful control increased, the distance from the avatar that participants judged tolerable decreased. This result is supported by a previous behavioral study (Iachini et al., 2016). Second, we observed that as the probability of successful control decreased, the number of button presses increased. This is consistent with the notion that the closer a threatening stimulus is to the self, the more likely the danger and the stronger the elicited defensive responses (Bufacchi, 2017). In our experiment, the button press was regarded as a defensive behavior. As the chances of successfully stopping the approaching avatar became higher, the number of button presses (defensive behavior) decreased.

At the neural level, we have three major findings. Seeing a threatening body expression (angry avatar) increased the amplitude of early ERP components (N170 and VPP) compared to non-threatening body expressions (neutral avatar). Furthermore, threatening body expressions elicited a smaller N3 than neutral body expressions. Finally, full control (100% controllable cue) increased the amplitude of the late component LPP as compared to the 75% controllable cue. Taken together, we show that social threat is detected in the early stages and independently of the possibility of control. In contrast, the impact of perceived control over the threat is reflected in the electrophysiological responses at later stages.

Early threat detection. Our results indicate that participants were more sensitive to affective stimuli than neutral ones in the early stages of full body avatar processing. There are consistent but relatively few findings on body perception, a situation reflecting that whole body perception is still much less studied than face perception. Previous

studies have reported that not only facial expressions but also whole body images trigger this early brain activity (Farzmahdi et al., 2021; Meeren et al., 2005; Stekelenburg & de Gelder, 2004; Van Heijnsbergen et al., 2007) and that the activity in this time window is sensitive to the emotional expression as shown by larger VPP amplitudes for a fearful than a neutral body (Stekelenburg & de Gelder, 2004). Also, consistent with our results, N170 and VPP seem to derive from a common source in the brain (Joyce & Rossion, 2005). An interesting finding consistent with the present results is that presenting a target stimulus preceding the body stimulus did not influence the N170 amplitudes to the body stimulus (Hietanen et al., 2014), indicating that body expression perception is an automatic stimulus driven process. Here we add to this by showing that clear knowledge of subjective control of the threat does not impact the course of early body expression perception. This result suggests that we are observing here the early stages of threat perception, that are then followed by calculations of alternative escape decisions (Qi et al., 2018). Given this interpretation of the processes associated with N170, it is worth stressing that our results were obtained in a VR setting which is characterized by an immersive experience of realism but also at the same time, a subjective understanding that the experience is not real, in our case that the participant is not really threatened. An alternative outcome might have been that participants knowledge of the danger being 'unreal' would have overruled this early signature of threat experience.

Temporal dynamics of behavioral control. The middle-late component N3 is related to source allocation and response preparation. A lower amplitude of the N3 component is thought to reflect that more cognitive resources and brain resources are being mobilized to prepare for a response to the threat (Coenen, 1995; Ke et al., 2022; Mayer et al., 2021). E.g., higher cognitive tasks have been shown to elicit lower N3

amplitudes than simpler tasks (Michida et al., 1998). Moreover, negative emotional visual stimuli have been observed to evoke lower N3 than positive emotional ones (Ke et al., 2022). In our experiment, we found threatening body expressions to elicit lower N3 than neutral body expressions, suggesting that the threatening stimuli elicited negative emotions and required more cognitive resources than the neutral stimuli.

Concerning the late positive potential (LPP), previous studies reported that LPP refers to task-relevant, motivational engagement and action preparation during the later stage (Di Lemma et al., 2020; Gable et al., 2015; Gantiva et al., 2020). Johnen and Harrison found that LPP amplitude was larger under conditions of certainty compared to less certain conditions (Johnen & Harrison, 2020). In line with this study, we found that perfect control (100% controllable cue) elicited larger LPP than the 75% controllable cue. This suggests that perfect control opportunity resulted in more motivation engagement than 75% control success.

We also examined oscillatory brain responses in relation to differences in successful control probability for threatening and neutral body expression. Our data show that theta power in frontal central regions was only modulated by avatar emotion. There was a significant increase in response to the threatening body expression (angry avatar) compared with the neutral body expression (neutral avatar). This is consistent with findings showing that increased theta power is related to higher emotional arousal (Aftanas et al., 2001; Aftanas et al., 2002; Sulpizio et al., 2021) and that greater theta power may be induced by social threat compared with non-threat stimuli (Diao et al., 2017).

Our ECG results are consistent with the literature showing a higher heart rate for social threat than for non-threat (Eisenbarth et al., 2016; Weeks & Zoccola, 2015), although another study found a lower

heart rate for threatening vs neutral body expressions (Mello et al., 2022). In that study, participants passively viewed a threatening avatar coming closer, which induced the freezing response reflected in a reduced heart rate. In our paradigm, participants could actively stop the approaching avatar from coming closer by pressing the button. Thus, the increased heart rate might reflect emotional arousal to the threatening body expression rather than a freezing response.

In conclusion, the amplitudes of the earlier components (N170/VPP/N3) are elicited by viewing a threatening body expression and seem to be independent of control opportunities, while the latter modulate the later LPP component. Our findings on N170/VPP effects show that these two components may be modulated by threatening/neutral body expressions, which may reflect mechanisms involved in rapid detection of social threat in an early-middle stage, such as decoding the meaning of a threatening body expression. The social threat is further processed in later stages, as indicated by the effects of avatar emotion on the middle-late cognitive components N3. The ability to control the threat shows in the late cognitive evaluation stages, as reflected by the LPP effects. In addition, the increased frontal central theta power and heart rate are related to social threat processing. In sum, our study provides behavioral and neural insights into how humans process social threat under varying levels of control. On the methodological side, our study presents a novel VR-EEG-ECG setup that will be useful also for future VR and EEG studies investigating social interaction situations in a naturalistic fashion.

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Chapter 3

Behavioral and neural evidence for perceptual predictions in social interactions

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3.1 Abstract

The ability to predict others' behavior is crucial for social interactions. The goal of the present study was to test whether predictions are derived during observation of social interactions and whether these predictions influence how the whole-body emotional expressions of the agents are perceived. Using a novel paradigm, we induced social predictions in participants by presenting them with a short video of a social interaction in which a person approached another person and greeted him by touching the shoulder in either a neutral or an aggressive fashion. The video was followed by a still image showing a later stage in the interaction and we measured participants' behavioral and neural responses to the still image, which was either congruent or incongruent with the emotional valence of the touching. We varied the strength of the induced predictions by parametrically reducing the saliency of emotional cues in the video.

Behaviorally, we found that reducing the emotional cues in the video led to a significant decrease in participants' ability to correctly judge the appropriateness of the emotional reaction in the image. At the neural level, EEG recordings revealed that observing an angry reaction elicited significantly larger N170 amplitudes than observing a neutral reaction. This emotion effect was only found in the high prediction condition (where the context in the preceding video was intact and clear), not in the mid and low prediction conditions. We further found that incongruent conditions elicited larger N300 amplitudes than congruent conditions only for the neutral images. Our findings provide evidence that viewing the initial stages of social interactions triggers predictions about their outcome in early cortical processing stages.

3.2 Introduction

Primates live in complex social networks that are built and maintained by interactions between the members. The primate brain is fine-tuned to perceive nonverbal communication signals from conspecifics. In the domain of vision, social signals are predominantly provided by movements of the face and the body, whether these are displayed by single agents or in interactions. The pioneering research by Heider and Simmel (Heider & Simmel, 1944) demonstrated that humans discern intricate details about others' interactions based on simple movement cues. In the last two decades, cognitive and affective neuroscientists have started exploring the brain basis of the competences required to engage actively in social interactions and to understand the meaning of observed social interactions (Poyo Solanas & de Gelder, 2025). The centrality of social interaction is underscored by findings showing that an individual's expressive postures are judged differently depending on whether they are viewed as part of an interaction with another individual. Using well-controlled computer animations, Christensen et al (2024) showed that the emotional expression of an individual agent is perceived differently when the agent is shown in isolation vs. as part of a social interaction (Christensen et al., 2024). Another behavioral study found that emotions were perceived differently in a social interaction context in which two agents interacted vs. did not interact (Abramson et al., 2021). Participants were instructed to categorize the target agent's emotions (either fear or anger), with the other agent serving as contextual cues. It was found that recognizing fear was easier when participants interacted with an angry emotion compared to a fearful emotion. This effect was observed when participants viewed body or body-face compound stimuli, but not when they viewed faces alone. These studies indicate that body gestures and movements play an important role in emotion perception during social interaction.

Research on the neural basis of affective signals from whole-body postures and movements is still a relatively underexplored field (de Gelder, 2006; de Gelder & Solanas, 2021). Functional magnetic resonance imaging (fMRI) and electroencephalography (EEG) studies have shown that the brain is fine-tuned to details of whole-body postures and movements. Furthermore, observers are not passively registering the visual input from whole-body expressions, but the brain is actively preparing for an adaptive response, such as when a defensive reaction is called for (de Gelder et al., 2004). Importantly, for many familiar actions, once the goals of the action are understood, the end stages can be successfully predicted, as shown in studies comparing basketball novices vs. experts. The latter needed less information to accurately predict where a ball was going to land (Abreu et al., 2012; Özkan et al., 2019). This ability to predict the outcome of an ongoing action is especially relevant when we observe two agents in the course of a social interaction (McMahon & Isik, 2023). One study used short video clips of real-life interactions between dyads and asked participants to predict the outcome of the observed social interaction (Epperlein et al., 2022). They found that participants predicted the outcome of a social interaction less accurately in an aggressive context compared to a playful or neutral context, indicating that predictions depend on the emotional information available during observations of social interactions.

A few studies have examined how prediction operates in the course of neural processing of emotional stimuli (Baker et al., 2023; Vogel et al., 2015). For example, Baker et al. (2023) found that N170 and N300 responses to face stimuli are sensitive to emotion-prediction errors, showing stronger responses to unpredictable facial emotional expressions than predictable ones. Similarly, Vogel et al. (2015) found that the mismatch negativity (MMN), a mid-latency event-related

potential (ERP) component thought to reflect regularity violations, is sensitive to prediction errors based on facial emotional expressions. Their study showed that incongruent emotional faces (e.g., a neutral face followed by a fearful face) elicited larger MMN amplitudes compared to congruent faces (e.g., a neutral face followed by another neutral face). Another ERP study found that perceiving two consecutive emotional expressions elicits a stronger N400 response when the two expressions are incongruent rather than congruent (Calbi et al., 2017). This effect was observed regardless of whether the expression was conveyed by still images of the face or the body, and it might hint at a prediction error response.

Other studies have focused on the N170, as it is linked to the processing of not only faces but also bodies (Baker et al., 2023; Calbi et al., 2017; He et al., 2018; Stekelenburg & de Gelder, 2004; Van Heijnsbergen et al., 2007). Some studies have found effects of emotional expression on the body-evoked N170 (Lu et al., 2023), while others have not (Stekelenburg & de Gelder, 2004; Van Heijnsbergen et al., 2007). Given the previous observation of an emotion-prediction effect on the face-evoked N170 (Baker et al., 2023), it is still an open question whether the body-evoked N170 is affected by emotion predictions when observing social interactions. Taken together, the N300 and N400 may serve as neural markers of violations of higher-order visual predictions, whereas the N170 may specifically reflect the visual processing of bodies.

We hypothesized that: 1) Observers of a social interaction derive predictions from their observations about the outcome of the interaction; and 2) These putative social predictions automatically and rapidly influence how the outcome of the ongoing social interaction is perceived. We tested our hypotheses with a novel paradigm: Participants watched a short video clip of a social interaction between

two agents, in which agent A approached agent B and touched him on the shoulder, whereupon agent B turned around to face agent A. The videos were stopped before the end and then followed a by a still probe image, which was the final frame of the full clip disclosing agent B's reaction to the interaction. In the perceptual task, participants judged the appropriateness of the agents' reaction from the agent's bodily expression. For the neural measures, we focused on the ERP components N170, N300, and N400, as reviewed above. By presenting the video clip prior to the still probe we could temporally separate the putative prediction effects of the video from its (shorter-lived) sensory effects. To investigate the impact of social prediction on observing social interactions, we varied both the strength and the correctness of the predictions that observers could derive from the clip. Prediction strength was varied across three levels as follows: in the main "high prediction" condition, the video clearly showed how agent A approached and touched agent B. In the "mid prediction" condition, social interaction information was reduced by backward presentation of the video. Finally, in the "low prediction" condition, each video frame was scrambled, effectively removing any social cues from the video and preventing emotion prediction.

Prediction correctness, referred to below as prediction error, was varied by manipulating the emotional congruence between the probe image and the preceding video. This was implemented by preceding each probe condition (image of a neutral or angry reaction; see above) with either a "neutral" video (in which agent A gently touched agent B's shoulder) or an "angry" video (in which agent A abruptly pulled agent B's shoulder). The incongruent condition was designed to trigger prediction errors in participants.

We expected that: 1) If observers of a social interaction derive predictions from it about its outcome, our participants should show

more accurate responses in the perceptual task when the preceding clip allows for stronger predictions. 2) If these social predictions influence the processing of the ongoing social interaction, our participants should show neural changes in response to the probe. Specifically, body-related responses (N170) and prediction-related responses (N300 and N400) should reflect variations in prediction strength and prediction errors.

3.3 Methods

3.3.1 Participants

Thirty healthy participants were recruited from the student population at Maastricht University. Two participants' data were rejected because one participant did not follow the task instructions and another participant's ERPs data (N170, N300 and N400) exceeded 3 standard deviations (SD) above the mean. Twenty-eight participants' data were included in the analysis (aged 19-34 years, 24.0 ± 4.9 (mean \pm SD); 15 male and 14 female; one left-handed). All participants had normal or corrected-to-normal vision, and no history of brain injury, psychiatric disorders, or current use of psychotropic medication. Before the experiment, participants provided written consent. They received compensation of 7.5 Euros or one study credit point for their participation. The Ethics Committee of Maastricht University approved the study, and all procedures adhered to the principles outlined in the Declaration of Helsinki (approval number: OZL_263_16_02_2023).

3.3.2 Stimuli

The stimuli consisted of video clips of social interactions and still images extracted from the end section of the videos. The videos showed

a person on the right (agent A) approaching a person on the left (agent B). At the onset, agent B had his/her back turned away from agent A. Agent A approached and touched agent B on the shoulder whereupon agent B reacted to this by turning around toward agent A.

The video recordings were made with ten actors (six females and four males) who were combined to create five gender-matched pairs. For each actor pair, five “angry” social interactions and five “neutral” social interactions were recorded, resulting in ten videos per pair (50 videos in total). The still images were created by taking the last frame of the video. These images served as the probes for the participants’ task, which was to rate whether the reaction of agent B (to the touch by agent A) was appropriate. The images and videos were processed using Adobe Premiere Pro and all faces were blurred. Videos and still images were presented on a black background (size: 1150×1088 pixels), covering approximately 15×13 degrees of the participants’ visual angle in the experiment. To ensure that participants focused on the interaction between the two actors, they were instructed to fixate a white fixation cross placed at the center of the screen, located between the two actors. The videos are available in the supplementary materials.

3.3.3 Experimental design and procedure

Each trial started with a 1000-ms fixation period, followed by the presentation of the video. After a short gap (400-500ms) during which the screen was blank, the probe image was presented for 1000ms revealing agent B’s reaction. Subsequently, participants were instructed to answer the following question, which was shown on the screen: “Does the reaction of the person on the left match the action of the person on the right?”. Participants chose one of two response

alternatives (“I guess yes” and “I guess no”) during this response interval, which lasted 2000ms (Fig 1A).

An example of the probe image in the two *emotion reaction* conditions (angry reaction or neutral reaction) is shown in Figure 1C. The different *prediction strength* conditions are illustrated in Figure 1D. This manipulation was implemented by playing the video either normally (high prediction), or as time-reversed or scrambled versions. In the backwards videos (mid prediction), the visibility of the actors’ movements was preserved, while the interpretation of the social action was hampered. In other words, the clip began with agent A already touching agent B’s shoulder, then releasing the hand, and finally walking away backwards (from left to right). In the scrambled videos (low prediction), each frame was masked with Gaussian masks so that both movement and social action information were largely reduced (Figure 1D).

The manipulation of *prediction error* was implemented by pairing each video clip with either its original last frame (*congruent* condition: angry video followed by angry image, or neutral video followed by neutral image) or the last frame of the clip in which the same actors exhibited the other emotion (*incongruent* condition: angry video followed by neutral image, or neutral video followed by angry image). Example frames from the neutral and angry videos are shown in Figure 1C. Participants’ “Yes” responses on congruent trials and “No” responses on incongruent trials were considered as correct, whereas “No” responses on congruent trials and “Yes” responses on incongruent trials were considered as incorrect.

The study used a fully balanced $2 \times 3 \times 2$ within-subject design. As described above, the first factor was *emotion reaction* (angry or neutral), the second factor was *prediction strength* (high, mid, or low),

and the third factor was *prediction error* (emotional valence of image and video: congruent or incongruent). Each of the twelve conditions was presented in 25 unique trials, resulting in a total of 300 trials that were randomly presented in 4 runs, each lasting 7 minutes. Participants took a short break after the first two runs. Before the experiment, participants practiced the task on 24 trials. The whole experiment lasted around 28-35 minutes.



Fig. 1 A-D. Experimental design. (A) Trial procedure. Participants watched a social interaction video followed by a still probe image. At

the end of each trial, participants responded to the question on the screen by pressing one of two buttons (yes/no). ERP analysis was time-locked to the still image, see red rectangle. (B) Experimental design matrix. The study used a $2 \times 3 \times 2$ within-subject design with factors *emotion reaction* (angry, neutral), *prediction strength* (high, mid, low), and *prediction error* (congruent, incongruent). (C) Examples of *emotional reaction* that are included in the matrix of *prediction error*. The left column of figures shows the middle frame of the "angry" video and the "neutral" video. The right column of figures shows the *emotional reaction*: the "angry" reaction and the "neutral" reaction. The solid arrows indicate congruent conditions: an angry reaction preceded by an angry video or a neutral reaction preceded by a neutral video. The dashed arrows indicate incongruent conditions: an angry reaction preceded by a neutral video or a neutral reaction preceded by an angry video. (D) Examples of prediction strength in the video, showing the first frame of high, mid and low conditions.

3.3.4 EEG acquisition

EEG data were recorded using an elastic cap with 64 electrodes placed according to the international 10-20 system and sampled at a rate of 1000Hz (BrainVison Products, Munich, Germany). Electrode Cz was used as the reference during recording and the forehead electrode (Fp1) was used as a ground electrode. Four electrodes were used to measure the electrooculogram (EOG). Two of them were used as vertical electrooculograms (VEOG). One was placed above the right eye, and another was placed below the right eye. The other two electrodes were used as a horizontal electrooculogram (HEOG), with one placed at the outer canthus of the left eye, and the other at the outer canthus of the right eye. The remaining 60 electrodes included FPz, AFz, Fz, FCz, CPz, Pz, POz, Oz, AF7, AF8, AF3, AF4, F7, F8, F5, F6, F3, F4, F1, F2, FC5, FC6, FC3, FC4, FC1, FC2, T7, T8, C5, C6, C3, C4, C1, C2, TP9, TP10,

TP7, TP8, TP9, TP10, CP5, CP6, CP3, CP4, CP1, CP2, P7, P8, P5, P6, P3, P4, P1, P2, PO7, PO8, PO3, PO4, O1, and O2. Impedances for reference and ground were maintained below 5kOhm and for all other electrodes below 10kOhm.

3.3.5 EEG data preprocessing

EEG data were preprocessed and analyzed using FieldTrip version 20220104 (Oostenveld et al., 2011) in Matlab R2021b (MathWorks, U.S.). Recordings were first segmented into epochs from 500ms pre-stimulus (i.e., before the onset of the probe image) to 1500ms post-stimulus and then filtered with a 0.3-30 Hz band-pass filter. EEG data at each electrode were re-referenced to the average of all electrodes. Artifact rejection was done using independent component analysis (logistic infomax ICA algorithm (Bell & Sejnowski, 1995)); on average, 2.97 ± 1.08 (mean \pm SD) components were visually identified as artifacts and removed per participant. Moreover, single epochs during which the EEG peak amplitude exceeded 3 SD above/below the mean amplitude were rejected. On average, $71.04\% \pm 9.14\%$ of trials were preserved and statistically analyzed per participant.

3.3.6 Event-related potential analyses

The EEG analysis focused on neural responses to the probe (reaction) image. Baseline correction was applied and involved subtracting the average amplitude in the baseline interval (-200 to 0ms) from the overall epoch. Trials were averaged for each experimental condition, resulting in ERPs used for further statistical analyses, which were performed using IBM SPSS Statistics 27 (IBM Corp., Armonk, NY, USA). We spatially separated the EEG electrodes into a temporal cluster (P7, P8, TP7, TP8, TP9, TP10) and central cluster (FCz, FC1, FC2, Cz, C1, C2, CPz, CP1, CP2), and averaged the channels within

each cluster. For each cluster, we pooled all conditions and visually identified a prominent ERP component based on visual inspection of the overall ERP waveform, topographical distribution of grand-averaged ERP, and previous studies (Chen et al., 2022; Hietanen et al., 2014). The identified ERP components and their associated time windows were as follows: N170 (180-230ms) in the temporal cluster, N300 (250-350ms) in the central cluster, and N400 (350-500ms) in the central cluster. The mean amplitude was computed as the average of all electrodes within each cluster for the specific time window.

A repeated-measures $2 \times 3 \times 2$ ANOVA (*Emotion reaction*: angry/neutral; *Prediction strength*: high/mid/low; *Prediction error*: congruent/incongruent) was applied to the mean amplitudes; this was done for each ERP component separately. Degrees of freedom for F-ratios were corrected with the Greenhouse–Geisser method. Bonferroni’s method was used to correct for multiple comparisons. Statistical results were considered as significant given a p-value < 0.05 .

3.4 Results

3.4.1 Behavior

To verify whether our manipulation of the video induced variations in participants’ predictions, we examined the effects of prediction strength (high, mid and low) and prediction error (congruent and incongruent) on response accuracy (proportion of correct responses), pooled across *emotion reaction*. We found that the main effect of prediction strength was significant ($F(2, 54) = 49.23, p < 0.001, \eta_p^2 = 0.65$) (high vs. mid: $t(27) = 6.91, p < 0.001$; high vs. low: $t(27) = 8.89, p < 0.001$; mid vs. low: $t(27) = 4.85, p < 0.001$). Accuracy was highest for the high

prediction condition (0.77 ± 0.15), followed by the mid prediction condition (0.68 ± 0.15), and lowest for the low prediction condition (0.54 ± 0.06). These findings indicate that our manipulation of contextual information was effective: reducing the amount of information in the preceding video led to a decrease in prediction accuracy. We found that the main effect of prediction error was not significant ($F(1, 27) = 0.39, p = 0.536, \eta_p^2 = 0.01$), suggesting that task difficulty did not differ significantly between congruent (0.68 ± 0.14) and incongruent (0.65 ± 0.16) conditions.

To test whether participants' choices/accuracy were above chance level, we conducted a one-sample t-test comparing participants' accuracy in each prediction strength (high/mid/low) and prediction error (congruent/incongruent) condition vs. 0.5. The accuracy in all conditions was significantly above chance level ($ps < 0.002$).

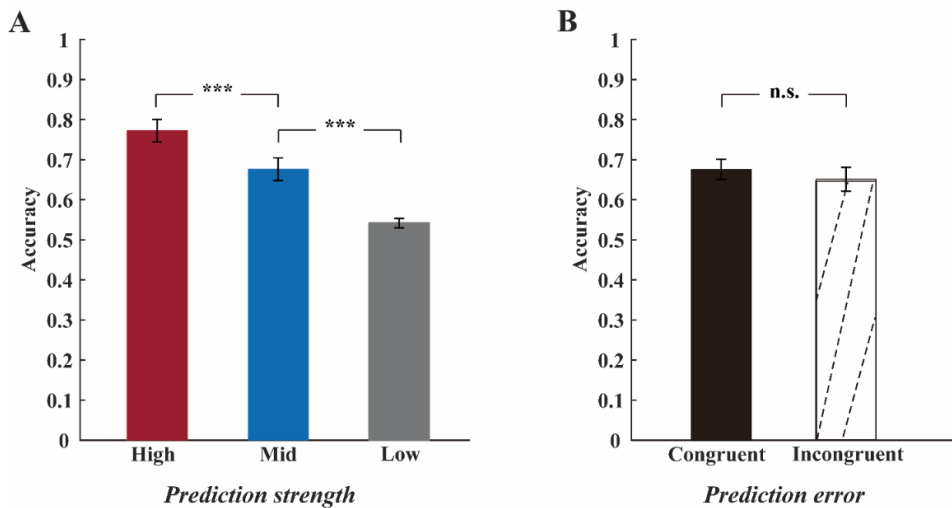


Fig. 2. (A) Means and standard error (SE across participants) of accuracy per prediction strength condition (high, mid and low). (B) Means and SE of accuracy per prediction error condition (congruent and incongruent). ***: $p < 0.001$, n.s.: non-significant.

3.4.2 ERPs

Our hypothesis concerned the effect of emotional valence (*emotion reaction*) and its modulation by contextual factors (*prediction strength* and *prediction error*). Before testing for a main effect of *emotion reaction* and its interaction with *prediction strength* and *prediction error*, we assessed the three-way interaction (*emotion reaction* \times *prediction strength* \times *prediction error*). This was found to be non-significant for each ERP component (N170: $F(2, 54) = 2.44, p = 0.097, \eta_p^2 = 0.08$; N300: $F(2, 54) = 0.56, p = 0.573, \eta_p^2 = 0.02$; N400: $F(2, 54) = 0.83, p = 0.443, \eta_p^2 = 0.03$). Next we analyzed the two-way interactions, which revealed a significant *emotion reaction* \times *prediction strength* interaction for N170 ($F(2, 54) = 3.48, p = 0.040, \eta_p^2 = 0.11$), but not the other ERP components (N300: $F(2, 54) = 0.92, p = 0.40, \eta_p^2 = 0.03$; N400: $F(2, 54) = 0.18, p = 0.83, \eta_p^2 = 0.01$), and a significant *emotion reaction* \times *prediction error* interaction for N300 ($F(1, 27) = 6.47, p = 0.017, \eta_p^2 = 0.19$), but not the other ERP components (N170: ($F(1, 27) = 0.05, p = 0.829, \eta_p^2 = 0.00$), N400: ($F(1, 27) = 0.11, p = 0.745, \eta_p^2 = 0.00$)). These results are in line with our hypothesis. However, unlike hypothesized, we found no significant *prediction strength* \times *prediction error* interaction for any ERP component (N170: $F(2, 54) = 2.05, p = 0.146, \eta_p^2 = 0.07$; N300: $F(2, 54) = 1.32, p = 0.28, \eta_p^2 = 0.05$; N400: $F(2, 54) = 0.83, p = 0.44, \eta_p^2 = 0.03$). In the following sections, we investigated the nature of the observed interactions by testing for simple effects of the interacting factors. We also explored main effects of the factors that showed no significant interactions; these effects were not a focus of the current study and therefore the results are presented in the supplementary data.

Interaction effect of emotion reaction \times prediction strength on N170

To disentangle the observed interaction effect of *emotion reaction* \times *prediction strength* on N170, we analyzed simple effects of *emotion reaction* (i.e., per *prediction strength*), which revealed a significant simple effect of *emotion reaction* for the high prediction condition ($t(27) = -5.18, p < 0.001$) as expected, but not for the mid or low prediction conditions (mid: $t(27) = -1.41, p = 0.507$; low: $t(27) = -1.74, p = 0.277$). More specifically, angry reactions ($-1.45 \pm 2.00 \mu\text{V}$) elicited larger N170 amplitudes than neutral reactions ($-0.52 \pm 1.87 \mu\text{V}$) in line with previous results (Lu et al., 2023), and interestingly, this enhancing effect occurred only when the images were preceded by a fully intact video (high prediction condition).

We further observed a significant simple effect of *prediction strength* for the angry reaction. Both high and mid prediction were followed by larger N170 amplitudes than low prediction when the following reaction in the probe image was angry; the difference between high and mid prediction was not significant (Angry reaction: high vs. low: $t(27) = -4.51, p < 0.001$; mid vs. lows: $t(27) = -2.62, p = 0.014$; high vs. mid: $t(27) = -2.20, p = 0.109$). Interestingly, this simple effect of prediction strength was found only for the angry reaction, not for the neutral reaction (Neutral reaction: high vs. low: $t(27) = -1.76, p = 0.272$; mid vs. low: $t(27) = -1.88, p = 0.214$; high vs. mid: $t(27) = 0.59, p = 1.000$).

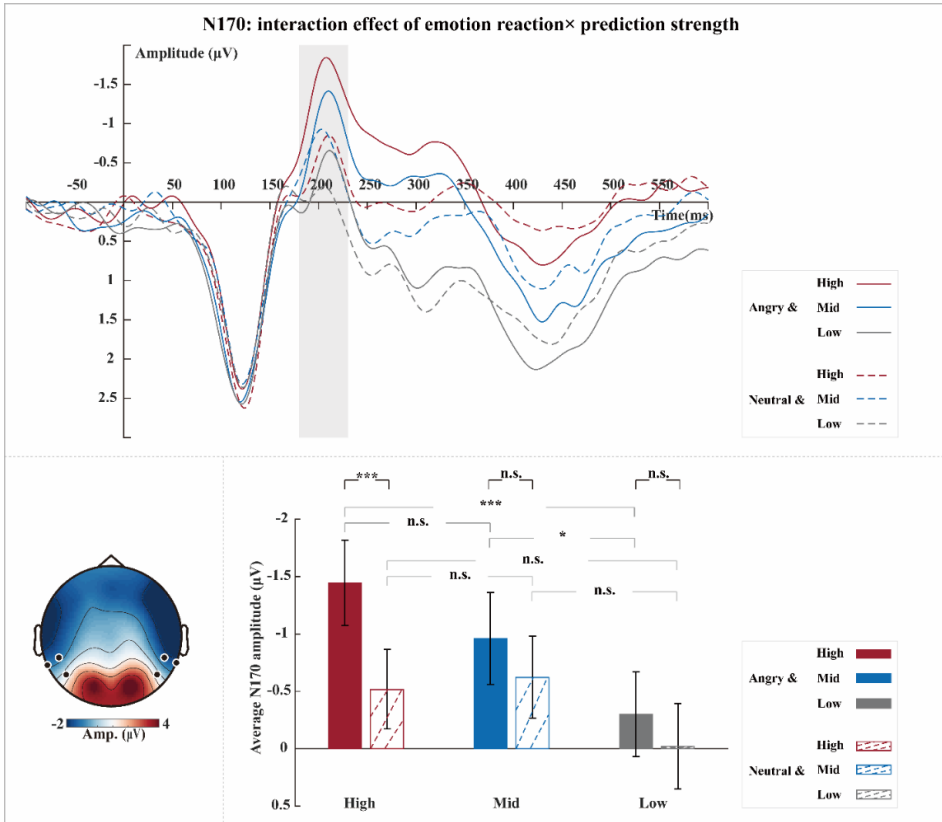


Fig. 3. Interaction effect of *emotion reaction* × *prediction strength* on N170. Grand-averaged ERP waveforms of N170 per condition (angry-high, neutral-high, angry-mid, neutral-mid, angry-low, and neutral-low) (top). Waveforms were calculated by averaging the data at the electrodes P7, P8, TP7, TP8, TP9, and TP10 (see black dots in scalp map). The shaded rectangle visualizes the time window from which the average ERP amplitude was extracted (180-230ms). The topographic map was calculated by averaging the data of all conditions within a time window of 180-230ms after the onset of the probe image (bottom left). Bar plots (bottom right) illustrate the mean and SE across participants of the average N170 amplitude per condition. ***: $p < 0.001$, *: $p < 0.05$, n.s.: non-significant.

Interaction effect of emotion reaction and prediction error on N300

Further investigation of the observed interaction effect of *emotion reaction* \times *prediction error* on N300 revealed a significant simple effect of *prediction error* for the neutral reaction ($t(27) = 3.87, p = 0.001$) as expected, but somewhat surprisingly not for the angry reaction ($t(27) = -0.08, p = 1.000$). More specifically, compared with neutral videos ($-0.60 \pm 1.38 \mu\text{V}$), angry videos ($-1.04 \pm 1.44 \mu\text{V}$) resulted in the subsequent neutral reaction eliciting larger N300 amplitudes.

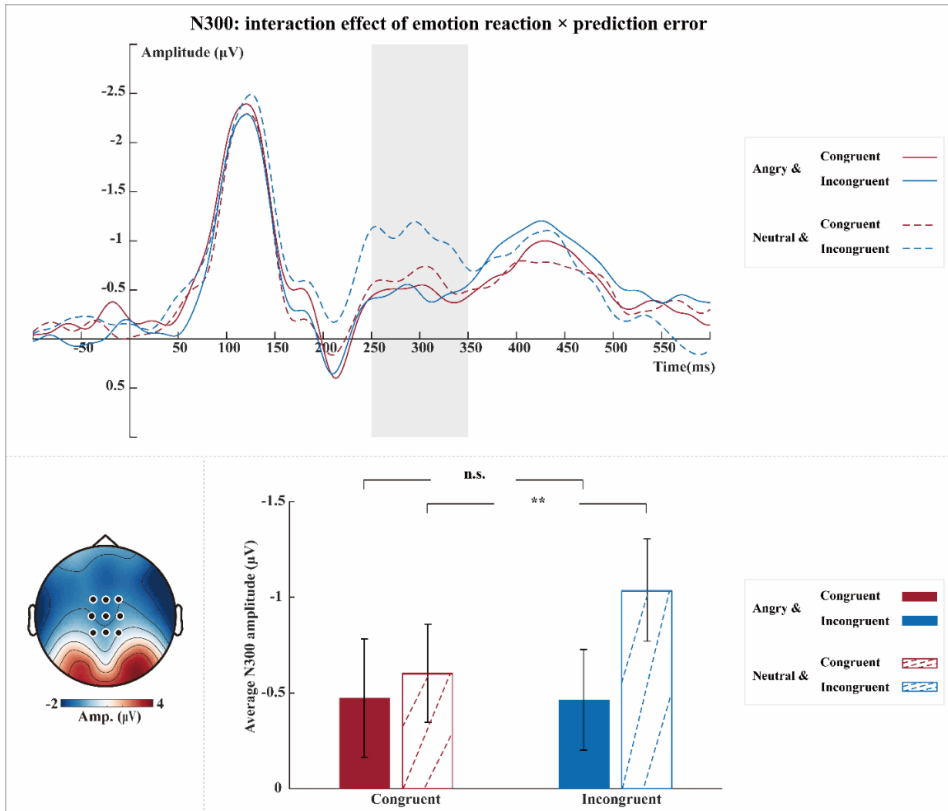


Fig. 4. Interaction effect of *emotion reaction* \times *prediction error* on N300. Grand-averaged ERP waveforms of N300 per condition (angry-congruent, neutral-congruent, angry-incongruent, and neutral-incongruent) (top). Waveforms were calculated by averaging the data at electrodes FCz, FC1, FC2, Cz, C1, C2, CPz, CP1, and CP2 (see black dots in scalp map). The shaded rectangle visualizes the time window from which the average ERP amplitude was extracted (250-350ms). The topographic map was calculated by averaging the data of all conditions within a time window of 250-350ms after the onset of the probe image (bottom left). Bar plots (bottom right) illustrate the mean and standard SE across participants of the average N300 amplitude per condition. ***: $p < 0.001$, **: $p < 0.01$, n.s.: non-significant.

3.5 Discussion

The goals of the present study were to test first, whether observers of a social interaction derive predictions about its outcome and second, whether these predictions influence how information about the outcome is processed? Our study used a novel paradigm that measures the impact of viewing the initial stages of a social interaction on how the final stages are processed. This involved manipulation of the prediction context in two different ways, by manipulating prediction strength and prediction error.

At the behavioral level, the accuracy of appropriateness judgments was highest in the high prediction condition, followed by the mid prediction condition, and lowest in the low prediction condition. Thus, our behavioral results show that participants were able to successfully judge the appropriateness of the emotional reaction (the still probe image) when the preceding video provided clear social cues

(high prediction condition). Performance gradually diminished to guessing behavior when the context provided fewer emotional cues (mid and low prediction conditions). These results confirm our hypothesis that observing social interactions may lead to predictions about the outcome. At the neural level, observing an angry reaction elicited significantly larger N170 amplitudes than observing a neutral reaction. This emotion effect was only found in the high prediction condition (where the context in the preceding video was intact and clear), not in the mid and low prediction conditions. Moreover, we found that the high prediction condition elicited larger N170 amplitudes than the mid and low prediction conditions. This prediction effect was found only in response to angry reactions. Additionally, observing social interactions can trigger prediction error effects. We found that incongruent conditions elicited larger N300 amplitudes than congruent conditions. This prediction error effect was found only in neutral reactions, not in angry reactions. Our results confirm our hypothesis that social predictions may influence the perceptual and neural processing of social interactions.

Emotion effect on the early component N170 depends on prediction strength

Our first neural finding was that observing social interactions containing dyadic bodies evoked a clear N170 response. Previous studies have shown that the N170 is a marker of visual body processing (Borhani et al., 2015; de Gelder et al., 2004; Lu et al., 2023; Meeren et al., 2005; Stekelenburg & de Gelder, 2004). Here, we extend these previous findings by showing that the N170 is sensitive not only to a single body but also to body expressions in interactions involving two agents. Hence, our results are consistent with findings about the

primacy of social interactions (Abassi & Papeo, 2020). Concerning the sensitivity of the N170, we further observed that the N170 is stronger for angry compared to neutral expressions. This is consistent with our recent finding (Lu et al., 2023) and, more importantly, extends previously observed emotional expression effects from single images and single-body expressions to social interaction situations.

Our main finding here is that the emotional expression effects during observation of interactions are only seen in the high prediction condition. In other words, neural discrimination between angry and neutral interaction images, as reflected by the N170, was not evident when the preceding social context videos did not allow emotion predictions (mid and low prediction conditions). Moreover, we found that predictions were impacted by emotional context, such that high predictability elicited larger N170 amplitudes than lower predictions for videos of angry body interactions. This result indicates that the N170 is not only sensitive to social predictions triggered by the videos but also to the specific emotional content.

Prediction error effects on the late component N300 depend on emotional whole-body interaction

Next, we found an effect of prediction error on the processing of observed social interactions, as reflected by the N300, in line with our expectations and previous results relating the N300 to higher-order visual prediction errors (Chen et al., 2022). More specifically, enhancements of the N300 have been related to unexpected and violating conditions compared to expected and confirming conditions (Baker et al., 2023; Kumar et al., 2021; Truman & Mudrik, 2018). In line with these studies, we found a prediction error response

(incongruent > congruent) for social interactions. Interestingly, this effect was only significant when the emotional reaction was neutral, indicating that neutral reactions may violate emotion predictions more strongly than angry ones.

These results indicate that the appropriateness of the reaction to an emotional interaction was extracted in the time window of the N300 (or 250-350ms post-stimulus onset) in our study. Unexpectedly, we found no effect of prediction strength on prediction-error responses in the N170 or N300, suggesting that these error responses do not necessarily depend on the availability of social predictions.

3.6 Conclusion

In sum, our results show that observing a social interaction generates perceptual predictions about how the behavior of the agents and these predictions affects cortical processing in the time window of the N170. The strength of this prediction effect measured at the final image is a function of how informative the preceding video is. This signifies that combined emotional expressions of interacting agents can be rapidly detected in early processing stages and that social interaction predictions influence information processing at perceptual and neural levels. Later prediction errors are reflected in the N300 amplitude, and this prediction error processing is most pronounced when observing a neutral bodily reaction. This suggests that later prediction may involve deeper cognitive processing reckoning with the emotional context in social interactions.

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3.8 Supplementary

Main effect of prediction error on N170 and N400

Analysis for main effects revealed a significant effect of *prediction error* (i.e., pooled across *reaction emotion* and *prediction strength*) on N170 and N400. More specifically, the incongruent condition elicited smaller N170 amplitudes and larger N400 amplitudes than the congruent condition (N170: incongruent: $-0.51 \pm 1.76 \mu\text{V}$, congruent: $-0.78 \pm 1.90 \mu\text{V}$, $F(1, 27) = 7.13$, $p = 0.013$, $\eta_p^2 = 0.21$; N400: incongruent: $-0.88 \pm 1.36 \mu\text{V}$, congruent: $-0.71 \pm 1.35 \mu\text{V}$, $F(1, 27) = 5.79$, $p = 0.023$, $\eta_p^2 = 0.18$).

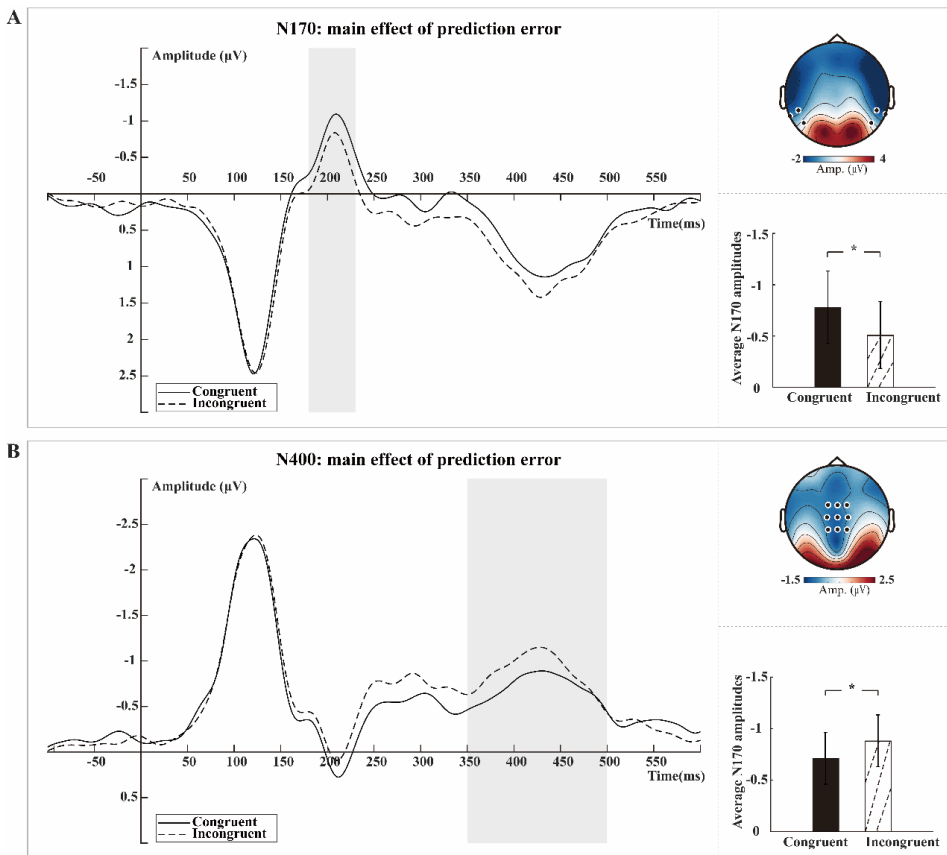


Fig. 5 A-B. Main effect of *prediction error* on N170 and N400. Grand averaged ERPs are depicted per condition (congruent and incongruent) for N170 and N400 components separately (left). The shaded rectangle visualizes the time window (180-230ms for N170, and 350-450ms for N400) from which the average ERP amplitude was extracted. The highlighted black dots on the topographic map (right top) represent the electrodes from which the grand-averaged ERP for each component was extracted across all conditions. Bar plots (right bottom) illustrate the mean and SE across participants of each component's amplitude per condition. *: $p < 0.05$

Main effect of prediction strength on N300 and N400

We further observed a significant main effect of *prediction strength* (i.e., pooled across *reaction emotion* and *prediction error*) on N300 and N400. More specifically, high prediction resulted in subsequent still images eliciting smaller N300 amplitudes and N400 amplitudes, compared with mid and especially low prediction (N300: high: $-0.26 \pm 1.51 \mu\text{V}$, mid: $-0.62 \pm 1.74 \mu\text{V}$, low: $-1.05 \pm 1.33 \mu\text{V}$, $F(1, 27) = 9.54$, $p = 0.001$, $\eta_p^2 = 0.26$; N400: high: $-0.26 \pm 1.51 \mu\text{V}$, mid: $-0.84 \pm 1.53 \mu\text{V}$, low: $-1.12 \pm 1.31 \mu\text{V}$, $F(1, 27) = 10.13$, $p = 0.001$, $\eta_p^2 = 0.27$).

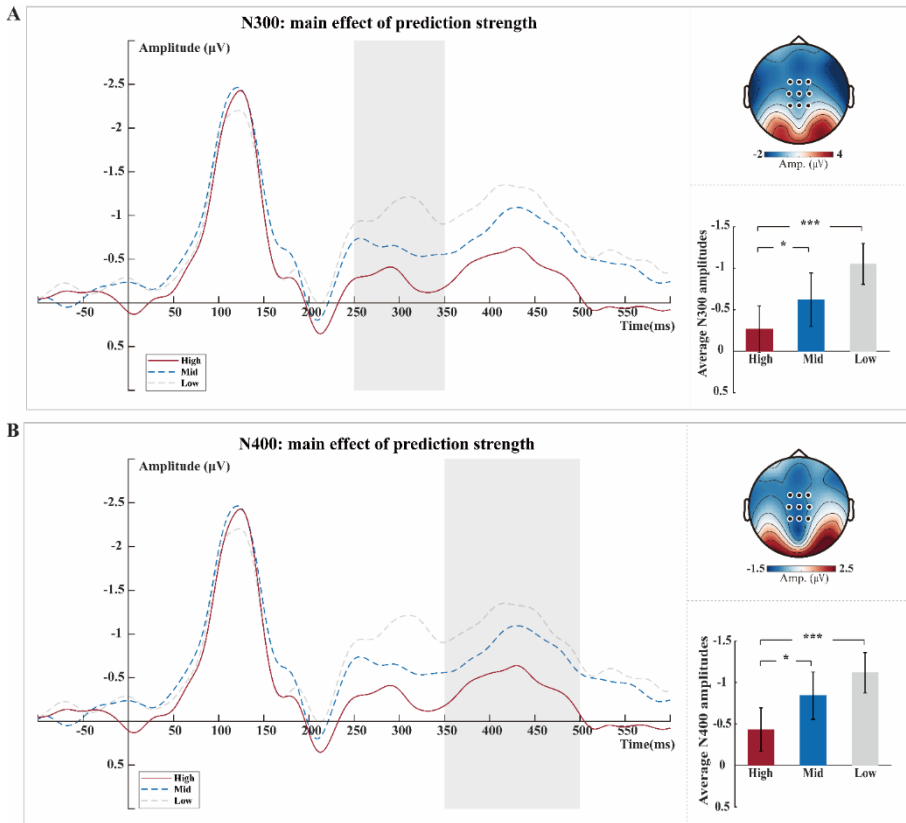


Fig. 6 A-B. Main effect of *prediction strength* on N300 and N400. Grand averaged ERPs are depicted per condition (high, mid and low) for N300 and N400 components separately (left). The shaded rectangle visualizes the time window (250-350ms for N300, and 350-450ms for N400) from which the average ERP amplitude was extracted. The highlighted black dots on the topographic map (right top) represent the electrodes from which the grand-averaged ERP for each component was extracted across all conditions. Bar plots (right bottom) illustrate the mean and SE across participants of each component's amplitude per condition. ***: $p < 0.001$, *: $p < 0.05$

Chapter 4

The contribution of body perception to self-identity. An ERP study

Based on:

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4.1 Abstract

This study used EEG and personalized avatars to investigate the neural mechanisms underlying personal identity perception. Compound avatar images combining participants' own faces and bodies, as well as those of others, were generated from photographs. Participants underwent an embodiment training for each avatar type in a virtual reality (VR) environment, where they controlled the avatar's actions during physical exercise tasks. Subjective assessments by participants confirmed a stronger identification with avatars representing their own identity compared to those representing others. Analysis of event-related potentials (ERPs) revealed that avatars representing the participants' self-identity elicited weaker N2 and P1 responses compared to avatars representing other identities. No significant effects on N170 responses were observed. Control conditions utilizing avatars with modified body characteristics confirmed that the reduction in N2 amplitude was specifically related to identity perception rather than variations in visual body size. These findings suggest that the perception of self-identity occurs rapidly, within approximately 200 milliseconds, indicating the integration of visual face and body information into identity representation at an early stage.

4.2 Introduction

Understanding and processing someone's identity is fundamental to our social interactions. We effortlessly recognize familiar individuals and distinguish between acquaintances and strangers. Furthermore, we have a unique ability to recognize our own physical appearance, often scrutinizing our own facial and bodily features when faced with a mirror. Previous research on self-perception has primarily focused on facial stimuli to investigate the behavioral and neural processes involved in identity perception and recognition (Gonzalez-Franco et al., 2016; Maister et al., 2013; Sui et al., 2009). The significance of self-face recognition has long been debated and recent meta-analyses confirm that individuals identify their own face more quickly than others' faces (Bortolon & Raffard, 2018). Much less is known about self-perception based on the body and the combined perception of the self face and body. The importance of body perception for self-perception is illustrated by clinical studies showing that body perception-based self-awareness can sometimes lead to dissatisfaction with our physical appearance, contributing to conditions like eating disorders and body dissatisfaction, as evidenced by clinical studies (Karazsia et al., 2017). But despite its importance, the neural mechanisms underlying self-body perception remain poorly understood.

EEG studies exploring the neural basis of self-facial identity perception have identified the N2 component, an event-related negativity occurring at ~200ms, to be associated with self-identity and self-relevance (Bola et al., 2021; Muñoz et al., 2020; Woźniak et al., 2018). Woźniak et al. (2018) found that self-associated faces elicit smaller N2 amplitudes than faces associated with others, such as friends or strangers, indicating an early neural process for self-face perception. Consistently, Bola et al. (2021) demonstrated that self-face stimuli, but

not other-face stimuli, elicit the N2pc component within 200ms. Muñoz et al. (2020) found that personal objects elicited lower N2 amplitudes compared to non-personal objects, further supporting the role of the N2 in self-relevance processing. These findings collectively suggest that the attenuation of N2 associated with self-identity from self-relevant stimuli, such as one's own face, occurs rapidly within ~200ms.

To date, only a few studies have delved into the perception of self-identity from bodies or used personalized body images. In a functional magnetic resonance imaging (fMRI) study, researchers utilized full-body photos of participants clad in dark bathing suits and found that photos conveying self-identity triggered responses in the extrastriate, parietal regions, and middle frontal gyrus in the right hemisphere (Hodzic et al., 2009). An event-related potential (ERP) study employed participant photos, presenting naturalistic, enlarged, and reduced body images to investigate the perception of self-body versus other-body under various attention tasks (Uusberg et al., 2018). Their findings indicate that the distinction between self-body and other-body influences the N170 component, renowned for its role in the initial stages of face or body perception (Stekelenburg & de Gelder, 2004). However, our comprehension of the neural dynamics underlying the perception of self and other identities based on body images remains limited.

A related inquiry concerns the relative significance of the face and body. Based on the literature where studies on self-facial identity largely outnumber those on self-body identity, one might assume that face identity drives self-recognition, with the body playing only a minor role. If so, the presence of the personalized body would not make a difference to self-identity perception. However, studies on the perception of emotional expressions have shown that body expression can influence how facial emotion is processed already in the early

processing stages as seen in the EEG on the P1 (Meeren et al., 2005). Thus, it is conceivable that face and body information are integrated in early neural processes to form a self-identity percept.

To test this hypothesis in the current study, we explored the neural basis of self-identity perception using avatars synthesized from personalized face and body images. To enhance the participants' sense of body ownership of the avatar, we devised an embodiment task employing a virtual reality (VR) environment for physical exercise. Participants faced a virtual mirror displaying their avatar and engaged in physical activities (e.g., moving their arms to catch bubbles and reaching for crystals). This VR session aimed to bolster the participants' identification with the avatar and their sense of body ownership. During the experiment proper, participants viewed various categories of avatars and performed an oddball task while EEG was recorded. EEG provides exceptional temporal precision, offering millisecond-level resolution, which is ideal for investigating the temporal dynamics of self-identity processing. Building upon previous findings with personalized face images and body, we anticipated that the perception of self-identity based on avatars with the own face and the own body would modulate N2 and N170 responses compared to perception of other-identity avatars. As previous studies have linked P1 to sensory input such as image size (Busch et al., 2004; Pfabigan et al., 2015), we also included avatars with altered body sizes and analyzed P1 responses, to control for visual image size differences between self and other avatars.

4.3 Methods

4.3.1 Participants

Twenty-nine healthy participants (aged 18-24 years, mean = 19.9; standard deviation (SD) = 1.7; one left-handed) were recruited from the female student population at Maastricht University. All participants had a body mass index within the ideal range (18.5-24.9), normal or corrected-to-normal vision, and no history of brain injury, psychiatric disorders, or current use of psychotropic medication. Before the experiment, participants provided written consent. They received compensation of 7.5 Euros or one credit point per hour for their participation. The Ethics Committee of Maastricht University approved the study, and all procedures adhered to the principles outlined in the Declaration of Helsinki.

4.3.2 Experimental design and stimuli

Personalized avatars for each participant were created from frontal photographs showing a full frontal view body and face with a neutral posture and expression. These images served as the basis for generating individualized avatar body trunks, closely matching the participant's body shape, and avatar faces that accurately replicated the participant's facial features. We refer to these components as “self” or “own”. Additionally, we generated avatar body trunks and avatar faces from images of averaged Dutch body and face profiles. We refer to these components as “other”. We digitally manipulated all body images to generate additional, heavier-weighted versions of avatars with big body trunks.

To elicit a full self-identity percept, we combined the participants' own avatar face with the participants' own avatar body. Similarly, to elicit an other-identity percept, we combined the other avatar face with the other, big body trunk avatar. Examples of these two main avatars are illustrated in Fig. 1A. As these avatars differed in both (putative) identity percept and body-trunk size, we included two

altered-body conditions that served to assess potentially confounding body-size effects in the absence of strong identity differences. These control avatars combined the participants' own avatar face with the participants' big body trunk avatar (Fig. 1B left) and the other avatar face with the other, medium body trunk avatar (Fig. 1B right). All avatars were generated using the Character Creator 3 software.

In order to increase the naturalness and variability of the avatar images during the EEG recordings, we pseudorandomly varied the color of the avatar's T-shirt (blue, purple, or green) and the avatar's orientation (frontal, 90 degrees left, or 90 degrees right), resulting in nine unique avatar images for each condition. The avatar was presented on a transparent background (size: 700×1000 pixels) covering approximately 3.2×4.5 degrees of participants' visual angle in the experiment. In order to make participants focus on the whole body, we centered a white fixation cross onto the avatar's body near the waist (Fig. 1).

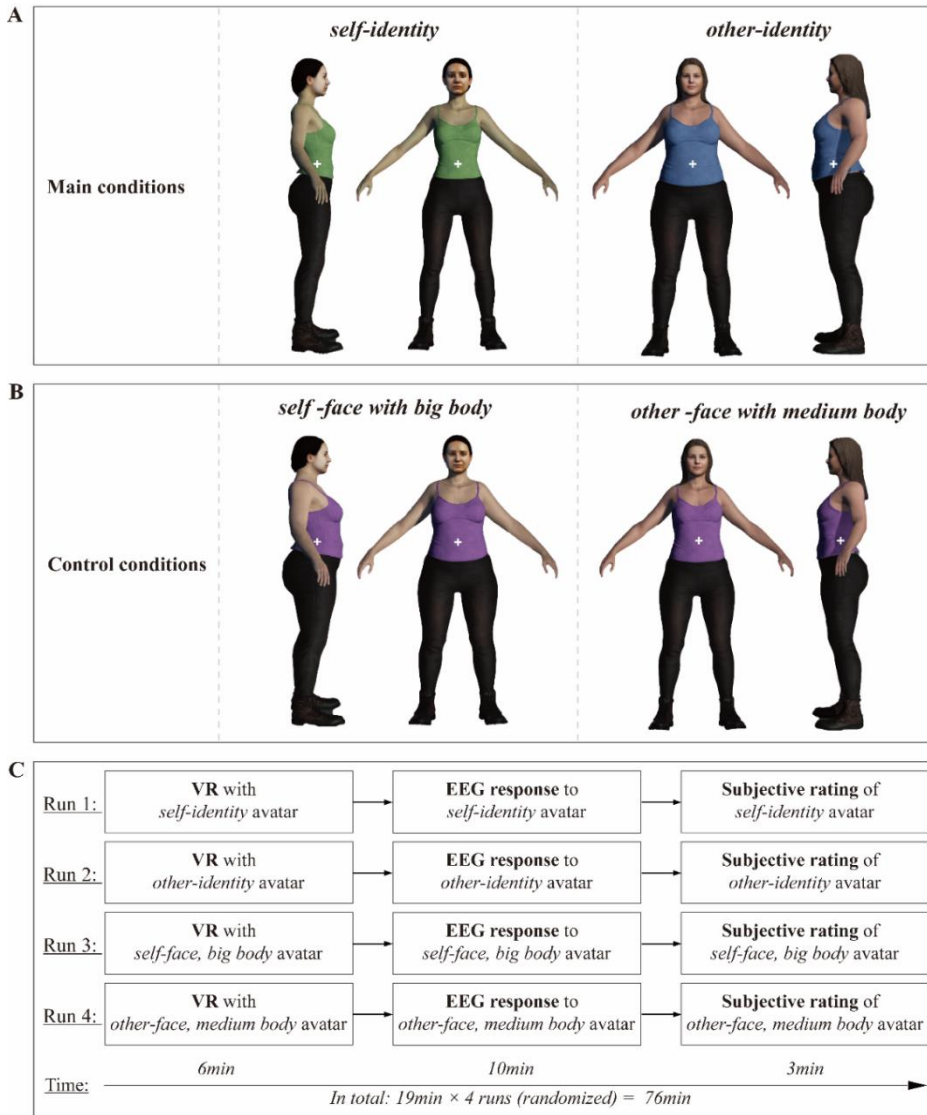


Fig. 1. Experimental design. Four example avatars are shown (one per condition). Panel A depicts the main conditions, featuring the participant's self-identity avatar (composed of the participant's own face and own body) on the left, and the other-identity avatar (composed of others' face and body) on the right. These avatars were expected to elicit strong self-identity percepts and a clear other-identity percept,

respectively. Panel B depicts the control conditions, featuring an avatar composed of the participant's own face and a big body and another avatar composed of other-face and a medium body. The latter avatars were expected to elicit body-size effects in the absence of strong identity differences. Avatar orientation and shirt color were pseudorandomly varied within each condition. This figure is used with permission of the participant resembled in the self-identity condition images. Panel C depicts the experimental protocol. The order of runs was randomized across participants.

4.3.3 Experimental procedure

Before admitting participants to the EEG study, their ability to recognize and distinguish their own avatar image from other avatar images was assessed with an online pre-questionnaire. When participants passed this initial screening they were invited to the lab, where the experimenters introduced the experiment, prepared the EEG (see below, section *EEG acquisition*) and seated them in a comfortable chair. Participants underwent four runs of the experiment lasting in total ~1h. Each run consisted of three parts that directly followed each other: VR task, EEG task, and post-questionnaire. In the VR task, participants performed a behavioral task in a VR environment while being embodied in an avatar corresponding to one of the four conditions. The purpose of this task was to create embodiment in the current avatar condition. In the subsequent EEG task, participants performed a behavioral task on 2D images of the same avatar as in the VR task; the images were shown on a computer screen while EEG was recorded. In the subsequent post-questionnaire, participants answered three questions related to the VR and avatar. The order of runs (i.e., conditions) was randomized across participants. Details about pre-questionnaire, VR task, EEG task and post-questionnaire are described in the sections below.

Pre questionnaire

To assess whether participants could recognize their personalized self-identity avatar and distinguish it from other avatars, we presented them with images of the self-identity avatar and images of the control avatar composed of other-face with medium body. We asked participants to rate whether the avatar looked similar to themselves ('similarity') and whether they could recognize the avatar ('recognizability') on a seven-point Likert scale (1: not agree at all, 7: strongly agree) before the experiment (Table 1, light shading).

VR Embodiment task

The VR scenario was programmed in Unity software in collaboration with Virtual Bodyworks Company (Barcelona, Spain). Participants stood upright wearing a VR headset (Oculus Quest 2). In the VR environment, they viewed a given avatar (depending on the experimental condition) in a mirror from a first person perspective and performed a target catching task. This task required them to manually catch bubbles and reach crystals through different circles in the VR by executing corresponding arm movements in the physical world.

EEG task

In the EEG experiment, each trial consisted of the presentation of an avatar image for 1000ms, preceded by a fixation cross for 500 ± 100 ms. To make participants focus on the avatar, an oddball task was used. This task required them to press a button when they detected a deviant avatar, which consisted of different physical features (hair style, skin color, and facial features). The deviant avatars were also presented in nine variations (3 shirt colors \times 3 orientations) and they never occurred on two consecutive trials. We instructed participants to press the button

when they saw the deviant avatar, and emphasized response accuracy (we did not encourage response speed; therefore we did not analyze reaction time below). In each run, each standard image was repeated 42 times and each deviant image was repeated 4 times, resulting in 378 standard trials and 36 deviant trials per run (i.e., condition). Each EEG run lasted about 10 minutes.

Post questionnaire

To assess the participants' subjective feelings about their embodiment, avatar identification, and avatar liking (Marchiondo et al., 2015; Mello et al., 2022) we asked them three questions after each EEG run. These questions are described below (Table 1, dark shading).

Table 1. Pre-questionnaire and post-questionnaire.

<i>Questionnaire</i>	<i>Aim</i>	Question	Rating
Pre-questionnaire	Similarity	The avatar looks like me.	1 (do not agree at all) to 7 (strongly agree)
	Recognizability	I can recognize myself in this avatar.	1 (do not agree at all) to 7 (strongly agree)
Post-questionnaire	Embodiment	I felt that the virtual body I saw when I was in VR was my own body.	1 (do not agree at all) to 7 (strongly agree)
	Identification	The body I saw physically looked like me.	1 (do not agree at all) to 7 (strongly agree)
	Liking	How did you feel about the avatar?	1 (do not like it at all) to 7 (I like it very much)

4.3.4 EEG acquisition

EEG data were recorded using an elastic cap with 64 electrodes placed according to the international 10-20 system, and sampled at a rate of 1000Hz (BrainVison Products, Munich, Germany). Electrode Cz was

used as the reference during recording and the forehead electrode (Fp1) was used as a ground electrode. Two electrodes were used to measure the vertical and horizontal electrooculogram (EOG). The remaining 58 electrodes included FPz, AFz, Fz, FCz, CPz, Pz, POz, Oz, AF7, AF8, AF3, AF4, F7, F8, F5, F6, F3, F4, F1, F2, FC5, FC6, FC3, FC4, FC1, FC2, T7, T8, C5, C6, C3, C4, C1, C2, TP9, TP10, TP7, TP8, CP5, CP6, CP3, CP4, CP1, CP2, P7, P8, P5, P6, P3, P4, P1, P2, PO7, PO8, PO3, PO4, O1, and O2. Impedances for reference and ground were maintained below 5kOhm and for all other electrodes below 10kOhm.

4.3.5 EEG data preprocessing

EEG data were preprocessed and analyzed using FieldTrip version 20220104 (Oostenveld et al., 2011) in Matlab R2021b (MathWorks, U.S.). Recordings were first segmented into epochs from 500ms pre-stimulus (the avatar image) to 1500ms post-stimulus and then filtered with a 0.3-30 Hz band-pass filter. EEG data at each electrode were re-referenced to the average of all electrodes. Artifact rejection was done using independent component analysis (logistic infomax ICA algorithm (Bell & Sejnowski, 1995); on average, 1.56 ± 0.70 (mean \pm SD) components were visually identified as artifacts and removed per participant. Moreover, single epochs during which the EEG peak amplitude exceeded 3 SD above/below the mean amplitude were rejected. On average, $71.36\% \pm 10.43\%$ of trials were preserved and statistically analyzed per participant.

4.3.6 Event-related potential analyses

Epochs from 200ms before until 1000ms after stimulus onset were extracted from the preprocessed data. Baseline correction was applied and involved subtracting the average amplitude in the baseline interval (-200 to 0ms) from the overall epoch. Trials were averaged for each

experimental condition, resulting in ERPs used for further statistical analyses, which were performed using IBM SPSS Statistics 27 (IBM Corp., Armonk, NY, USA). Only trials comprising standard stimuli were analyzed. We spatially separated the EEG electrodes into an occipital cluster (POz, Oz, PO3, PO4, O1, O2), temporal cluster (P7, P8, TP7, TP8, CP5, CP6, P5, P6) and frontal cluster (F1, F2, Fz, FC1, FC2, FCz) and averaged the channels within each cluster. For each cluster, we pooled all conditions and visually identified a prominent ERP component based on visual inspection of the overall ERP waveform, topographical distribution of grand-averaged ERP, and previous studies (Lu et al., 2023; Muñoz et al., 2020; Xu et al., 2017). The identified ERP components and their associated time windows are as follows: P1 (80-130ms) in the occipital cluster; N170 (140-190ms) in the temporal cluster; N2 (200-250ms) in the frontal cluster. The mean amplitude was computed as the average of all electrodes within each cluster within the specific time window.

Outliers (data points further than 3 SD away from the mean) were rejected; this affected one participant's dataset in the analyses of N170. All other datasets were normally distributed as assessed with Shapiro-Wilk test. Paired t-tests were applied to compare the mean ERP amplitudes (or differences between these amplitudes) across conditions. Statistical results were considered as significant given a p-value < 0.05.

4.4 Results

4.4.1 Pre questionnaire results

Rating scores for similarity and recognizability were significantly larger for the self-identity avatar than the control avatar, which was

composed of other-face with medium body (Similarity: self-identity avatar: 5.45 ± 1.40 , altered-body avatar: 2.72 ± 1.46 , $t(28) = -10.21$, $p < 0.001$; Recognizability: self-identity avatar: 5.86 ± 1.27 , altered-body avatar: 2.59 ± 1.48 , $t(28) = -9.96$, $p < 0.001$). These observations indicate that participants could successfully identify and discriminate their personalized avatar.

4.4.2 Post questionnaire results

The rating scores of embodiment showed a significant difference between self-identity and other-identity conditions ($t(28) = 13.15$, $p < 0.001$). Specifically, the embodiment scores for self-identity (5.03 ± 1.37) were substantially higher than those for other-identity (1.79 ± 0.98). Additionally, a significant difference was observed between the control conditions ($t(28) = 3.58$, $p = 0.001$), with higher embodiment scores for other-faces with medium bodies (3.13 ± 1.55) than self-faces with big bodies (2.44 ± 1.32). Notably, the difference between main conditions was significantly larger than that between control conditions ($t(28) = 7.23$, $p < 0.001$, difference between main conditions (self-identity minus other-identity): 3.24 ± 1.33 , difference between control conditions (other-faces with medium bodies minus self-faces with big bodies): 0.69 ± 1.04). Applying the same analyses to identification scores and liking scores yielded results qualitatively identical to those above, except that the identity had no significant effect on identification scores in the control conditions. Overall, the subjective rating data indicate that participants identified more strongly with the self-identity avatar than the other-identity avatar (Fig. 2).

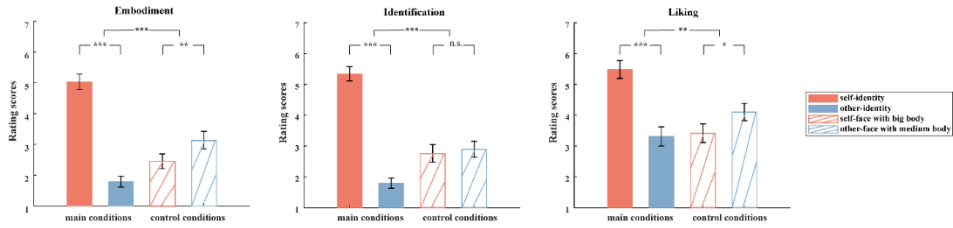


Fig. 2. Post-questionnaire results. Means and standard error (SE) of rating scores for embodiment (left), identification (middle) and liking (right) per condition. ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, n.s.: non-significant

4.4.3 ERPs

Effect of self- vs. other-identity perception

To investigate the temporal dynamics of brain activity during the perception of self-identity versus other-identity, we compared ERPs elicited by viewing participants' own avatar (self-identity condition) vs. another avatar (other-identity condition). Figure 3A shows that the self-identity condition ($4.40 \pm 2.97 \mu\text{V}$) elicited smaller P1 amplitudes than the other-identity condition ($5.34 \pm 3.36 \mu\text{V}$). This observation was confirmed by a significant effect of identity on P1 amplitude ($t(28) = -2.09$, $p = 0.046$). In line with our hypothesis, we found a similar effect of identity on N2 ($t(28) = 2.82$, $p = 0.009$; self-identity: $-0.46 \pm 1.54 \mu\text{V}$, other-identity: $-1.08 \pm 1.59 \mu\text{V}$). We found no effect on N170 ($t(27) = -1.20$, $p = 0.240$).

Effect of identity perception vs. effect of body size

To exclude that the observed effect on P1 and N2 reflected merely visual body differences (rather than identity, i.e., the integration of the own face with the own body), we compared the other-face, medium body avatar *versus* the self-face, big body avatar. Compared to the main

conditions, these control conditions significantly reduced overall identity differences (due to the mismatching self-face and body; see Post-questionnaire results above) while preserving differences in physical body size. Unlike the main results above, comparison of these control conditions yielded no effect on P1 or N2 (P1: $t(28) = -1.45, p = 0.158$; N2: $t(28) = -0.24, p = 0.815$) but on N170 ($t(27) = 2.67, p = 0.013$; other-face with medium body: $-1.17 \pm 1.46 \mu\text{V}$, self-face with big body: $-1.38 \pm 1.46 \mu\text{V}$), suggesting that the main results above do not reflect merely visual body differences.

To confirm this notion, we statistically compared the observed effect of identity perception versus the observed (null) effect of body size. We found a significant difference only for the N2 component, such that the difference between the main conditions was larger than the difference between the control conditions ($t(28) = 2.55, p = 0.017$; self-identity minus other-identity: $0.62 \pm 1.19 \mu\text{V}$; other-face with medium body minus self-face with big body: $-0.03 \pm 0.72 \mu\text{V}$). This result suggested that the effect on N2 can be attributed to identity perception, rather than body size. We found no significant difference for P1 ($t(28) = -1.64, p = 0.113$), suggesting that the effect on P1 cannot be attributed to identity perception alone, but also to body size.

Comparison of self-identity condition vs control conditions

We further explored differences between the self-identity condition and the control conditions, for which participants gave reduced identification ratings as stated above (see post-questionnaire results above). Consistent with the identification-rating results, we found that the self-identity condition elicited smaller N2 amplitudes than the self-face with big body ($t(28) = 2.13, p = 0.042$) and the other-face with medium body ($t(28) = 2.04, p = 0.051$). Applying the same analyses to P1, yielded a significant difference to the self-face with big body ($t(28)$

= -2.13, $p = 0.042$), but not to the other-face with medium body ($t(28) = -1.73, p = 0.095$), further supporting the above notion that P1 was modulated by body rather than identity. Overall, the N2 responses and identification ratings showed a strikingly similar pattern across conditions (Fig.3C vs Fig.2 middle). These observations further support the notion that N2 was modulated by identity perception, whereas P1 was affected more by visual body size.

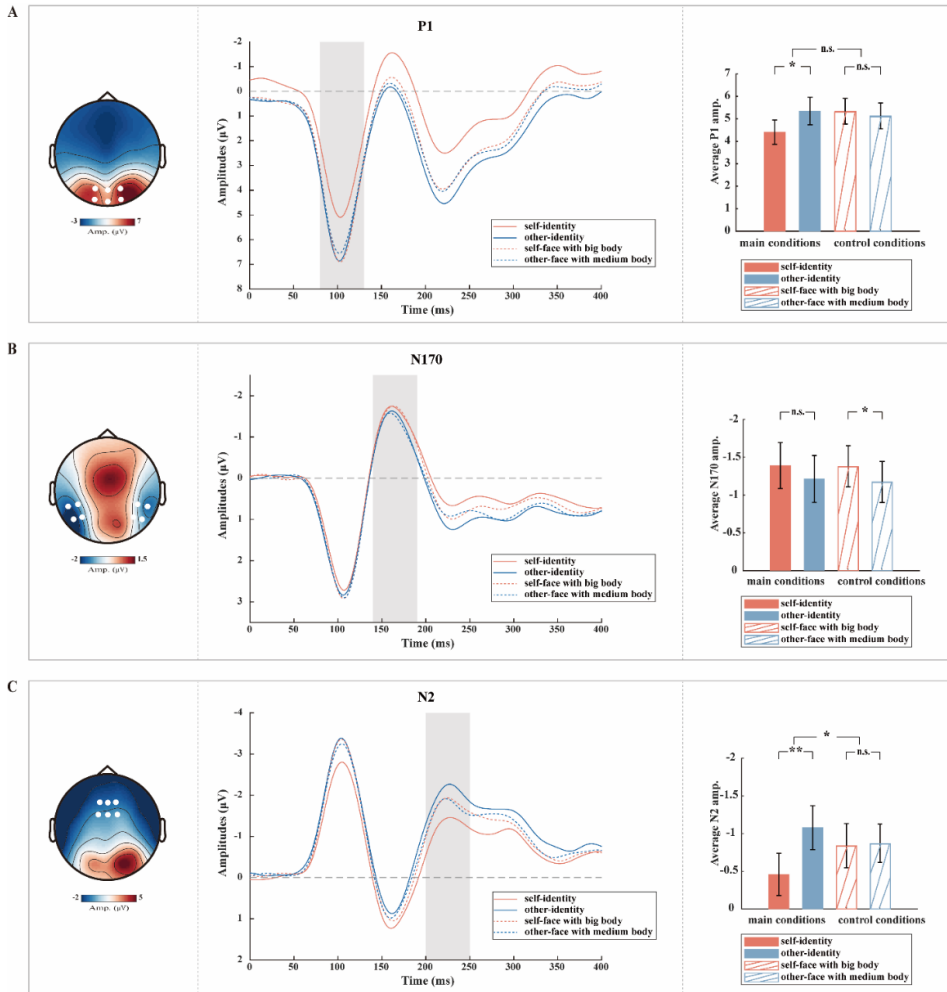


Fig. 3 A-C. EEG results. Grand averaged ERPs are depicted per

condition for P1, N170, and N2 components separately (middle). The shaded rectangle visualizes the time window from which the average ERP amplitude was extracted. The highlighted white dots on the topographic map (left) represent the electrodes from which the grand-averaged ERP for each component was extracted. Bar plots (right) illustrate the mean and standard error (SE) across participants of each component's amplitude per condition. **: $p < 0.01$, *: $p < 0.05$, n.s.: non-significant.

4.5 Discussion

We investigated neural responses to self-identity, other-identity and altered-body avatar images. In line with our hypothesis on the importance of body identity, we found a clear effect of self-identity based on the face and the body on the N2 component: avatars with whom participants could strongly identify elicited significantly smaller N2 amplitudes than avatars with whom participants identified less. Importantly, this suppressive effect on N2 was caused by self-identity as defined *jointly by the face and the body*: self-face avatars elicited smaller N2 amplitudes only when also the avatar's body resembled the participant. In contrast, the earlier P1 component showed a clear effect of visual body size: avatars with bigger bodies elicited significantly larger P1 amplitudes than avatars with smaller bodies, regardless of how strongly participants could identify with these avatars. We further observed that self-face avatars elicited stronger N170 amplitudes than other-face avatars; however, like the P1 results, this observation showed no systematic link to self-identity.

Effect of face and body on subjective ratings of identity, embodiment, and liking

Behavioral results showed that participants strongly identified with avatars that contained both their own face and body. Avatars with a face and/or a body that did not resemble the participant received significantly lower identification ratings. Surprisingly, the self-face avatar with the big body was rated similarly as the other-face avatar with the medium body. This suggests that the presence of facial identity alone is insufficient for triggering self-perception regardless of body self-identity. Instead, self-identity seems to be perceived based on a combination of the body and the face. In line with this, it has been shown that a task-irrelevant body expression can influence face identity (Stock & Gelder, 2014). Our finding contrasts with the traditional emphasis on the role of the face for identity perception. A review of previous studies about combined face-body perception for person identity found that observers tend to attend selectively to the face and ignore the body, unless the facial information is insufficient to provide identity information (Hu et al., 2020). But previous studies did not use personalized avatar images that the participants had become acquainted with through VR embodiment. Still, we cannot exclude that the instructions to fixate on the center of the image (which was de facto on the body) may have contributed to a reduced the impact of the face component.

Unlike the identification ratings, participants' ratings of embodiment and liking showed a significant difference between the control conditions. Participants embodied and liked more the other-face avatar with the medium body than the self-face avatar with the big body. The main conditions showed a similar effect, with higher ratings for the self-face, self-body avatar than the other-face avatar with the big body. Together, this shows that participants embodied and liked more the medium (more self-like) body than the bigger body, regardless of face identity. And face identity alone may not be not as important for

embodiment and liking as one may have expected.

Overall, these subjective rating data indicate that embodiment and liking seem to be driven primarily by the perception of the body, whereas identification may be driven more by a combination of face and body perception.

Effect of self-identity on N2

Our main finding is that perception of self-identity based on the face and the body reduces N2 responses. In the main conditions, we observed that self-face, self-body avatars elicited smaller N2 amplitudes than other-face, big-body avatars. In contrast, in the control conditions, we found no significant N2 difference between self-face, big-body avatars and other-face, medium-body avatars. Moreover, N2 responses showed a significantly larger difference between the two main conditions than between the two control conditions. These observations rule out that the effect observed in the main conditions reflects body-size differences and instead support a genuine effect of self-identity perception. Our interpretation is further supported by our observation that the N2 responses followed a pattern across conditions that closely resembled that of participants' identification ratings. This strongly suggests that both measures reflect the same phenomenon.

Our finding that self-identity perception reduces the N2 amplitude is consistent with results from previous studies that showed N2 reduction related to self-relatedness, familiarity, and ownership (Carver et al., 2006; Kotlewska et al., 2023; Muñoz et al., 2020; Woźniak et al., 2018). Noteworthy, reduction of N2 has been attributed to a rather automatic process (Todd et al., 2008), suggesting that self-identity perception as reflected by N2 suppression might emerge with relatively little cognitive effort.

We further observed that self-identity avatars elicited smaller N2 amplitudes than avatars combining the self-face with a big body or the other-face with a medium body. This indicates that the N2 reduction is sustained by the identity of not only the face but also the body. Previous studies reported that self-faces elicit smaller N2 amplitudes than other-faces including famous faces (Kotilewska et al., 2023), indicating that N2 is sensitive to self-identity. While consistent with this interpretation, our results further reveal that when a body is present its identity *needs to fit that of the face*. Thus, our findings extend the previous N2 findings by showing that the previously observed suppressive, self-face related effect on N2 is largely attenuated when the self-face is combined with a big body. This further suggests that the N2 suppression does not reflect the self-face alone, but the self-identity as defined by the combination of face and body.

It should be noted that the observed N2 reduction might reflect a process that is more general than self-perception alone. Muñoz et al., 2020 found significantly smaller N2 response to personal objects than non-personal objects (Muñoz et al., 2020). Similarly, unfamiliar objects have been found to elicit more negative N2 responses than familiar objects (Carver et al., 2006). Therefore, the N2 reduction might reflect more general percepts of personal identity and/or familiarity.

Effect of body size on P1

We found that the self-identity avatar elicited significantly smaller P1 amplitudes than the other-identity avatar with the big body. A similar trend was observed in the control conditions: other-face avatars with medium-sized body elicited significantly smaller P1 amplitudes than self-face avatars with a big body. Therefore, unlike the N2 results, the effect on P1 reflected visual differences in body size, rather than self-identity. Several previous studies have shown that the P1 component is

related the visual stimulus size (Busch et al., 2004; Niu et al., 2008; Pfabigan et al., 2015; Schindler et al., 2019), with larger-sized stimuli eliciting larger P1 amplitudes. Our results confirm these previous findings and further reveal that the size-sensitivity of P1 persists even when visual input elicits distinct identity percepts.

Effect of face, but not self-identity, on N170

In contradiction with our hypothesis, we found no clear effect of self-identity (face and body) on the N170 component. We observed that self-face avatars with big bodies elicited significantly larger N170 amplitudes than other-face avatars with medium bodies. A similar trend was observed in the main conditions: self-face avatars with self-bodies elicited slightly larger N170 amplitudes than other-face avatars with big bodies. Therefore, unlike the N2 results, the effect on N170 reflected differences between self-face and other-face, with little relation to the body or overall identity. This interpretation is in line with previous findings showing larger N170 responses to self-faces vs faces of friends or strangers (Keyes et al., 2010).

4.6 Conclusion

Perception of self-identity (as defined jointly by the face and the body) reduces the N2. Therefore, self-identity perception emerges rapidly in the brain within 200ms, suggesting that visual face and body information have been integrated into identity at this stage. Conversely, image size and face identity are processed in earlier stages as reflected by increases in P1 and N170 responses respectively.

4.7 References

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Chapter 5

General discussion

5.1 Overview of the findings

In this thesis, we used EEG techniques to investigate the neural basis of the perception of body expressions in social threat, social interaction, and self-identity. The empirical work is divided into three chapters.

In chapter 2, we investigated the perception of social threat and how it is impacted by the controllability of the threat. Behaviorally, we found that participants' response times were shorter when facing threatening body expressions (angry avatars) compared to non-threatening body expressions (neutral avatars). In the ERP results, we found that the amplitudes of early ERP components (N170 and VPP) increased, while the middle component N3 decreased when viewing an angry avatar compared to a neutral avatar. The amplitude of the late component LPP increased under the full control (100% controllable cue) condition compared to the 75% controllable cue condition. Taken together, the findings of this empirical chapter are twofold, showing that, first, social threat is rapidly detected in the early stages of cortical stimulus processing (within approximately 180ms), independent of the ability to control. Second, the perceived control over the threat impacts only later processing stages (within approximately 500 milliseconds).

In chapter 3, we explored body expression perception and how it is influenced by emotion predictions with social interaction stimuli. Behaviorally, we found that the accuracy (participants' judgement of the appropriateness of the emotional reaction in the image following a social interaction video) decreased as prediction strength decreased. Accuracy was highest in the high prediction condition (i.e., when the social context in the video was clear and intact), lower in the mid prediction condition (when the video was played backwards), and lowest in the low prediction condition (when the video was scrambled). At the neural level, we found that the early component N170 was larger

when participants viewed an angry body expression compared to a neutral body expression, and this effect was only significant in the high prediction condition. We further found that neutral whole-body emotional reactions facilitated cortical detection of prediction errors, compared to angry reactions. This was shown by a significant increase in the discriminability of N300 responses to matching versus mismatching body-emotion images. In sum, the findings of this chapter highlight the interplay between emotion-expression processing and emotion predictions in early cortical processing stages. Whole-body emotion expressions are processed in the brain in a flexible manner depending on the dynamic social context.

In chapter 4, we focused on the processing of self-identity by creating personalized avatars for each participant. Compound avatar images, combining participants' own faces and bodies as well as those of others, were generated from photographs. Subjective assessments from participants confirmed a stronger sense of identification with avatars depicting their own face/body compared to those representing others. Analysis of ERPs revealed that avatars depicting the participants' self-identity elicited weaker N2 and P1 responses compared to avatars representing other identities. No significant effects on N170 responses were observed. These findings suggest that the perception of self-identity occurs rapidly, within approximately 200 milliseconds, indicating the integration of visual face and body information into identity representation at an early stage.

In the following sections, I will first describe how our findings extend our understanding of the N170 component, which is one of the most relevant ERP components related to the encoding of body expressions, particularly concerning its emotional effects. Next, I will embed the aforementioned findings within the broader context of existing literature and discuss their implications for our understanding

of body expression perception, focusing on the themes of social threat, social interaction, and self-identity.

5.2 N170: an ERP marker of body expression processing

Our results from three studies (Chapters 2-5) align with previous findings that the N170 component is elicited by body stimuli and face-body compound stimuli (Chapter 5) (Farzmahdi et al., 2021; He et al., 2018; Hietanen & Nummenmaa, 2011; Meeren et al., 2005; Stekelenburg & de Gelder, 2004; Tanaka & Jiang, 2024; van Heijnsbergen et al., 2007; Wang et al., 2017). Moreover, we found that N170 and VPP amplitudes were modulated by emotional valence, such that angry body expressions elicited larger N170/VPP amplitudes than neutral body expressions. Many studies have found that the N170 is more sensitive to affective faces, such that angry and fearful faces elicit larger N170 amplitudes than neutral faces (Hinojosa et al., 2015; Schindler & Bublatzky, 2020). These studies suggest that the N170 is more responsive to emotional stimuli than neutral stimuli, and our results provide further empirical support for this. They also show clearly that this effect is observable for not only faces but also whole body expressions.

Compared to face studies, fewer studies have focused on body expressions. Earlier findings reported that N170 and VPP are related to the processing of whole body expressions. Most of these studies failed to observe an emotion effect on N170 (Farzmahdi et al., 2021; Meeren et al., 2005; Stekelenburg & de Gelder, 2004; van Heijnsbergen et al., 2007), but found an emotion effect on VPP, with fearful bodies eliciting larger VPP amplitudes than neutral bodies, which is consistent with the ERP results in Chapter 2 (Stekelenburg & de Gelder, 2004). Moreover,

one study suggested that N170 and VPP seem to derive from a common source in the brain (Joyce & Rossion, 2005). A possible reason for why earlier studies did not find an emotion effect on body expressions may be the small number of participants (12-17 participants). In the current thesis, we tested 25 or more participants in each experiment, which may have led to higher statistical sensitivity to emotion effects on ERPs compared to previous studies.

In summary, our findings on N170 show that this early processing stage is modulated by both angry and neutral body expressions, which may reflect mechanisms involved in the rapid detection of emotional body expressions (e.g., social threat). We propose that the N170 may serve as a marker for the processing of body expressions.

In the next section, I will discuss the relationship between social threat and control ability over threat.

5.3 Social threat perception is independent of control ability

In Chapter 2, we integrated EEG with VR to investigate social threat perception using avatars displaying angry and neutral expressions. The VR technology allowed us to create a more naturalistic and immersive environment. Our experimental design included both static avatars, which facilitated strong image-evoked ERP data and the analysis of the temporal dynamics of social threat processing, as well as dynamic avatars, which provided realistic scenarios to elicit control behavior. We found that social threat (an angry body expression) elicited a larger N170/VPP and a smaller P3 than non-social threat (a neutral body

expression). The 100% control condition elicited a larger LPP than the 75% control condition. The ERP results showed no interaction effect between social threat and control condition. Furthermore, we did not find any interaction effect between social threat conditions and control conditions in behavioral results, time-frequency analysis, nor heart rate. Therefore, these results suggest that social threat can be detected rapidly, reflected in N170 effects which occur around 180ms. And consume more cognitive resources, reflected in P3 effects which occur around 280ms. However, it does not undergo further evaluation. There are no significant effects between social threat and non-social threat on the LPP, which occurs later around 500ms. Interestingly, the processing of social threat appears to not depend on the perceived control over the threat.

So far, only a few studies have explored social threat elicited by angry body expression and the relationship between which and the control ability over the threat, especially from the neuroscience aspect. Theoretically, we found that social threats, conveyed by angry body expressions, are rapidly detected, as reflected in the N170 effect. Furthermore, this effect is not influenced by control behavior. Methodologically, our study presents a novel VR-EEG-ECG setup that can be valuable for future studies investigating social interactions in a naturalistic manner. This novel setup can be useful in the future for other researchers to improve the naturalness of their paradigms.

Many studies on social threat have focused on anxiety and have found that social threat can elicit anxiety, which is modulated by various factors (e.g., attention) (Li et al., 2007; Mogg & Bradley, 2002; Roelofs et al., 2010; Staugaard, 2010). Indeed, this anxiety trait can help people prepare for upcoming threats and avoid danger (McNaughton & Corr, 2004). However, few studies have investigated how control ability or other preceding information impacts social threat perception.

One study used happy and angry facial expressions as cues for instructed threat-of-shock or safety, in which happy faces cue threat and angry faces cue safety, or vice versa. They found that physiological reactions (skin conductance responses and phasic heart rate changes) to threat cues emerged regardless of whether angry or happy facial expressions signaled shocks (Bublitzky et al., 2019). Our results are in line with this study, indicating that threat perception may not be strongly influenced by preceding information.

There are two possible reasons why we did not find a significant interaction effect between social threat and control ability. First, each trial presented a static image of the avatar before approaching the participant, with ERP analyses locked to the static avatar to obtain clean EEG data. The control behavior concerned the movements of the dynamic avatar aiming to stop the avatar's approaching. Even though the controllability cue preceded both the static avatar and dynamic avatar, participants knew that their control action would not apply to the static avatar. Second, it is worth noting that our experiment was conducted in a VR environment, which provided a realistic and immersive experience for participants. However, at the same time, they may have been aware that this was not the real world. The induction of a realistic threat experience is an experimental challenge, for ethical reasons. Inherently, this casts some doubt about the external validity of findings from social threat studies. In our case, participants may have subjectively felt that they were not truly threatened or vulnerable, especially since they could control the approaching avatar. This might also explain why we found no effect of control ability on threat perception. Our study goes one step further by using an immersive environment presumably giving a more naturalistic experience of threat. Despite these improvements, some caution should still be exercised when interpreting the behavioral null result on controllability. It

remains possible that in a real environment, such an effect would be observable.

In summary, Chapter 2 reveals that social threat induced by an angry body expression can be rapidly detected during the early processing stage (N170), approximately 180ms after the stimulus onset. Additionally, our novel VR-EEG-ECG setup allowed us to collect clean EEG data in a realistic scenario.

It is important to consider the social and clinical implications of this study. Social threats are often encountered in family or school settings, and individuals who have experienced social threats, such as domestic or school violence - often accompanied by angry body gestures - may exhibit different neural and behavioral patterns compared to others who did not experience such violence. This is especially true when they perceive their ability to control the threat. In the future, we could further explore social threat induced by whole body expressions in clinical studies.

However, there are some limitations to this study. First, while the VR environment was highly realistic, it would have been more effective to allow participants to move freely. On the one hand, if we take full advantage of VR's capabilities, then we cannot record clean EEG data. Thus, in our study, the participant was sitting on a chair. Second, the control ability in our experiment primarily affected the approaching avatars, whereas our ERP analyses focused on static avatars. This design may not allow us to get the interaction effect between social threat and control ability on the ERP results. In future research, it is better to take advantage of VR by, for example, allowing participants to move freely. In addition, directly using the dynamic avatar has the potential to test if control ability impacts social threat.

In the next section, I will focus on prediction effects in social interaction derived from two agents' whole body expressions.

5.4 Body expression perception in social interactions

In Chapter 3, we designed a novel paradigm to examine emotion prediction derived from social interactions using whole-body expressions. We discovered that whole-body emotional expressions are processed in the cortex in a flexible manner depending on the dynamic social context. While most studies have found that N170 amplitudes are modulated by emotional valence, these effects were often studied in isolation. Our study replicated previous findings of emotion effects on N170, and we further demonstrated that this body emotion effect was only observed in a high prediction condition where the social context (video) was clear, it was not significant in lower prediction conditions (mid and low prediction conditions). Additionally, we found that prediction errors elicited large N300 amplitudes which is in line with previous studies. Interestingly, this prediction error effect (incongruent > congruent) was observed in neutral reactions but not in angry reactions. It suggests that neutral emotional expressions may be more likely to violate emotion predictions in the cortex than angry ones.

5.4.1 Body-emotion effect was only observed in high prediction condition

In chapter 3, we found an emotional body effect on N170 (angry > neutral), which is in line with chapter 2 and previous studies (Borhani et al., 2015; de Gelder et al., 2004; Meeren et al., 2005; Stekelenburg & de Gelder, 2004). More importantly, we found this body-emotion effect only under conditions in which the emotion was presented in a

predictive emotional context (high prediction condition). This effect was not significant in the mid and low prediction conditions, where the predictive emotional context was less clear. Additionally, we did not find any interaction effect between reaction emotion and prediction error. Previous studies mainly focused on the different emotion impacts on body expression perception, while less is known about how different levels of predictability can impact body expression perception in the early processing stages. Our N170 results show that predictive emotional context plays a crucial role in emotional body expression perception. In the absence of this predictability, body emotion has only little impact on this early processing stage.

In Chapter 2, we found that angry body expressions elicited larger N170 amplitudes, and this effect was independent of the information about control of the threat. Another study found that nude bodies elicited larger N170 amplitudes than clothed bodies, and this body effect was not modulated by top-down attention (Hietanen et al., 2014). In line with these studies, our results indicate that the body-emotion effect on N170 effects is not influenced by higher-order information (prediction error). In one study, angry facial expressions elicited larger N170 amplitudes only in the intact stimulus condition, not in a scrambled condition (Schindler et al., 2021). In other studies, realistic body expressions elicited larger N170 amplitudes than scrambled body expressions, suggesting that N170 is influenced by low-level information in the early stages of body expression processing (Meeren et al., 2005; Soria Bauser & Suchan, 2013). Similarly, we observed the body-emotion effect on N170 only under high prediction conditions, where the social context was intact and clear.

In summary, our findings on N170 show that this early processing stage is modulated by both angry and neutral body expressions, which may reflect mechanisms involved in the rapid

detection of emotional body expressions. Furthermore, this emotion effect on N170 is influenced by different levels of emotion predictability. When predictability is lower, body emotion has only little impact on the early processing stage. Therefore, we propose again that the N170 may serve as a marker for the processing of body expressions.

5.4.2 Prediction error effect on N300 was only observed in neutral reaction

In Chapter 3, we found that incongruent conditions elicited larger N300 amplitudes than congruent conditions, which aligns with previous studies (Baker et al., 2023; Kumar et al., 2021; Truman & Mudrik, 2018). N300 is a negative ERP component that occurs around 250-350ms in the central region (Chen et al., 2022; Vö & Wolfe, 2013; Wu & Coulson, 2007). It is related to prediction errors in response to emotional stimuli and higher-order visual information (Baker et al., 2023; Baker et al., 2022; Chen et al., 2022). Interestingly, this prediction error effect (incongruent > congruent) seems to occur only when the emotional reaction is neutral (neutral body expression), not angry (angry body expression).

In our study, the ERP results were time-locked to the reaction image. This suggest that what participants saw in the prediction video impacted their brain activity when processing the subsequent reaction image. We observed more pronounced N300 amplitudes in the neutral reaction, not in the angry reaction, indicating that participants may have felt their predictions were more violated when the agent's reaction showed a neutral body expression compared to an angry body expression. These results further reveal that the prediction error effect on N300 depends on the emotional content of the body expression in the reaction.

Unlike previous studies, our stimuli were more realistic and natural, consisting of videos and images that depicted social interaction scenarios to elicit participants' emotional predictions and emotional responses. A few studies explored emotion prediction when observing social interaction, especially with interactive body expression (Baker et al., 2023). Our study not only extends the understanding of the ERP marker N300, which can be triggered by prediction error, but also reveals that this violation effect tends to occur more easily when the emotional response is neutral. In contrast, we did not observe this violation effect when the emotional response was anger.

One possible explanation is that when Agent A tries to capture Agent B's attention from behind, whether the touch is neutral (gentle) or angry (forceful), Agent B is unprepared and cannot predict the event since they cannot see what is happening or who is touching them. People might react more strongly to neutral stimuli when they are unprepared or cannot predict the situation. Additionally, it may be considered safer and more acceptable if Agent B reacts with anger in such an unpredictable scenario. This could explain why we did not find a significant prediction error effect for angry reactions after neutral touch and angry touch.

On the other hand, participants might feel that their expectations are more violated when Agent B responds neutrally after an aggressive or angry touch compared to a neutral touch. They may find it more acceptable when both the action and response are neutral, but they might perceive it as more disturbing or violating when the initial touch is angry, yet Agent B responds neutrally.

In summary, this study has both scientific and societal implications, offering new insights into prediction processes during social interaction, especially when it involves emotional information.

Our experimental design, using videos and images of social interactions as stimuli, made the lab experiment more engaging and realistic. Our findings also prompt us to consider how social context and prior information influence our judgments in daily interactions, and how our evaluations are affected by the outcomes following predictions.

Some individuals with emotional difficulties, such as those with alexithymia, - who are less sensitive to emotions, - or those with autism, who experience challenges in social interactions, could be valuable groups for testing our findings related to the N170 and N300 effects. These neural markers could also be useful in assessing changes after medical or psychological treatment, or in distinguishing these individuals from healthy groups. In the future, we could further investigate the prediction effect in social interactions in clinical studies.

As for the limitations of this study, there could be more behavioral assessments. For example, we can ask participants to judge the emotion of the approaching agent (agent A) in interaction video or judge the emotion of the reacting agent (agent B) in a later image. With more behavioral results, it would help us gather more data and test the relationship between behavioral ratings and ERP results.

In the above two studies, we used body stimuli with blurred faces to exclude any face impact during the processing of body expression perception. In the next section, I will discuss the topic of self-identity which uses face and body compound stimuli.

5.5 Self-identity and the importance of body expression

In Chapter 4, we used fully personalized avatars, as well as avatars with faces and bodies completely different from the participants, to

investigate self-identity perception. We designed an embodiment VR task that preceded a computer-based task. The VR scenario enabled participants to connect with the personalized (or other) avatars. We found that the N2 component can serve as an index of self-identity processing. Notably, we discovered that facial identity information alone may be insufficient to trigger participants' identification but that information from the body helps this identification. Participants preferred avatars with medium-sized bodies (similar to their own) over avatars with larger bodies, even when the latter featured their own faces. This study has significant implications for understanding the importance of body identity and shape in self-identity perception and offers new insights into issues related to body size, a topic of growing concern for mental and physical health. Methodologically, it introduced a novel approach to studying self-identity by using VR to create embodied experiences with different avatars, allowing us to tap into participants' feelings of connection with these avatars. Our data further highlight the critical role of the body in self-identity.

5.5.1 N2 is related to encoding self-identity

In our ERP results, we found that self-identity elicited smaller P1 and N2 amplitudes than other-identity. The earlier component, P1, is mainly related to processing the body size of the avatar images. Although N2 exhibited a similar pattern to P1, we suggest that N2 is specifically linked to the processing of self-identity. There are three reasons for this.

First, when comparing the main conditions (self-identity vs. other-identity), both P1 and N2 amplitudes showed significant effects. To further confirm the identity effect, we compared the effects between the main conditions and control conditions (main conditions > control conditions). We found a significant difference only for the N2 component, where the difference between the main conditions was

larger than the difference between the control conditions. This result suggests that the effect on N2 can be attributed to identity perception, rather than body size.

Second, many studies have linked the early P1 component to attention or the visual processing of stimuli's physical attributes (e.g., size), with larger P1 amplitudes elicited by larger-sized stimuli (Busch et al., 2004; Niu et al., 2008; Pfabigan et al., 2015). In contrast, N2 is related to more advanced cognitive processes, such as self-identity. Most studies on self-related topics have found that the N2 component is associated with processing self-relevant stimuli, such as faces, objects, and names (Bola et al., 2021; Guan et al., 2014; Keyes et al., 2010; Knyazev, 2013; Scott et al., 2005; Shi, 2016; Sui et al., 2009; Tacikowski & Nowicka, 2010). Higher self-relevance in stimuli elicited smaller N2 amplitudes, which is consistent with our results. Another EEG study found that the reduction in N2 amplitude has been attributed to a relatively automatic process (Todd et al., 2008), suggesting that self-identity perception, as reflected by N2 suppression, might emerge with relatively little cognitive effort.

Third, behaviorally, we found that the rating scores for identification shared a similar pattern to the N2 effects. The identity scores were higher in the self-identity condition than in the other-identity condition, and the difference between the main conditions was larger than the difference between the control conditions. This indicates that participants identified more with the self-identity condition compared to the other-identity condition.

Taken together, these findings suggest that N2 is related to self-identity perception, which occurs approximately 200 milliseconds after stimulus onset in the frontal-central region.

5.5.2 The importance of body identity

In the behavior results, we found a significant difference between the main conditions (self-identity vs. other-identity) in identification scores, such that participants identified more with the self-face, self-body avatar (self-identity) than with the other-face, other-body avatar (other-identity). However, this difference was not significant between the control conditions (other-face, medium-body avatar vs. self-face, big-body condition). This indicates that the presence of facial identity alone may be insufficient for triggering self-perception when body self-identity is not present.

Additionally, we observed that participants' ratings of embodiment and liking showed significant differences between the main conditions, as well as between the control conditions. Participants embodied and liked the other-face avatar with the medium body more than the self-face avatar with the big body. The main conditions showed a similar effect, with higher ratings for the self-face, self-body avatar than for the other-face avatar with the big body. Together, these findings suggest that participants embodied and liked the medium (more self-like) body more than the bigger body, regardless of face identity. This implies that face identity alone may not be as crucial for embodiment and liking as one might have expected.

In summary, our data highlight the critical role of body expression in self-identity. Interestingly, participants embodied and liked medium bodies (closer to their own body size) more compared to bigger body regardless of the face-identity. These findings have important social and clinical implications, particularly for understanding attitudes toward obesity. Participants preferred the medium body even when the larger body had a different face, suggesting that body size plays a significant role in perception.

Moreover, VR technology could serve as a tool to help individuals with obesity engage in physical exercise or training by allowing them to embody avatars of varying body sizes in realistic, immersive environments.

However, there are limitations to this study. To eliminate potential confounds related to gender matching between participants and avatars, we only recruited female participants. Thus, our findings may not generalize to males. Additionally, our sample consisted exclusively of Caucasian participants, so cultural differences (e.g., among Asian populations) may also influence the results. Further research is needed to explore these variables.

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Appendix

Impact paragraph

Body and facial expressions are ubiquitous in our daily lives, yet most research focuses predominantly on facial expressions, often overlooking the significance of body expressions. The findings have significant scientific, social, and clinical implications.

In Chapter 2, we broaden the understanding of body expression perception by showing that N170 amplitude can be modulated by social and non-social threats, induced by angry and neutral body expressions. While previous studies found no significant deviation in N170 for fearful versus neutral bodies in the context of social threat, our findings indicate that social threat can be rapidly detected during the early stages of body expression processing, approximately 180ms after the onset of the threatening stimulus.

Methodologically, we developed a novel VR-EEG-ECG setup, which allowed us to collect clean EEG data in a VR environment. From a social and clinical perspective, social threats are often encountered in familial or educational settings. Individuals who have experienced social threats, such as domestic or school violence—often accompanied by threatening body gestures—may display different neural and behavioral patterns compared to those who have not.

N170 could serve as a neural marker for assessing individuals' sensitivity to social threats. While our experiment did not find that control over a threat influenced social threat perception, this could be due to the lack of ecological validity in lab settings. In real life, a sense of control may help people manage social threats, such as domestic or school violence.

In Chapter 3, we replicated the results from Chapter 2, showing that angry body expressions elicit larger N170 amplitudes than neutral body expressions in a social interaction context. Few studies have explored how emotional predictions influence the perception of emotional body expressions within social interactions. We found that low-level information modulates emotional effects in the early processing stage (N170). Additionally, we identified the N300 component as a potential neural marker of prediction error.

These findings suggest that social context and prior information play crucial roles in shaping our judgments during daily interactions. Individuals with emotional difficulties, such as those with alexithymia—who have reduced sensitivity to emotions—or individuals with autism, who experience challenges in social interactions, may be ideal candidates for testing the N170 and N300 effects. These neural markers could be used to assess changes following medical or psychological treatment or to differentiate these individuals from healthy populations.

In Chapter 4, we explored self-identity perception using fully personalized avatars and avatars with faces and bodies completely different from the participants. This study provided evidences that body expression plays an important role in self-identity and offers new insights into the growing issue of body size and its impact on mental and physical health. We found that the N2 component serves as an index of self-identity processing. Notably, facial expression alone was insufficient to trigger self-identification. Participants preferred avatars with medium-sized bodies similar to their own over larger avatars, even when the larger avatars featured the participant's face. This highlights the critical role body expression plays in self-identity.

Previous studies have primarily used facial stimuli to investigate self-identity perception, whereas our research implemented

personalized face-body compound stimuli. Additionally, we employed VR techniques and an embodiment task to deepen participants' connection with each avatar. Technologically, this introduces a novel method for studying self-identity by using VR to create embodied experiences with different avatars, tapping into participants' feelings of connection.

These findings hold important social and clinical implications, particularly regarding attitudes toward obesity. Participants preferred medium-sized bodies over larger bodies, suggesting that body size plays a significant role in self-perception. Furthermore, VR technology could be a valuable tool for helping individuals with obesity engage in physical exercise by allowing them to embody avatars of varying body sizes in immersive, realistic environments.

In summary, this doctoral thesis makes multiple contributions. First, it advances the theoretical understanding of body expression in social environments. Second, it offers valuable experimental paradigms and methodological innovations for collecting clean EEG data in VR contexts. Finally, it has significant societal implications, enhancing our understanding of non-verbal communication and its impact on human life.

Summary

This thesis explored the behavior and neural basis of body expression, focusing on the topics of social threat, social interaction, and self-identity. It emphasizes the crucial role of body expression in emotion perception and body identity. By combining high temporal resolution EEG with realistic VR technology, this research aimed to gain a deeper understanding of the neural processing involved in body expression.

Firstly, the ERP component N170, occurring approximately 180ms after stimulus onset, was found to be linked to the encoding of body expressions. The results showed that this early processing stage is modulated by both angry and neutral body expressions, which may reflect mechanisms involved in the rapid detection of emotional body expressions, such as those related to social threat. We propose that N170 may serve as a neural marker for processing body expressions. Additionally, the perception of social threat from angry body expressions is independent of control ability over that threat.

Secondly, the effect of emotion on N170 amplitude was influenced by the strength of prediction. This effect was only significant under conditions of high prediction strength, where the social context remained intact. Moreover, the prediction error effect on the N300 component was dependent on the emotional reaction, being more pronounced when the agent's emotional reaction was neutral.

Finally, the perception of self-identity (as defined by both face and body) was found to reduce N2 amplitude. This indicates that self-identity processing occurs rapidly in the brain, within 200ms, suggesting that visual information from the face and body is integrated into identity recognition at this stage. Behavioral ratings further demonstrated that participants embodied and preferred the medium-

sized (more self-like) avatar body over the larger one, regardless of face identity. Interestingly, face identity alone did not seem as crucial for embodiment and preference as previously expected.

Overall, this thesis provides new insights into the behavioral and neural basis underlying body expression perception. The experimental setup, combining VR, EEG, and ECG, and the use of personalized avatars in a VR environment, allowed participants to engage in a more immersive and realistic setting during the lab experiments. This offers valuable examples for future research in the field.

Samenvatting

Dit proefschrift onderzoekt het gedrag en de neurale basis van lichaamsuitdrukkingen, met de focus op sociale dreiging, sociale interactie en zelfidentiteit. Het benadrukt de cruciale rol van lichaamsuitdrukking in emotieperceptie en lichaamsidentiteit. Aan de hand van experimenten die EEG met een hoge temporele resolutie combineren met realistische en immersieve VR-technologie, was het mogelijk voor dit onderzoek om zich te richten op het verkrijgen van een dieper begrip van de neurale verwerking die betrokken is bij lichaamsuitdrukking.

Ten eerste werd de ERP-component N170, die ongeveer 180 ms na het begin van de stimulus optreedt, in verband gebracht met de codering van lichaamsuitdrukkingen. De resultaten toonden aan dat deze vroege verwerkingsfase wordt beïnvloed door zowel boze als neutrale lichaamsuitdrukkingen. Dit weerspiegelt mogelijkwijze de mechanismen die betrokken zijn bij de snelle detectie van emotionele lichaamsuitdrukkingen, zoals bijvoorbeeld in het geval van ateed sociale bedreiging. We stellen voor dat N170 kan dienen als een neurale marker voor de verwerking van lichaamsuitdrukkingen. Bovendien is de perceptie van sociale dreiging door boze lichaamsuitdrukkingen onafhankelijk van de mate van controle die de waarnemer zou hebben over die dreiging.

Ten tweede werd onderzocht of predictie een rol speelt bij de observatie van het verloop van interacties tussen twee personen. Het effect van emotie op de amplitude van N170 beïnvloed door de sterkte van voorspellingen. Dit vroege effect was voornamelijk duidelijk als de voorspellenden waarde van de voorafgaande informatie hoog was. Daarnaast was het voorspellingsfouteffect op de N300-component afhankelijk van de emotionele reactie, waarbij het effect sterker was

wanneer de emotionele reactie op een agressieve beweging van de agent neutraal was.

Tot slot bleek dat de perceptie van zelfidentiteit (zoals gedefinieerd door zowel gezicht als lichaam) de amplitude van N2 verminderde. Dit geeft aan dat de verwerking van zelfidentiteit snel in de hersenen plaatsvindt, binnen 200 ms, wat suggereert dat visuele informatie van gezicht en lichaam in deze fase wordt geïntegreerd in identiteitsherkenning. Gedragmatige beoordelingen toonden verder aan dat deelnemers zich meer identificeerden met en de voorkeur gaven aan de middelgrote (meer op zichzelf lijkende) avatar-lichaam boven de grotere avatar, ongeacht de gezichtsidentiteit. Opmerkelijk is dat gezichtsidentiteit alleen niet zo cruciaal leek voor belichaming en voorkeur als eerder werd verwacht maar dat het lichaam ook een duidelijke rol speelt.

Al met al biedt deze scriptie nieuwe inzichten in de gedragsmatige en neurale basis van lichaamsuitdrukkingsperceptie. De experimentele opzet, die VR, EEG en ECG combineerde, en het gebruik van gepersonaliseerde avatars in een VR-omgeving, stelde de deelnemers in staat om tijdens de labexperimenten in een meer meeslepende en realistische omgeving te opereren. Dit biedt waardevolle voorbeelden voor toekomstig onderzoek op dit gebied.

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舍，您担心我在这边没有朋友，不习惯寒冷的气候和饮食。上次从家里回荷兰，你从家门口目送我们上车，然后又跑到另外一个路口等我们路过。我看着您孤单的身影，心里暖暖的也有点想落泪。您一直说希望我以后过得比您好，您对我的好是希望我成为更好的人。在我心里，您和妈妈一直都是我最坚强的后盾。亲爱的妈妈，家里大大小小的事情都是您在打点。我们都很信任你，所以您身上的责任和担子也很重。您常常为他人考虑，却少了考虑自己。我在您身上看到了责任感和善良，还有您对事和人都非常包容。感谢您也给了我这些美好的品质，虽然我常常感觉到自己没能向您一样包容。来荷兰之后经常和您视频，我喜欢听您说家里大大小小的事情，以前可能毫不在意，现在反而很享受这样的温暖。以前习惯了您做饭，来了荷兰之后非常想念您做的饭菜，非常地道的湘菜非常美味。自己独立生活之后才知道，您做家务的不容易。亲爱的妹妹，感谢你照顾家里，有你真好。还有在天堂的外公，我时常怀念您。从小您就对我很偏爱，觉得我是您的骄傲。您给的偏爱，从您去世之后，我再也没有感受过了。我常常希望如果您能看到我的成长，那有多好啊。最后，亲爱的爷爷奶奶，希望你们身体健康，幸福快乐。

写在 2024 年日历年年底（于马城）

About the author

Juanzhi Lu (陆娟芝) was born in Hunan, China, on 8th April 1995. She completed her secondary education at Hengyang No.8 Senior High School in 2013. After that, she enrolled at the Faculty of Education, Hunan Agricultural University, where she obtained a bachelor's degree in applied psychology in 2017. Given her interest in psychology and science, as well as her excellent performance during her bachelor's, she earned a postgraduate recommendation and started her master's research in social neuroscience at Shenzhen University under the supervision of Prof. dr. Fang Cui. During the master's period, she also worked as a research assistant for Prof. dr. Ning Lu. After obtaining her master's degree, she gained the support of the Chinese Scholarship Council (No. CSC202008440538) for studying as PhD student under the supervision of Prof. Beatrice de Gelder and Dr. Lars Riecke. Her research focused on body expression perception under social threat, social interaction and self-identity. In October 2024, Juanzhi will continue work with Prof. dr. Beatrice de Gelder as a postdoctoral fellow, where she will focus her research on the project of biomechanically possible vs. impossible bodies by using the EEG technique.

Publications

Peer-reviewed publications

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Lu, J., Riecke, L., & de Gelder, B. Behavioral and neural evidence for perceptual predictions in social interactions. *Imaging Neuroscience*. Major revision.

Conference contributions

Lu, J., Kemmerer, S. K., Riecke, L., & de Gelder, B. (2023). Early threat perception is independent of later cognitive and behavioral control. A virtual reality-EEG-ECG study. The Ettore Majorana Foundation and Centre for Scientific Culture (Eric, Italy). [Poster presentation]

Lu, J., Riecke, L., Ryan B. & de Gelder, B. (2024) The contribution of body perception of self-identity. An ERP study. European Society for Cognitive and Affective Neuroscience (Gent, Belgium). [Poster presentation]