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From Motion to Emotion:
A Multilevel Investigation of Affective Intention Decoding

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Summary

Understanding others' affective states is fundamental to successful social interaction. However, inferring such states poses a challenge — emotions and intentions are inherently inaccessible and must be expressed or communicated through observable cues. While facial expressions have been extensively studied, the human body also serves as a key channel for communicating affective intentions, offering high adaptive value. Prior research has identified several factors influencing how we perceive others' affect, including movement features and the bodily states of the observer. The action observation network (AON) reliably activates during the observation of other people's actions. Within this network, regions such as the inferior frontal gyrus, inferior parietal lobule, and premotor cortex are thought to support understanding by mapping observed movements onto motor representations, thereby providing a neural foundation for inferring others' actions and intentions. However, the precise role of the AON in affective intention decoding remains under debate. Emerging evidence also suggests that the observer's own motor repertoire and physiological states, such as acute inflammation, may modulate how affect is perceived in others' body movement — yet, how these internal factors interact with specific movement cues is still poorly understood.

This dissertation investigates which features of body movement contribute to affect perception in complex social interactions, and whether similarity between observed and internal motor representations modulates this process. Four experiments were conducted. Project 1 employed a computational feature-based approach to analyze whole-body movements in affective interactions. Project 2 targeted brain regions involved in action observation and valence processing. Project 3 examined how exercise-induced inflammation affects perception of emotional interactions. Project 4 combined methods from Project 1 and 2 to test how movement similarity influences both perception and neural activation.

The findings show that kinematic features support emotion recognition, while postural cues relate more closely to subjective valence ratings. Interactive movement enhances recognition of socially salient emotions such as affection. Neural data revealed that a fronto-parietal network — especially the inferior parietal lobule — encodes valence from movement and responds more strongly to dissimilar movements, suggesting a central role in affective intention decoding. Inflammation was found to alter gaze behavior and reduce both sensitivity and emotion recognition, linking internal altered physiological states to perceptual processes. These results point to a close interaction between movement features, physiological states, movement similarity, and the fronto-parietal system in decoding affective intentions.

Table of Contents

List of Figures

List of Abbreviations

AON	Action Observation Network
BOLD	Blood Oxygenation Level Dependent
CRP	C-reactive Protein
dPMC	dorsal Premotor Cortex
DMM	Direct Matching Model
EBL	Emotional Body Language
fMRI	functional Magnetic Resonacne Imaging
FLD	Full Light Displays
IFG	Inferior Frontal Gyrus
IL-6	Interleukin-6
IPL	Inferior Parietal Lobule
MCP-1	Monocyte Chemoattractant Protein-1
mOFC	Medial Orbiofrontal Cortex
MVPA	Multivoxel Pattern Analysis
PLD	Point Light Displays
RSA	Representational Similarity Analysis
SAMI	Similarity Analysis of Human Movements and Interactions
SMA	Supplementary Motor Area
SPL	Superior Parietal Lobule
SVM	Support Vector Machine
TNF-α	Tumor Necrosis Factor alpha
vPMC	Ventral Premotor Cortex

1 Background

"The only true discovery, would not be to visit strange lands but to possess other eyes, to behold the universe through the eyes of another." ***Marcel Proust***

1.1 The Importance of Affect Perception in Humans

In the rush of a train station, emotions unfold in motion. Someone might run down the stairs, exhausted, trying to catch a train – only to miss it and throw their arms up in frustration. A family reunion may take place as one member rushes toward their loved ones, or a lone traveler may stand still, looking despondent as the train pulls away. These scenes highlight our ability to observe, interpret, and evaluate the inner states of others in their embodied expressions, as though seeing the world through someone else's eyes.

As a social species, humans are able to intuitively understand and accurately interpret others' internal states without conscious effort. This ability holds significant adaptive value, guiding our responses and facilitating successful social interactions (Bradley et al., 2001; Darwin, 1872). Conversely, difficulty in decoding affective states can lead to interpersonal misunderstandings, social withdrawal, or even isolation (Persad & Polivy, 1993). Moreover, neurodevelopmental, neurodegenerative and psychiatric conditions — such as major depressive disorder, autism spectrum disorder, or Parkinson's disease — are often characterized by impairments in perceiving and evaluating others' emotional states, complicating social navigation and interpersonal connections (Archer, Hay, & Young, 1994; Bellot et al., 2021; Kaletsch et al., 2014; Krüger et al., 2018; Nackaerts et al., 2011; Trevisan & Birmingham, 2016).

Just as these processes influence social interactions, they are now also central to the field of affective computing. The ability to accurately infer emotions can enhance human–computer interactions across diverse domains, including gaming, mental health support, education, and everyday life (see Sreeja & Mahalakshmi, 2017; Wang et al., 2022, for reviews). Yet, the challenge remains: How can we understand another's internal state, let alone teach this skill to a machine (Picard, 2003; Frith & Frith, 2006; Barrett et al., 2011)? Understanding observed actions depends on a wide range of interacting factors, including prior experiences, cultural background, current mood, and the need to anticipate future outcomes (Liew et al., 2011; Molenberghs et al., 2012; Kemmerer, 2021) — for instance, whether to approach or avoid the person who just missed the train.

In the following, I provide an overview of recent research on the factors shaping affective judgments of others' internal states, with particular attention to movement features, neural correlates, and physiological states, as well as their interplay in understanding actions and emotions.

1.2 Communication of Emotions: from Faces to Bodies to Interactions

> *"People do not have direct information about others' mental states and must therefore base their inferences on whatever information about others' mental states they do have access to."*
> **Epley and Waytz**, 2010, p. 499

Emotions can be conveyed through various channels, providing information about the inner state, with much research traditionally emphasizing facial expressions and prosody (Cowen & Keltner et al., 2020; Matsumoto & Willingham, 2009). The human face, for example, carries distinct features that allow us to identify individuals as well as their inner states, such as emotions. Focusing on facial expressions, research has provided evidence that at least six basic emotions — anger, happiness, sadness, fear, surprise, and disgust — are expressed through universal facial patterns that appear from birth and are recognized with a high level of intercultural stability (Ekman & Friesen, 1971; Jack et al., 2012). However, categorical approaches such as Basic Emotion Theory (BET) have been criticized for oversimplifying emotional experience and neglecting contextual influences (Barrett et al., 2019; Cowen & Keltner, 2017; Crivelli et al., 2016; Jack et al., 2012; Lindquist et al., 2012, 2016; Ortony et al., 2022). In contrast, dimensional frameworks such as circumplex models represent emotions along dimensions like valence and arousal, providing a more nuanced representation (see Calvo & D'Mello, 2010, for a review).

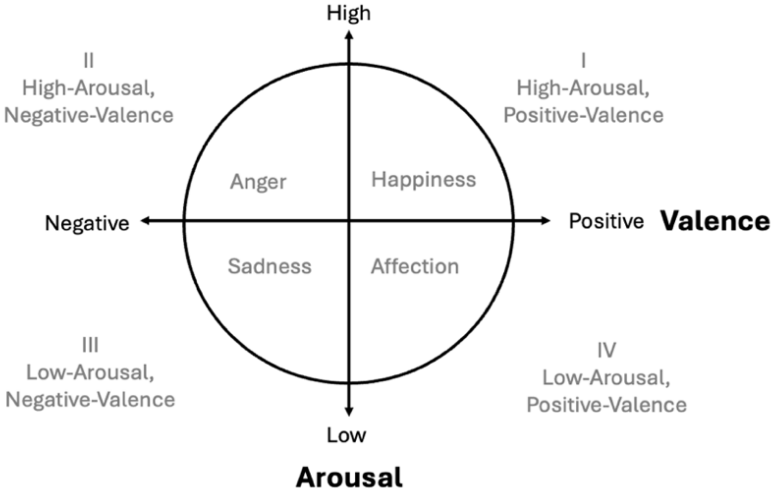

Figure 1: Circumplex Model Model of Emotions. Four categorical emotions positioned within the valence–arousal space (adapted from Wang et al., 2022).

Figure 1 illustrates the four categorical emotions — happiness, affection, sadness, and anger — used in this dissertation. The model was adapted from Wang et al. (2022) and adjusted to reflect the relative positions of these emotions within the dimensional space defined by valence and arousal.

1.2.1 Emotional Body Language

Although facial expressions have long dominated the study of emotion, they represent only part of the picture. Increasing attention has been given to the body as a powerful and complementary channel of affective information. Research by de Gelder and colleagues highlights key differences between emotions communicated via the face versus the body (de Gelder, 2006, 2009). While fearful faces primarily signal the presence of a threat, fearful body movements convey direct information about the actions taken to avoid or respond to it. Darwin (1872) already emphasized the link between emotions and their associated actions, noting that bodily movements stem from adaptive behaviors and thereby reveal the evolutionary roots of emotional expressions. Consistent with this view, the body provides access to internal states such as intentions and emotions (Atkinson et al., 2004; Cavallo et al., 2016; de Gelder, 2009; Poyo Solanas et al., 2020a, 2020b), remains informative even when the face is obscured, and can trigger immediate and automatic responses (Lorey et al., 2012; Michalak et al., 2009). Different emotions are associated with distinct body regions — for example, anger and happiness in the arms, sadness in the chest, and love throughout the whole body — suggesting that these same areas help express and perceive those emotions (Nummenmaa et al., 2018).

The coordinated expression of emotions through whole-body movements — often involving multiple joints and paired with meaningful actions — is commonly referred to as *emotional body language* (EBL; see de Gelder, 2007, for a review). Studies have shown that recognizing EBL is comparable in accuracy to recognizing facial expressions and that kinematic and postural configurations vary based on the expressed emotion, which in turn influences how EBL is perceived (Atkinson et al., 2004; Atkinson et al., 2023; de Gelder et al., 2009; Poyo Solanas et al., 2020a). For instance, Michalak et al. (2009) demonstrated that gait patterns associated with sadness and depression are characterized by reduced velocity, limited arm swing, and decreased vertical head motion. In contrast, more active emotions tend to involve greater gestural movement, faster velocity, and more expansive motions (de Meijer, 1989; Wallbott, 1998; Wallbott & Scherer, 1986). Furthermore, more recent work by Poyo Solanas et al. (2020a) revealed that specific postural features — such as limb angles and limb contraction —

are among the best predictors for discrete emotion categories. Consequently, the arrangement of body posture, gestures, trunk, and arm movements serves as an expressive means by which the body conveys emotions, intentions, or interpersonal signals (Blair, 2003; Campos et al., 1989; de Gelder, 2007, 2009) — such as the collapsed posture of a person who has just missed their train.

Nevertheless, the methods used to quantify body-movement features are highly heterogeneous. Some studies employ quantitative descriptions of posture and movement (see Kleinsmith & Bianchi-Berthouze, 2013, for a review), others focus on specific body segments (Pollick et al., 2001), and still others lack an explicit computational approach. This variability underscores the need for systematic frameworks to capture the multidimensionality of whole-body movements in affective perception.

1.2.2 Emotion Dynamics in Social Interactions

Emotions can be understood as dynamic, communicative processes between individuals and their environment (Clarke et al., 2005). While most research has focused on single-person displays, studies show that emotions are more accurately recognized in interactive, dyadic contexts (Atkinson et al., 2023; Clarke et al., 2005; Lorey et al., 2012). Dyadic interactions not only enhance recognition of emotions like joy and affection but also increase subjective perception in how positive or negative interactions are judged, as well as the confidence in those judgments. Contextual cues — such as physical distance, body orientation, and synchrony — further shape emotion perception (Lahnakoski et al., 2020; Moreau et al., 2016; Yokozuka et al., 2018). The sequencing of actions between interacting individuals helps observers anticipate behavior and decode affective intent (Manera et al., 2012, 2013). Abramson et al. (2021) demonstrated that bodies alone, even without facial cues, can improve fear recognition during social interaction, underscoring the body's critical role in emotional communication. Similarly, Bachmann and colleagues (2022) provided evidence that movement patterns emerging within an interaction enhance emotion understanding in dyadic contexts. Research on joint action also emphasizes the need for shared representations to enable effective social interaction (Sebanz & Knoblich, 2009). While context clearly influences affective interpretation, it remains unclear which specific interpersonal movement features contribute to affective perception in social settings.

1.3 The State of the Body, the Brain and Movement: from Inflammation to Action Observation and Movement Similarity

Whereas the previous chapters highlighted what is observed, individuals may nonetheless interpret the same situation differently — for instance, the frustration of missing a departing train might be perceived as anger by one observer and as sadness by another (Harmon-Jones et al., 2017; Murray et al., 2024). The following chapter therefore shifts focus from the observed actions to the factors modulating the perception within the observer.

1.3.1 Factors Modulating Affect Perception

If someone has just run down the stairs to catch a train, their physiological state may influence how they perceive the emotional tone of the surrounding scene. Among such influences, systemic inflammation is particularly relevant: key inflammatory markers such as interleukin-6 (IL-6) and tumor necrosis factor-α (TNF-α) interact with brain circuits involved in interpreting emotional cues. Elevated cytokine levels, commonly observed in mood disorders, have been linked to impaired emotion recognition and negative perceptual biases (Hansson et al., 2021; Moieni et al., 2015a, 2015b; Rosenblatt et al., 2014). For example, in patients with bipolar disorder, higher TNF-α levels have been associated with poorer recognition of sadness (Chang et al., 2024). Importantly, inflammation does not only alter internal emotional processing but also manifests in observable motor behavior. Lasselin et al. (2020) showed that experimentally induced systemic inflammation in healthy adults leads to distinct changes in movements — slower and shorter strides, reduced arm swing and knee flexion, and a downward-tilting head posture. Therefore, inflammation could alter the expression of emotional body language (EBL). This altered movement behavior could, in turn, shape the perception of others, since evidence suggests that one's own motor behavior also affects how social cues are understood. For instance, an individual's typical walking speed can bias how they interpret others' gait: fast walkers may perceive slow gaits as sad, whereas slow walkers may perceive fast gaits as angry (Edey et al., 2017). Movement similarity enhances action recognition and intention understanding, as shown by studies linking movement resemblance to improved perceptual accuracy (Casile & Giese, 2006; De Marco et al., 2020). Thus, people who move similarly may better interpret each other's emotions, leading to smoother social interactions. Conversely, those with dissimilar movement patterns — or in an altered physiological state such as acute inflammation — may misread emotional cues, potentially disrupting social understanding. While previous research has emphasized factors such as gender, mood, and perspective-taking, this thesis focuses on how physiological states and movement similarity shape affect perception. Evidence supports the influence of inflammation through neural and behavioral pathways (Lasselin et al., 2021; Peters et al., 2021; Smith, 2000), but the role of movement similarity remains less clear — raising the question: *How does movement similarity affect the perception of emotion?*

1.3.2 The Action Observation Network

To understand how movement similarity might shape affect perception, it is essential to consider the action observation network (AON) — a distributed system of brain regions engaged during the observation of human movement and thought to link the actions we observe in others with our own motor repertoire. Through this mechanism, the brain is believed to interpret actions by generating motor simulations grounded in existing motor programs (Bachmann et al., 2018; Caspers et al., 2010; Kilner et al., 2007). The AON comprises the inferior frontal gyrus (IFG), dorsal and ventral premotor cortices (dPMC, vPMC), supplementary motor area (SMA), inferior and superior parietal lobes (IPL, SPL), and primary sensory cortex (SI). These areas allow observed actions to be mapped onto the observer’s own motor system, supporting prediction, imitation, and affective interpretation (Balser et al., 2014; Bachmann et al., 2018; Caspers et al., 2010; Iacoboni et al., 1999; Kilner et al., 2007; Pichon et al., 2008, 2012; Rizzolatti et al., 1996, 2001; Sinke et al., 2010). Within the AON, the IPL, IFG, and PMC are especially important for movement similarity. The IPL processes emotional and intentional information, using fine-grained movement cues to infer others’ mental states. It also maintains internal body models and matches observed actions to one’s own motor repertoire (Blakemore & Sirigu, 2003; Engelen et al., 2015, 2018; Patri et al., 2020). Disrupting IPL activity impairs intention recognition in the observer for simple reach-to-grasp or reach-to-pour kinematics, underlining its essential role in processing discriminative kinematic features (Patri et al., 2020). The IFG is particularly responsive to socially and emotionally meaningful actions, showing stronger activation during complex, whole-body movements and social interactions (Iacoboni et al., 2005; Keysers & Gazzola, 2007). The PMC primarily contributes to motor simulation and preparation during action observation, enabling imitation and appropriate behavioral responses (Fogassi et al., 2005; Molenberghs et al., 2012).

1.3.3 Movement Similarity as a Mechanism for Affective Intention Decoding

While the AON provides the neurophysiological basis for encoding and recognizing affective actions, different frameworks attempt to explain its functioning. *Embodied simulation* proposes that observers understand others by internally simulating their actions and emotional states

(Gallese & Sinigaglia, 2011). The underlying process is motor resonance, whereby action observation activates corresponding motor representations in the observer, creating a shared neural substrate for perception and understanding (Gentile et al., 2023; Rizzolatti & Craighero, 2004). This mechanism is formalized in the direct-matching hypothesis (see Figure 2), which posits that observed actions are mapped onto the motor system in a feedforward, bottom-up manner, enabling intuitive understanding without higher-level inference (Rizzolatti et al., 2001; Rizzolatti & Craighero, 2004). In this view, no iterative feedback between areas of the AON is needed.

By contrast, predictive coding models describe action understanding as a hierarchical and dynamic process in which the brain generates predictions about others' goals and movements and compares them with incoming sensory input (Kilner et al., 2007). Here, interaction between AON regions involves continuous, bidirectional exchanges between top-down predictions and bottom-up signals (see Figure 2). Both accounts, however, depend on the observer's internal representations, which are shaped by prior experience, bodily states, and motor repertoire (Decety & Sommerville, 2003). Yet, it remains under debate what exactly needs to be reproduced in the observer from the observed actions (e.g., joint angles, velocity of motion) and whether action mirroring is based on reproducing movements or intentions (Csibra, 2007).

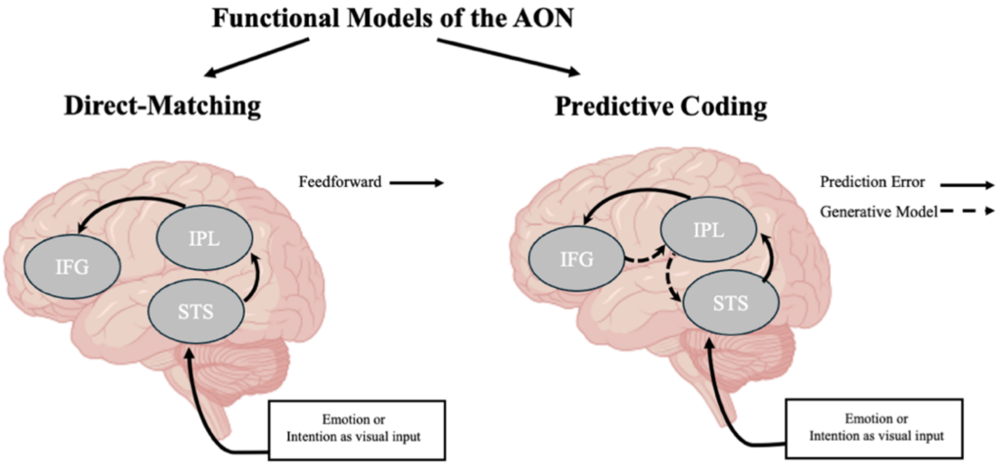

Figure 2: Schematic Overview of the Two Theoretical Frameworks within the AON.

The Direct Matching model posits a feedforward process in which observed actions are directly mapped onto the observer's motor system for immediate resonance. In contrast, the Predictive Coding model assumes a hierarchical loop where prior expectations guide perception, and mismatches (prediction errors) between expected and observed actions update internal models (adapted from Kilner et al., 2007).

So far, we have outlined a resonance mechanism that transforms visual input into (affective) action understanding (see Figure 3). This process acts as a bridge between the motor system of the actor and the perceptual and motor systems of the observer, shaped by past experience, motor repertoire, and even internal physiological states such as inflammation. Uithol and colleagues (2011) provided a presumable causal pathway through which the executor's planned action is mapped onto the observer's system, which is adapted for affective action understanding in Figure 3.

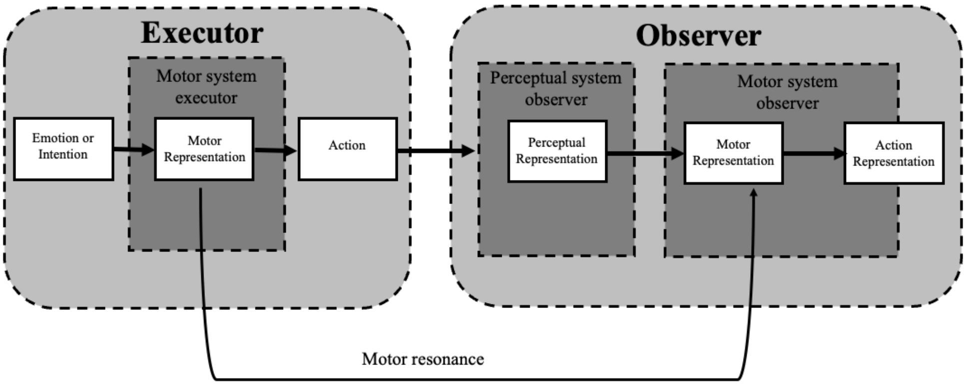

Figure 3: A Causal Chain for Affective Intention Decoding.

Adapted from Uithol (2011) schematic representation of linear affective intention decoding from movements of the executor through obervations and motorical representations within the observer.

While this dissertation primarily focuses on body movements within social interactions — specifically how inflammation and similarities between the executor's and observer's motor systems influence expression and perception — it is important to recognize that action observation is a multidimensional process. A recent review by Kemmerer (2021) identified twenty-two distinct factors that modulate activity within the Mirror Neuron System (MNS), underscoring its complexity. These factors span multiple domains, including properties of the action itself, characteristics of the actor and the observer, their relationship, and the broader context. For example, factors such as attention, perspective, motivation, or contextual elements like the presence of food on a table can all influence activation within the AON.

1.3.4 Measuring Perception, Physiological States and Movement Similarities in Affective Understanding

Returning to the train station, imagine sprinting down the stairs yourself or watching someone rush past at a much faster pace. Both situations illustrate key modulators of affective perception, but they raise the question of how to study what is observed and from whom. Sprinting itself can alter the physiological state of the observer, for example, by inducing inflammation. Inflammation is typically induced experimentally through endotoxin administration, vaccinations, or direct injection of proinflammatory cytokines (Hansson et al., 2021). Physical exercise, however, provides a noninvasive alternative. Intense, unfamiliar, or prolonged endurance activity reliably triggers a mild and temporary proinflammatory response — marked by increased cytokines such as interleukin-6 (IL-6) and tumor necrosis factor-α (TNF-α) — followed by anti-inflammatory recovery (Peake et al., 2017; Pedersen & Hoffman-Goetz, 2000). This makes exercise a valuable tool for exploring how inflammatory states influence mood and emotional processing. The second scenario relates to the characteristics of observed movements. Stimuli can range from static images to full-light displays (FLDs), which present naturalistic motion but are harder to control, and point-light displays (PLDs), which isolate kinematic information using minimal visual input (Johansson, 1973). While PLDs may be slightly less accurate in conveying emotion, they allow for highly controlled investigation and recruit largely the same brain networks as FLDs — excluding regions such as the amygdala involved in urgent affective responses (Bachmann et al., 2018). Advances in marker-based and markerless motion capture now allow precise tracking of whole-body movement and the creation of both FLDs (Poyo Solanas et al., 2020a) and PLDs (Bachmann et al., 2020). Using optoelectronic systems or computer vision, anatomical landmarks can be analyzed to study affective expression. Two main approaches exist for quantifying such movement: feature-based methods and data-driven methods such as principal component analysis, which enable objective analysis of emotional kinematics (Kleinsmith & Bianchi-Berthouze, 2013; Roether et al., 2009). The same techniques can also be applied to capture an individual’s motor repertoire. For example, De Marco et al. (2020) recorded participants’ reach-to-grasp movements and compared them with observed reach-to-grasp actions in the stimuli, quantifying the degree of similarity between them.

This overview illustrates not only the modulators of affective perception but also the methodological tools required to capture them. These tools — ranging, for example, from exercise-based manipulations to PLDs and motion capture — provide the foundation for the empirical studies presented in this thesis.

2 Own Research Program

2.1 Aims and Objectives

The present work investigated how movement features of emotional body language, neural correlates of the AON, and internal bodily states such as inflammation or movement similarities shape affect perception in social interactions. Specifically, there were two main aims. The first goal was to specify how different kinematic, postural and interpersonal features of emotional body language influence the perception of social interactions, and to identify which areas of the AON represent affective information carried by movement kinematics (Project 1 & Project 2). The second aim was to examine how physiological states and movement similarities shape the perception of emotional interactions (Project 3 & Project 4). The broader goal of this dissertation is to advance our understanding of how affect is recognized from body movement in social contexts. Such knowledge can not only help understand why perception may be impaired in certain disorders such as depression or autism spectrum disorder but also informs technological applications, such as social robots or AI agents, while enhancing precision, fluidity, and mutual understanding in everyday encounters. Accordingly, the causal chain for understanding others intention based on their actions is adapted and extended to contribute for movement similarities and physiological states. Figure 4 outlines the updated causal chain of affective intention decoding, shown linearly but reflecting a reciprocal and dynamic process.

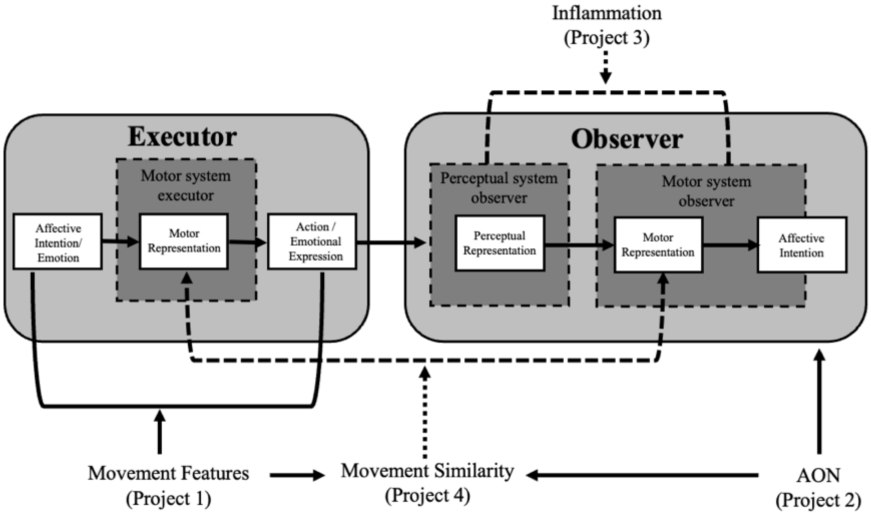

Figure 4: Updated Causal Cahin of Affective Intention Decoding.

Schmeatic illustration of affective intention understanding linking affective expression, neural encoding, and modulatory influences of physiological states and movement similarity between executor and observer..

Project 1 examines how affect is expressed in movement, while Project 2 investigates their neural decoding; Projects 3 and 4 highlight modulatory influences of physiological states and movement similarity (dotted lines).

2.2 Project 1: Decoding Spatiotemporal Features of Emotional Body Language in Social Interactions

By Keck, Zabicki, Bachmann, Munzert & Krüger (Scientific Reports, 2022)

2.2.1 Aim

The project pursued two main goals. First, we aimed to provide a quantitative and computational description of movement features in social interactions. Second, we sought to examine how these features contribute to emotion category recognition and valence perception.

2.2.2 Methods

Participants (n = 31) viewed 48 point-light displays of dyadic interactions expressing four emotions: happiness, affection, sadness, and anger. They categorized the observed emotion and rated perceived valence on a scale from –5 to +5. Movement features of emotional body language were extracted from thirteen anatomical markers and their 3D coordinates. Intrapersonal features included kinematic parameters such as velocity, acceleration, and vertical movement, as well as postural parameters such as limb angles, contraction, symmetry, and volume. Interpersonal features were calculated to capture proximity (distance and time in personal space), orientation, balance in motion energy, synchronization of velocity and acceleration, and correlations between spatial distance and other features. Full details of feature calculation appear in Table 1 and the supplementary material of the publication.

2.2.3 Analysis

We compared emotion categories using ANOVAs, applied decision tree classifiers to assess the predictive value of different feature sets (M1: interpersonal, M2: intrapersonal, M3: combined), and used Representational Similarity Analysis (RSA) to link perceptual ratings to the extracted features.

2.2.4 Results

Both intrapersonal (i.e. vertical movement) and interpersonal features (i.e. motion energy balance) systematically varied across the four emotions. Classification accuracy was highest for the combined model, demonstrating that integrating both intra- and interpersonal features enhanced prediction performance. Kinematic features best predicted emotion categories, whereas valence perception was more strongly linked to postural features.

2.2.5 Conclusion

In sum, Project 1 demonstrated that movement features at both the individual and interpersonel level contribute to the perception of emotion and valence in social interactions. The findings emphasized the importance of integrating these layers to decode affective content in bodily expressions.

2.3 Project 2: Decoding Affect in Emotional Body Language: Valence Representation in the Action Observation Network

By Keck, Bachmann, Zabicki, Munzert & Krüger (Social Cognitive and Affective Neuroscience, 2025)

2.3.1 Aim

The aim of this project was to investigate the brain mechanisms involved in inferring affective states from body movements during social interactions. Specifically, we sought to examine how areas within the AON and valence-sensitive regions contribute to perceiving valence based purely on movement kinematics.

2.3.2 Methods

Twenty participants viewed twenty point-light displays, comprising ten positive and ten negative social interactions, while undergoing fMRI. During scanning, participants rated the emotional valence of each interaction on an 11-point Likert scale ranging from –5 to +5.

2.3.3 Analysis

We used parametric modulation to identify brain regions where BOLD signal scaled with subjective valence ratings, thereby indicating sensitivity to affective perception. To further explore how these impressions were represented, we applied multivoxel pattern analysis (MVPA) such as RSA and Support Vector Machines (SVM) to assess whether neural activity patterns could reliably distinguish between positive and negative stimuli.

2.3.4 Results

Regions within the AON, specifically the IPL, IFG, dPMC, and vPMDC, reflected the perceived valence of PLD interactions more strongly than classical valence-sensitive regions such as the amygdala and mOFC. The IPL emerged as a key region for decoding the affective content of observed movements. Importantly, valence was not encoded in the amplitude of BOLD responses but rather in the representational similarity of neural activity patterns.

2.3.5 Conclusion

The findings demonstrate that valence perception in social interactions is primarily represented in distributed neural patterns within the AON rather than in activation amplitudes of classical valence-sensitive regions. This highlights the IPL as a central region for decoding affective content from observed body movements.

2.4 Project 3: Exercise-Induced Inflammation Alters the Perception and Visual Exploration of Emotional Interactions

By Keck, Honekamp, Gebhardt, Nolte, Linka, de Haas, Munzert, Krüger K. & Krüger B. (Brain, Behavior, & Immunity – Health, 2024)

2.4.1 Aim

This project investigated modulatory influences on affective perception by examining how internal physiological states of the observer, specifically exercise-induced systemic inflammation, alter the recognition and visual exploration of emotional body language in social interactions. The central goal was to test whether a pro-inflammatory response, mediated by cytokines such as interleukin-6 (IL-6), affects the perception of emotion and attention allocation to emotional body cues.

2.4.2 Methods

Nineteen male participants completed a within-subject design consisting of three conditions: a 45-minute downhill run at 70% VO_2max to induce peak myokine release and a pro-inflammatory state, a treadmill run without decline as an active control, and a passive resting condition. Blood samples were collected at four time points (T0 = before exercise, T1 = directly after exercise, T3 = 3h after exercise, T24 = 24h after exercise) to measure inflammatory markers (IL-6, CRP, MCP-1) and muscle damage (myoglobin). Three hours post-exercise (T3), participants viewed point-light displays of dyadic social interactions depicting happiness, affection, sadness, and anger. They categorized the emotional content, rated intensity, indicated confidence, and provided self-reported mood ratings. Concurrently, eye movements were recorded during the PLD task.

2.4.3 Analysis

Visual exploration was analyzed via number of fixations, glance duration, first fixation metrics, and dwell time. Emotion recognition performance was assessed through classification accuracy, absolute valence ratings, and sensitivity to detect emotion-specific cues. Blood analyses provided verification of the inflammatory response.

2.4.4 Results

The downhill run significantly elevated inflammatory markers compared to the control conditions. This pro-inflammatory state was accompanied by a decrease in emotion recognition accuracy and sensitivity across all emotion categories. Eye-tracking data revealed a shift in visual exploration, with more fixations directed toward sad interactions under inflammation, whereas happy interactions attracted more fixations in the resting condition.

2.4.5 Conclusion

The findings demonstrate that transient, exercise-induced inflammation dampens the recognition and discrimination of emotional cues in body language and systematically alters visual exploration patterns. These results highlight how internal physiological states can modulate affective processing of social interactions.

2.5 Project 4: The Social Brain: Motor Similarity Sharpens Affective Intention Decoding

*By Keck, Bachmann, Hegele, Munzert & Krüger (****PsyArxiv, September 2025****; under review in Plos Biology)*

2.5.1 Aim

The aim of this project was to investigate whether similarity between an observer's own motor repertoire and the observed movements shapes affective perception and neural representation of EBL. Building on the findings of the previous projects, this study integrated the movement features identified in Project 1, the neural decoding methods established in Project 2, and the observer-related perspective introduced in Project 3.

2.5.2 Methods

Eighteen participants first performed emotional interactions of varying affective intensity in a motion capture session, from which individual motor signatures were derived using key features identified in Project 1. Participants then rated the valence of point-light displays showing interactions with the same content acted by different executor's on two separate occasions. During a subsequent fMRI session, they viewed the same PLDs again. Each trial was classified as movement-similar or movement-dissimilar based on the degree of feature alignment with each participant's own recordings.

2.5.3 Analysis

We examined how movement similarity affected subjective ratings of valence, how it modulated BOLD responses within core AON regions such as the inferior frontal gyrus (IFG) and inferior parietal lobule (IPL), and how it influenced MVPA-based decoding accuracy of valence across movement-similar and movement-dissimilar trials. Theoretical interpretations were considered within the frameworks of direct matching theory, which predicts enhanced resonance and stronger activation for similar movements, and predictive coding theory, which proposes sharpened representations in IFG and reduced prediction error signals in IPL under conditions of movement similarity.

2.5.4 Results

Movement-similar actions led to more accurate valence decoding in the IFG and reduced IPL activation, whereas dissimilar actions elicited stronger subjective intensity ratings. While IPL patterns distinguished between positive and negative valence regardless of similarity group, IFG performance scaled with increasing affective intensity.

2.5.5 Conclusion

The findings are more consistent with a predictive coding account of the mirror neuron system than with direct matching. They suggest that the body functions as an embodied prior in decoding affective intent. Together, the results demonstrate that movement similarity modulates affective intention decoding in core regions of the AON by shaping subjective perception, dampening IPL responses, and sharpening IFG representations.

3 General Discussion

Research on emotion perception has long centered on facial expressions. In line with a recent shift in literature, this thesis focuses on affective information in body movements and the role of the observer. Across four studies, I show that movement features within social interactions, internal bodily states, and movement similarity shape how emotions are perceived. Together, the findings highlight that emotional meaning in body actions is not fixed but emerges from a dynamic behavioral, physiological, and neural interplay between stimulus and observer. Below, I outline key insights and their implications for embodied models of affective understanding.

3.1 Motion as Information: Intra- and Interpersonal Movement Cues in Affective Interactions

Bodily expressions are increasingly recognized as a rich channel for emotional communication (Witkower & Tracy, 2019). Projects 1 and 3 demonstrated that emotion recognition from body movements is on par with facial expressions, with specific movement features and bodily states contributing to this ability. To address this, Project 1 systematically decomposed expressive body movements in social interactions into kinematic and postural features, as well as interactive features. Using analytic techniques from univariate to multivariate tools, we provided evidence that emotion recognition is mainly driven by kinematic features. Our feature-based approach showed that, for example, vertical movement is significantly greater for happiness, compared to anger, affection and sadness. Among all analysed parameters, vertical movement emerged as the most distinctive and informative feature for predicting emotion categories based on movement alone and for explaining participants' emotion perception to a higher degree than any other feature when observing purely kinematic information. Moreover, different classes of features contribute differently to emotional judgments: kinematics were more predictive of discrete emotion categories, while postural parameters (e.g., body openness and contraction) were more aligned with valence attribution.

These findings are consistent with existing literature. For example, Michalak et al. (2009) showed that sad gait is expressed through reduced arm swing and vertical head movement. Differentiating emotions like fear and anger, Poyo Solanas and colleagues (2020a) showed that postural features like limb angles and symmetry distinguished emotions on the same valence spectrum. More recent work from Chen et al. (2023) showcased the importance of temporal kinematics like velocity and acceleration in emotion inference from gait, as well as the expression (Homagain & Martens; 2023). While our interpersonal feature approach aligns with existing models of emotion recognition (Kleinsmith & Bianchi-Berthouze, 2013), Project 1 is the first to computationally and systematically quantify dyadic interactions using interpretable motion features. Unlike prior work focused on individual cues, our method captures relational dynamics — such as proximity, orientation, and kinematic asymmetry — offering objective metrics for affect perception in social contexts (Schilbach et al., 2013). This approach advances the understanding of interpersonal emotions in two key ways: First, it helps distinguish reciprocal emotions like affection from sadness, which may be kinematically similar but differ in interactional features, such as time spent in personal space. Second, it allows differentiation between emotions with similar intensity but opposite valence — such as happiness and anger — by quantifying kinematic imbalances between interacting individuals. Emotions differ in both the degree and direction of these imbalances; for example, anger typically involves greater motion energy asymmetry than happiness.These findings build on work by Clarke et al. (2005) and Kret & de Gelder (2010), showing how social context and interaction-dependent features shape emotional interpretation.

In summary, Project 1 showed that affective information in body movements can be objectively categorized using kinematic, postural, and interactive features. Emotion categories were primarily encoded in kinematics, valence perception aligned with postural cues, and interactive features helped differentiate emotions within the same valence spectrum.

3.2 The Fronto-Parietal Network of Affective Intention Decoding

The AON plays a central role in deriving emotional meaning from observed actions, integrating perceptual and motor processes to support intention understanding. Within this network, frontoparietal regions are particularly important for decoding subtle kinematic cues. Koul et al. (2018) demonstrated that small variations in reach-to-grasp actions are distinguished in these areas, with MVPA highlighting the SPL, IFG and especially the IPL as key regions for intention decoding. To test whether this extends to complex, socially embedded body movements in affective interactions, Project 2 applied MVPA and parametric modulation and found that the IPL reflects both subjective valence impressions and validated valence categories, showing stronger encoding than other AON areas or classically valence-sensitive regions such as the amygdala and medial orbitofrontal cortex (mOFC). The IFG and premotor cortex (PMC) also contributed, though to a lesser extent. These findings support two conclusions: (1) the IPL functions as a central hub for intention decoding — from simple reach actions to affectively charged, whole-body social interactions — and (2) observing abstract biological motion activates AON regions more strongly than traditional valence-sensitive regions, suggesting that motor-based systems play a dominant role in affective interpretation when movement is present.

This contributes to a long-standing debate: Does the AON simulate the movement itself or the intention and affect it conveys? Jacob (2013) proposed that strong motor tuning reduces flexibility for goal attribution, implying mutual exclusivity between motor and intention coding. However, our results suggest that the motor system encodes affective intent directly from movement dynamics, even in minimalistic stimuli such as point-light displays (PLDs). In line with Koul et al. (2018) and theoretical work by Becchio et al. (2024), this supports the view that intentions are embodied in motor cues—from subtle kinematics to full social interactions. Project 1 showed that affect can be decoded from spatiotemporal features, and Project 2 confirmed that even subtle kinematic differences in PLDs evoke distinguishable neural and perceptual responses. This reinforces findings by Chikazoe et al. (2014) that affect is encoded in fine-grained neural patterns, though our results challenge their broader claim of modality independence for whole-body movements. While Chikazoe's work focused on static emotional stimuli involving OFC activation, our dynamic stimuli revealed modality-specific encoding within the AON, especially the IPL, highlighting a motor-informed mechanism for decoding affective meaning.

While Project 1 provided strong behavioral and feature-based evidence for decoding affect from body movements, and Project 2 showed that the AON encodes emotional valence during social interactions, neither directly linked these processes to motor resonance. Project 4 fills this gap by integrating Project 1's feature-based approach and Project 2's fMRI methods with a novel measure of movement similarity, advancing the discussion within the frameworks of the AON. Behavioral studies have shown that intention recognition improves when observed movements resemble the observer's own motor patterns (De Marco et al., 2020; Edey et al., 2017). Building on this, Project 4 demonstrated that movement similarity acts as an embodied prior in affective intention decoding. Two key findings emerged: (1) greater movement similarity led to less intense subjective impressions, higher neural pattern distinctiveness in the IFG, and reduced IPL activity, and (2) lower similarity resulted in more intense affective perception and less accurate decoding in the IFG, while IPL decoding remained stable across similarity levels. This reinforces the IPL's role — highlighted in both Projects 2 and 4 — as a central hub for linking movement and intention in observing interactive scenarios (Atkinson et al., 2023; Urgen & Orban, 2021), independent of movement similarity. Together, these findings point toward two interrelated conceptual mechanisms underlying the AON: motor resonance and predictive coding.

First, interpreting motor resonance as a mirroring mechanism supports the idea that movements themselves carry affective intentions (Projects 1–4) and that the observer's internal motor representations shape perception (Project 4). This supports the view that affective understanding can emerge from motor feature encoding, challenging the traditional dichotomy between movement and intention — as evidenced by Project 2 and further reinforced by Project 4. Intention recognition is not solely a visuomotor process; it depends both on the visual discriminability of actions (Project 1) and the degree of resonance with the observer's motor repertoire (Project 4). While it could be argued that motor resonance arises from visual familiarity, our findings align with Calvo-Merino et al. (2006, 2007), who showed that motor experience, not visual exposure, drives resonance — extending these insights from expert performance to everyday social interactions.

Second, our results contribute to the ongoing debate between direct matching models (DMM; Rizzolatti et al., 2006) and predictive coding models (PCM; Frith & Frith, 2005; Kilner, 2007). Our data support predictive coding, revealing a hierarchical organization between the IPL and IFG in decoding affective intentions. Using a feature-based movement similarity measure as an embodied prior, Project 4 showed that high similarity results in weaker affective impressions, more distinct IFG patterns, and reduced IPL activity — indicating efficient top-down matching. In contrast, low similarity leads to stronger affective responses, less accurate IFG decoding, and increased IPL activation, consistent with prediction error processing. Importantly, greater IPL activation for unfamiliar actions contradicts DMM predictions, which would expect reduced activation where matching fails. This suggests that DMM's feedforward model lacks the capacity to integrate contextual and affective priors (Kemmerer, 2021). This could explain the absence of parametric effects in Project 2 due to the lack of an interaction between movement similarity and valence perception, although this should be interpreted with caution as outlined in the following. Valence encoding is still present in AON areas, as indicated by multivariate results, but not captured by the linear assumptions of parametric modulation. Further support comes from causal evidence: only IPL disruption (theta-burst stimulation) impairs affective intention decoding, while IFG disruption does not (Patri et al., 2020). Additionally, Schippers and Keysers (2011) observed a top-down flow from the IFG to visual areas, consistent with the IFG forming predictions and the IPL refining them through prediction error. High-temporal-resolution studies (Amoruso et al., 2014; Panasiti et al., 2016; van Schie et al., 2004) further support this model, showing that motor familiarity dampens early prediction error signals, mirroring our observed early IPL suppression and later IFG refinement.

To conclude, affective intention decoding from observed movements relies on motor resonance, shaped by movement similarity and supported by a hierarchical frontoparietal network. Within this architecture, the IPL consistently emerges as a central hub for interpreting intentions embedded in kinematic features based on one’s own motor representation (Bischoff et al., 2012). While movement similarity enhances this process by providing internal motor priors, it is important to note that physiological states — such as inflammation — can also modulate how these intentions are perceived.

3.3 Physiological States Shape Perception: Inflammation as a Modulator of Affective Intention Decoding

Project 3 demonstrated that exercise-induced inflammation alters affective perception, leading to reduced recognition and sensitivity of emotional signals in body movements while also altering visual exploration. The resulting inflammatory response increased levels of IL-6, CRP, MCP-1, and myoglobin —biomarkers associated with inflammation and muscle damage. Given IL-6’s key role in neuroimmune signaling (Miller et al., 2009), these findings suggest that affective intention decoding is shaped not only by motor priors but also by internal physiological states. This interpretation aligns with the neuroimmune network hypothesis, which proposes that immune system activity influences brain function and social cognition (Nusslock et al., 2024). Previous studies have shown that inflammation can lower the ability to interpret the mental state of others (Balter et al., 2018) and empathy (Flasbeck et al., 2024). Interestingly, Swartz et al. (2021) found that elevated TNF-α levels in adolescents were associated with decreased functional connectivity between the IFG and IPL. Thus, one could speculate that acute inflammation disrupts affective intention decoding by weakening the connection between IFG and IPL, impairing motor resonance and the integration of social information. Support for this hypothesis also comes from gaze behavior observed in Project 3. Under inflammation, participants showed more fixations on sad stimuli, in contrast to a focus on happy stimuli under resting conditions. This shift may reflect altered fronto-parietal dynamics. The IPL, responsible for reorienting attention (Corbetta & Shulman, 2002), may assign greater relevance to negative information under inflammation. At the same time, the IFG, involved in detecting behaviorally salient cues, inhibitory control and regulation of emotional distraction (Corbetta & Shulman, 2002; Aron et al., 2004), may be less effective in modulating attention, allowing gaze to linger on negative content. This pattern aligns with findings from antisaccade tasks showing that emotional stimuli, especially anger, require coordinated IPL and IFG activation to override reflexive gaze (Llamas-Alonso et al., 2022).

Future studies could investigate this connection given the work of Project 3 and Project 4. Up until now there is no direct evidence, whether the immune-brain interactions directly impact the neural substrates of embodied social cognition in the fronto-parietal network.

3.4 Future Implications, Contributions and Limitations

The four projects presented in this thesis collectively advance our understanding of affective intention decoding, yet they also highlight methodological, clinical, and theoretical issues that point the way for future research and applications.

3.4.1 Methodological Advancements

A central methodological feature of this thesis was the consistent use of point-light displays (PLDs), which isolate movement and exclude confounding cues such as facial expressions or contextual information. This abstraction allows for precise analysis of spatiotemporal features underlying affective body language but reduces ecological validity, since real-world emotion perception depends on multimodal integration. Previous work has shown that PLDs may under-engage classical valence-sensitive regions such as the amygdala (Bachmann et al., 2018), suggesting that future studies should apply the feature-based framework to more naturalistic stimuli and leverage modern image-processing tools. In Projects 1 and 4, predefined movement features were employed, guided by perceptual approaches (Wallbott & Scherer, 1986; Kleinsmith & Bianchi-Berthouze, 2013) and integrated into the open-source SAMI toolbox (Zabicki & Keck, 2021). However, alternative data-driven dimensionality reduction techniques, such as PCA (Troje, 2002), factor analysis (Ivanenko et al., 2004), or blind-source separation (Roether et al., 2009), may provide greater objectivity. Although prior work has shown strong alignment between perceptually defined and computationally extracted features (Roether et al., 2009), it remains an open question whether purely computational methods, such as deep neural networks trained to recognize emotions from movements, can capture the perceptual and neural processes underlying affect recognition. Future studies could employ Representational Similarity Analysis (RSA) to compare feature-based and computational approaches and their respective contributions to behavioral perception. Finally, although this thesis applied parametric, univariate, and multivariate fMRI analyses (e.g., RSA, SVM), future work should explore network-level dynamics using methods such as Dynamic Causal Modeling or Granger

Causality. Incorporating stimuli of varying emotional intensity, as done in Project 4, would also improve ecological validity and allow a better understanding of graded affective perception.

3.4.2 Clinical Relevance

The similarity framework developed in Project 4 provides promising applications for clinical populations with restricted motor repertoires, such as those with hypokinesia. For example, patients with Parkinson's disease can often recognize categorical emotions but show attenuated intensity ratings, suggesting impairments in embodied simulation within the AON (Bellot et al., 2021). The present framework could therefore be used to test whether IPL attenuation is lowest for self-similar movements and whether IFG decoding scales linearly with movement similarity. More broadly, it offers a valuable tool for studying other populations with overlapping motor and socio-cognitive impairments (Eddy et al., 2018). Additionally, gaze patterns observed under exercise-induced inflammation in Project 3 parallel those reported in unmedicated depressed patients, who show increased fixation on negative and reduced attention to positive stimuli (Suslow et al., 2020). This suggests that combining movement similarity measures, eye-tracking, and inflammatory markers could provide new insights into the mechanisms underlying affective disorders.

3.4.3 Theoretical Advancements

The present work also contributes to theoretical developments in the study of affective perception. Project 1 demonstrated that emotional categories can be predicted from movement features, providing partial support for discrete emotion models. At the same time, the results of Project 4 showed that movement similarity shapes affective impressions and attenuates perceived intensity for similar movements, underscoring the limitations of a purely categorical approach. These findings align more closely with continuous models of affective perception, which can account for graded responses and individual variation, consistent with the neurophysiological process of motor resonance. Furthermore, the results address the debate between direct matching and predictive coding accounts. While direct matching theory predicts stronger resonance and higher activation for similar movements, the findings from Project 4 support predictive coding. Specifically, motor similarity appears to sharpen neural representations in the IFG and reduce prediction errors in the IPL, suggesting that the body functions as an embodied prior in decoding affective intent. Finally, it is important to distinguish between perception and direct experience of valence. For instance, Chikazoe and colleagues (2014) showed that gustatory stimuli engage distinct neural processes when experienced versus when perceived. Future work could use immersive technologies such as virtual and augmented reality to bridge this gap and investigate affective processing in more naturalistic social contexts.

In addition to these methodological, clinical, and theoretical considerations, several broader limitations must be acknowledged. These include the restricted ecological validity of PLDs, the relatively low ambiguity of many stimuli, and the limited attention to sex differences. Except for Project 3, all studies included mixed-gender samples despite evidence for differences in emotion perception (Alaerts et al., 2011) and inflammatory sensitivity (Engler et al., 2016; Lasselin et al., 2018). Future research should therefore implement controlled approaches to capture variability across sexes and enhance generalizability at the population level.

4 Conclusion

The outcomes of the four studies presented here provide evidence that body movements influence the decoding of affective intentions both through the movements we observe in others and through the way we move ourselves. This process is further modulated by acute inflammatory states. Specifically, we found that kinematic features contribute to emotion recognition, while postural features shape the perceived valence of the observed interactions. Social information in affective interactions enrich the perception through certain interactive features, such as the balance in motion energy, and enhance emotion categorization. While those movement features contribute to visual discrimination they enable a comparison between one's own movement and the movement of another, highlighting the attenuative nature of similiar movement within fronto-parietal regions of affective intention decoding. Thus, the subjective feeling of watching someone miss the train may differ depending on the observer — less intense for one whose own movements resemble the action, but more pronounced for another whose motor repertoire is dissimilar. But why? We interpret our findings in a predictive coding manner, where higher-order brain areas, such as the IFG, decrease prediction errors in the kinematic affective intention hub (IPL), while also showing that areas of the AON contain affect specific information based on movement alone. Yet, it is not only the movement I observe and the comparison with my own movement. Acute inflammation further alters affective intention decoding by attenuating sensitivity to bodily cues and shifting visual exploration toward negative social information.

Affective Intention Decoding

We started this thesis on a crowded train station with a quote from Proust. Across the four projects, we explored this very idea: the attempt to understand others by observing how they move — and through this, accessing their affective states. By decoding the emotional language of the body, examining how internal (physiological) states and motor (dis)similarity shape this decoding, and uncovering how the fronto-parietal network represent affective meaning, we have departed the train station closer to perceiving the world through the eyes of another.

5 Publications

Keck J., Zabicki, A., Bachmann, J., Munzert, J., Krüger, B. (2022) Decoding spatiotemporal features of emotional body language in social interactions. *Scientific Reports, 12, 15088.*

Bachmann J., Krüger, B., **Keck, J.,** Munzert J., Zabicki, A. (2022) When the timing is right: The link between temporal coupling in dyadic interactions and emotion recognition. *Cognition, 229, 105267.*

Preißler, L., **Keck, J.,** Krüger, B., Munzert, J., Schwarzer, G. (2023) Recognition of emotional body language from dayadic and monadic point-light displays in 5-year-old children and adults. *Journal of Experimental Child Psychology, 235, 105713*.

Hacker, S.[1], **Keck, J.[1],** Reichel, T., Eder, K., Ringseis, R., Krüger, K., & Krüger, B. (2023). Biomarkers in endurance exercise: individualized regulation and predictive value. *Translational Sports Medicine*, *2023*(1), 6614990.

Keck, J.[1], Honekamp, C.[1], Gebhardt, K., Nolte, S., Linka, M., de Haas, B., Munzert, J., Krüger, K. & Krüger, B. (2024). Exercise-induced inflammation alters the perception and visual exploration of emotional interactions. *Brain, Behavior, & Immunity-Health*, *39*, 100806.

Keck, J., Bachmann, J., Zabicki, A., Munzert, J., & Krüger, B. (2025). Decoding affect in emotional body language: Valence representation in the action observation network. *Social Cognitive and Affective Neuroscience*, nsaf021.

Nolte, S., Malhan, D., Klemmer, A., Kastner, T., Walter, N., Fleckenstein, D., **Keck, J.,** Klügel, S., Maier, C., Gebhardt, K., Stauber, T., Relogio, A., Krüger, K., Hollander, K. (2025) Training in normobaric hypoxia induces hematological changes that affect iron metabolism and immunity. *Scientific Report 15, 17757.*

Keck, J., Bachmann, J., Munzert, J., Hegele, M., & Krüger, B. (2025). The Social Brain: Motor Similarity Sharpens Affective Intention Decoding. https://doi.org/10.31234/osf.io/9ak4m_v1; under review in *PLOS Biology, submitted 17 of September 2025*

Software:

Zabicki, A., & **Keck, J.** (2021). SAMI: Similarity Analysis of Human Movements and Interactions (v0.1.0). Zenodo.

[1] shared 1st authorship

6 Appendix

Project 1 published as

6.1 Decoding Spatiotemporal Features of Emotional Body Language in Social Interactions

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Decoding spatiotemporal features of emotional body language in social interactions

Johannes Keck[1,2]✉, Adam Zabicki[1], Julia Bachmann[1], Jörn Munzert[1,2] & Britta Krüger[1]

How are emotions perceived through human body language in social interactions? This study used point-light displays of human interactions portraying emotional scenes (1) to examine quantitative intrapersonal kinematic and postural body configurations, (2) to calculate interaction-specific parameters of these interactions, and (3) to analyze how far both contribute to the perception of an emotion category (i.e. anger, sadness, happiness or affection) as well as to the perception of emotional valence. By using ANOVA and classification trees, we investigated emotion-specific differences in the calculated parameters. We further applied representational similarity analyses to determine how perceptual ratings relate to intra- and interpersonal features of the observed scene. Results showed that within an interaction, intrapersonal kinematic cues corresponded to emotion category ratings, whereas postural cues reflected valence ratings. Perception of emotion category was also driven by interpersonal orientation, proxemics, the time spent in the personal space of the counterpart, and the motion–energy balance between interacting people. Furthermore, motion–energy balance and orientation relate to valence ratings. Thus, features of emotional body language are connected with the emotional content of an observed scene and people make use of the observed emotionally expressive body language and interpersonal coordination to infer emotional content of interactions.

In everyday life, the expression of emotions is an essential part of human social interaction[1–3]. It is linked inseparably to the ability to observe, recognize, and evaluate the emotions of our conspecifics[4–8].

Affect expression occurs through combinations of verbal and nonverbal communication channels[9]. To judge other people's emotional states reliably, information can be decoded through nonverbal communication channels such as facial expressions or body movements and posture[10–17]. Up to now, most research in the field has focused on facial expressions. It has shown not only that people can express at least six different emotional states through their faces—anger, happiness, sadness, fear, surprise, and disgust—but also that these expressions demonstrate a high level of intercultural stability[18]. In recent decades, however, the focus of research has also shifted towards bodies. It has been suggested that recognition performance for bodily expressions is very similar to that for faces, and evidence has been provided that movements of the body or its segments also contain significant aspects of nonverbal communication[1,2,9,11,13,19]. For example, Michalak et al. have shown that gait patterns associated with sadness are characterized by reduced velocity, arm swing, and vertical motion of the head[2]. More recently, Poyo Solanas et al. demonstrated that fear is expressed through configurations of limb angles[9].

These studies indicate that postural and kinematic features vary depending on the emotional state, and that they influence the perception of emotion categories[2,3,9,20–24]. Postural and kinematic features can be summarized under the heading emotional body language (EBL). EBL is described as behaviour used to express emotions via the whole body coordinated in its movements across multiple joints and often accompanied by a meaningful action[11,25]. Thus, the use of space or the arrangement of body posture, gestures, and trunk and arm movements are tools through which the body can express an emotion[2,9,17,20,21,24]. In contrast to facial expressions, EBL is often more action-oriented, and it can be identified even when the face is not clearly visible[15,16,26]. It further enables the observer to recognize a situation and simultaneously acknowledge the action undertaken by an individual[11,26].

Consequently, EBL carries important information about not only the emotional state but also interindividual signalling[15,16]. Therefore, in this context, emotions can preferably be described as a dynamic relational process occurring between the individual and the environment[10]. In this vein, it has been demonstrated that contextual social information provided by interacting persons enhances the recognition of the emotional content of a scene and increases the observer's confidence in their perceptual judgement[7,10]. Important contextual cues in social

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interactions might be embodied synchronization or proxemic measures such as distance and orientation[27–29]. Taken together, the aforementioned studies suggest that interaction-specific parameters also contribute to the perception and identification of emotions. However, up to now, it remains largely unknown which features drive emotion perception in social interactions on the intra- and interpersonal level.

Here, we investigate for the first time both levels of body features in social interactions and their influence on the perception of emotions from body language. We provide a quantitative description and computational framework of movement features in social interactions using univariate and multivariate analysis. In detail, we investigated intrapersonal EBL by computing several kinematic and postural features and relating them to emotion perception. Moreover, we focused on interaction-specific characteristics that contribute to emotion perception. We used 48 point-light displays (PLDs) of human interactions portraying four emotions (happiness, affection, sadness, and anger). Participants observed these stimuli and were asked to categorize both the depicted emotional content and the valence of the perceived stimulus. We quantified different intra- as well as interpersonal movement features and analysed differences between emotional categories. To evaluate the relative importance of each calculated feature in the classification of emotional content, we trained different decision tree classifiers. Finally, we explored the correspondence of both the perceived emotional content and the perceived valence of a scene to the computational features on intra- and interpersonal levels via representational similarity analysis (RSA).

Materials and methods

Participants.

A total of 31 participants (16 women) with a mean age 23.58 ± 3.54 years participated in the experiment. None reported any history of psychiatric or neurological disorders and they had no history or current use of psychoactive medication. All procedures were approved by the local ethics committee of the Department of Psychology and Sports Science of the Justus Liebig University Giessen and adhered to the declaration of Helsinki. All participants provided written informed consent prior to participating.

Stimuli.

Stimuli were selected from a larger motion-capture data set[17]. Eight pairs of non-professional actors were instructed to perform an interaction portraying one out of four emotional scenes depicting either happiness, affection, sadness, or anger. To ensure a congruent behavioural pattern, actors were given a script of emotional situations and directed specifically to perform the same emotion. They were instructed to express their emotions intuitively within the context of the given situation, thereby allowing freedom and enhancing the variability of expression[17]. Interactions were recorded with an optical motion capture system (Vicon Motion Systems, Oxford, England) operating at 100 Hz. MATLAB software (Mathworks, Natick, MA) was used to create video files of 4-s sequences from the original coordinate 3D (C3D). In each video, 15 markers per person were plotted as white spheres on a black background to present a standard PLD model[30].

The final stimulus selection was based on prior validation of emotion category and perceived valence from 24 participants who did not take part in the present experiment. Valence was judged on an 11-point scale ranging from − 5 (*extremely negative*) to + 5 (*extremely positive*). There were two validation criteria: first, at least 50% of the participants had to recognize the displayed emotion (e.g., anger); second, the second-highest emotion rating should not exceed 25%. This allowed us to identify and exclude ambiguous scenes in which a specific emotion could not be recognized reliably. After validation, 12 stimuli that met both criteria were selected randomly for each emotion category. This resulted in a set of 48 (4 emotions × 12 scenes) stimuli. For more information on stimulus creation and validation, see Supplementary Figs. S1, S11 and [17].

Experimental procedure.

Prior to the present experiment, participants were given instructions and acquainted with the task. They subsequently performed a test run containing 12 trials that were not included in the main experiment.

In the experiment, each sequence was presented once, resulting in a series of 48 sequences. Sequences were displayed in a pseudo-randomized order on a 12-in. screen (refresh rate 60 Hz). The distance between each test person's eyes and the screen was approximately 40 cm. Each trial started with a fixation phase (1 s) followed by a stimulus sequence (4 s) and two behavioural ratings. After observing this sequence, participants were asked to assess the emotional valence of the videos on the same scale that had been used for stimulus validation (7 s). The second step was to sort emotions into one of the following categories: happiness, affection, sadness, or anger (4 s) (Fig. 1A).

Feature definition.

To investigate EBL characteristics that drive the perceptual judgement on an intra- and interpersonal level, we calculated several features using MATLAB software. From the 15 markers displayed, we chose 13 anatomical points (excluding sternum and sacrum) that presented anatomical landmarks on the upper body (including shoulders, elbows, wrists, and head) and the lower body (including hips, knees, and ankles). Features were calculated from the x, y, and z coordinates.

On an intrapersonal level, the three kinematic features (calculated for each anatomical point) addressed *velocity, acceleration*, and *vertical movement*. We implemented *symmetry*, *limb angles* (shoulder, elbows, hips, knees), *limb contraction* (distance from head to wrist and ankles), *volume,* as well as its *standard deviation (volume STD)* as postural features[9,24]. Each feature was calculated within each of the 400 frames and averaged across time and actors.

In a next step, we computed 12 interpersonal parameters. Proximity measures included *interpersonal distance* (*IPD*) and its variance over time (*IPD STD*), the percentage of time spent in the personal space of the other agent *(personal space),* as well as *interpersonal orientation* (*IPO*) and the ratio of orientation from one person to another to detect imbalances *(IPO balance)* in which the persons are turned towards each other[9,28,31,32]. To

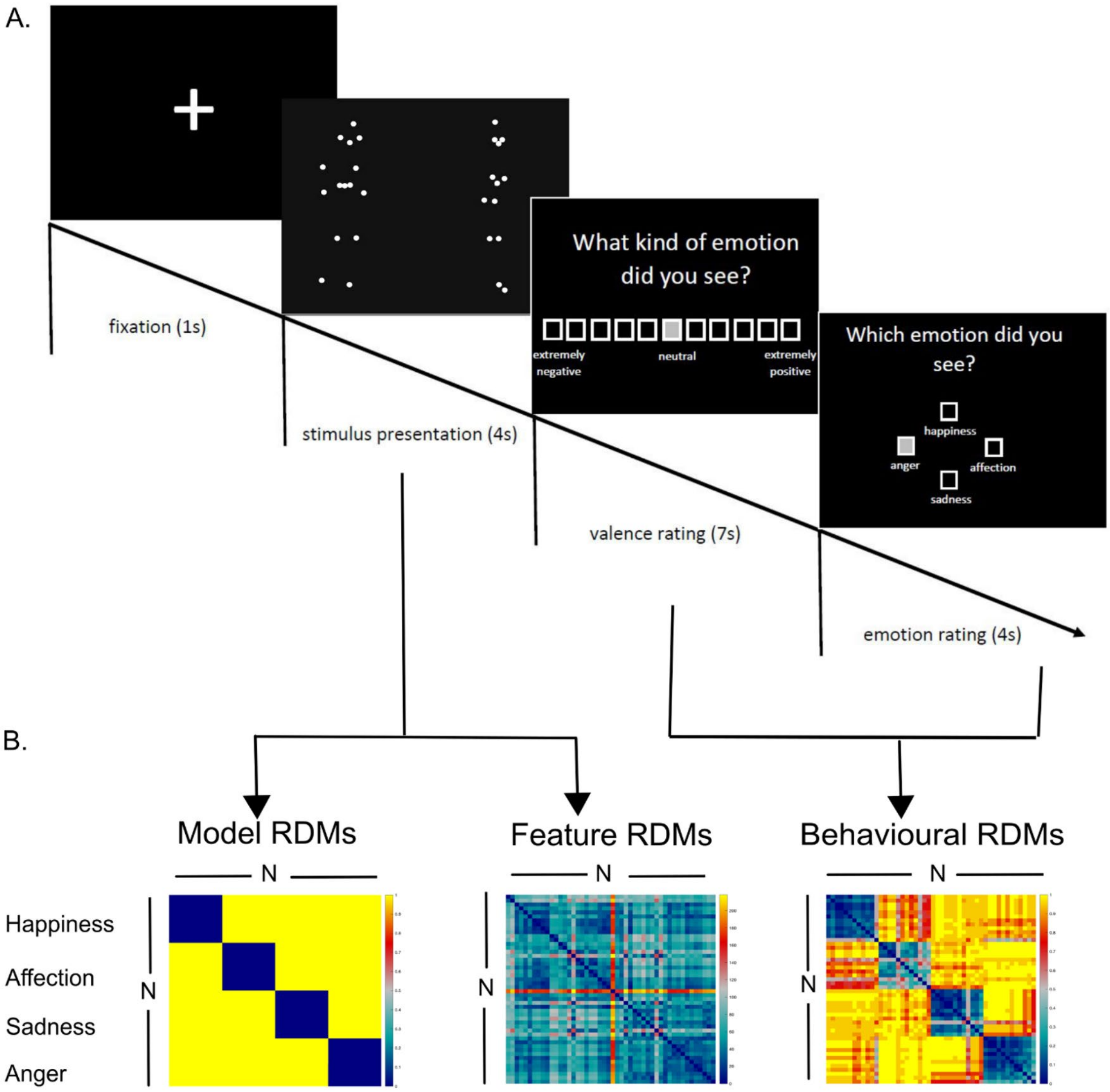

Figure 1. Experimental timeline and RDM creation. (**A**) Temporal structure of one trial. (**B**) Three different RDM types were created: first, model RDMs assuming categorical differences between emotions and valences by using binary variables (0 if identical, 1 otherwise); second, feature RDMs representing each parameter on the intra- and interpersonal level using Euclidean distance as similarity measure; third, behavioural RDMs using binary variables for emotion (1 if correct, 0 otherwise) and Euclidean distance for valence ratings.

investigate how the spatial distance between two people affects velocity, acceleration, limb angles, and limb contraction (with included time information), we correlated these measures with the distance profile (*distance correlations*). We also examined the synchronization of the velocity and acceleration profiles (*synchronization velocity & acceleration)*[29,33]. Finally, we calculated the proportion of the displayed motion energy *(motion–energy balance)* of each person[9,20,34]. For more detailed information on feature definitions and calculations, see Table 1, supplementary information, and[35].

Data analysis and statistics. As a first step, we calculated the recognition rates (accuracy) of stimuli for each emotional category by comparing the target emotion with the behavioural response. To ensure a sufficient degree of stimuli recognizability, we tested each emotional category against chance (25%) using Bonferroni-corrected one-sample t tests.

Influence of emotional categories. We tested for the emotion specificity of EBL features with a one-way ANOVA. The intrapersonal and interaction-specific features calculated from each stimulus were averaged across anatomical points and used as input. The ANOVA contained a four-level factor of emotion (happiness, affection, sadness, anger). Alpha was set at 0.05 for all statistical tests and post hoc pairwise comparisons were Bonferroni-corrected. Due to violations of the normal distribution in the values of interaction-specific features (*distance correlation, synchronization*), we normalized our data with a Fisher Z transformation[37,38].

	Abbr	Short description
Intrapersonal Features		
Acceleration	ACC	Derived from the calculated velocity
Velocity	VEL	Marker from the 3-dimensional motion trajectories divided by the according time interval (1/100 Hz = 10 ms)
Vertical Movement	VM	Absolute amount of displacement of each marker along the z-axis of subsequent frames
Volume	VOL	Multiplication of the distances between the minimum and maximum anatomical point of a agent along the x-, y-, and z-axes for each frame,
Volume Standard Deviation	VOL STD	respectively the standard deviation
Symmetry	SM	Symmetry contains height difference in z direction, the distance as well as circular segment to a predefined line of symmetry for each agent from corresponding left and right anatomical points
Limb Angles	LA	Shoulder (shoulder to elbow and hip), elbow (elbow to shoulder and wrist), hip (hip to shoulder and knee), and knee joint angles (knee to hip and ankle).
Limb Contraction	LC	Distances from the left and right ankle and the left and right wrist to the head
Interpersonal Features		
Average of Interpersonal Distance	IPD	Spatial distance between both agents. Calculated as the mean over time
Variance in Interpersonal Distance	IPD STD	respectively the standard deviation.
Average of Interpersonal Orientation	IPO	Time spent facing each other + time spent by one agent facing the other and vice versa.
Balance of Interpersonal Orientation	IPO BAL	Absolute value of the difference between orientation times of each agent divided by the sum of orientation times; higher value indicating greater balance level
Correlation between Spatial Distance and Velocity	DC VEL	Relationship of spatial distance between both agents and mean velocity of whole-body movements
Correlation between Spatial Distance and Acceleration	DC ACC	Relationship of spatial distance between both agents and mean acceleration of whole-body movements
Correlation between Spatial Distance and Volume	DC VOL	Relationship of spatial distance between both agents and volume
Correlation between Spatial Distance and Limb Contraction	DC LC	Relationship of spatial distance between both agents and limb contraction
Synchronization of Velocity	SYNC VEL	Correlation between agent's velocity profiles over time
Synchronization of Acceleration	SYNC ACC	Correlation between agent's acceleration profiles over time
Motion Energy Balance	ME BAL	Difference between amount of body movement (sum of averaged inter-frame Euclidean displacements of each marker) from each agent divided by the total amount of body movement in the scene; higher value indicating greater balance level
Personal Space	PS	Time spent in the personal space (within one arm length) of the interactive partner

Table 1. Summary of interaction-specific intrapersonal and interpersonal features calculated with the SAMI toolbox[35]. For a detailed explanation, see supplementary information.

Emotion classification with decision trees.

To evaluate the relative importance of each calculated feature in the classification of emotional interactions, we trained decision tree classifiers using Matlab Statistics and Machine Learning Toolbox (Version 11.6). Classification of stimuli was based on the weighted majority of multiple decision trees (bootstrap-aggregating approach) to avoid overfitting and enhance generalization[24,39,40].

Three different classifiers were trained for classification of emotions using averaged time information and averaged anatomical landmarks with different predictors: (1) M1 = intrapersonal features, (2) M2 = interpersonal features, and (3) M3 = combination of the two feature sets (M1 + M2).

To minimize the influence of randomly splitting the displayed 48 stimuli into the training and the validation dataset, we used leave-one-out-cross validation to estimate the performance of the different classifiers. To avoid imbalanced datasets and hence bias, each category was presented equally in training and test data (leave one stimulus out per category). For more information, see Supplementary Fig. S2.

Representational similarity analysis.

We used representational similarity analysis (RSA)[41,42] to characterize the relationship between the perceptual ratings and computed EBL feature sets for each of the 48 stimuli. By relating the stimuli to each other and arranging the values horizontally and vertically in the same order, we created a symmetrical representational dissimilarity matrix (RDM) (48 × 48). Each entry describes the relation between two stimuli. In the main diagonal, the stimuli values are compared with themselves, resulting in a diagonal defined as zeros.

In a first step, we created two different model RDMs by assuming a categorical distinction between the emotion and the valence category of the stimuli. Therefore, the dissimilarities between identical categories were 0 and those between different categories were 1 (Fig. 1B).

Second, we calculated 31 individual single-subject RDMs for emotion categorization by also using binary variables (0 if identical emotional rating, 1 otherwise). Furthermore, we used individual valence ratings to create RDMs in which each cell corresponded to the pairwise absolute difference. Here and in the following step, we used the Euclidean distance measure (Fig. 1B)[24,35].

To test which of the features related to the geometry of the model RDMs and the behavioural rating RDMs, we built feature RDMs representing the intrapersonal and interpersonal level (Fig. 1B). This step resulted in eight intrapersonal RDMs and 12 interpersonal RDMs.

To describe and test the relationship between all RDMs, we calculated a matrix of pairwise correlations (Kendall's τ_A) between model and feature RDMs separately on the intrapersonal and interpersonal level. To account for multiple testing, we applied Bonferroni corrections based on the number of features in each set. We used multidimensional scaling (MDS) to gain a graphical impression of representational distances (computed as 1 − Kendall's τ_A).

Furthermore, each feature RDM was tested against the behavioural RDMs using Kendall's τ_A for emotion categorization and Pearson correlation coefficients for valence ratings. Multiple testing was Holm–Bonferroni corrected, and the false-discovery rate was set at 0.05. The variance within the emotions and valence ratings across participants was represented by the noise ceiling and determined the amount of variance a model could explain.

In the last step, we aimed to explore perceptual judgements by merging the intra- and interpersonal level, analogous to M3. Therefore, we focused on the feature that best explained the behavioural rating on both levels and additionally outperformed the remaining features in pairwise comparisons. We normalized the representational geometry and created a common feature space by averaging the corresponding RDMs (Fig. S3). Next, we investigated the relationship between the produced feature combination RDM and single-participant behavioural RDMs and tested the resulting model against all other feature RDMs in the same manner as described above.

To calculate features and perform data analysis we used the SAMI toolbox, which is available on Github and archived in Zenodo[35].

Results

Emotion recognition of full body stimuli interactions. The present data revealed that overall emotion recognition was high. Anger sequences were categorized with the highest accuracy (M = 91.9%, SEM = 1.75), followed by happiness (M = 90.6%, SEM = 1.59), sadness (M = 87.63%, SEM = 1.77), and affection (M = 80.38%, SEM = 2.72). All four emotions were classified above chance level (happiness: $t(30) = 41.48$, $p < 0.001$; affection: $t(30) = 20.36$, $p < 0.001$; sadness: $t(30) = 35.48$, $p < 0.001$; anger: $t(30) = 38.27$, $p < 0.001$). For more information, see Supplementary Fig. S4.

Feature-based discrimination between emotion categories. On the intrapersonal level, the kinematic feature *velocity* revealed a significant main effect of emotion category. Bonferroni-corrected post hoc pairwise comparisons showed significantly faster movements for happiness compared to affection and sadness as well as for anger compared to sadness. *Vertical movement* also presented a significant main effect of emotion category: happiness was associated with more vertical displacement than anger, affection, and sadness. *Volume average* was significantly higher for happiness and anger than for sadness. The same was found for *volume STD* in which happiness and anger interactions were depicted through higher variance in volume than sadness.

For the interpersonal features, we found a significant main effect for *IPD* showing that the distance between two people was smaller when affection was expressed compared to happiness and anger. Likewise, *IPD STD* revealed smaller variability while expressing sadness compared to affection.

Examining distance correlation features (relation between IPD and intrapersonal features) revealed that *IPD* was associated more strongly with *limb contraction* when expressing affection compared to anger. The distance between interacting people affected *volume* to a higher degree when showing affection compared to anger.

A further main effect of emotion category was revealed for *personal space*. *Personal space* differed significantly between affection and happiness and between sadness and anger, showing that interacting people spent significantly more time in the *personal space* of their counterpart while expressing affection. Additionally, *IPO* revealed a significant main effect of emotion category showing that actors turned more towards each other while expressing affection compared to happiness, sadness, or anger. Regarding the *motion–energy balance*, we found a significant main effect of emotion revealing a lower *motion–energy balance* for sadness and anger compared to happiness and affection. Finally, balance in the time facing each other showed a main effect of emotion category with the highest *IPO balance* being for interacting agents portraying affection compared to sadness and anger. All results of the conducted ANOVAs can be found in Table 2. For more information, see Supplementary Figs. S5, S6, and Supplementary Table S1.

Feature importance for emotion classification. To examine the relative importance of specific features for emotion classification, we trained and tested three decision tree classifiers. The models differed in terms of the features used as predictors. Model M1 (intrapersonal features) provided an overall classification accuracy of M = 62.50% (happiness: M = 50.00%, affection: M = 50.00%; sadness: M = 75.00%; anger: M = 75.00%) compared to M = 68.75% for Model M2 (interpersonal features; happiness: M = 58.33%, affection: M = 83.33%; sadness: M = 66.67%; anger: M = 66.67%). Highest overall classification accuracy was provided by the combined Model M3 with an overall classification accuracy of M = 79.17% (happiness: M = 66.67%, affection: M = 91.67%; sadness: M = 91.67%; anger: M = 66.67%). M1 revealed the highest predictor importance for *vertical movement* and *limb angles* on an intrapersonal level (Fig. 2A). M2 showed that *IPD* and *motion–energy balance* were the most relevant features for classification on an interpersonal level (Fig. 2B). The combination model (M3) revealed the highest importance of *vertical movement*, *velocity, IPD*, IPO, and *motion–energy balance* (Fig. 2C).

Representational similarity analysis: relatedness of perceived emotions and EBL features. To determine the relationship between the perceptual impression and EBL features, we carried out an RSA. The visual comparison between the model RDMs (Fig. 3A) and the average rating RDMs (Fig. 3B) revealed a high structural similarity. In a first step, we compared model RDMs (Fig. 3A) and feature RDMs on the intrapersonal and interpersonal levels (Fig. 3C,D). Representational distances (computed as "1 − Kendall's τ_A correlation") of the categorical and feature RDMs are depicted via MDS plots. Visual inspection of the intrapersonal MDS plot (Fig. 4A) showed a clear separation between kinematic and postural features. Within the interpersonal RDMs (Fig. 4B) *motion–energy balance* was located closest to emotion and valence category RDMs.

	Happiness	Affection	Sadness	Anger
Intrapersonal Features				
VEL (mm/s) F(3,44) = 10.87, $p < 0.001$, $\eta^2 = 0.43$	M = 374 SEM = 41.30	M = 204.71 SEM = 31.16	M = 124.14 SEM = 14.80	M = 335.24 SEM = 45.05
VM (mm) F(3,44) = 21.69, $p < 0.001$, $\eta^2 = 0.6$	M = 748.63 SEM = 88.53	M = 248.46 SEM = 31.44	M = 188.81 SEM = 31.72	M = 497.18 SEM = 47.63
VOL (m^3) F(3, 44) = 5.66, $p < 0.01$, $\eta^2 = 0.3$	M = 0.38 SEM = 0.05	M = 0.32 SEM = 0.03	M = 0.22 SEM = 0.02	M = 0.38 SEM = 0.02
VOL STD (m^3) F(3, 44) = 5.58, $p < 0.01$, $\eta^2 = 0.3$	M = 0.1 SEM = 0.02	M = 0.07 SEM = 0.01	M = 0.04 SEM = 0.01	M = 0.11 SEM = 0.01
Interpersonal Features				
IPD (mm) F(3, 44) = 8.47, $p < 0.001$, $\eta^2 = 0.4$	M = 1023 SEM = 89.65	M = 622 SEM = 38.14	M = 910 SEM = 89.38	M = 1191 SEM = 97.89
IPD STD (mm) F(3, 44) = 3.02, $p < 0.05$, $\eta^2 = 0.2$	M = 97.99 SEM = 19.55	M = 122.34 SEM = 23.33	M = 45.90 SEM = 9.58	M = 99.12 SEM = 19.1
DC LC (Pearson's r) F(3, 44) = 4.18, $p < 0.05$, $\eta^2 = 0.22$	M = 0.43 SEM = 0.05	M = 0.55 SEM = 0.05	M = 0.62 SEM = 0.6	M = 0.39 SEM = 0.03
DC VOL (Pearson's r) F(3,44) = 3.49, $p < 0.05$, $\eta^2 = 0.19$	M = 0.42 SEM = 0.07	M = 0.49 SEM = 0.06	M = 0.53 SEM = 0.07	M = 0.28 SEM = 0.04
PS (%) F(3,44) = 7.49, $p < 0.001$, $\eta^2 = 0.34$	M = 33.71 SEM = 11.96	M = 88.91 SEM = 6.92	M = 46.86 SEM = 13.50	M = 24.25 SEM = 7.85
IPO (%) F(3, 44) = 9.01, $p < 0.001$, $\eta^2 = 0.4$	M = 40 SEM = 9 52	M = 79.63 SEM = 8.56	M = 32.21 SEM = 7.96	M = 25.15 SEM = 5.91
ME BAL (AU) F(3, 44) = 6.83, $p < 0.001$, $\eta^2 = 0.32$	M = 0.93 SEM = 0.01	M = 0.90 SEM = 0.02	M = 0.78 SEM = 0.05	M = 0.76 SEM = 0.04
IPO BAL (AU) F(3, 44) = 8.42, $p < 0.001$, $\eta^2 = 0.36$	M = 0.55 SEM = 0.13	M = 0.85 SEM = 0.08	M = 0.17 SEM = 0.1	M = 0.31 SEM = 0.11

Table 2. ANOVA of feature emotion categories.

Feature RDMs of *vertical movement, velocity, limb angles, limb contraction,* and *volume & volume STD* correlated positively with the emotion category model RDM. *Limb angles* and *limb contraction* also correlated positively with the valence model RDM. Regarding interpersonal features, we found weak positive correlations between *IPO balance*, *IPD*, *personal space*, *IPO*, and *motion–energy balance* and the emotion category model RDM; as well as between *IPO Balance*, *motion–energy balance*, and *IPD* and the valence model RDM (Fig. 4A,B).

Second, we determined the relatedness between EBL features and perceptual impressions by correlating emotion- and valence-rating RDMs and intra- and interpersonal model RDMs. Regarding the relationship between perceived emotion and intrapersonal features, we found significant correlations for all kinematic and postural parameters except *acceleration* (Fig. 5A). The highest correlations were for *vertical movement* ($r = 0.1$) and *velocity* ($r = 0.08$). It has to be noted that all correlations were rather low ranging from 0.01 to 0.1. Nevertheless, it is worth mentioning that *vertical movement* performed better than the remaining features as revealed by pairwise comparisons between the feature RDMs (Fig. 5A). None of the feature RDMs came close to the noise ceiling (0.29–0.31).

When comparing intrapersonal features with valence ratings, we identified significant correlations for each kinematic and postural feature ranging from 0.03 to 0.14. Data revealed that postural parameters performed better than kinematic parameters. As revealed by pairwise comparisons, *limb angles* correlated most strongly ($r = 0.12$) with valence ratings and performed significantly better than all other models (Fig. 5C). The second strongest correlation ($r = 0.08$) was found for *limb contraction,* which additionally outperformed all kinematic features. Hence, kinematic intrapersonal EBL features related more strongly to the perceived emotion category, and postural intrapersonal EBL features related more strongly to perceived valence.

The comparison between interpersonal feature RDMs and emotion category rating RDMs (Fig. 5B) revealed the highest correlation for *personal space* ($r = 0.07$). Furthermore, *IPO balance* ($r = 0.06$) and *motion–energy balance* ($r = 0.06$), as well as *IPD* ($r = 0.06$), *IPO* ($r = 0.06$), and *distance correlation limb contraction* ($r = 0.03$) performed significantly better than the remaining models ($p < 0.001$).

Regarding the comparison between interpersonal features and valence ratings (Fig. 5D), the highest explanatory value was provided by *IPO balance* ($r = 0.18$). This also outperformed all other models ($p < 0.001$) with the exception of *motion–energy balance* ($r = 0.18$). Except for the four *distance correlation* RDMs, all interpersonal

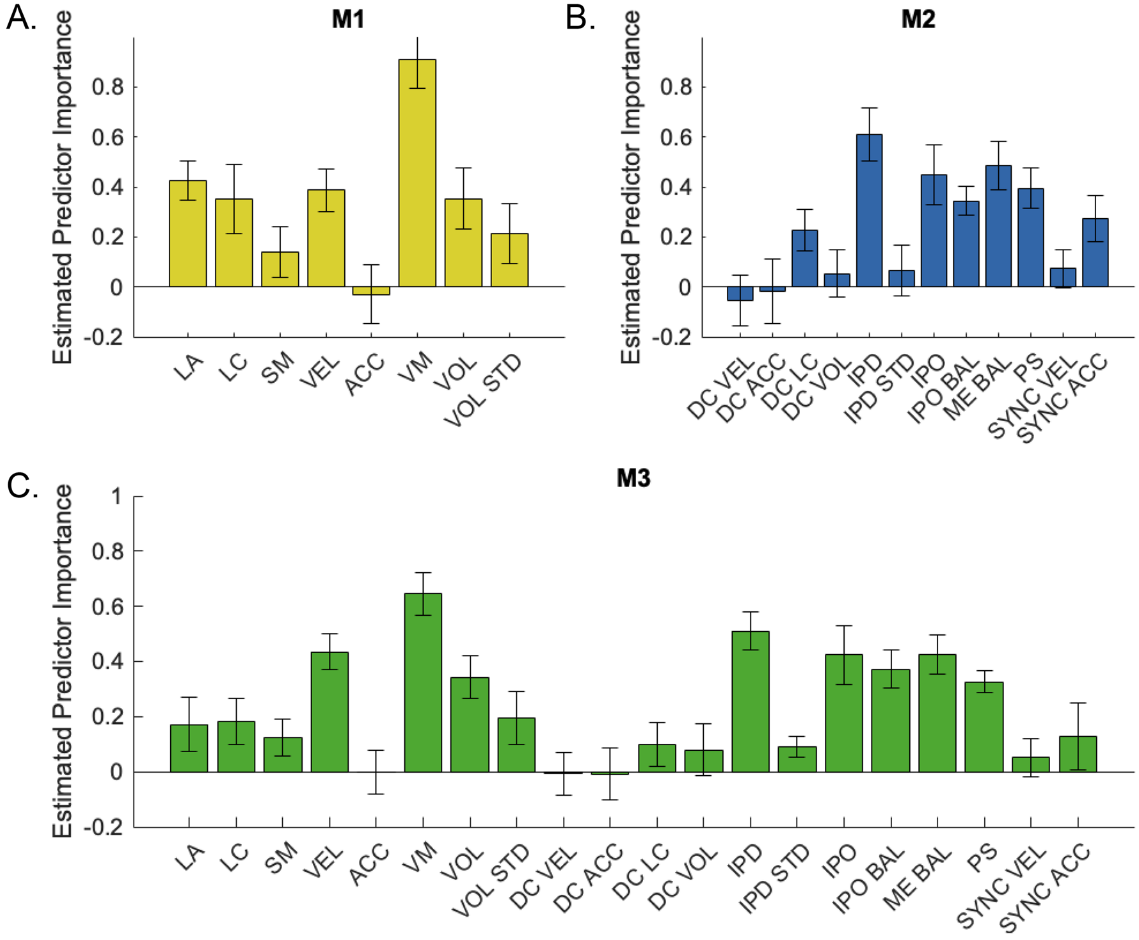

Figure 2. Estimated feature importance for emotion classification. (**A**) Model M1 = intrapersonal features as predictors (overall classification accuracy 56.75%). (**B**) Model M2 = interpersonal features as predictors (overall classification accuracy = 59.41%). (**C**) Model M3 = M1 + M2 combination model (overall classification accuracy of 69.54%). Bars and error bars show means and standard deviations of predictor importance for different validation samples. Chance level of emotion classification at 25%. *LA* limb angles, *LC* limb contraction, *SM* symmetry, *VEL* velocity, *ACC* acceleration, *VM* vertical movement, *VOL* volume, *VOL STD* volume standard deviation, *DC VEL* distance correlation velocity, *DC ACC* distance correlation acceleration, *DC LC* distance correlation limb contraction, *DC VOL* distance correlation volume, *IPD* interpersonal distance, *IPD STD* interpersonal distance standard deviation, *IPO* interpersonal orientation, *IPO BAL* interpersonal orientation balance, *ME BAL* motion energy balance, *PS* personal space, *SYNC VEL* synchronization velocity, *SYNC ACC* synchronization acceleration.

features attained weak significant correlations with valence ratings. Thus, emotion and valence perception of interacting people seems to depend most strongly on the displayed *motion–energy balance* and orientation as well as on proxemic measures (*IPD*, *IPO*, *personal space*).

Furthermore, we conducted an explorative analysis of feature combinations (Fig. 3E). Regarding emotion perception, we averaged vertical movement with each of the six highest performing interpersonal features (*IPO balance, personal space, motion–energy balance, IPO, IPD, DC LC*). Only feature combinations between *vertical movement* and *IPO* (r = 0.11) as well as between *vertical movement* and *motion–energy balance* (r = 0.11) performed significantly better than the remaining combination models and all intra- and interpersonal models ($p < 0.001$) except for the combination between *vertical movement* and *IPO balance.* This indicates that emotion perception of EBL was best predicted not by a single feature in isolation, but by a combination of several features.

Regarding valence perception, averaging *limb angles* and *IPO balance* (r = 0.21), as well as *limb contraction* and *IPO balance* (r = 0.2) revealed higher correlations. Furthermore, pairwise comparisons revealed significant differences between all combination RDMs and feature RDMs on both levels ($p < 0.001$), except for the combination between limb angles and *motion–energy balance* as well as the single feature *motion–energy balance*. For more information, see Supplementary Figs. S9, S10 and Supplementary Table 2.

Discussion

Our data provide a detailed quantitative description of movement features in emotional interactions that are related to emotion perception. The systematic decomposition of an interaction into an intrapersonal and interpersonal level reveals that both levels relate substantially to the emotional content of the scene as well as to

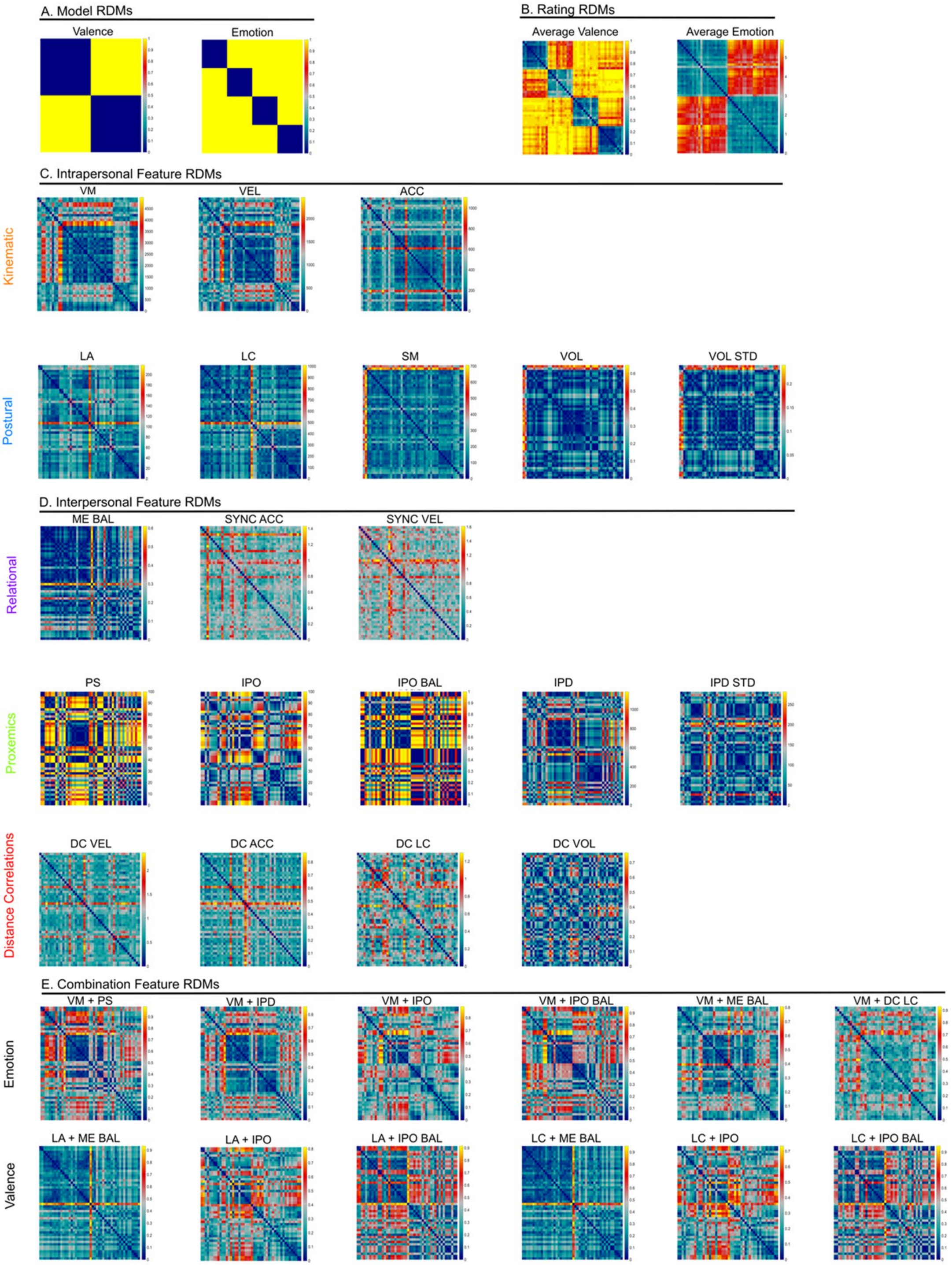

Figure 3. Representational dissimilarity matrices. (**A**) Theoretical model RDMs that assume different similarities based on emotion and valence categories (0 if identical, 1 otherwise). (**B**) Behavioural, averaged over participants emotion (1 if correct, 0 otherwise) and valence rating RDMs (Euclidean distance as similiarity measure). RDMs for (**C**) intrapersonal features, (**D**) interpersonal features and (**E**) combination features using Euclidean distance as similarity measure. *LA* limb angles, *LC* limb contraction, *SM* symmetry, *VEL* velocity, *ACC* acceleration, *VM* vertical movement, *VOL* volume, *VOL STD* volume standard deviation, *DC VEL* distance correlation velocity, *DC ACC* distance correlation acceleration, *DC LC* distance correlation limb contraction, *DC VOL* distance correlation volume, *IPD* interpersonal distance, *IPD STD* interpersonal distance standard deviation, *IPO* interpersonal orientation, *IPO BAL* interpersonal orientation balance, *ME BAL* motion energy balance, *PS* personal space, *SYNC VEL* synchronization velocity, *SYNC ACC* synchronization acceleration.

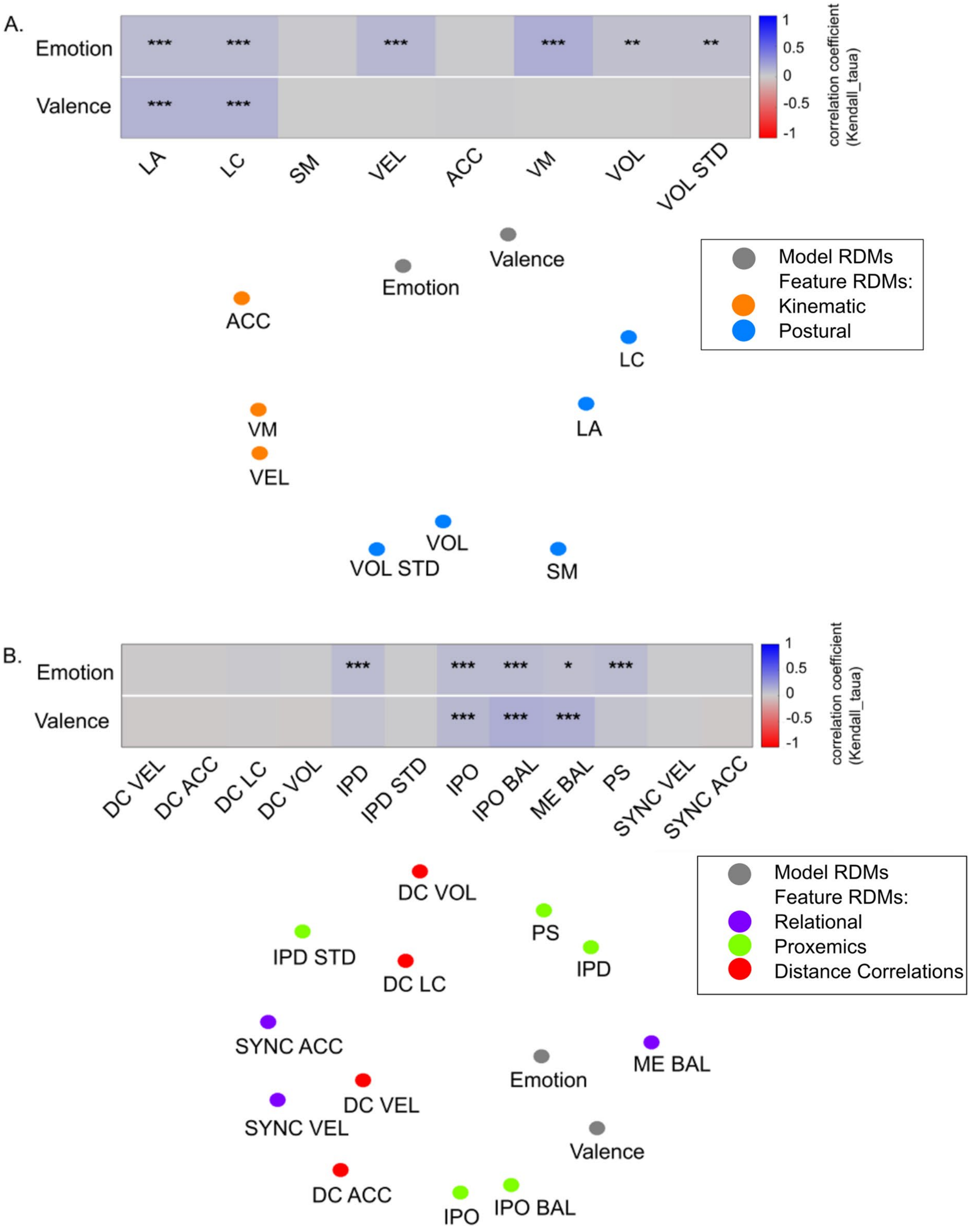

Figure 4. Relationship between model RDMs and feature RDMs for (**A**) intrapersonal features, (**B**) interpersonal features, as indicated by Kendall's τ_A correlation. Significant correlations shown by asterisks (*ns* not significant; *p < 0.05; **p < 0.01; ***p < 0.001). MDS plots approximate Kendall's τ_A correlation distance (1 – Kenadll's τA) among RDMs: the closer the points to each other, the more similar their corresponding RDMs.

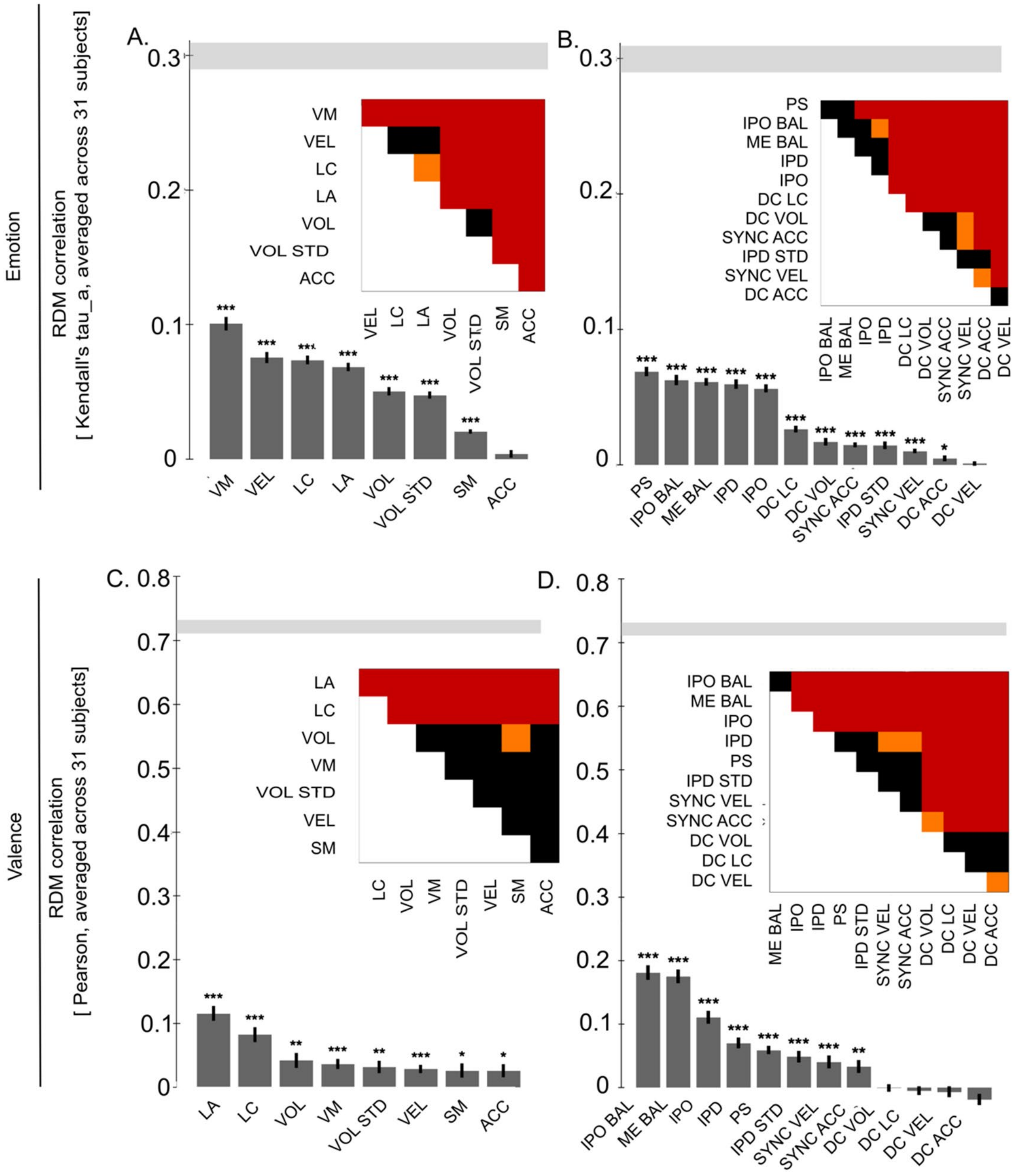

Figure 5. Relationship between behavioural RDMs and feature RDMs. (**A**,**C**) Intrapersonal Features; (**B**,**D**) Interpersonal Features; Kendall's τ_A correlation between emotion rating RDMs and Pearson correlation between valence rating RDMs. Significant correlations shown by asterisks (*ns* not significant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$, controlling FDR at 0.05). Lower and upper bounds of the noise ceiling are depicted by a grey bar. Pairwise comparisons indicate which feature RDMs perform significantly differently. Colour corresponds to significance level (black: ns; orange: $p < 0.05$; red: $p < 0.01$; calculated via two-sided signed-rank test across subjects, controlling FDR at 0.05). *LA* limb angles, *LC* limb contraction, *SM* symmetry, *VEL* velocity, *ACC* acceleration, *VM* vertical movement, *VOL* volume, *VOL STD* volume standard deviation, *DC VEL* distance correlation velocity, *DC ACC* distance correlation acceleration, *DC LC* distance correlation limb contraction, *DC VOL* distance correlation volume, *IPD* interpersonal distance, *IPD STD* interpersonal distance standard deviation, *IPO* interpersonal orientation, *IPO BAL* interpersonal orientation balance, *ME BAL* motion energy balance, *PS* personal space, *SYNC VEL* synchornization velocity, *SYNC ACC* synchronization acceleration.

its perception. We show that the emotional content of social interactions has a specific kinematic and postural fingerprint and can be described via quantitative intra- and interpersonal parameters. Both levels are linked to each other inseparably. This linkage is reflected not only by a model that integrates intra- and interpersonal features (M3) exhibiting the best performance but also by the explorative analysis of feature combinations. We further show a strong correspondence between those features that characterize the emotional content of a stimulus and the features that are critical for emotion perception[3]. Representational similarity analysis reveals that it is especially kinematic parameters that contribute to the perception of emotional content on an intrapersonal level; whereas on an interpersonal level, balance and proxemics parameters are important cues for the observer. It also becomes apparent that observers use mainly interaction-specific information to decode relational emotions such as affection. We further found that intrapersonal postural parameters such as *limb angles* and interpersonal balance parameters such as *motion–energy balance* and *IPO balance* show the strongest relation to the valence percept.

Recently, de Gelder and Poyo Solanas have proposed a framework in which perceptually relevant information from bodies via movement and posture is coded in the brain through midlevel features such as limb contraction and head-to-hand distance[43]. Our results support the importance of these midlevel features and add computational interaction-specific parameters to their framework. The present data show that the emotional content of a scene is characterized by midlevel features such as *velocity* or *motion–energy balance*. For example, happy interactions are characterized by higher *velocity* profiles than affection and sadness, but not higher than anger. These findings are broadly consistent with those reported in the existing literature[2,3,19,20,22]. Affectional and sad interactions show a high degree of similarity regarding their intrapersonal kinematic and postural parameters. These emotions, however, reveal characteristic differences on the interpersonal level (e.g., *IPO, IPO Balance, IPD STD, personal space*).

Regarding emotion perception, our findings show an association to characteristic body expressions on both the intra- and the interpersonal level. Representational similarity analysis reveals that *vertical movement*, *IPO (average & orientation)*, and *motion–energy balance* are best suited to explain emotion perception. In contrast to some research reports[12,24,36,44], we were unable to distinguish emotional categories via postural features such as *limb angles* and *limb contraction*. Here, it has to be taken into account that most former studies used stimuli depicting a single person mainly in a frontal view and not social interactions observed from a third-person perspective as in the present study. The present data show that participants confused happiness with anger, although only to a small extent. Conversely, anger trials were more often confused with sadness than with happiness. Most often, affection stimuli were confused with happiness. A study investigating emotions in gait[3] has demonstrated that confusions occur preferentially between emotions that share a similar level of movement activation: angry gaits tend to be confused with happy gaits, and sad gaits with fearful ones. Thus, these authors concluded that *velocity* is particularly important for the perception and expression of emotions[3,20,22]. Our findings also suggest that velocity of movements is important in the process of emotion recognition. However, velocity is not sufficient to distinguish between emotions such as anger and happiness, especially within social interactions where interpersonal cues such as proxemics or balance are available for the observer. Interpersonal cues such as *motion–energy balance* between two agents allow a perceptual distinction between happiness and anger. *Motion-energy balance* explains (1) the high degree of confusion between happiness and affection and (2) the low degree of confusion between anger and happiness when social information is available. *Motion-energy balance* within interactions, therefore, seems to be an important property for the observer to generate an emotional percept. Hence, social context information is particularly important for recognizing emotional content, especially when the depicted emotions depend more on reciprocal interactions (e.g., affection)[10,45]. The present results provide a computational framework for this observation. For example, affection differs from other emotions only regarding its interpersonal movement characteristics. This is underpinned by the calculated classification trees: the intrapersonal model is less accurate than the interpersonal model, underlining that emotions such as affection have a strong interpersonal character and that the spatiotemporal coupling of two moving agents seems to be of great significance especially for perceiving socially expressible emotions[10,17].

Besides emotion recognition, we were interested in the perceived emotional valence—a dimension that reflects the subjective impression of a scene related to approach–avoidance tendencies[46]. Our data reveal that on the intrapersonal level, postural features such as limb angles best explain the participants' valence perception. Regarding interpersonal features, *motion–energy balance* and orientation between interacting people are the best predictors of perceived valence.

Finally, we observed a noteworthy, albeit not significant, trend towards a synchronization of *velocity* profiles, indicating that higher synchronization between people is associated with a positive impression of the perceived interaction. A study investigating interpersonal behaviour in a social task has shown that patterns of proxemic behaviours and interpersonal distance predicted the subjective quality of interactions[28]. Thus, balance and spatiotemporal harmony are predictors for both the experienced and the observed quality of an interaction.

Interestingly, our RSA results show that emotion category recognition is better predicted by kinematic features, whereas valence perception is related more to postural features of the stimuli. Basically, human emotions can be conceptualized within a two-dimensional model comprised of emotional valence (the subjective value—i.e., positive vs negative) and arousal (intensity)[47,48]. The present results reveal that emotions possessing the same valence (e.g., anger and sadness) are more similar in terms of the actors' postural features. Further, we observed that emotions that differ in terms of their valence but are similar in terms of their intensity (e.g. happiness and anger) resemble each other regarding their kinematics. Thus, one might assume that postural features might be more likely to reflect the valence and kinematic features might be more likely to reflect the arousal or intensity of the presented stimuli.

Altogether, we found a set of EBL features that characterizes emotional content and predicts the perception of the emotional quality of human interactions. These features are defined on an intra- and interpersonal level and include kinematic, and postural characteristics as well as proximity, balance, and synchronization. We conclude that the perception of human emotional interactions is a function of not only inherent kinematics of the agent but also interpersonal balance and proximity between agents.

Limitations and future implications. It should be noted that the present and comparable studies differ with respect to the stimulus material used, stimulus length, emotional content, contextual information, and feature calculation[17,24]. These differences explain the partly heterogeneous results on emotion perception. Despite this heterogeneity, perception and recognition of emotional content are robust regardless of the stimulus material used. Thus, humans seem to weigh the relative importance of different movement features flexibly depending on the specific stimulus properties presented to them.

We have to acknowledge that neither an intrapersonal nor an interpersonal feature correlates with the perceptual performance on the noise ceiling level, and that we found only weak positive correlations in the present study[24]. One reason for this may be that many features are similarly pronounced in different emotion categories. For example, happiness and anger are characterized by similar velocities. Hence, it would seem appropriate to develop models that integrate multiple feature dimensions of the observed scene. First solutions are offered by the present attempt to use a combination of features to classify the emotional content as well as to predict the emotional percept. Future studies, however, might apply more ecologically valid stimuli and combine different features in a multidimensional space in order to phenotype emotion specific properties of EBL in social interactions. Such approaches that aim to decode emotional human states from a combination of nonverbal signals on multiple levels are highly relevant in the context of human–robot interaction in order to ensure natural communication[47–50].

Data availability

The datasets used and analyzed during the current study are available from the corresponding author on reasonable request. The source code is available at https://zenodo.org/record/4764552#.YiXYKi9Xb0p (MATLAB).

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Author contributions

Conceived and designed the experiments: J.K., A.Z., J.B., J.M., B.K. Performed the experiments and analyzed the data: J.K., J.B., A.Z. Discussed the results and wrote the paper: J.K., A.Z., J.B., J.M., B.K. All authors approved the final version of the manuscript.

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Competing interests

The authors declare no competing interests.

Additional information

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6.2 Decoding Affect in Emotional Body Language: Valence Representation in the Action Observation Network

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Decoding affect in emotional body language: valence representation in the action observation network

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Abstract

Humans are highly adept at inferring emotional states from body movements in social interactions. Nonetheless, it is under debate how this process is facilitated by neural activations across multiple brain regions. The specific contributions of various brain areas to the perception of valence in biological motion remain poorly understood, particularly those within the action observation network (AON) and those involved in processing emotional valence. This study explores which cortical regions involved in processing emotional body language depicted by kinematic stimuli contain valence information, and whether this is reflected either in the magnitude of activation or in distinct activation patterns. Results showed that neural patterns within the AON, notably the inferior parietal lobule (IPL), exhibit a neural geometry that reflects the valence impressions of the observed stimuli. However, the representational geometry of valence-sensitive areas mirrors these impressions to a lesser degree. Our findings also reveal that the activation magnitude in both AON and valence-sensitive regions does not correlate with the perceived valence of emotional interactions. Results underscore the critical role of the AON, particularly the IPL, in interpreting the valence of emotional interactions, indicating its essential function in the perception of valence, especially when observing biological movements.

Keywords: valence; point light displays; action observation network; social interactions; biological motion

Introduction

Imagine observing two people from a distance. One person is gesticulating violently, while the other shifts their gaze to the ground. Without even discerning their facial expressions, you quickly form the impression that one person appears to be very angry, whereas the other seems concerned. Simultaneously, you get an idea of the positivity or negativity of the observed scene. This example showcases our astonishing ability to swiftly gather rich information from people's movements, enabling us not only to understand their inner states but also to evaluate them subjectively.

Humans can express and recognize emotions through various channels, including voice, face, and body (de Gelder 2006). In recent years, the study of whole-body emotion expressions referred to as "emotional body language" (EBL) has gained significant prominence in the cognitive sciences (de Gelder 2006, Atkinson et al. 2012, de Gelder et al. 2015, Bachmann et al. 2018). EBL describes the expression of emotion by the body using not only coordinated and distinctive movement patterns associated with certain emotions containing different stereotypical body postures and gestures but also interpersonal and interactional cues (Johansson 1973, De Meijer 1989, Wallbott 1998, Pollick et al. 2001, Clarke et al. 2005, Keck et al. 2022, Atkinson and Vuong 2023).

Neurophysiological research has extensively explored the brain regions involved in the perception and recognition of EBL. These studies have demonstrated convincingly that perceiving emotional bodily expressions involves a large neural network. This network is organized around the action observation network (AON) containing the premotor cortex (PMC), the inferior frontal gyrus (IFG), and the inferior parietal lobule (IPL) and superior parietal lobule (SPL) (Grèzes et al. 2007, Pichon et al. 2009, Kret et al. 2011a, 2011b). Further regions belonging to the AON are the dorsomedial prefrontal cortex, the supplementary motor area (SMA), and regions attuned to bodies (e.g. extrastriate body area and fusiform body area) and biological motion [superior temporal sulcus (STS); see Caspers et al. (2010), Downing and Peelen (2011), Grossman and Blake (2001), and Schwarzlose et al. (2005) for meta-analyses]. Structures involved in emotion and valence processing such as the lateral orbitofrontal cortex (OFC) and amygdala are also activated when perceiving EBL, especially

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when full light displays are observed (Gallagher and Frith 2003, Saxe 2006, Carrington and Bailey 2009).

How emotional valence is represented in the human brain has been investigated intensively across various stimulus categories [see Lindquist et al. (2016) for a meta-analysis]. Emotional valence refers to the subjective impression of an object, experience, or scene in terms of its pleasantness or unpleasantness, thereby reflecting its subjective value (Frijda 1986, Kuppens et al. 2013). Neurophysiological studies point to a central role of the OFC (Ongür and Price 2000). Both the lateral and medial OFC regions appear to contain affective representations of stimuli from various modalities (Small et al. 2003, Chikazoe et al. 2014, Lindquist et al. 2016). For instance, the medial OFC and the adjacent ventromedial prefrontal cortices have been linked to reward expectancy, outcome values, and the experience of positive valence. Regarding the preference for negative valence, particularly the left amygdala shows consistent increased activation (Lindquist et al. 2016). However, Lindquist et al. (2016) have suggested a lack of truly valence-specific processing pathways. Instead, they claimed that a flexible affective workspace correlates with positive and negative valence across several brain regions. In this context, Chikazoe et al. (2014) found that neural populations in various brain regions, including the OFC, encode both positive and negative affect.

Despite our advanced understanding of how EBL is processed and how we perceive emotional valence from various types of stimuli, the neural underpinnings that enable humans, as observers, to discern the emotional valence depicted through others' kinematics are still not fully understood. In particular, the roles of specific areas within the AON and regions sensitive to emotional valence require further exploration. This study focuses on two primary objectives: first, we seek to identify which AON and valence-sensitive regions convey valence information when processing EBL depicted by kinematic stimuli. Second, we investigate whether the processing manifests through the magnitude of activation or through distinct patterns within the identified regions of interest by using representational similarity analysis (RSA) and multi-voxel pattern analysis (MVPA). Given the need to infer the emotional content of biological movements exclusively from their kinematics, we hypothesize that certain areas within the AON, which are pivotal for intention recognition from kinematics, play a specialized role in interpreting the emotional valence of the observed stimuli.

Materials and methods

Participants

Twenty adults (11 females; mean age: 26.8 years; SD = 5.85 years) with normal or corrected-to-normal vision participated in our study. None reported any history of psychiatric, neurological, immunological or physical disorders, or a current use of psychoactive medication. Prior to participation, all participants gave written informed consent in compliance with the Declaration of Helsinki. The procedure was approved by the local ethics committee of the Department of Psychology and Sports Science of Justus-Liebig-University Giessen.

Stimuli

Emotional interactions were depicted using point-light displays (PLDs), drawn from a motion-capture dataset developed by Lorey et al. [see Lorey et al. (2012) for full details]. The stimulus set employed here includes 20 emotional PLD interactions that differ in terms of their valence and difficulty. PLD interactions are short-video sequences (4 s, third-person view) showing white dots on a black background with each dot representing specific anatomic landmarks of the actors' bodies covering both upper (shoulders, elbow joints, wrists, and forehead) and lower body parts (hips, knee joints, and ankles) and providing only kinematic information. They depict the movements of two actors portraying one of four emotions: anger, sadness, happiness, and affection. Interactions containing anger and sadness were grouped in the category "negative" emotion, and interactions with affection and happiness were pooled in the category "positive" emotion. Easy stimuli were those interactions on which 91%–100% of viewers agreed on the emotion being portrayed. The difficult stimuli were those with a consensus rate of 50%–70% [see Lorey et al. (2012) for further details].

Additionally, for each stimulus, a scrambled version was created to serve as a control by eliminating form and body information while retaining the dynamic aspects of the motion. These scrambled versions were generated using PLAViMoP software (Decatoire et al. 2019). All stimuli did not differ with respect to their kinematics (see Supplementary Fig. S1).

Design and task

During fMRI scanning, participants performed six runs of 40 trials employed in an event-related paradigm. Each run contained 10 positive trials (5 easy and 5 difficult) and 10 negative trials (5 easy and 5 difficult). We further added a control condition using a scrambled version of each stimulus. This resulted in a total of 240 trials and a 50-min scanner session overall. Stimuli from all conditions were presented in a pseudorandomized order within each run and counterbalanced across participants. Each trial started with a fixation for 1 s followed by a jitter (0%–90% of Repetition Time (TR) in 10% steps, average 1.5 s) (Fig. 1a). Then PLD or scrambled sequences (4 s) were presented. After observing the sequence, participants were asked to rate the perceived emotional valence on an 11-point Likert scale ranging from −5 ("very negative") to +5 ("very positive") (4 s). After each valence rating, a second rating assessed rating confidence from 0% to 100% confidence (4 s). Figure 1a depicts the whole procedure, except for confidence rating since the analysis presented here was centered on valence perception.

fMRI: image acquisition

fMRI data were collected on a Siemens Prisma 3-T whole-body scanner (Siemens Prisma, Erlangen, Germany) using a 20-channel head coil. A structural image was acquired from each participant consisting of 176 T1-weighted sagittal images (1-mm slice thickness; MPRAGE) and a fieldmap (40 slices; TR = 1000 ms; Echo Time (TE) = 10 ms). For functional imaging, six runs with 265 volumes per run (i.e. a total of 1590 volumes) were registered using a T2*-weighted gradient echo-planar imaging sequence covering the whole brain with 40 slices (slice thickness = 3 mm; 0.75 mm gap; descending interleaved; TR = 2000 ms; TE = 30 ms; flip angle = 75°; field of view = 210 mm × 210 mm, 2 mm in-plane isotropic resolution). The orientation of the axial slices was parallel to the Anterior Commisure - Posteriore Commisure line. Trial onsets were jittered within 0%–90% of the TR Image.

Data analysis and statistics

Univariate analysis

Image preprocessing was carried out using SPM 12 (Wellcome Department of Imaging Neuroscience, University College London, UK). Origin coordinates were adjusted to the anterior commissure,

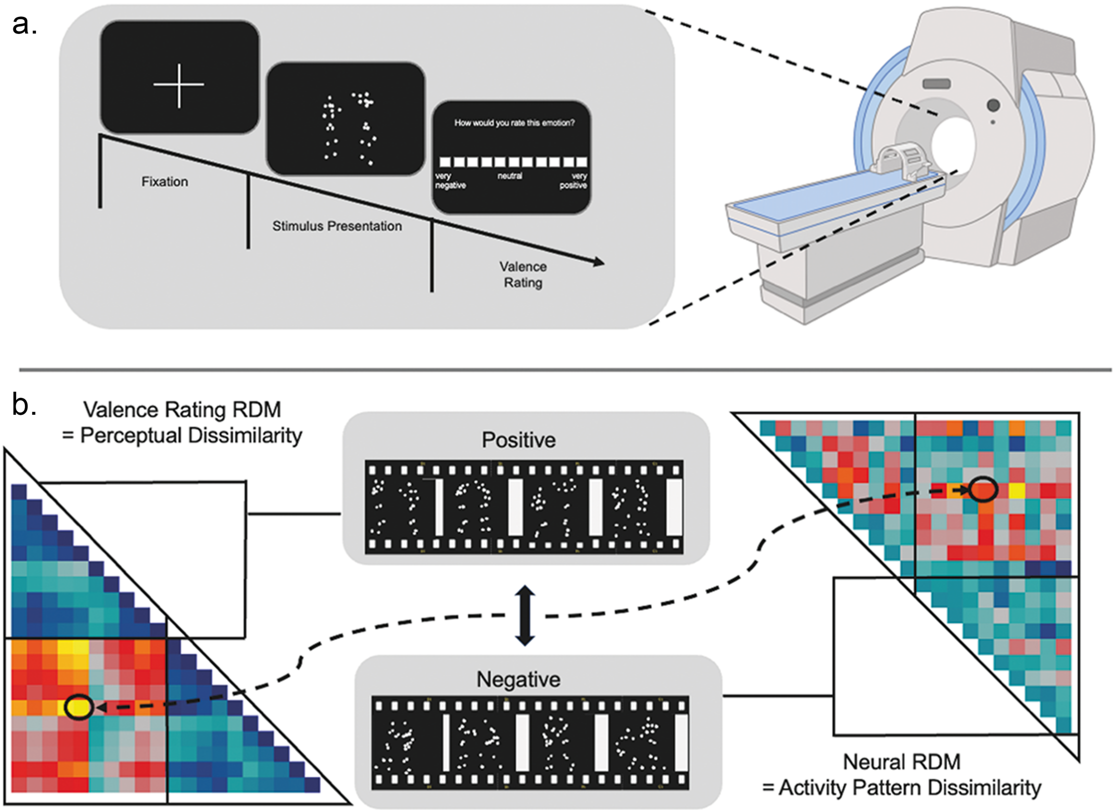

Figure 1. Experimental timeline and RDM creation. (a) Temporal structure of one trial. (b) Example interaction of positive and negative scenes (center). In the upper and lower triangle of RDMs, each entry describes the relation between two stimuli. In the main diagonal, the stimuli values are compared with themselves, resulting in a diagonal defined as zeros. In the lower triangle on the left, behavioral RDMs are created by calculating the absolute distance between valence ratings. In the upper triangle on the right neural RDMs are created by calculating the cross-validated Mahlanobis distance between each pair of neural activities. All RDMs are arranged horizontally and vertically in the same order going from positive (10 stimuli) to negative (10 stimuli).

and realignment (2nd Degree B-spline interpolation to the first volume of each functional run) and unwarping were performed using voxel displacement maps generated from the fieldmaps (Hutton et al. 2002). Sinc interpolation was utilized to correct for timing differences in slice acquisition within a single volume. The anatomical data were corrected for B1-field inhomogeneities. Furthermore, the functional images were coregistered with the anatomical scan for each subject. Smoothing was executed with an isotropic three-dimensional Gaussian filter with a full-width-at-half-maximum (FWHM) kernel of 5 mm. Furthermore, normalization to the standard space of the Montreal Neurological Institute brain was performed.

The first-level analysis was computed participant-wise using the general linear model (GLM). A boxcar function was convoluted with the hemodynamic response function. The observation phases for each condition were entered into the model. Boxcar function length covered the respective observation intervals. Moreover, six movement parameters of the rigid-body transformation of the motion-correction procedure were introduced into the GLM as covariates. The voxel-based time series were filtered by a low-pass filter (FWHM = 4 s) and a high-pass filter (time constant = 256 s).

Parametric analysis

Prior to multivariate analysis, we examined brain regions showing increased BOLD signal with increased ratings of emotional valence via a parametric analysis. The parameter values were included as a modulator of the observation regressors representing the main regressor of the GLM. We investigated the hypothesis that valence-sensitive regions would reflect the perceived positivity or negativity of a stimulus. Regarding the modulation of activation magnitude by valence, we tested the positive correlation between the parameter and the brain activation for each participant (the more positive the rated valence, the higher the activation), and vice versa (the more negative the valence rating, the higher the activation). Then, the resulting parameter estimates were entered into a second-level, one-sample *t*-test in which the mean estimate across participants at each voxel was tested against zero (random effects model). The statistical threshold was set at $P = .05$, corrected for multiple comparisons using the family-wise error (FWE) criterion.

Multivariate analysis

Regions of interest

The anatomical scan was used to reconstruct the cortical surface of each hemisphere using FreeSurfer (http://surfer.nmr.mgh.harvard.edu). Regions of interest (ROIs) were selected on the basis of previous findings reported in the literature on EBL observation (Caspers et al. 2010, Bachmann et al. 2018) and valence perception (Lindquist et al. 2016). These were defined anatomically on an individual basis using the FreeSurfer parcellation algorithm (Destrieux et al. 2010). We defined 10 ROIs bilateral as follows: "IPL," "SPL," "IFG," "SMAprop," "preSMA," "dorsal PMC (dPMC)," "ventral PMC (vPMC)," and "STS" (AON regions), as well as “mOFC” and “amygdala” (valence-sensitive regions). Defining ROIs on an individual basis allowed us to work with high anatomic precision and avoided the need for spatial normalization. See Supplementary Table S1 for details on ROI sizes.

Preprocessing

For the multivariate analyses, we carried out a separate preprocessing. First, realignment and unwarping were performed using voxel displacement maps generated from the fieldmaps (Hutton et al. 2002). The functional images were coregistered with the anatomic scan for the respective subject. Smoothing was executed using an isotropic three-dimensional Gaussian filter with an FWHM kernel of 2 mm.

General linear models

A first-level analysis was computed with SPM 12 using separate GLMs for each subject and each of the six runs. We created 20 boxcar regressors corresponding to the 10 positive (5 easy and 5 difficult) and 10 negative (5 easy and 5 difficult) scenes. The boxcar functions of each regressor spanned the observation (4 s) and rating period (8 s). Each regressor was convoluted with a canonical hemodynamic response function. Moreover, six movement parameters from the rigid-body transformation of the motion-correction procedure were entered as covariates in the GLM. The voxel-based time series were filtered with a high-pass filter (time constant = 128 s).

Representational similarity analysis

We employed an RSA to characterize the geometry of neural representations of perceived valence while observing different affective interactions. Representational dissimilarity matrices (RDMs) characterize the pairwise dissimilarity of activation patterns evoked by all observed emotional interactions and, therefore, allow a direct comparison between representational spaces from the behavioral measures and fMRI activation patterns by mapping the correspondence between their similarity structures. For this analysis, we used the toolbox from Nili et al. (2014). For each ROI, all pairwise comparisons were assembled in an RDM. Our first step was to estimate the true activity patterns by applying multivariate noise normalization to the beta coefficients obtained for each stimulus (Walther et al. 2016). In the second step, we calculated the cross-validated Mahalanobis distance to quantify the dissimilarity between each stimulus pair, resulting in a 20 × 20 representational dissimilarity matrix (RDM) (10 positive scenes, 10 negative scenes; see Fig. 1b). Cross-validation was achieved by using the six runs as inputs for a six-fold cross-validation procedure. RDMs were calculated separately for each experimental run and averaged for each subject. This yielded 20 brain RDMs (one per subject) for each of the 10 ROIs that were used to calculate the average similarity between activity patterns across participants. Then, we used multidimensional scaling (MDS) to project the high dimensional RDM space onto two dimensions and gain a graphical impression of representational distances. For this purpose, the 20 subject RDMs were averaged to obtain a single RDM per ROI.

Association between valence rating and its neural representation

We tested the association between the subjectively perceived valences and the geometry of neural representations that might cause them. For this purpose, we first created rating dissimilarity matrices (rating DMs) representing the structure of the stimulus ratings for each stimulus. For each subject, we compared the mean stimulus valence ratings to each other by calculating the absolute difference between them. This difference served as the dissimilarity, again leading to a 20 × 20 rating DM. To compare brain and behavioral RDMs, we used Pearson’s product-moment correlation coefficients and a one-sided signed-rank test across the single-subject RDM correlations. To test differences between fits across ROIs, we used two-sided signed-rank tests across subjects for each pair of brain RDMs. To account for multiple testing, we controlled the false-discovery rate at 0.05. The amount of variance in the behavioral response that a brain RDM can explain is limited by the variability across subjects and indicated by a noise ceiling (gray bar, Fig. 3d).

Decoding stimulus valence

In a last step, we carried out a multi-voxel pattern analysis (MVPA) in order to analyze whether the neural patterns during observation were distinct enough to decode the observed experimental condition. To assess the specific response patterns within a specific ROI, we employed a support vector machine (SVM). The analysis included leave-one-run-out cross-validation for each subject and ROI. To reduce the number of features, we applied a principal component analysis. In each iteration of the cross-validation, we split the corresponding vectors into a set of tests (one run out of six) and training data (all remaining runs), with 100 vectors (5 runs × 20 stimuli). SVM was provided with labels indicating each condition of the training samples, a decision boundary was extracted based on these data, and this boundary was applied to predict the condition of the test data. We compared each of the assigned valence labels and counted correct and incorrect assignments as 1 and 0. The whole procedure was repeated until each run had served as test data. Then, we calculated the proportion of correct assignments across the six-folds of the cross-validation process. This proportion was derived for each subject and each ROI.

To assess the significance of the decoding accuracies, we conducted a permutation analysis involving random labeling of the valence condition (positive vs. negative interaction). This approach offers a more robust evaluation of statistical significance compared to a one-sample *t*-test against chance (cf. Stelzer et al. 2013). Across 2000 iterations per subject and ROI, the condition labels for the 100 data samples (training data) underwent random shuffling. The classification accuracy of this randomly labeled dataset was then computed using the leave-one-run-out cross-validation approach outlined earlier. Probability values were determined by calculating the proportion of random shuffles that resulted in an accuracy equal to or greater than the one observed for the actual (unshuffled) labels. All *P*-values underwent correction for multiple ROIs using the Holm–Bonferroni method (Holm 1979).

Results

Parametric analysis

Prior to multivariate analyses, we conducted a parametric modulation analysis to determine which brain sites were modulated by the perceived stimulus valence. Results revealed no valence-dependent variation of neural activation with respect to the magnitude. No brain areas were found to show either a positive or negative correlation with the perceived valence (FWE-corrected).

Multivariate fMRI results

Representational similarity analysis

Visual inspection of MDS plots (Fig. 2) showed a spatial organization of positive and negative interactions within the IPL, IFG, vPMC, and dPMC (Fig. 2b). In these regions, positive and negative

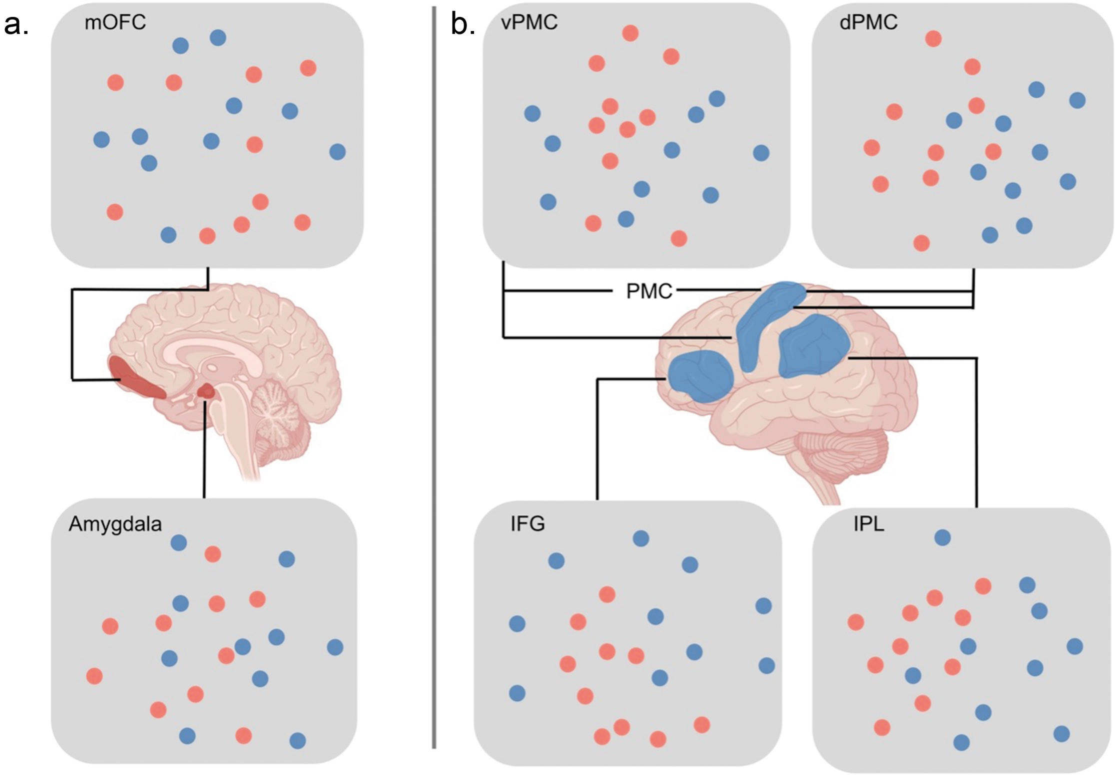

Figure 2. MDS plots of brain RDMs. For each ROI, an MDS plot (minimizing metric stress) shows the similarities of the neural pattern elicited by positive (blue) or negative (red) social interactions. The closer the dots are to each other, the more similar their neural patterns. The brain in the middle shows the anatomic location of ROI labels. (a) valence-sensitive regions & (b) Action-Observation Network.

interactions were nearly separated into two clusters in which especially the perceived negative scenes were located closer to each other and thus showed a more similar pattern than perceived positive scenes. This was especially true for the IPL. MDS plots of the mOFC and the amygdala revealed that the scenes were not as sharply separated as in the AON areas (Fig. 2a).

Subjective valence representations

Cross-subject results yielded a behavioral RDM with a high degree of similarity within but not between the two valence categories (Fig. 3b), showing that subjects were able to distinguish very reliably between positive and negative interactions. The described high similarity in the behavioral ratings can be seen in the near upper (Pearson's $r = 0.85$) and lower (Pearson's $r = 0.83$) bounds of the noise ceiling.

Via RSA, we aimed to explore whether the perceived valence (subject ratings) could be explained by the neural geometry of the investigated ROIs. Results showed that the RDM of the left IPL correlated significantly with the rating RDM. It should also be noted that IPL RDM correlated significantly more strongly with perceived valence than all other investigated brain RDMs (Fig. 3d; Table 1). Other AON areas whose RDMs correlated significantly with the behavioral RDM were the RDMs of the IFG, the dPMC, the vPMC, and the STS of both hemispheres, as well as the RDM of the left SPL. It should be noted that the brain RDM of the left and right IFG and the left dPMC also correlated more strongly with the behavioral RDM than all remaining brain RDMs (Fig. 3d). The brain RDM of the amygdala and the mOFC of both hemispheres also correlated significantly with the behavioral RDM, but to a significantly lesser degree than the RDMs of nearly all AON regions. All other investigated brain RDMs did not correlate significantly with the behavioral RDM. All results are reported in Table 1, and remaining RDMs can be found in Supplementary Fig. S2.

Decoding

To investigate whether the neural patterns in the investigated ROIs were distinct enough to differentiate between the observed positive and negative interactions, a decoding was carried out. Regarding the stimulus valence, a significant classification was possible only for the left IPL (Fig. 3c). Accuracies and SEM for decoding results are reported in Table 1.

Discussion

We found that neural patterns within the AON—specifically, within the IPL and IFG, as well as within the dPMC and vPMC—display a neural geometry reflecting the valence impression of observed PLD interactions. Notably, the IPL demonstrates a distinct valence-dependent gradient, transitioning from the highest similarity between the negative scenes to the lowest similarity between the negative and positive scenes. This neural signature in the IPL is crucial for the successful decoding of the affective content of the observed scenes. Interestingly, areas often associated with valence processing (i.e. the mOFC and the amygdala) do not allow a decoding of stimulus valence, and their representational geometry reflects to a lesser extent the valence impression of the observed scenes compared to AON areas. Our findings also indicate that it is not the activation magnitude within AON and valence-sensitive regions that reflects the perceived valence of PLD interactions but the representational codes.

This study highlights the specific role of the IPL within the AON in deciphering the emotional valence of observed interactions. The representational geometry of the IPL most closely reflects the

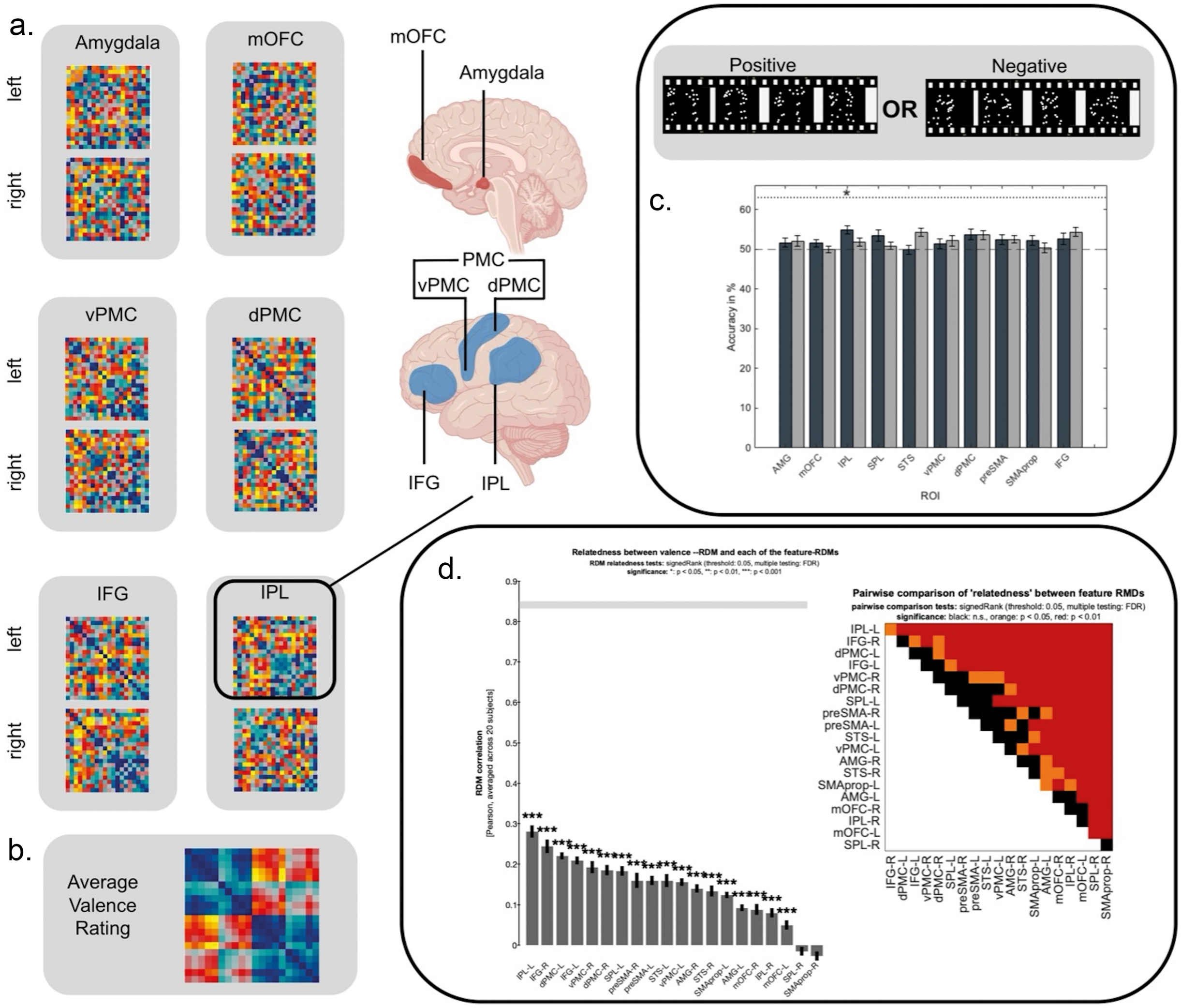

Figure 3. Representational dissimilarity matrices, decoding accuracies, and relationship between neural RDMs and valence rating RDMs. (A) Neural RDMs for left and right amygdala, mOFC, vPMC, dPMC, IFG, and IPL (Mahlanaobis distance as similarity measure). (B). Valence rating RDM averaged across participants (absolute distance as similarity measure). (C) Decoding accuracies for each investigated ROI and permutation analysis. Significant correlations shown by asterisks (*$p < .05$). (D). Pearson linear correlations between valence rating RDMs and averaged neural RDMs. Significant correlations shown by asterisks (*$p < .05$; **$p < .01$; ***$p < .001$, controlling FDR at .05). Lower and upper bounds of the noise ceiling are depicted by a gray bar. Pairwise comparisons indicate which neural RDMs perform significantly differently. Color corresponds to significance level (black = not significant; orange = $p < .05$; red = $p < .01$; calculated via two-sided signed-ranks test across subjects, controlling false-discovery rate at .05).

perceived emotional valence of the scenes, indicating its crucial role in perceiving valence in kinematic stimuli. Areas traditionally associated with processing emotional valence and subjective affect appear to have a secondary role in the present task.

The AON: valence coding when perceiving kinematics of emotional interactions

It has been suggested that the AON plays an important role in understanding other people's actions and their underlying intentions by integrating observed actions with the personal motor repertoire (Caspers et al. 2010). The IPL plays a key role in this. It is known to be relevant for the sensory-to-motor mapping of visual input (i.e. an observed action) onto the observer's body coordinates (Buccino et al. 2004). Neural activity within the IPL can even use subtle kinematic features of observed acts to discriminate between different intentions (Koul et al. 2018, Patri et al. 2020). Regarding the processing of EBL, several neurophysiological studies have demonstrated that the IPL plays a prominent role in processing emotional content of human actions (Sinke et al. 2010, Engelen et al. 2018). Whereas univariate studies underline the notion that the IPL exhibits a sensitivity toward the processing of negative emotions (Engelen et al. 2015, 2018, Meeren et al. 2016, Poyo Solanas et al. 2018), multivariate studies further indicate that it exhibits emotion-specific stimulus-independent representations (Downing and Peelen 2011, Cao et al. 2018).

This study elucidates that the IPL exhibits distinct neural response patterns associated with negative and positive scenes. The analysis further demonstrates that the neural geometry of the left IPL is best aligned with the behavioral RDM. Specifically, the IPL's neural codes for observed negative scenes show a high degree of similarity, whereas codes for negative and positive scenes show a notable dissimilarity, thus reflecting the rating behavior of participants. These findings underscore that the IPL's neural geometry represents both the affective content of scenes as well as the perceived affect. The pronounced similarity in neural patterns for negative scenes

Table 1. Decoding accuracies and RDM correlations. Average decoding accuracy and standard error of the mean regarding the distinction between positive and negative valence of a scene. Pearson linear correlation coefficients between brain regions and perceptual RDMs and their respective standard error of the mean.

		Decoding		RSA	
ROI	L/R	Accuracy (%)	SEM	Correlation to behavioral RDM	SEM
Amygdala	L	51.62	1.17	0.10	0.01
	R	52.06	1.30	0.14	0.01
mOFC	L	52.46	1.23	0.05	0.01
	R	52.46	1.01	0.09	0.01
IPL	L	**55.01**	1.00	**0.28**	0.02
	R	51.71	1.03	0.08	0.01
SPL	L	49.87	1.15	0.18	0.02
	R	54.17	1.03	−0.02	0.02
STS	L	51.45	1.26	0.16	0.02
	R	52.15	1.31	0.13	0.01
vPMC	L	52.63	1.37	0.16	0.01
	R	54.34	1.12	0.20	0.02
dPMC	L	53.73	1.28	0.22	0.01
	R	53.55	1.11	0.18	0.01
preSMA	L	52.24	1.22	0.16	0.01
	R	50.35	1.30	0.16	0.02
SMAprop	L	53.46	1.38	0.12	0.01
	R	50.83	0.89	−0.03	0.02
IFG	L	51.49	0.85	0.21	0.01
	R	49.87	0.85	0.24	0.02

suggests that the IPL is particularly attuned to negative emotional content within human actions. Affective actions articulate specific expressions of an individual's needs and intentions, thereby also enabling the prediction of future behaviors (Flanagan and Johansson 2003, Wilson and Knoblich 2005). This capability, especially in recognizing negative emotions, is vital for ensuring one's physical and psychological safety (Baumeister et al. 2001, Vaish et al. 2008). This suggests that the IPL may have evolved a specialized adaptation for processing negative affect.

The IPL is suggested to be a shared neural substrate between action and perception and, thus, involved in the process of internal simulation (Rizzolatti et al. 2006). Recent findings underscore its role in processing spatiotemporal contingencies of social interactions and generating somatosensory representations of body states with perceived emotions (Ross and Atkinson 2020, Atkinson and Vuong 2023). Our findings underlie the importance of the IPL in the process of understanding kinematic information with emotional content through simulation.

The RSA revealed additional AON sites exhibiting a representational geometry that, to some extent, maps the valence impressions of the observed scenes. The neural pattern in the IFG as well as vPMCs and dPMCs correlated strongly with the behavioral RDMs. Yet, the patterns in these regions—specifically, in the IFG and both the dorsal and ventral sections of the PMC—were not sufficiently distinct to decode the content of the observed stimulus.

The IFG is, like the IPL, involved in action understanding (Iacoboni et al. 2005, Rizzolatti et al. 2006, Li et al. 2020), thereby inferring intentions and action outcomes (Buccino et al. 2004, Patri et al. 2020). It is particularly active when observing complex and goal-directed actions (Caspers et al. 2010), whole-body actions, and interactions, but less active when observing independently acting individuals (cf. Caspers et al. 2010, Centelles et al. 2011). Furthermore, the IFG has a specific sensitivity to emotions transported via body language (Saygin et al. 2004, Gazzola et al. 2007, Keuken et al. 2011, Quadflieg and Koldewyn 2017).

It becomes apparent that neural responses of both regions—the IFG and the IPL—are modulated by action intention as well as by emotion in actions (Keuken et al. 2011, Ansuini et al. 2015, Cao et al. 2018). A recent study by Patri et al. (2020) tried to clarify the specific roles of the IFG and the IPL in action observation. It found that disruption of activity in the IPL, but not in the IFG, impaired an observer's ability to interpret the intentional significance of changes in discriminative kinematic features. This provides causal support for an architecture in which especially the IPL represents goals or intentions during action observation. This observation could account for our result that the IPL outperformed the IFG and other AON regions in representing the affective intention of the observed kinematic stimuli.

Besides the IPL and IFG, the PMC displays the affective valuation of the observed scenes. The PMC exhibits a particular sensitivity for emotional body movements (Grèzes et al. 2007, Pichon et al. 2009, Sinke et al. 2010), as well as for social scenes, thereby underscoring the notion that it contains a tuning to more complex action representations than meaningless movements (Centelles et al. 2011). Hoshi and Tanji (2006) have further demonstrated that important functions of the PMC are to match motor acts with sensory inputs (vPMC) and to plan and prepare for potential actions the observer might need to perform in response (dPMC). Whereas the IFG and the PMC areas are both central nodes of the AON and active during the observation of (emotional) actions, their roles might differ to a certain degree. The IFG is more involved in the cognitive and interpretative aspects of action observation, focusing on understanding the meaning and intentions behind actions (Iacoboni et al. 2005). In contrast, the PMC is involved more directly in the motor aspects, including the simulation, prediction, and preparation to imitate the observed action or to respond to it appropriately (Fogassi et al. 2005, Molenberghs et al. 2012). Therefore, the better representation of the affective content within the IPL and the IFG compared to the PMC in the present task of observing affective PLD interactions might be explained by the fact that subjects did not have to react to the observed scene. The present task is more about understanding the content of the PLD scenes than preparing an action. This might be especially facilitated by the stimuli used here. The observation of kinematic PLD stimuli, which have a certain degree of abstraction, can further reduce the urge to (re)act.

Valence-sensitive areas when observing biological motion in social interactions

Limbic areas such as the amygdala and several cortical areas such as the OFC often reveal increased activity when affective valence is being represented during emotion experience and perception, pain, aversion, and orgasm [see Lindquist et al. (2012) for a review]. Studies examining the neural processing of EBL also showed an involvement of the OFC (Pichon et al. 2009, Sinke et al. 2010) and the amygdala (Pichon et al. 2009, Mattek et al. 2020). For example, Pichon et al. (2009) showed an increased BOLD response in the OFC when observing angry compared to fearful stimuli in a person presented from a frontal viewpoint. Similarly, several studies revealed an increased amygdala activation, especially when participants observed full-light displays of fearful or angry bodies (Hadjikhani and De Gelder 2003, Hortensius et al. 2017), thereby underlining the notion that the amygdala is a central node for the neural processing of negative affect (especially fear- and anger-related stimuli) (LeDoux 2003). However, our data revealed that neural activation within neither the amygdala nor the OFC is modulated when perceiving an interaction that is more negative. Furthermore, it was not possible to decode the positive or negative valence of a scene, and the neural geometry of AON areas more accurately reflects the perceived valence rather than the neural geometry of valence-sensitive areas.

The present experiment's findings suggest that valence perception is less apparent in valence-sensitive areas and more pronounced in AON regions. This distinction may arise from the different types of stimuli used compared to those in other studies. For instance, previous experiments often employed stimuli that either evoked emotional responses directly in observers or used images and videos of people displaying emotions—typically negative ones—from a frontal view (Pichon et al. 2009, Chikazoe et al. 2014). In contrast, our experiment utilized kinematic depictions of human movements observed from a third-person perspective, because we aimed to explore how movement information from others can contribute to perceiving emotional valence. It seems possible that these depictions of interactions from a third-person perspective may not evoke strong feelings of pleasure or discomfort in observers due to their abstract nature and that they therefore might not engage the amygdala in assessing signal relevance (de Gelder 2006). This observation aligns with findings from studies employing PLDs, which also did not report amygdala activation in response to affective actions (Heberlein and Saxe 2005, Centelles et al. 2011, Atkinson et al. 2012).

Conclusion

The present study investigated whether AON and valence-sensitive regions convey valence information when processing EBL depicted by kinematic stimuli. Our findings show that a decoding of stimulus valence is possible within the IPL, thereby suggesting a distinctiveness of the neural codes underlying the observation of positive and negative scenes. Furthermore, we observed that the neuronal geometry of AON and valence-sensitive areas, albeit to a lesser degree, reflects the geometry of subjective valence ratings as indicated by RSA. We found the closest match of neural activation patterns and behavioral responses within the IPL. Because this cortical site is considered as representing action intention from observed kinematics, the accentuated role of the IPL in the present study can also be explained by the notion that the decoding of affect via kinematic stimuli is a form of intention recognition.

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Supplementary data

Supplementary data is available at SCAN online

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Data availability

All data are available upon request.

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6.3 Exercise-induced Inflammation Alters the Perception and Visual Exploration of Emotional Interactions

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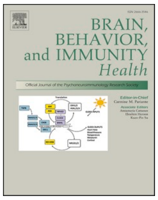

Exercise-induced inflammation alters the perception and visual exploration of emotional interactions

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ABSTRACT

Introduction: The study aimed to investigate whether an exercise-induced pro-inflammatory response alters the perception as well as visual exploration of emotional body language in social interactions.
Methods: In a within-subject design, 19 male, healthy adults aged between 19 and 33 years performed a downhill run for 45 min at 70% of their VO_{2max} on a treadmill to induce maximal myokine blood elevations, leading to a pro-inflammatory status. Two control conditions were selected: a control run with no decline and a rest condition without physical exercise. Blood samples were taken before (T0), directly after (T1), 3 h after (T3), and 24 h after (T24) each exercise for analyzing the inflammatory response. 3 h after exercise, participants observed point-light displays (PLDs) of human interactions portraying four emotions (happiness, affection, sadness, and anger). Participants categorized the emotional content, assessed the emotional intensity of the stimuli, and indicated their confidence in their ratings. Eye movements during the entire paradigm and self-reported current mood were also recorded.
Results: The downhill exercise condition resulted in significant elevations of measured cytokines (IL6, CRP, MCP-1) and markers for muscle damage (Myoglobin) compared to the control running condition, indicating a pro-inflammatory state after the downhill run. Emotion recognition rates decreased significantly after the downhill run, whereas no such effect was observed after control running. Participants' sensitivity to emotion-specific cues also declined. However, the downhill run had no effect on the perceived emotional intensity or the subjective confidence in the given ratings. Visual scanning behavior was affected after the downhill run, with participants fixating more on sad stimuli, in contrast to the control conditions, where participants exhibited more fixations while observing happy stimuli.
Conclusion: Our study demonstrates that inflammation, induced through a downhill running model, impairs perception and emotional recognition abilities. Specifically, inflammation leads to decreased recognition rates of emotional content of social interactions, attributable to diminished discrimination capabilities across all emotional categories. Additionally, we observed alterations in visual exploration behavior. This confirms that inflammation significantly affects an individual's responsiveness to social and affective stimuli.

1. Introduction

Imagine a person walking towards you, expanding their chest, clenching and lifting their fists. Instantly, we may feel that the person we are looking at is filled with anger and that we should draw away from this potential threat. This example makes clear that humans are able to quickly retrieve a wealth of information through mere observation of a person's Emotional Body Language (EBL) (Atkinson et al., 2004; Bachmann et al., 2018; de Gelder et al., 2015; Keck et al., 2022; Poyo Solanas et al., 2020).

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Despite the general ability to recognize emotions of conspecifics through EBL (de Gelder, 2006), it is assumed that human perception of the world and the people around is shaped by individual states and experiences (for a review, see Gallese, 2007) such as an individual's mood, gender or mental illness (e.g., Alaerts et al., 2011; Van Den Stock et al., 2007). In addition, bodily conditions like systemic inflammation can also influence perceptual functioning. Literature states that pro-inflammatory cytokines such as interleukin-6 (IL-6) and tumor--necrosis-factor-α (TNF-α) act as key mediators in the crosstalk between inflammatory pathways and neurocircuits in the brain influencing behavioral responses (Smith, 2000; Turnbull and Rivier, 1999). These cytokines activate the hypothalamus via different pathways (Dantzer et al., 2000, 2008; Dantzer and Kelley, 2007; Maier and Watkins, 1998) and, thereby influence the metabolism of serotonin and dopamine which play an important role in a variety of mood-, depression- and sickness related behaviours (Elenkov, 2008; Engler et al., 2016; Konsman et al., 2002; Miller et al., 2009; Schedlowski et al., 2014).

One of the most used research tools for investigating the relationship between mood, emotion perception and inflammatory states, is the experimental use of endotoxin, vaccinations or the direct injection of pro-inflammatory cytokines (Hansson et al., 2021). These interventions result in a reliable increase of pro-inflammatory cytokines, such as TNF-α and IL-6, in healthy subjects without inducing an actual infection (Balter et al., 2018; Benson et al., 2017; Bollen et al., 2017; Eisenberger et al., 2009; Grigoleit et al., 2011; Kotulla et al., 2018; Kullmann et al., 2014; Moieni et al., 2015b; Schedlowski et al., 2014; Wright et al., 2005). Typical symptoms of sickness-behaviour, such as increase in self-reported depressed mood, anxiety, fatigue, and uneasiness (e.g., Engler et al., 2016; Grigoleit et al., 2011; Kullmann et al., 2014), feelings of social disconnection (Eisenberger et al., 2010; Moieni et al., 2015a) and even lower self-esteem (Kotulla et al., 2018) were repeatedly induced in individuals via endotoxemia. It has been demonstrated that endotoxin injection also leads to alterations in emotion perception. For instance, impaired emotion recognition accuracy (of Reading-the-Mind-in-the-Eyes-Test - RMET) (Balter et al., 2018; Moieni et al., 2015a), negatively biased information processing (Benson et al., 2017; Bollen et al., 2017; Hansson et al., 2021), disturbed reward processing (Harrison et al., 2016) and altered emotion-regulation were shown (Hansson et al., 2021). Those alterations were accompanied by heightened brain activity in areas that are associated with different aspect of neural processing of emotions and motion (for a review, see: Harrison et al., 2016; Lasselin et al., 2018).

Besides inflammation-induction via endotoxemia, there are potentially sterile options, such as physical exercise-induced stress that also induce temporarily pro-inflammatory processes. Particularly intense and prolonged endurance exercise induces a mild pro-inflammatory response characterized by an increase of circulating leukocytes and inflammatory cytokines, such as IL-6 and TNF-alpha, which is followed by an anti-inflammatory counter regulation in the post-exercise period (Peake et al., 2015b). The physiological basis for this exercise-induced immune response is a stress response associated with the release of catecholamines, increased blood flow, a rise in body temperature, ultrastructural tissue trauma, and increased challenges on energy metabolism (Hodgman et al., 2023). The pro-inflammatory exercise response is even more pronounced after acute exercise that is unfamiliar and involves high muscle tension combined with eccentric components (Peake et al., 2005).

Given that both familiar and unfamiliar forms of exercise have been linked to the systemic release of pro-inflammatory cytokines (Suzuki, 2018), it is hypothesized that there exists a reciprocal relationship between neuronal and immunological mechanisms during exercise. This interplay is posited to influence social cognitive processing (Proschinger and Freese, 2019).

On this background, our within-subject design aims to explore the impact of exercise-induced pro-inflammatory responses on the perception and visual exploration of emotions conveyed through body language during social interactions. We employed 45 min downhill treadmill running at 70% VO2max, as an intensive eccentric exercise bout to induce a high level of pro-inflammatory cytokines, leading to a systemic pro-inflammatory status. Two control conditions were selected: a control run level run and a rest condition without physical exercise. Three hours later, participants observed point-light displays (PLDs) of human interactions portraying four emotions (happiness, affection, sadness, and anger). Participants were asked to categorize the depicted emotional content, the emotional intensity of the perceived stimulus as well as their confidence regarding their ratings. We furthermore assessed eye movements of the participants during the whole paradigm as well as their self-reported current mood. We hypothesize that exercise-induced inflammation alters emotion perception with respect to its accuracy, the perceived emotional intensity and the subjective confidence of these ratings as well as the visual exploration behaviour.

2. Materials & methods

2.1. Participants

Altogether 19 male adults aged 19–33 (mean age: 23.89 years; SD = 3.78 years) with normal or corrected-to-normal vision participated in our study. None of the participants reported any history of psychiatric, neurological, immunological or physical disorders, a current use of psychoactive medication or performance of endurance exercises on more than 4 days a week. Prior to participation, all participants gave written informed consent in compliance with the Declaration of Helsinki. Due to Corona policy all participants had to wear surgical or FFP2 masks. Additionally, they had to be symptom-free and give written confirmation thereof. All participants were either vaccinated against COVID-19 prior to or during participation in this study. Additionally, the state of health of each subject was checked with a blood count before exercise. In case of anomalies, subjects were excluded from participation. The procedure was approved by the local ethics committee of the Department of Psychology and Sports Science of Justus-Liebig-University Giessen. We used the German version of the Emotional Competence Questionnaire (Emotionale-Kompetenz- Fragebogen, EKF; Rindermann, 2009) to assess the participant's ability to recognize and understand one's own emotions; the ability to recognize other's emotions; the ability to regulate and control one's emotions; the ability to express one's emotions (nonverbally and verbally). Normalized standard mean EKF values were in a normal range (90.1–109.9) for all four main domains. Additionally, the German version of the Interpersonal-Reactivity-Index (IRI-SPF, Saarbrückener Persönlichkeitsfragebogen zur Messung von Empathie, V 7.0 Paulus, 2009) was used to estimate the participant's empathic competence within four emotional and cognitive empathic factors. The *empathy scores* were all in a normal range (mean 43.77, SEM 1.30). Participants' scores for EKF items and IRI-SPF did not differ between the experimental conditions.

2.2. Experimental procedure

The study was conducted as a within-subject cross-over design. Participants visited our laboratories on four different days, with at least one week between each testing day: Pre-test, downhill running (INFL), control running (CON) and rest (REST). Order of INFL and CON treadmill running were randomized across participants, REST was always scheduled for the last session. This was necessary because blood cells derived from REST blood sampling had to be directly used in another experiment in which these cells were incubated with the different sera of the two exercise conditions (Gebhardt et al., 2024). An overview of general procedure is shown in Fig. 1 A.

On the first day, each individual's anthropometric data (height, age, weight), pulmonary function (vital capacity, forced expiratory volume), electrocardiogram and blood pressure at rest, as well as a body fat analysis (via bioelectrical impedance analysis) were assessed by a

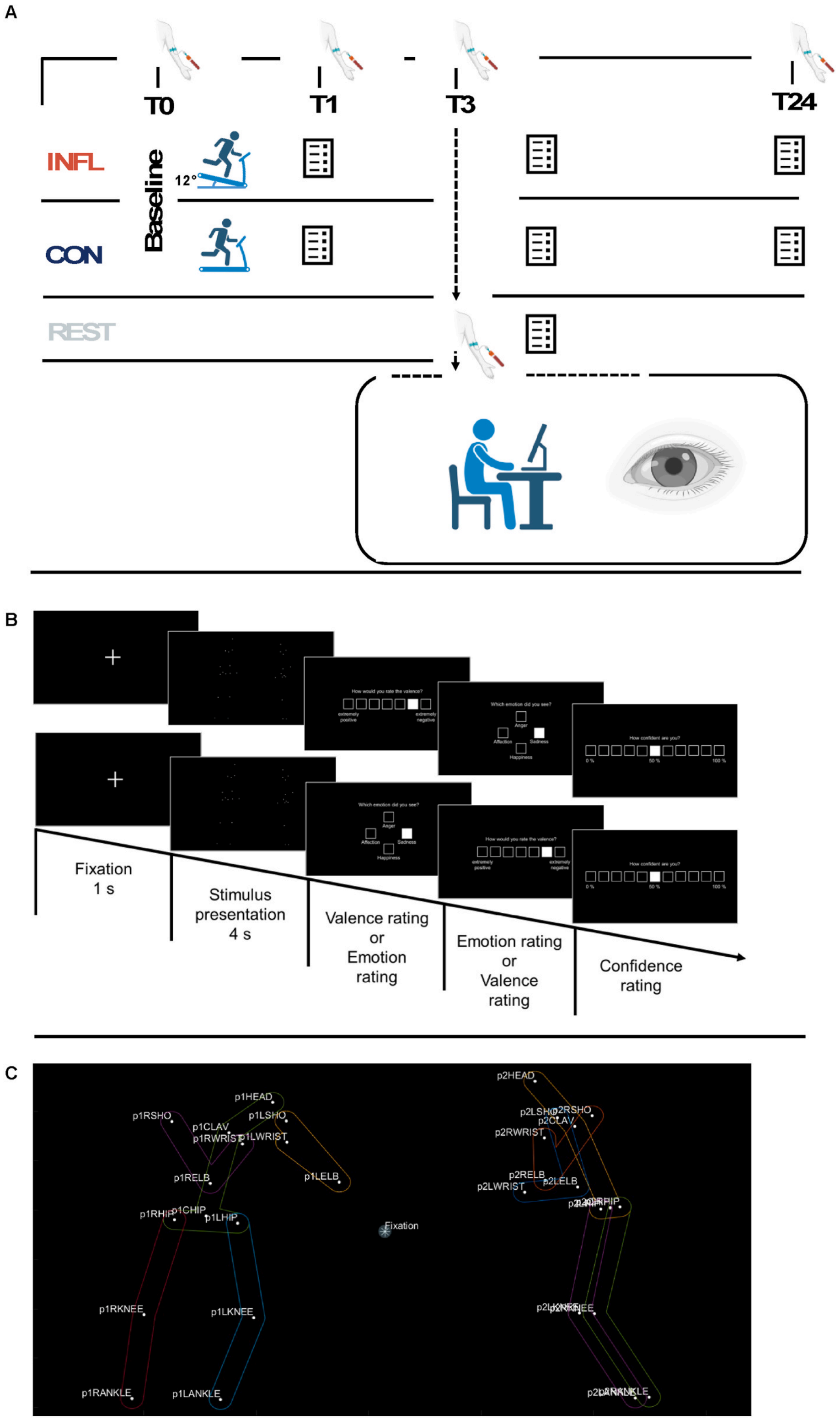

Fig. 1. *Experimental Procedure and Timeline.* A) Time-schedule of experimental conditions, blood-sampling, experiment and questionnaires. B) Temporal structure of two trials, each trial started with a fixation phase (1s) followed by the stimulus sequence (4s). Subsequent to the stimulus presentation, an emotion and valence rating (upper row) were presented. In half of the trials, the ratings were inverted (lower row). These ratings were followed by a confidence rating. C) Anatomical landmarks and predefined AOIs for eye-tracking analysis.

physician. After that, participants were tested to obtain their individual maximal oxygen uptake (VO_{2max}) using a step protocol on the treadmill starting at 8 km/h with a step height of 2 km/h and step length of 2 min until subjective exhaustion. VO_2 (via spiroergometry), heart rate (via chest strap) and the subjective exhaustion (via BORG-scale) were assessed at every step. VO_{2max} was used to determine the individual's running speed for INFL and CON protocols (Gebhardt et al., 2024).

Downhill treadmill running (12% decline) with a VO_2 corresponding to 70% of the individual's VO_{2max} was selected as an inflammatory stimulus (INFL). This type of eccentric exercise containing high intensity and a long duration is known to induce a reliable and notable increase in circulating pro-inflammatory cytokine levels (e.g., IL-6, TNF-α, CRP, MCP1) without inducing significant effects on sickness symptoms such as fever (Peake et al., 2005; Steensberg et al., 2002). As a control condition for possible effects related to running itself, such as cardiopulmonary stimulation etc., control treadmill running with the same intensity at 1% incline was selected (CON).

Durations of both running protocols were set to 45 min unless the participants were forced to quit earlier due to exhaustion or other reasons. Participants had to run for at least 30 min to be included into data analysis. Only one of the participants had to stop the run after 35 min in the downhill condition. Both runs were completed on a treadmill by h/p/cosmos (h/p/cosmos quasar med 4.0, h/p/cosmos Sports & Medical GmbH, Nussdorf, Traunstein, Germany) and began with a short warm-up of 10 min in which VO_2 was regulated to match the 70% VO_{2max} via adjustments in velocity. For each condition and participant, the sessions have been scheduled between 8 a.m. and 12 p.m. to account for potential variations in the blood concentration of inflammatory markers that could occur in the afternoon (Nakao, 2014).

2.3. *Assessment of inflammatory status*

Venous blood samples were collected at four points in time in each experimental condition (INFL, CON) (prior to exercise = T0; immediately after exercise = T1; 3 h after exercise = T3; 24 h after exercise = T24) in vacutainers. The level prior to exercise (T0) served as baseline for the two exercise conditions (see Fig. 1. A). Plasma vacutainers were anticoagulated with EDTA. They vacutainers were centrifuged at 2500×*g* for 10 min at 4 °C immediately after sampling, while serum samples had clotted for 30 min before centrifugation. Samples were separated into aliquots and stored in Eppendorf tubes at −80 °C until analysis. IL-6, TNF-α, CRP, MCP1 levels as well as Myoglobin (Mb) as a marker of muscle damage were determined by Luminex Multiplex Assay (Luminex LX200, Biotechne, Minneaplois, USA).

2.4. *Assessment of mood state*

To describe participants' current mood state at each testing day, a short version of the German mental state scales (Befindlichkeitsskalen – BFS, Abele-Brehm and Brehm, 1986) was used. Since negative mood and anxiety were reliably induced by endotoxemia before (e.g., Engler et al., 2016; Grigoleit et al., 2011; Kullmann et al., 2014), Anger, Positive Mood, Calm, Arousal and Depressed were selected to describe mood-related items due to their relevance for the connection between mood and inflammation. The BFS contains 21 5-point-scaled items ranging from 1 (never) to 5 (always).

2.5. *Emotion recognition experiment*

Three hours after exercise, participants were given instructions and acquainted with the task. They subsequently performed three example trials that were not included in the main experiment. In the experiment, each video was presented once, resulting in a series of 48 sequences. Video sequences were displayed in an intra- and interindividually randomized order on a 19-inch screen (display resolution: 1280x720, refresh rate 60 Hz). The distance between each test person's eyes and the screen was approximately 65 cm. After completing a calibration and validation procedure for the eye tracker, each trial started with a fixation phase (1 s) followed by a stimulus sequence (4 s) and three behavioural ratings. The ratings consisted of: 1.) an emotional valence rating, rating the video sequences on a 7-point Likert scale from very negative (−3) to very positive (+3). 2.) Sorting emotions into one of the following categories: happiness, affection, sadness, or anger. 3.) Confidence ratings on an 11-point Likert scale ranging from 0% (−5) to 100% (+5). The order of emotional valence ratings and sorting emotions to categories were alternating to avoid order effects, confidence ratings were always provided last. This procedure is visualized in Fig. 1 B.

To control for potential influences of the inflammatory state on cognitive functions, such as working memory, participants engaged in a spatial span task. This task required them to replicate the location of an object displayed on a computer screen. At the initial level, participants were asked to replicate one location. With each subsequent level, the task's difficulty increased by requiring the replication of an additional location. The highest level at which a participant accurately replicated all locations was assessed and utilized as a control parameter.

2.6. *Stimuli*

The observed stimuli were selected from a larger motion-capture data set from Bachmann et al. (2020). Eight pairs of non-professional actors were instructed to perform an interaction portraying one out of four emotional scenes depicting either happiness, affection, sadness, or anger. To ensure an emotion-congruent behavioural pattern, actors were given a script of emotional situations and directed specifically to perform the same emotion. They were instructed to express their emotions intuitively within the context of the given situation, thereby limiting restrictions and enhancing the variability of expression (Bachmann et al., 2020). Interactions were recorded with an optical motion capture system (Vicon Motion Systems, Oxford, England) operating at 100 Hz. MATLAB software (Mathworks, Natick, MA) was used to create video files of 4-s sequences from the original coordinate 3D (C3D). In each video, 15 markers per person were then plotted as white spheres on a black background to present a standard PLD (point-light display) model.

The final stimulus selection was based on prior validation of emotion category (anger, sadness, affection, happiness) and perceived valence from 24 participants who did not take part in the present experiment. Valence was judged on an 11-point scale ranging from −5 (extremely negative) to +5 (extremely positive). There were two validation criteria: 1.) At least 50% of the participants had to recognize the displayed emotion; 2.) The second-highest emotion rating should not exceed 25%. This allowed us to identify and exclude ambiguous scenes in which a specific emotion could not be recognized reliably and those which were overly easy to recognize, avoiding both floor and ceiling effects. After validation, 12 stimuli that met both criteria were selected randomly for each emotion category, which resulted in a set of 48 (4 emotions × 12 scenes) stimuli.

2.7. *Eye tracking*

During the whole experiment, a video-based pupil- and corneal reflection Tobii Nano Pro eye tracker (Tobii AB, Danderyd, Sweden) was used to track participant's gaze behavior during stimulus presentation at a sampling rate of 60 Hz and mounted on the bottom of the screen. According to the manufacturer, the eye tracker operates with a precision of 0.1° RMS and an accuracy of 0.3° in optimal conditions with a total system latency of 1 frame (17 ms). To determine fixations, we identified events in between saccades with a minimum event duration of 100 ms and a saccade velocity threshold of 30 deg/s (de Haas et al., 2019). Note that this definition of fixation also encompasses pursuit phenomena, as it can be assumed that with dynamic stimuli, the eyes wander along, and this is equally essential for a corresponding fixation.

Within all 48 PLD stimuli, for each actor separately and within every frame of the video, five areas of interests (AOI) based on the 2D dot coordinates of the markers were created using Matlab (2022b) with the corresponding labels: right arm, left arm, trunk, right leg and left leg. In order to determine which fixation or pursuit events fell into which area, two criteria were used. 1.) All distances between the event and all markers were calculated to find the minimum distance across all relevant frames. 2.) Additionally, this resulting minimum distance had to be below a threshold of 50 pixels to count as a fixation of the area, which served as a tolerance margin to account for oculomotor drift and potential accuracy limits (see Fig. 1 C).

2.8. Data analysis and statistics

Prior to statistical analysis, several pre-processing steps of the data were carried out. First, the current mood state was determined by summing up the selected items of the BFS after each exercise condition. Higher values in the sum score reflect increasing negative mood and anxiety. To determine emotion recognition accuracy in the EBL paradigm, the percentage of correct category ratings of each emotion was calculated by comparing the rating of a given stimuli to the actual validated emotional category. To determine intensity perception of the PLDs, absolute valence values were determined to be able to make an inference about how intense a stimulus was perceived. Thus, higher intensity can therefore be interpreted as more negative or more positive, depending on the category. Confidence ratings were calculated to gather information about the subjective impression of the participants' confidence regarding the given rating. For the sensitivity measurement d', we calculated the proportion of hits (HR) (identified and displayed emotion are consistent) and false alarms (FAR) (identified and displayed emotion are inconsistent). Proportions of 0 were replaced with $0.5/N_{p/a}$:

$$d' = z(HR) - z(FAR)$$

Sensitivity reflects the observer's ability to discriminate whether the 'signal' (here, the respective emotional category) is present or not. High d' values indicate a good discrimination ability for the respective emotional category, i.e., the category can be distinguished from the other ones. Each participant's d' values were calculated as the mean for each emotion, separately for all three conditions.

2.9. Exercise-induced inflammation

To ascertain whether a given exercise-intervention leads to an inflammatory response, we tested whether there was a condition-dependent change of cytokine concentrations from T0 to T1 to T3 to T24. Therefore, we conducted a 2 (condition: INFL vs. CON) x 4 (timepoint: T0, T1, T3, T24) repeated-measures ANOVA for IL-6, TNF-α, CRP and MCP1 as markers for inflammation, as well as for myoglobin (Mb) as a marker for muscle damage. It has to be noted that missing values exist for each parameter. This is because the measured values lie outside the normal curve and, therefore, cannot be determined.

2.10. Influence of exercise-induced inflammation on mood

To determine possible influences of exercise-induced inflammation on current mood state of participants, we performed a one-way ANOVA with a three-level factor exercise condition (INFL, CON, REST).

Influence of exercise-induced inflammation on emotion recognition, intensity perception, confidence and sensitivity.

To ensure adequate recognizability of the displayed emotions, emotion recognition accuracy was tested against chance (25 %) for all conditions via Wilcoxon signed-ranks test.

To determine the possible influence of exercise-induced inflammation on emotion recognition accuracy, intensity perception as well as perceived confidence, for each parameter a 3 (condition: INFL, CON, REST) x 4 (emotion category: happiness, affection, anger, sadness) repeated-measures ANOVA was conducted.

To investigate whether inflammation induced changes in perceptual sensitivity, we calculated a 3 (condition: INFL, CON, REST) x 4 (emotion category: happiness, affection, anger, sadness) repeated-measures ANOVAs using d'.

To assess the impact of exercise-induced inflammation on working memory performance, we conducted a one-way ANOVA with the exercise condition as a three-level factor (INFL, CON, REST).

2.11. Influence of exercise-induced inflammation on eye movements

To determine the possible influence of exercise-induced inflammation on gaze behavior, we quantified different eye movement measurements (Suslow et al., 2020).). Visual scanning was described by the numbers of fixations (NF) and average glance duration (AGD). The so-called initial attention was measured by the latency of the first fixation (First Fixation Latency = FFL) as well as the duration (First Fixation Duration = FFD). The maintenance of attention was evaluated by calculating dwell time (DT). For more detail on the calculation see Table 1.

For simplicity we refer to both pursuit and fixation events as 'fixations'.

For all parameters of gaze behavior, we calculated separate 3 (condition: INFL, CON, REST) x 4 (emotion category: happiness, affection, anger, sadness) repeated-measures ANOVAs.

For each conducted repeated-measures ANOVA, Mauchly's test of sphericity was conducted. Violations were treated by using Greenhouse-Geisser ($\varepsilon < 0.75$) correction (Girden, 1992). If repeated-measures ANOVA displays significant effects, post hoc pairwise comparisons were calculated and Bonferroni-corrected. For all pre-processing steps and statistical tests, Matlab R2022b and JASP 0.15.0.0 were used. Alpha significance levels were set to 0.05 for all statistical tests.

3. Results

3.1. Muscle damage and inflammation after exercise

Using a 2 × 4 repeated-measures ANOVA, we investigated whether the levels of IL-6, TNF-α, CRP, MCP1 and Mb were affected differentially by the different exercise conditions in order to verify that INFL leads to a significant systemic inflammation which is more pronounced than the inflammatory response after CON (see Fig. 2).

Our results revealed an interaction effect of experimental condition x time point for IL-6 (see Fig. 2 D) concentrations ($F(3,16) = 7.535$, $p < 0.05$, $\eta^2 = 0.079$). Bonferroni-corrected post hoc analyses showed that blood concentration levels of IL-6 were significantly higher for INFL T3 compared to INFL T0 ($p < 0.001$) and CON T24 ($p < 0.05$). We found no main effect of condition for IL-6.

For CRP (see Fig. 2 A), a main effect of condition was found ($F(1,16) = 4.558$, $p < 0.05$, $\eta^2 = 0.05$). Post hoc analysis revealed higher blood concentration of CRP for INFL compared to CON ($p < 0.05$). Furthermore, Greenhouse-Geisser corrected values revealed an interaction effect of experimental condition x time point ($F(1.73,16) = 6.650$, $p < 0.01$, $\eta^2 = 0.074$). Bonferroni-corrected post hoc analyses highlights differences between INFL T0, T1, T3 and CON T0, T1, T3, T24 compared to INFL T24 ($p < 0.001$).

Results for MCP1 (see Fig. 2 C) revealed an interaction effect between condition x time point ($F(3,16) = 23.643$, $p < 0.05$, $\eta^2 = 0.034$)

Table 1
Description of gaze parameters.

Parameter	Abbr.	Short description
Number of Fixations	NF	Number of fixations for each trial averaged across emotions
Average Glance Duration	AGD	Average amount of time each subject's gaze stays within boundaries of the AOIs (calculated by dividing fixation time by fixation frequency)
First Fixation Duration	FFD	Duration of first fixation in ms
First Fixation Latency	FFL	Time between stimulus onset and first fixation in ms
Dwell Time	DT	Sum of durations from all fixations that hit AOI in ms. Calculated for each AOI and each trial and then averaged for each subject

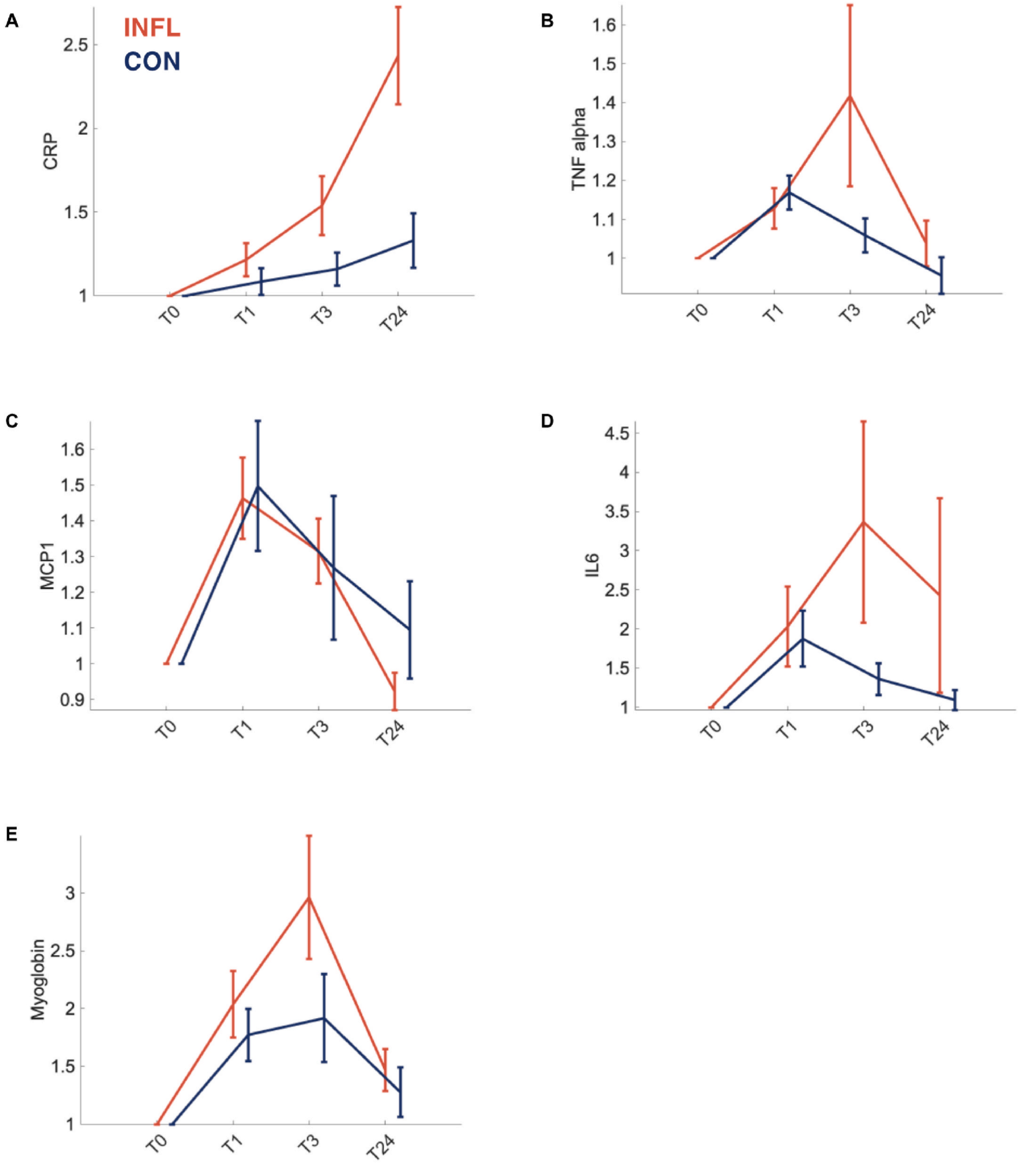

Fig. 2. *Concentration of various cytokines (B, C, D) and plasma proteins (A, E)* prior to exercise = T0; immediately after exercise = T1; 3 h after exercise = T3; 24 h after exercise = T24; downhill-running (INFL/red) or control-running (CON/blue). The depicted data are the means and the SEMs of biomarker increases relative to T0.

but no effect of experimental condition. Regarding the interaction effect, INFL T1 showed a higher MCP1 concentration compared to CON T0, T3 and T24 as well as to INFL T0, T24 (all $p < 0.01$). Likewise, CON T1 was higher compared to CON T0 and CON T24 ($p < 0.001$) as well as to INFL T24 ($p < 0.01$). Lastly, INFL T3 MCP1 concentration was higher compared to both T0 and T24 of both conditions ($p < 0.01$).

Mb concentrations (see Fig. 2 B) were measured as a possible inflammation-driving factor under INFL. For Mb concentrations, a significant main effect for condition ($F(1,18) = 5.214$, $p < 0.05$, $\eta^2 = 0.042$) was found. However, there was no interaction effect. Post hoc analysis showed that the Mb concentrations were higher for INFL compared to CON ($p < 0.05$). Furthermore, paired sample t-tests indicated a higher Mb concentration for INFL T3 compared to CON T3 ($p < 0.05$).

There was no main of experimental condition and no interaction between condition and time point for TNF-α.

3.2. Mood state

Regarding the mood state (Anger, Positive Mood, Calm, Arousal, Depressed), we found no differences of any of the investigated mood scales between the different experimental conditions (all $p > 0.05$).

3.3. Influence of exercise-induced inflammation on emotion recognition

Overall, emotion category ratings given here show a high consistency with the ratings from the validation study (see Fig. 3 A). The Wilcoxon signed-rank test revealed that sequences of each emotional category were classified significantly above chance level (all $p < 0.001$) and thus ensuring a high degree of recognizability.

Using a 2 × 4 repeated-measures ANOVA, we investigated whether the recognition of emotional interactions was affected by exercise-induced inflammation. Results revealed a main effect of experimental condition on recognition performance ($F(1.790,18) = 4.465$, $p < 0.05$, $\eta^2 = 0.023$). Bonferroni-corrected post hoc analyses showed that recognition rates for REST were significantly higher compared to INFL ($p < 0.05$) but not to CON. Furthermore, a main effect of emotion category was found ($F(2.279,18) = 5.823$, $p < 0.05$, $\eta^2 = 0.147$) with post hoc analyses indicating that affection scenes were accompanied by significantly lower recognition rates compared to happiness and anger scenes ($p < 0.05$) while other pairwise comparisons revealed no significant differences (all $p > 0.05$). We found no interaction effect between condition and emotion (see Fig. 3 A).

Regarding intensity ratings, we found no main effect of condition as well as no interactions between condition and emotion category (all $p > 0.05$). However, a main effect was present regarding emotion category ($F(2.153,18) = 44.559$, $p < 0.001$, $\eta^2 = 0.483$) with post hoc analysis showing that interactions portraying happiness were perceived more intense compared to the all other emotions (all $p < 0.001$). Further, affection stimuli were perceived more intense compared to sadness stimuli ($p < 0.005$).

The same main effect of emotion category was present for confidence ratings ($F(3,18) = 15.860$, $p < 0.001$, $\eta^2 = 0.253$) with participants confidence in their rating being higher for happy interactions compared to all other emotional interactions (all $p < 0.001$). No further effects were revealed regarding the perceived confidence.

To investigate how inflammation influences participants' discrimination abilities, we calculated d' (see Fig. 3 B). We found a main effect of condition, ($F(2,18) = 5.784$, $p < 0.001$, $\eta^2 = 0.093$) with increasing sensitivity for REST compared to INFL ($p < 0.05$). The present data revealed no main effect of emotion category and no interaction between condition and emotion category for d'.

In the control analysis, we found no differences in working memory performance across the experimental conditions ($F(2,18) = 1.441$, $p > 0.05$).

3.4. Influence of exercise-induced inflammation on eye movements

Using 2 × 4 repeated measures ANOVAs for all eye movement related parameters, results showed that the exercise induced inflammation status of participants influenced the number of fixations (NF) ($F(2,18) = 3.947$, $p < 0.05$, $\eta^2 = 0.011$) (see Fig. 3 C). Post hoc comparisons revealed more NFs for INFL compared to CON ($p < 0.05$), as displayed in Fig. 3C. Additionally, a significant main effect of emotion occurred ($F(3,18) = 4.395$, $p < 0.01$, $\eta^2 = 0.058$) with less fixations when viewing affectionate interactions compared to both negative emotion displays (all $p < 0.05$). Greenhouse-Geisser-corrected interactions between emotion and condition ($F(3.951,18) = 15.765$, $p < 0.001$, $\eta^2 = 0.302$) showed that happy interactions were less fixated in INFL compared to REST, whereas they were more often fixated in REST compared to CON (all $p < 0.05$). Sad interactions under INFL were more fixated compared to REST. Furthermore, angry interactions in INFL were less fixated than angry interactions in CON (all $p < 0.05$). Under INFL, happy and affectionate as well as angry interactions were less often fixated than sad interactions (all $p < 0.05$). For CON, both positive interactions were less often fixated than angry interactions (all $p < 0.05$). In the REST condition, happy interactions were significantly more often fixated than affectionate and sad interactions (all $p < 0.05$).

In addition to the number of fixations, we examined the average glance duration (AGD). Greenhouse-Geisser-corrected values indicated a main effect of emotion category ($F(1.944,18) = 3.782$, $p < 0.05$, $\eta^2 = 0.06$) with post hoc analysis showing longer AGDs for affectionate compared to sad and angry interactions ($p < 0.05$). There was no significant effect of experimental condition regarding average glance duration. However, Greenhouse-Geisser-corrected values indicated an interaction effect ($F(3.142,18) = 6.680$, $p < 0.001$, $\eta^2 = 0.154$) between condition and emotion category. Post hoc comparisons revealed longer AGDs for happiness stimuli in INFL compared to REST and anger stimuli in INFL compared to CON (all $p < 0.05$). Sad interactions were accompanied by shorter AGDs in INFL compared to REST ($p < 0.05$). In INFL, observing happy interactions led to longer AGDs than sad interactions ($p < 0.05$). In CON, anger scenes led to shorter AGDs compared to happy and affectionate scenes (all $p < 0.05$).

Focusing on the effect of emotion category regarding the initial attention, we found a main effect concerning the duration of the first fixation duration (FFD) ($F(3,18) = 2.828$, $p < 0.05$, $\eta^2 = 0.05$) revealing longer FFDs when observing affectionate compared to sad scenes ($p < 0.05$). We found no effects of experimental condition regarding the duration of the first fixation. However, Greenhouse-Geisser corrections revealed a significant interaction between emotion and condition ($F(3.767, 18) = 5.365$, $p < 0.001$, $\eta^2 = 0.128$). Post hoc comparisons further elucidated that initial fixations in anger scenes were notably longer in CON than INFL ($p < 0.05$). Also, angry scenes in CON elicited longer initial fixations than in INFL ($p < 0.05$).

For the latency of the first fixation (FFL), we did not find a main effect of experimental condition or emotion category. However, there was an interaction between experimental condition and emotion category ($F(6,18) = 2.384$, $p < 0.05$, $\eta^2 = 0.06$). All post hoc comparisons did not reveal statistically significant differences concerning the latency of the first fixation.

Attention maintenance of participants depicted through dwell time (DT) showed no main effect of either experimental condition or emotion category. Though, an interaction effect ($F(2.995,18) = 7.206$, $p < 0.001$, $\eta^2 = 0.151$) with Greenhouse-Geisser-corrected values indicating longer DTs for affectionate interactions in REST compared to happy and sad interactions in the same condition (all $p < 0.05$). Overall, observing affectionate interactions was accompanied by shorter DTs for REST compared to INFL and CON (both $p < 0.05$).

4. Discussion

An increasing number of studies (e.g. Eisenberger et al., 2009; 2010; Moieni et al., 2015a,b) have explored the impact of systemic inflammatory conditions on emotion perception and theory of mind. This study employed a within-subject design in a cohort of young, healthy males to explore the potential impact of exercise-induced sterile inflammation on the recognition and visual scanning behavior of emotions conveyed through body language during emotional interactions. Specifically, we induced an inflammation-like state using a downhill running exercise model. This is evidenced by elevated muscle damage markers and an increase in pro-inflammatory cytokines and serum proteins. The eccentric downhill exercise condition resulted in greater elevations of

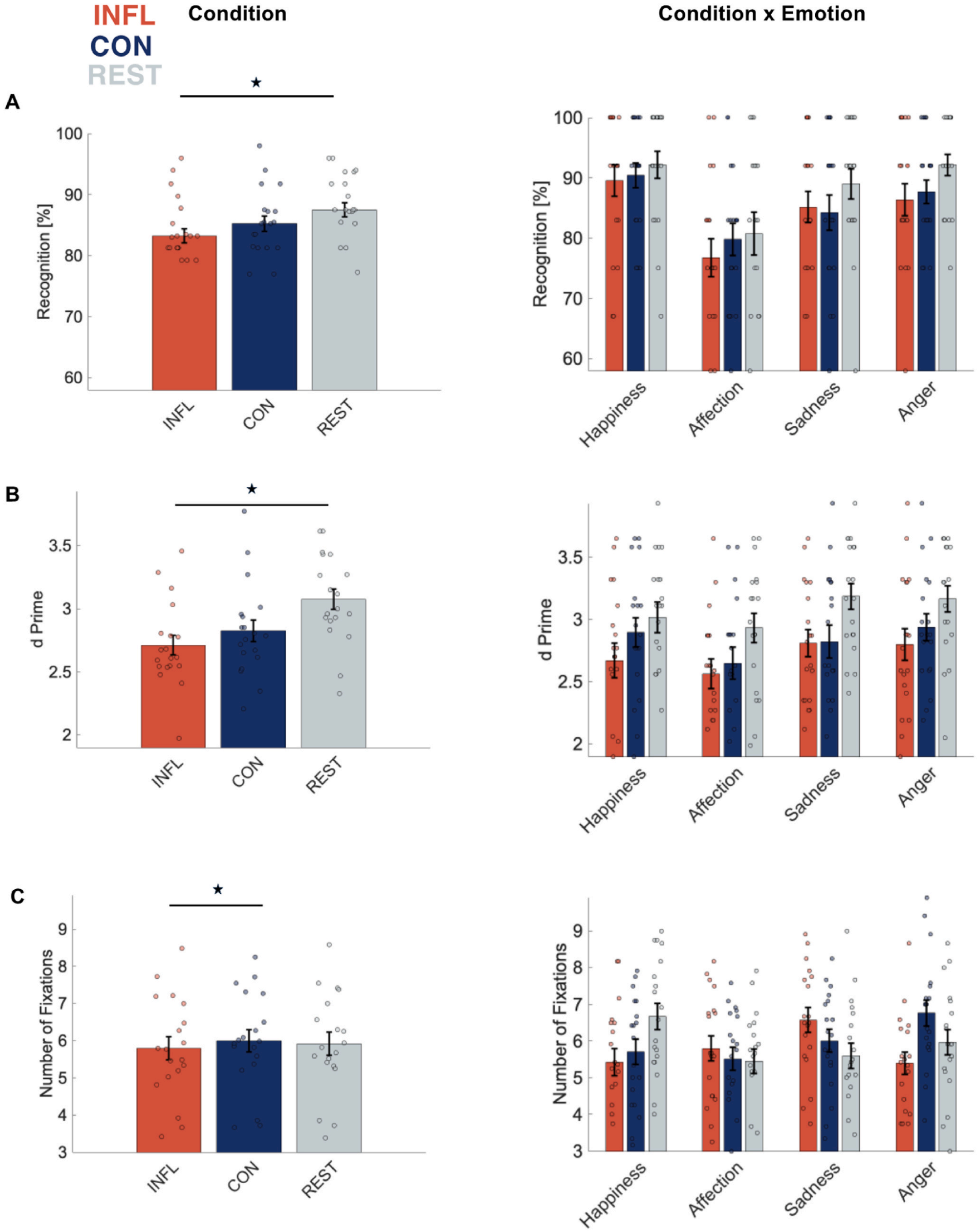

Fig. 3. *Influence of experimental condition on recognition performance and gaze behavior.* A) Emotion recognition rates of interactions for all emotion categories (i.e, happiness, affection, sadness, anger). B) Average sensitivity (d') and C) Number of Fixations by condition and emotional category. Bars and error bars show means and SEMs. Significance level between conditions is indicated by asterisk. (★ $p < 0.05$).

measured cytokines (IL6, CRP, MCP-1) and markers for muscle damage (Mb) compared to the control running condition (Bruunsgaard et al., 1997; Peake et al., 2005; Pedersen and Febbraio, 2008; Steensberg et al., 2002). Notably, we observed significant increases in IL-6 and MCP1 between T0 and T3 only in the downhill running condition, while CRP levels differed between both conditions only at T24. There were no significant differences between the conditions regarding TNF-α levels. Particularly at T3, the time point of the behavioral experiment, myoglobin concentrations substantially increased in the downhill run compared to the control run, indicating the presence of a noticeable muscle damage as a driver of inflammation.

Regarding emotion perception, we demonstrated significantly decreased recognition rates of the emotional state of two interacting PLD agents for 3 h after downhill running compared to the rest condition, but no such effect was observed for 3 h after control running compared to rest. The experimental condition had no effect on the perceived emotional intensity or the perceived subjective confidence of the given ratings. Regarding participants' discrimination abilities, our findings indicate that the inflammation condition is accompanied by a reduced ability to differentiate between emotion categories compared to the rest condition. We also observed that the inflammatory condition is associated with changes in participants' visual scanning behavior, potentially causing them to exhibit more fixations on sad stimuli, in contrast to the control condition, where they exhibited more fixations while observing happy stimuli. In the next sections, our results are discussed in more detail.

4.1. Strenuous exercise as an experimental model to induce inflammation

An important feature of the present study is that we used an exercise model to induce a pro-inflammatory condition. It has been repeatedly shown that strenuous bouts of endurance exercise and particularly exercise with eccentric components induce a pro-inflammatory response (Peake et al., 2017b). Indicators of inflammation, for example, are mild increases in systemic IL-6 and TNF-α in the post exercise period, which occur immediately and are often present for up to 48 h (Paulsen et al., 2012). While this is fundamentally part of the exercise-induced immune response, the eccentric load of the downhill run adds muscle damage, resulting in a more pronounced sterile inflammatory process. In the present study, this component of downhill exercise is indicated by elevated myoglobin levels as a marker of muscle damage, as well as more increased IL-6, CRP and MCP1 levels compared to the control condition (Peake et al., 2005). Yet, regarding TNF-α only a trend was visible in our data.

Notably, the exercise intervention employed in this study elicited a much smaller inflammatory response in comparison to the endotoxin manipulations utilized in related research (Eisenberger et al., 2009, 2010; Engler et al., 2016; Grigoleit et al., 2011; Kotulla et al., 2018; Kullmann et al., 2014; Moieni et al., 2015a, b; Wright et al., 2005; Lasselin et al., 2018). For instance, Moieni et al. (2015) employed endotoxin as an inflammatory challenge to investigate inflammation-induced alterations in a theory of mind task. The endotoxin injection resulted in a 100-fold increase in IL-6 and TNF-α levels, accompanied by various mood-worsening effects, whereas the current exercise intervention led to an average increase of only 3–4 fold of IL-6 compared to baseline.

However, inducing smaller increases in inflammation may offer advantages for studies focusing on the social cognitive consequences of low-grade inflammation (cf. Balter et al., 2018) as the level of immune activation demonstrated in this study more closely resembles the low-grade inflammatory levels observed in individuals with depression, as well as in medical conditions like diabetes. For example, IL-6 levels in people with type-2 diabetes or depression often range between 2 and 10 pg/ml (Kadoglou et al., 2007). Thus, the current model appears to provide a more accurate representation of the inflammatory state in the mentioned medical conditions compared to many endotoxin studies. The relatively modest increases in inflammatory markers observed in this study can be attributed to the nature of sterile inflammation, which elicits milder levels of inflammatory cytokines compared to inflammation induced by bacteria or bacterial components. This approach minimizes potential confounding side effects, such as sickness symptoms or significant mood deterioration, previously reported in other studies. (e.g., Dowlati et al., 2010; Maes et al., 1995). Furthermore, the present method offers advantages, including sterility, by avoiding skin and tissue injury, eliminating infection risks, and circumventing administration challenges, as noted in prior research (Shek and Shephard, 1998; Wright et al., 2005). Another benefit of our exercise-induced inflammatory treatment is its adaptability to each participant's baseline fitness level, making the approach suitable for individuals with varying physical activity levels.

4.2. The influence of inflammatory processes on emotion perception

Regarding emotion perception, we revealed inflammation-driven changes in emotional state recognition of two interacting PLD agents. Specifically, in a pro-inflammatory state induced by downhill running, individuals showed reduced emotional content recognition during observed interactions irrespective of the displayed emotion. Moreover, their sensitivity to emotion-specific cues, quantified by d', declined.

The present findings not only reinforce but also enrich the existing body of literature, which has consistently demonstrated that the injection of endotoxins and the ensuing inflammatory response result in significant alterations in emotion perception. This phenomenon has been explored from various angles in prior research. On one front, studies have unveiled a proclivity for inflammation to engender a perceptual bias skewed towards negativity (Benson et al., 2017; Bollen et al., 2017). Simultaneously, other investigations showed that endotoxin-induced inflammation appears to impair one's capacity to interpret emotions portrayed through facial expressions, as assessed by instruments like the Reading-the-Mind-in-the-Eyes-Test (Balter et al., 2018; Moieni et al., 2015). Collectively, these findings, along with those of the current study, suggest that inflammation detrimentally affects the precise recognition of emotional states in others, regardless of the emotion's valence. Furthermore, Muscatell et al. (2016) demonstrated the influence of endotoxin-induced inflammation on neural activity within regions integral to mentalizing, the process of attending to and comprehending others' thoughts and feelings. Notably, individuals subjected to the endotoxin condition exhibited heightened activity in the dorsomedial prefrontal cortex, a pivotal node in the mentalizing network, when exposed to both negative and positive social feedback, in contrast to those in the placebo condition. Consequently, it becomes evident that inflammation exerts a discernible impact on the brain's responsiveness to social and affective stimuli.

In contrast to the frequently reported findings in related literature, our study did not observe an increase in aroused, depressed, or angry mood following exercise-induced inflammation at both the 3-h and 24-h time points after downhill running. This contrasts with several studies that induced inflammatory status via endotoxemia, which showed an increase in self-reported depressed mood, anxiety, fatigue, uneasiness (e.g., Engler et al., 2016; Grigoleit et al., 2011; Kullmann et al., 2014), feelings of social disconnection (e.g., Eisenberger et al., 2010; Moieni et al., 2015a), as well as low self-esteem (Kotulla et al., 2018). As previously mentioned, the exercise intervention used in our study elicited a smaller inflammatory response compared to endotoxin manipulations, which may explain the absence of depression-like mood alterations in our findings. A further noteworthy point concerning this case is raised by studies of Eisenberger et al. (2009) and Moieni et al. (2015b). They found no differences in mood changes following endotoxins for men but for women independently from cytokine elevations, indicating different hormonal contributions to cytokine induced depressed mood changes. It is important to highlight this aspect to contextualize our results, which were collected from a male cohort.

4.3. The influence of inflammatory processes on eye movements

Gaze patterns are recognized as indicators of various conscious and unconscious cognitive processes, including attention allocation, initial vigilance, gaze direction, and focus of attention, as well as attentional engagement and maintenance (Suslow et al., 2020). These processes play a crucial role in regulating emotional responses by shaping initial attention and subsequent processing filters (Todd et al., 2012). However, prior research on the impact of low-grade inflammation on emotion perception has not yet explored eye movement behavior. In our study, we used eye tracking parameters to investigate participants' initial attention, attention maintenance, and visual scanning under different inflammatory conditions. Specifically, we found an effect of experimentally induced inflammation on eye movements, focusing on the number of fixations made. Our findings revealed that the number of fixations increased nearly linearly from the inflammatory (INFL) to the control (CON) and rest (REST) condition when participants observed happy interactions. Conversely, for sad interactions, the number of fixations decreased from INFL to CON to REST. This suggests that participants tended to explore sad stimuli more when experiencing a more pronounced inflammation, and to explore happy stimuli more when this is not the case. Interestingly, this eye scanning behavior aligns with patterns observed in unmedicated depressed patients, who tend to show fewer fixations on positive stimuli and more on negative scenes compared to healthy controls (Suslow et al., 2020). Affective cognition, such as negative biases, is a core aspect of depression (Elliott et al., 2011) and is linked to depression risk, exacerbation, and symptom maintenance. This similarity in gaze behavior suggests a potential indicator of an early depression-like behavior in the presence of acute inflammation.

However, it is important to note that the observed differences in gaze behavior cannot easily explain the present changes in perceptual performance during inflammation. Under inflammation, there was a reduction in emotion recognition for all emotions, while gaze behavior shifted towards exploring sad stimuli more. Interestingly, there was no sensitivity difference for recognizing sad stimuli between the INFL and CON condition, suggesting that the increased tendency to explore sad stimuli may have compensated the detrimental effect of inflammation for these stimuli. Futures studies could further investigate the potential role of affective attention in mediating effects of inflammation on emotion recognition, including a possible role of microsaccades.

4.4. Limitations

Firstly, we have to admit that the question of whether the observed effects are solely related to emotion perception or if participants would perform poorly on any perceptual or cognitive task under inflammatory conditions remains partially unanswered. To address this, future studies could incorporate a perceptual control task, such as assessing speed discrimination of randomized point-light displays. However, we showed in a control task that inflammation did not influence working memory capacity. This suggests that inflammatory conditions may primarily impact emotion perception rather than cognition itself. Furthermore, our work indicates that modulations of gaze behavior by inflammation strongly interact with emotional stimulus content, underscoring their affect-specific nature. In this vein, a literature review conducted by Bollen et al. (2017) did not find compelling evidence linking acute experimental inflammation to changes in attention, executive functioning, or consistent patterns in memory functions. In contrast, studies examining social and emotional processing consistently showed that these processes are more likely to be influenced by inflammation.

Second, we acknowledge that the effects of chronic inflammation, as seen in clinical populations, could differ substantially in both nature and magnitude from those observed in our current experimental paradigm (cf. Bollen et al., 2017). Therefore, further research involving individuals with chronic inflammatory conditions is essential to gain a clearer understanding of how chronic inflammation affects emotion perception.

Third, it is important to note that our study only included male participants to mitigate the influence of menstrual cycle fluctuations and enhance controllability. However, existing literature has demonstrated differences between male and female participants concerning emotion perception (Alaerts et al., 2011) and sensitivity to inflammation-induced changes (Engler et al., 2016; Lasselin et al., 2018; Moieni et al., 2015b; Wegner et al., 2017). Therefore, it is highly desirable to conduct studies that encompass both sexes to account for possible sex-specific differences.

A fourth critical concern relates to the current emotion recognition paradigm, which primarily consisted of stimuli with minimal ambiguity. As a result, the overall recognition rates were high, and the variation between conditions was relatively small, making it challenging to detect robust effects. For future investigations, it would be beneficial to incorporate more difficult and ambiguous stimuli to enhance the potential for significant findings.

Another aspect worth considering is the sequence of our experimental conditions, where the rest condition was consistently placed last due to methodological constraints, and the control condition resulted in slightly elevated cytokine levels. Despite this limitation, we want to emphasize that only the contrasts between the downhill running condition and the rest condition yielded significant results. This suggests that the observed perceptual differences are likely attributed to the inflammation condition.

5. Conclusion

In summary, our findings point out that exercise-induced inflammatory responses could alter emotion perception, manifesting primarily as diminished recognition rates of emotional content of social interactions. This effect can be attributed to a diminished sensitivity to emotion-specific cues across all emotional categories. While changes in visual scanning behavior were observed, they cannot account for the altered perceptual performance, as those effects were not observed irrespective of the emotion category. Thus, the effects of inflammation on perception likely stem from changes in neural activity within brain regions involved in emotion processing and mood regulation, such as limbic and cortical areas, which are susceptible to fluctuations in blood cytokine concentrations (Dantzer et al., 2008; Lasselin et al., 2018).

To the best of our knowledge, this study provides first evidence that exercise-induced low-grade inflammation potentially might impair the accurate and reliable comprehension of emotional information conveyed through perceived body language during social interactions. However, further research is warranted to gain a more comprehensive understanding of inflammation-induced changes in social cognition, including their implications for both healthy populations and individuals with neuropsychiatric disorders such as depression, but also lifestyle-related diseases, like diabetes-type 2 and arteriosclerosis.

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Ethics approval statement

Ethical approval was provided by the Ethics Commission of the FB06, JLU Giessen.

Patient consent statement

Following the guidelines of the Declaration of Helsinki, written informed consent was obtained from all participants before participation in the study.

Statement

During the preparation of this work the author(s) did not use generative AI and AI-assisted technologies.

CRediT authorship contribution statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bbih.2024.100806.

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6.4 The Social Brain: How Movement Similarity Sharpens Affective Intention Decoding

Article

The Social Brain:
Motor Similarity Sharpens Affective Intention Decoding

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Summary

Humans readily infer others' feelings from how they move, yet the computational principles that support this ability remain debated. Two prominent accounts propose either direct motor matching or predictive coding mechanisms. Here we combine motion-capture, behavior assessments, and fMRI multivoxel pattern analysis to test whether an observer's own motor repertoire operates as an embodied prior during affective action perception. We quantified motor similarity between each observer and stimulus kinematics and examined its impact on neural representations within the action observation network. Motor similarity sharpened affective representations in inferior frontal gyrus: cross-validated classifiers trained on high-similarity trials decoded valence reliably above chance and outperformed classifiers trained on low-similarity trials. In contrast, motor similarity attenuated univariate BOLD responses in inferior parietal lobule, consistent with reduced prediction error under more precise priors. Behaviorally, observers judged motorically dissimilar interactions as more intense, indicating greater perceptual salience when observed kinematics diverge from one's own repertoire. Affective intensity further modulated neural precision in inferior frontal gyrus, revealing an interaction between social salience and embodied priors. Together, these converging neural and behavioral results adjudicate between competing accounts by demonstrating a principled double dissociation: representational sharpening in inferior frontal gyrus without increased activation, alongside attenuation in inferior parietal lobule under higher similarity, supporting a hierarchical predictive coding framework for social perception. Beyond action observation, our results show that a person's own movement repertoire calibrates neural representations of affect, offering a general principle for efficient embodied inference.

Highlights

- Similar affective expressions enhance neural decoding of affect in the IFG while attenuating responses in the IPL
- Observers rate dissimilar actions, relative to their own expressions, as more emotionally intense
- Affective salience and motor similarity jointly enhance decoding accuracy in the IFG
- Results support a predictive coding account of affective intention decoding from body movements

Keywords: Mirror Neuron System, Motor Resonance, Affective Intention, Valence, Motor Similarity

Introduction

Social interactions hinge on our ability to rapidly and often unconsciously infer others' emotional states and intentions. A single movement can convey subtle yet crucial information about affect and intent. Consider a bustling restaurant in which glasses are clinking and laughter is rippling through the room. At a corner table, a man sits with arms tightly crossed, his foot bouncing, fingers rhythmically clenching and unclenching. His companion, without hearing a word, senses unease. But how does the brain extract such rich social meaning from mere movement? And how does the observer's own body with its incorporated habits, actions, and experiences shape this perception?

Mirror neurons are thought to form the neural foundation for understanding others' actions and intentions by converting visual input into motor representations (Rizzolatti and Craighero, 2004). One influential account, the direct matching model (Gallese et al., 2004; Rizzolatti & Craighero, 2004), posits that observing others' actions engages the same neural circuits as performing them, particularly those within the inferior frontal gyrus (IFG), premotor cortex (PMC), and inferior parietal lobule (IPL). This motor resonance enables intuitive action understanding and intentional inference by simulating the observed movement. Previous research indicates that observing familiar actions elicits greater activation within these motor-related areas, emphasizing the importance of prior experience in shaping neural responses during action observation (Balser et al., 2014; Calvo-Merino et al., 2006, 2007; De Marco et al., 2020). Motor familiarity, defined as observing a movement pattern that is part of one's own motor repertoire, enhances the efficiency of motor system engagement, thereby facilitating the perceptual processing of observed actions (Cross et al., 2006; Iacoboni, 2005; Rizzolatti & Craighero, 2004). Moreover, greater motor similarity amplifies resonance, thereby increasing activation in IFG, PMC, and IPL.

However, up to now, this modulatory influence of motor familiarity has been explored primarily by comparing individuals with extensive experience in specific movement patterns such as dancers or athletes to novices who lack any motor expertise related to the observed actions (Aglioti et al., 2008; Balser et al., 2014; Calvo-Merino et al., 2006, 2007; Pilgramm et al., 2009; for a review see Kemmerer et al., 2021). Yet, in everyday life, action understanding often relies on ordinary movements that are deeply familiar to all of us, such as walking and running during goal-directed locomotion, reaching and grasping when manipulating objects, or smiling and gesturing to express emotions. These expressions vary not only in their valence and category (e.g., anger, joy) but also in affective intensity (i.e., the degree to which an emotion is kinematically emphasized or subdued). Research has shown that emotional expressions contain rich kinematic information about the meaning of an action (Atkinson et al., 2004; de Gelder 2007; de Gelder et al., 2004; Hadjikhani & de Gelder, 2003; Poyo Solanas et al., 2020). Based on the modulatory influence of motor familiarity described so far, interindividual differences in the kinematic expression of anger, joy, fear, or sadness could, although being subtle in nature, affect the observer's ability to decode the affective content of observed actions. If an observed emotional expression is highly similar to the way one would express that same emotion oneself, the expression should resonate more strongly within the observer, enabling a more accurate internal simulation of the observed body movements and ultimately leading to a more precise decoding of the emotions expressed by others. Indeed, behavioral evidence supports this notion: Edey et al. (2017) showed that greater divergence between an observer’s own gait and the gait they observe can alter the perceived emotional valence of the movement.

However, this purely resonance-based view has been challenged by predictive coding theories. These propose that the brain continuously generates and refines expectations about observed actions on the basis of prior experience (Friston, 2005; Kilner et al., 2007). This framework posits a hierarchical process: Higher cortical areas generate top-down predictions about expected sensory input that are then compared to actual observations. Discrepancies (i.e., prediction errors) drive continuous model refinement (Clark, 2013). Specifically, the IPL processes goal-level representations by integrating sensory input and comparing it with prior expectations. When an observed action deviates from these expectations, prediction errors signal the need for model refinement. These errors are forwarded to the IFG that maps observed movements onto the observer’s own motor repertoire, refines these representations based on prior motor experience, and sends updated predictions back to the IPL to adjust the understanding of action goals. The key benefit is increased neural efficiency, because more resources are allocated to novel, unpredictable information (Barlow, 1961; Mumford, 1992). Recent perspectives even suggest that the mirror neuron system, once thought to function purely bottom up, is actually embedded within a hierarchical architecture potentially serving predictive functions (Keysers & Gazzola, 2014; Keysers et al., 2024).

Critically, both models agree that prior motor experience influences action perception—but they diverge in how they do this (for a review, see Kemmerer et al., 2021). The direct matching model predicts increased neural activation for motorically similar actions due to stronger resonance, whereas the predictive coding models suggest that greater motor similarity reduces prediction errors, resulting in attenuated sensory responses and sharpened neural representations. Although empirical studies have provided support for both scenarios (Alaerts et al., 2014; Calvo-Merino et al., 2006; Gardner et al., 2015; Kokal and Keysers, 2010; Sasaki et al., 2012; Schippers and Keysers, 2011; Ubaldi et al., 2015), they have not adjudicated between these two accounts or answered the question how one's own body representation alters sensory processing—especially in ecologically valid social contexts involving emotionally expressive whole-body movements of varying affective intensity.

To directly compare these accounts and examine how motor similarity modulates affective decoding in real-life social interactions, we employed kinematic analysis, behavioral measures, blood-oxygenation-level-dependent functional magnetic resonance imaging (BOLD fMRI), and multivariate pattern analysis (MVPA). Specifically, we investigated whether motor similarity between observer and observed agent influences the decoding of affective intentions from body movements, and whether the observer's own motor repertoire serves as a prior in this process of modulating perceptual and neural responses through motor resonance. According to direct matching theory, greater motor similarity should lead to enhanced motor resonance, resulting in stronger BOLD activation and higher decoding accuracy in the IFG and the IPL. In contrast, predictive coding accounts propose that motor similarity will improve prediction precision, thereby reducing prediction errors and attenuating BOLD responses in the IPL, while simultaneously sharpening neural representations in the IFG on the basis of adjusted neuronal representation through reciprocal interaction. We additionally hypothesize that the modulatory influence of motor similarity on affective decoding varies as a function of the affective intensity of the observed expression. More intense expressions characterized by higher kinematic salience should either amplify motor resonance (direct matching) or strengthen top-down priors, thus reducing uncertainty more efficiently (predictive coding), leading to more distinct neural signatures in frontoparietal regions. Given their central roles in motor simulation and predictive processing, the IFG and the IPL emerge as key regions of interest for testing these competing accounts. Both regions are consistently implicated in action observation and intention decoding (Keck et al., 2025; Koul et al., 2018; Patri et al., 2020), yet their functional contributions may diverge depending on whether motor resonance or predictive coding guides the process of affective intention decoding.

Our design enabled us to assess how individual differences in their affective motor repertoire shape the decoding of affective intentions across a range of affective intensities, providing novel insight into how embodied priors guide the understanding of affective intentions.

Materials & Methods

Participants

Twenty adults (10 female, mean age 25.1 years, *SD* = 3.4 years) with normal or corrected-to-normal vision participated in the study. Participants reported no history of psychiatric, neurological, immunological, or physical disorders, and none were currently using psychoactive medication. Two participants were excluded because they failed to attend either the behavioral experiment or the fMRI scanning session, leaving a total sample of 18. All participants provided written informed consent in compliance with the Declaration of Helsinki. The study procedure was approved by the local ethics committee of the Department of Psychology and Sports Science, Justus-Liebig University Giessen.

Motion Capturing

Ten participant pairs were instructed to enact different interactions with four different positive or negative affective states (happy, sad, angry, and affection). Each affective interaction was performed at three intensity levels (low, medium, and high) to capture a broad spectrum of affective behaviors in social interactions. To ensure consistency in their expressions, participants received scripted scenarios outlining specific affective contexts. They were also encouraged to respond intuitively within these scenarios, allowing for natural variability in their performances.

The interactions were recorded using a Vicon optical motion capture system (Vicon Motion Systems, Oxford, England) with 24 cameras. Reflective markers were placed on predetermined anatomical landmarks based on the Vicon “Plug-in-Gait” model that requires 39 markers per participant. The system captured three-dimensional marker trajectories with a spatial resolution of 1 mm at a sampling rate of 120 Hz. Data processing was performed using Nexus 2.12 software (Vicon Motion Systems, Oxford, England).

Behavioral Experiment

Each subject participated in the behavioral experiment twice, with an average interval of 7 days between sessions. Participants were presented with 24 affective point-light interactions (6 for each affective state, and 2 for each intensity within the valence categories) selected from a larger motion-capture dataset (Bachmann et al., 2020) based on identical scene contexts as the scripts provided for motion capturing. For additional details on stimulus creation, see Bachmann et al. (2020).

During the experiment, each sequence was shown once on a 12-inch screen with a refresh rate of 60 Hz. The viewing distance was approximately 40 cm. Each trial began with a 1-s fixation phase, followed by a 4-s stimulus sequence. After observing the interaction, participants rated the perceived affective valence of the videos on an 11-point scale ranging from -5 (*extremely negative*) to +5 (*extremely positive*).

fMRI: Scanning

During fMRI scanning, participants completed six runs of 48 trials using an event-related paradigm. Each run included the same stimuli as the behavioral experiment along with a control condition featuring scrambled versions of all stimuli. This design resulted in a total of 288 trials and a scanner session lasting approximately 60 min. Stimuli from all conditions were presented in a pseudorandomized order within each run and counterbalanced across participants.

Each trial began with a 1-s fixation period, followed by a jittered interval ranging from 0–90% of the repetition time (TR) in 10% increments (average jitter: 1.5 s) (see Figure 1B). Participants then viewed either a point-light display (PLD) or a scrambled sequence for 4 s followed by a blank screen for 8 s spanning the BOLD response.

fMRI: Image Acquisition

fMRI data were collected on a Siemens Prisma 3-T whole-body scanner (Siemens Prisma, Erlangen, Germany) using a 20-channel head coil. A structural image was acquired from each participant consisting of 176 T1-weighted sagittal images (1-mm slice thickness; MPRAGE) and a fieldmap (40 slices; TR = 1000 ms; TE = 10 ms). For functional imaging, six runs with 265 volumes per run (i.e., a total of 1,590 volumes) were registered using a T2*-weighted gradient echo-planar imaging sequence covering the whole brain with 40 slices (slice thickness = 3 mm; 0.75 mm gap; descending interleaved; TR = 2,000 ms; TE = 30 ms; flip angle = 75 degrees; field of view = 210 mm × 210 mm, 2 mm in-plane isotropic resolution). The orientation of the axial slices was parallel to the AC–PC line. Trial onsets were jittered within 0–90% of the TR Image.

Data Analysis and Statistics

Kinematic Analyses: Measurement of Motor Similarities

To calculate the motor similarity between agent and observer, we conducted a four-step data analysis: First, we calculated predefined movement features (see Figure 1 C) including kinematic and postural configurations such as motion energy, velocity, or limb angles for the presented PLD interactions (for more details on feature definitions, see Keck et al. 2022; Zabicki & Keck, 2021, see supplementary materials). Second, we computed the same movement features for the interactions captured from each participant during motion capture. Third, we quantified the similarity between the stimulus movements and those performed by participants during motion capture by calculating the normalized Euclidean distance for each feature across participants (see *Figure 1 E*). Finally, fourth, we approximated whole-body similarity by calculating the integral across all feature similarities. A value of 0 indicates perfect similarity, whereas values further from 0 correspond to greater dissimilarity. For a visual description, see Figure 1.

Classification of Similar and Dissimilar Movement Groups

To assess the characteristics of the proposed similarity measure, we calculated average, minimum, and maximum similarity scores as well as potential differences between the two affective valence categories. Movements were classified as similar or dissimilar by performing a median split across all participants and stimuli (18 participants × 24 stimuli = 432 movement similarities). Individual scenes above the median were classified as dissimilar, whereas those below the median were classified as similar (see Figure 1 G).

Behavioral Analyses: Influence of Motor Similarity on Valence Perception

To assess how motor similarity affects subjectively perceived valence, absolute mean valence ratings were computed and categorized via a median split. A Wilcoxon signed-ranks test evaluated differences in perceived valence between high and low motor similarity.

To improve reliability and reduce variability, we calculated the average valence ratings across both behavioral experimental days. This approach aimed to enhance consistency and minimize the effect of possible confounding effects such as mood or time of day (Hot et al., 2005; Hristova & Grinberg, 2011).

fMRI: Analyses

Regions of Interest

We defined two bilateral core regions of the action observation network as regions of interest (ROIs) based on previous findings (Keck et al. 2025; Kilner, 2007; Koul et al. 2018; Patri et al., 2020): the inferior frontal gyrus (IFG) and the inferior parietal lobule (IPL). ROIs were masked using custom-created masks for the left and right IFG and IPL in MNI space.

Univariate Analysis: Preprocessing

First, a univariate analysis was conducted. Functional images were spatially smoothed using an isotropic Gaussian kernel with a full width at half maximum (FWHM) of 6 mm. Each participant's data were modeled using an event-related approach. At the first level, a general linear model (GLM) was applied. Regressors differed between participants and represented either "similar movement" or "dissimilar movement" for each scene. In addition to the similarity regressors, the model included the six standard motion parameters from the realignment procedure.

Univariate Analysis: BOLD Activation Magnitude

Following model estimation, voxel-wise activation signals were extracted within the predefined ROIs. These activation signals were then averaged across voxels and across scenes within each similarity category for each participant. Finally, to assess whether motor similarity influences neural activation within the ROIs during action observation, a Wilcoxon signed-ranks test was performed to evaluate differences in BOLD activity within each ROI between similar and dissimilar movements.

Multivariate Analysis: Preprocessing

First, realignment and unwarping were performed using voxel displacement maps generated from the fieldmaps (Hutton et al., 2002), and the functional images were coregistered with the anatomic scan for the respective subject. Smoothing was executed using an isotropic three-dimensional Gaussian filter with a full-width-at-half-maximum (FWHM) kernel of 2 mm and normalized them to MNI space (http:// www.loni.ucla.edu/ICBM/).

Multivariate Analysis: General Linear Models

A first-level analysis was computed with SPM 12 using separate GLMs for each subject and each of the six runs. We created 24 boxcar regressors corresponding to the 12 positive (4 x low intensity; 4 x middle intensity; 4 x high intensity) and 12 negative (4 x low intensity; 4 x middle intensity; 4 x high intensity) scenes. The boxcar functions of each regressor spanned the observation phase (4s). Each regressor was convoluted with a canonical hemodynamic response function. Moreover, six movement parameters from the rigid-body transformation of the motion-correction procedure were entered as covariates in the GLM. The voxel-based time series were filtered with a high-pass filter (time constant = 128 s).

Multivariate Analysis: Decoding Stimulus Valence Based on Motor Similarity

In the next step, we conducted a multi-voxel pattern analysis (MVPA) to determine whether neural activity patterns during observation were sufficiently distinct to decode the observed valence (positive or negative) as a function of motor similarity. To examine response patterns within the IPL and the IFG, we employed two support vector machine (SVM) classifiers: one trained on brain activity associated with similar movements; the other, on brain activity associated with dissimilar movements.

Due to varying proportions of similar and dissimilar movements across participants, we employed cross-validation across subjects, ROIs, and classifiers. To reduce the dimensionality of the data, we applied principal components analysis (PCA). In each of the 10 cross-validation iterations, the dataset was randomly split into a training set (80%) and a test set (20%) resulting in 346 training vectors and 86 test vectors per iteration (based on 24 stimuli × 18 subjects). This procedure was performed separately for each of the six runs, yielding a total of 60 average accuracy scores (6 runs × 10 iterations). The SVM was trained on the labeled training data to predict the valence condition of each stimulus representative for the affective intention. A decision boundary was derived from the training data and applied to the test data, with correct and incorrect classifications scored as 1 and 0 respectively. Classification accuracies were calculated to assess the performance of the two SVMs within each ROI and were compared against chance level (50%). The normality of classification accuracies was assessed using the Shapiro–Wilk test. If the assumption of normality was violated, classification performance was tested against chance using the nonparametric Wilcoxon signed-ranks test; otherwise, a one-sample

Student's *t* test was used. To statistically compare classification performance between similar and dissimilar movements within each ROI, a Wilcoxon signed-ranks test was conducted.

If decoding based on motor familiarity exceeded chance level, we proceeded to examine whether affective intensity further modulated the distinctiveness of the neural patterns within the relevant ROIs. Therefore, we applied the same approach using a subset of the data (8 stimuli per intensity category × 18 subjects). To compare the classification performance with regard to affective intensity we performed a 3 (affective intensity: low, medium, high) × 2 (similarity: similar vs. dissimilar) repeated measures ANOVA. If significant effects emerged, post hoc pair-wise comparisons were conducted and Bonferroni-corrected. Futhermore each classifier was tested against chance level (50%). This approach allowed us to examine whether the effect of motor similarity on decoding performance varied systematically with the degree of affective intensity.

All analysis steps and statistical tests, were carried out using Matlab 2024a and JASP 0.15.00.

Results

Effects of Motor Similarity on Valence Perception

With regard to the influence of motor similarity on the subjective perception of valence in social interactions, results showed that dissimilar movements (M = 2.73, SEM = 0.14) were perceived as more intense than similar movements (M = 2.42, SEM = 0.12; Z = –3.19, p = .01; see Figure 2A). Thus, motor dissimilarity between the observer and the agent amplifies the perceived emotional intensity of affective social interactions.

fMRI Results: Effects of Motor Similarity on Activation Magnitude

Neuroimaging data showed that observing movements more similar to one's own (M = 0.11, SEM = 0.02) was associated with attenuated BOLD responses in the left IPL compared to dis-similar movements (M = 0.34, SEM = 0.06; Z = –3.59, p < .001; see Figure 2B). No significant effect of motor similarity on BOLD activation were found in the right IPL and the IFG of both hemispheres.

fMRI Results: Effects of Motor Similarity on Decoding Affective States

We used MVPA to assess whether the decodability of affective intention in social interactions differed as a function of motor similarity (see Figure 2 C). In the left IFG, classifiers trained on similar movements (*M* = 0.54 %, *SEM* = 0.01) predicted the valence of the observed interaction significantly above chance (*W* = 1568.5, *p* < .001) and outperformed classifiers based on dissimilar movements (*M* = 0.51%, *SEM* = 0.01; *Z* = 2.92, p < .01). In the right IFG, only classifiers trained on dissimilar movements (*M* = 0.53%, *SEM* = 0.01) performed above chance, *t*(59) = 2.8, *p* < .01, *d* = .036, with no significant difference between similarity conditions. In the left IPL, decoding performance was above chance for both similar (*M* = 0.53%, *SEM* = 0.01; *t*[59] = 3.01, *p* < .01, *d* = 0.39) and dissimilar movements (*M* = 0.54%, *SEM* = 0.01; *W* = 1104.5, *p* < .001)—again, without a significant difference between conditions. Finally, in the right IPL, neural response patterns did not support above-chance decoding of affective valence, nor did they differ across similarity conditions. The Shapiro–Wilk test and descriptive statistics for each classifier can be found in the supplementary material. In summary, MVPA revealed above-chance decoding of affective valence for both similar (left IFG, left IPL) and dissimilar movements (right IFG, left IPL). However, improved classification for similar compared to dissimilar movements between observer and agent was observed exclusively in the left IFG.

fMRI Results: Effects of Motor Similarity on Decoding Affective Intentions of Different Intensities

To examine whether affective intensity further modulated the distinctiveness of neural patterns, we grouped the scenes into low, medium, and high affective intensity levels and trained six separate classifiers within the left IPL and IFG for each motor similarity group. A 2 × 3 repeated measures ANOVA on classification performance in the left IFG revealed a significant interaction between stimulus intensity and motor similarity, *F*(2,59) = 10.46, *p* < .001, $\eta^2 = 0.07$. Bonferroni-corrected post hoc analyses showed that high-intensity scenes classified on the basis of similar movements yielded higher decoding accuracy than low-intensity scenes within the same condition (*p* < .01), and also outperformed high-intensity scenes classified based on dissimilar movements (*p* < .001). No significant main effects or interactions were found in the right IFG or left IPL. All classifiers were tested against chance; detailed results are reported in the supplementary material.

Discussion

Previous research has shown consistently that prior motor experience shapes action perception. However, two competing theoretical accounts—the direct matching hypothesis and the predictive coding model—differ in the mechanisms they propose and their predictions regarding the effects of motor familiarity on activity patterns in key regions of the human mirror system during action observation (Kemmerer et al., 2021). To adjudicate between these accounts, we investigated whether motor similarity affects the decoding of affective intentions from body movements, and how this effect would be modulated by the emotional intensity of complex, socially nuanced whole-body interactions. Direct matching theories emphasize bottom-up processes including stimulus-driven activation in motor-related areas such as the IFG and IPL (Giese & Poggio, 2003; Rizzolatti et al., 2014). In contrast, predictive coding models propose that perception is an inferential process, integrating sensory input with top-down predictions derived from the observer's own motor repertoire (Clark, 2013; Kilner, 2007). Our findings align more closely with predictive coding principles. We found that observing motorically similar actions led to reduced BOLD responses in the IPL, suggesting lower prediction error accompanied by an enhanced affective intention decoding in the IFG. This is indicative of less noisy, more efficient, and more precise neural representations (Friston, 2005; Keysers et al., 2024; Kilner et al., 2007). This divergence supports the view that embodied priors, reflecting an individual's motor experience and expressive repertoire in emotional interactions, affect the subjective impression by reducing error signals in parietal areas and sharpening representational accuracy in frontal regions during the observation of meaningful social actions.

Behaviorally, participants rated affective interactions as more intense when the affective movements were motorically dissimilar to their own. This suggests that unfamiliar actions increase perceptual salience, probably due to larger prediction errors stemming from mismatches between expected and observed kinematics (Edey et al., 2017; Pollick et al., 2001; Roether et al., 2009). This is in line with the heightened IPL activation found during the observation of kinematically dissimilar as compared to similar actions.

Additionally, we manipulated the affective intensity of the observed interactions in order to test whether classification performance would vary according to a social saliency gradient from low to high affective intensity. We found that higher intensity interactions enhance classification performance in the IFG specifically in conditions of high motor similarity. Thus, decoding performance in the IFG varies with both motor similarity and affective intensity, suggesting that affective decoding becomes particularly efficient when the own motor repertoire matches the observed action in scenes with highly salient social input. This interaction supports the idea that predictive coding is involved in affectively relevant experiences such as pain, and that affective states may influence how predictions and prediction errors are computed (Geuter et al., 2017).

In sum, our findings point to the notion that the observer's motor repertoire serves as a prior that modulates the perception of affective actions, highlighting the role of motor representations in socially relevant predictive processing.

Motor Similarity as an Embodied Prior for Affect Decoding

Our findings challenge the notion that motor similarity universally amplifies cortical responses. Instead, they suggest a bidirectional mechanism in which motor similarity differentially modulates representations within the IFG and IPL to facilitate affective intention decoding (Keysers et al., 2024). Contrary to the direct matching hypothesis that predicts increased activation in both regions, we observed attenuated BOLD responses in the IPL and no activation increase in the IFG for motorically similar actions. Despite the absence of increased IFG activity, decoding accuracy for the affective content improved, indicating that motor similarity sharpens IFG representations through enhanced pattern precision. The IPL, in contrast, exhibited above-chance decoding in both similarity conditions, suggesting that its role is less dependent on motor similarity in terms of representational specificity (pattern), but more so in terms of overall activation (BOLD). The attenuated BOLD in the IPL aligns with findings by Diersch et al. (2013) and Mou et al. (2024) who reported stronger IPL engagement when actions violated motor priors or observer expectations. Thus, the IPL seems to be especially responsive to (kinematic) mismatches, consistent with error-driven processing in predictive models.

In line with prior work, our data reinforce the notion that the IFG and the IPL contribute to the processing of kinematic stimuli particularly in decoding the (affective) intentions underlying observed movements. This aligns with recent studies demonstrating that both regions contain intention-relevant information. Koul et al. (2018), for instance, used multivoxel pattern analysis to show that grasping intentions can be decoded from IFG and IPL activity. Similarly, Keck et al. (2025) found that those two areas represent affective intentions during the observation of social interactions presented as point-light displays. Although these findings confirm the involvement of both regions in the interpretation of kinematic cues, they do not per se demonstrate a functional dissociation or hierarchical relationship. Subtle indications emerge from differences in decoding performance and representational similarity: In Koul et al. (2018), classifier weights were highest in the IPL, suggesting a stronger encoding of intention-related features; and Keck et al. (2025) reported more distinct representational patterns in the IPL compared to the IFG. Yet, such correlational results leave open the question of causal relevance. This question, however, had been addressed directly by Patri et al. (2020), who applied continuous theta burst stimulation (cTBS) to either IFG or IPL prior to an intention decoding task. Only stimulation of the IPL impaired performance, indicating that while these regions encode intention-relevant information, only the IPL is causally necessary for inferring intentions from movement alone. In contrast, the IFG may contribute to intention processing when additional semantic or contextual cues are available (El-Sourani et al., 2018, 2020), rather than being essential for interpreting kinematics in isolation. This functional dissociation suggests a possible hierarchical organization in which the IPL may serve as an evaluative node that integrates and refines predictions issued by higher-order regions such as the IFG.

The present data support the assumption of a hierarchical structure between the IPL and the IFG when decoding affective intentions. Notably, in our experiment, the hierarchical structure became apparent specifically through the manipulation of motor similarity. This manipulation acted as an embodied prior, guiding perceptual inference and thereby revealing a representational architecture that might otherwise have remained hidden. We propose that the IFG generates a top-down prediction grounded in the observer's motor repertoire that serves as such an embodied prior. This prediction is evaluated by the IPL through comparison with incoming sensory information. This is consistent with hierarchical predictive coding frameworks proposing that the IFG generates high-level expectations about action intentions that are subsequently assessed by the IPL (Sasaki et al., 2012; Urgen & Saygin, 2020). Support for this hierarchical organization also comes from dynamic connectivity analyses. For example, recent DCM findings showing that information flows from the STS to both IPL and IFG, and does this across different social-cognitive processes, suggesting the presence of a sensory-to-motor inverse model (Sadeghi et al., 2022).-These findings are consistent with hierarchical models of action understanding in which the IFG generates expectations that are tested against sensory kinematics in downstream areas such as the IPL. Prediction errors generated upon mismatch are then sent back upstream to refine top-down models.

Together with converging evidence from correlational, causal, and dynamic approaches, the present results support the concept of a predictive hierarchy in which the IFG provides an embodied prior or best guess about the (affective) intention, whereas the IPL compares this prior to observed kinematics, updating predictions or minimizing prediction errors depending on the degree of mismatch. This hierarchical mechanism seems to apply not only to the recognition of goal-directed actions but also to the interpretation of more complex social cues such as affective meaning. In line with evidence from other domains (Clark, 2013; Yon et al., 2019), these findings emphasize the brain's fundamental reliance on prediction in (action) perception. Motor experience thereby functions as a prior not only for recognizing others' movements but also for inferring socially and emotionally relevant information. Embodied motor knowledge thus contributes to understanding both what others are doing and how they are feeling.

Predictive Coding as a Mechanism in Social and Affective Cognition

A central contribution of our study lies in showing that affective intensity matters as a modulator. This speaks to the notion that not only affective intention understanding is improved through motor similarity, but that this is even more the case for socially salient interactions. Observing high-intensity interactions led to improved decoding performance in the IFG, particularly when the observed movement closely matched the observer's own motor repertoire. This interaction suggests that the IFG does not process motor and affective features in isolation, but rather combines both dimensions to extract the affective meaning of observed actions. Evidence for the IFG's sensitivity to the affective intensity or emotional content of observed movement stimuli is provided by studies demonstrating that the IFG is engaged during the observation of emotionally expressive body movements and that its activation varies with emotional intensity, especially in response to highly salient emotions such as anger and fear (Atkinson et al., 2004; Ferri et al., 2013; Grèzes et al., 2007; Peelen et al., 2007; Peelen & Downing, 2007; Pichon et al., 2009; Schmidt et al., 2020). Our findings extend this work by showing that affective intensity enhances classification performance in the IFG, particularly when accompanied by motor similarity. Thus, emotional salience increases the informational value of sensory input, whereas motor similarity enhances model precision. Both together optimize the extraction of affective meaning during action perception.

According to the hierarchical predictive coding model of action understanding (Kilner et al., 2007), the IFG operates at a higher level of the mirror neuron system and is responsible for generating abstract predictions about others' goals, intentions, and affective states (Erlhagen et al., 2006; Kilner et al., 2007; Ondobaka et al., 2015). In contrast, the IPL functions at a lower hierarchical level at which it compares incoming kinematic information to these top-down predictions and computes (kinematic) prediction errors (Grafton & Hamilton, 2007; Ondobaka et al., 2015; Patri et al., 2020; Saygin et al., 2012). This framework explains why the IFG is particularly sensitive to affective intensity and motor similarity: Both factors enhance the informativeness and precision of the observed input, facilitating more accurate matching with predictive models. The IPL, in contrast, processes the residual mismatch but is not modulated directly by the affective or motor-related salience of the input. This interpretation is supported by recent findings showing that the IFG integrates emotional expression recognition and motor simulation, and that it is especially engaged by emotionally charged or socially salient actions (Jabbi et al., 2008; Keysers et al., 2024; Simone et al., 2025). Thus, motor similarity and affective intensity probably converge in the IFG to optimize socially relevant predictive processing.

Beyond fundamental mechanisms, our findings may also inform clinical accounts of social cognition that involve affective perception. Predictive coding models have been proposed to explain social difficulties in conditions such as autism spectrum disorder (ASD) in which altered priors or impaired prediction error minimization may disrupt social inference (Keysers et al., 2024). Similarly, in Parkinson's disease (PD), impaired body expressivity and degraded motor predictions may diminish the accuracy of social perception (Bellot et al., 2020). Bellot et al. (2020) showed that PD patients evaluate emotional valence less intensely compared to healthy controls. They hypothesized that neural changes might compromise the recruitment of motor representations within core mirror neuron areas such as the IPL and IFG, a process that could impair their function as embodied priors, as proposed in predictive coding frameworks (Argaud et al., 2018; Bellot et al., 2020; for a review, see Eddy & Cook, 2018). Future research should explore whether and how embodied prediction errors relate to clinical impairments in embodied social cognition.

Limitations and Future Directions

Despite its contributions, this study has its limitations: First, the modest sample size may reduce statistical power and limit generalizability. Second, repeated stimulus exposure may have introduced familiarity effects that could confound perceived similarity and decoding performance. Third, it has been argued that intention decoding from kinematics might be confounded, because if different intentions involve distinct kinematic patterns, it might be difficult to determine whether observers each rely on low-level motion cues rather than making some inference about the mental state (Thompson et al., 2019). However, recent evidence counters this claim, showing that systematic kinematic variation can itself provide the informational substrate for intention inference (Scilatti et al., 2023, Becchio et al., 2024). Our results align with the latter view, indicating that variability in movement kinematics is not a nuisance factor, but the very basis on which perceivers infer intentions. Finally, it is important to acknowledge that classification performance in the IPL would also follow the predictions made by direct matching and motor resonance. Nonetheless, alongside reduced activity and sharpening of the IFG, our results align more closely with hierarchical models of action understanding. Future studies should manipulate repetition and familiarity independently and use continuous measures of motor similarity to provide a more nuanced account of its neural effects.

Conclusion

Our findings support a predictive coding account of affective intention decoding, demonstrating that motor similarity sharpens neural representations and reduces prediction errors during the perception of affective interactions, while also leading to attenuated perception of intensity. We propose that motor similarity functions as an embodied prior for affective inference, generating predictions about others' affective states by reducing uncertainty in the sensorimotor stream. Crucially, our results suggest that predictive coding operates not only to anticipate what an agent is going to do (Friston, 2005; Kilner et al., 2007), but also how they might feel while doing it. These results contribute to a growing body of evidence indicating that social cognition relies on embodied priors, and that this enables the brain to anticipate, interpret, and respond to others' affect in a resource-efficient manner. We further argue that the integration of predictive and embodied frameworks, grounded in the functional architecture of the mirror neuron system, provides a coherent model for understanding others through movement.

Figures

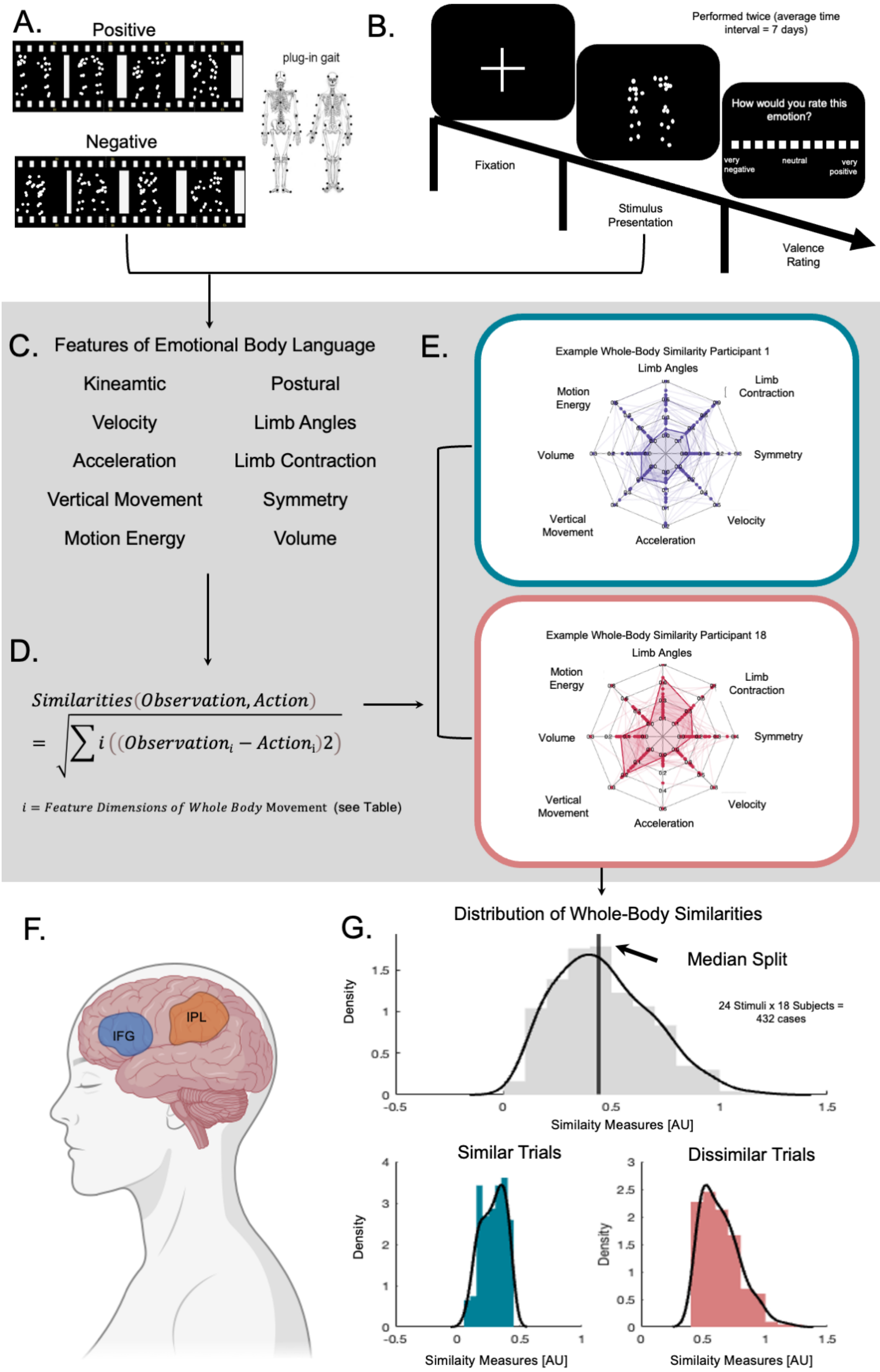

A.
Positive
Negative
plug-in gait
B.
Performed twice (average time interval = 7 days)
How would you rate this emotion?
very negative
neutral
very positive
Fixation
Stimulus Presentation
Valence Rating
C.
Features of Emotional Body Language
Kineamtic
Postural
Velocity
Limb Angles
Acceleration
Limb Contraction
Vertical Movement
Symmetry
Motion Energy
Volume
D.
Similarities(Observation, Action) = √(∑ i ((Observation_i − Action_i)2))
i = Feature Dimensions of Whole Body Movement (see Table)
E.
Example Whole-Body Similarity Participant 1
Limb Angles
Limb Contraction
Symmetry
Velocity
Acceleration
Vertical Movement
Volume
Motion Energy
Example Whole-Body Similarity Participant 18
Limb Angles
Limb Contraction
Symmetry
Velocity
Acceleration
Vertical Movement
Volume
Motion Energy
F.
IFG
IPL
G.
Distribution of Whole-Body Similarities
Median Split
24 Stimuli x 18 Subjects = 432 cases
Density
1.5
1
0.5
0
-0.5
0
0.5
1
1.5
Similaity Measures [AU]
Similar Trials
Dissimilar Trials
Density
4
3
2
1
0
-0.5
0
0.5
1
Similaity Measures [AU]
Density
3
2.5
2
1.5
1
0.5
0
0
0.5
1
1.5
Similaity Measures [AU]

Figure 1. Experimental timeline and movement-similarity analysis.

(A) Example scenes depicting negative and positive affective interactions. **(B)** Trial timeline with video presentation and rating period. **(C)** Kinematic and postural features extracted from each captured and shown interaction. **(D)** Calculation of whole-body motor similarity between executed and observed interactions. **(E)** Examples of high-similarity and low-similarity scores for different scenes and participants. **(F)** Anatomical locations of regions of interest in the action observation network. **(G)** Distribution of motor similarities scores across all observer–agent pairs with the median split used to create similarity groups.

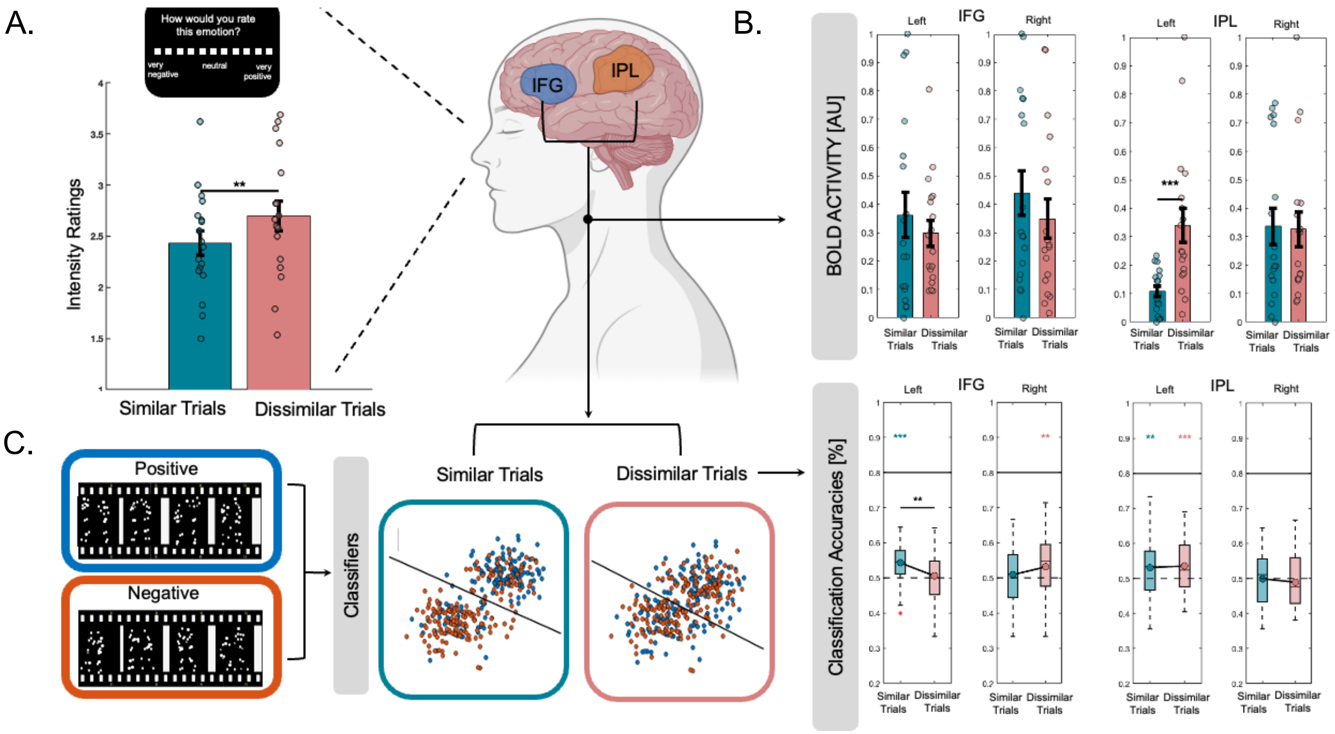
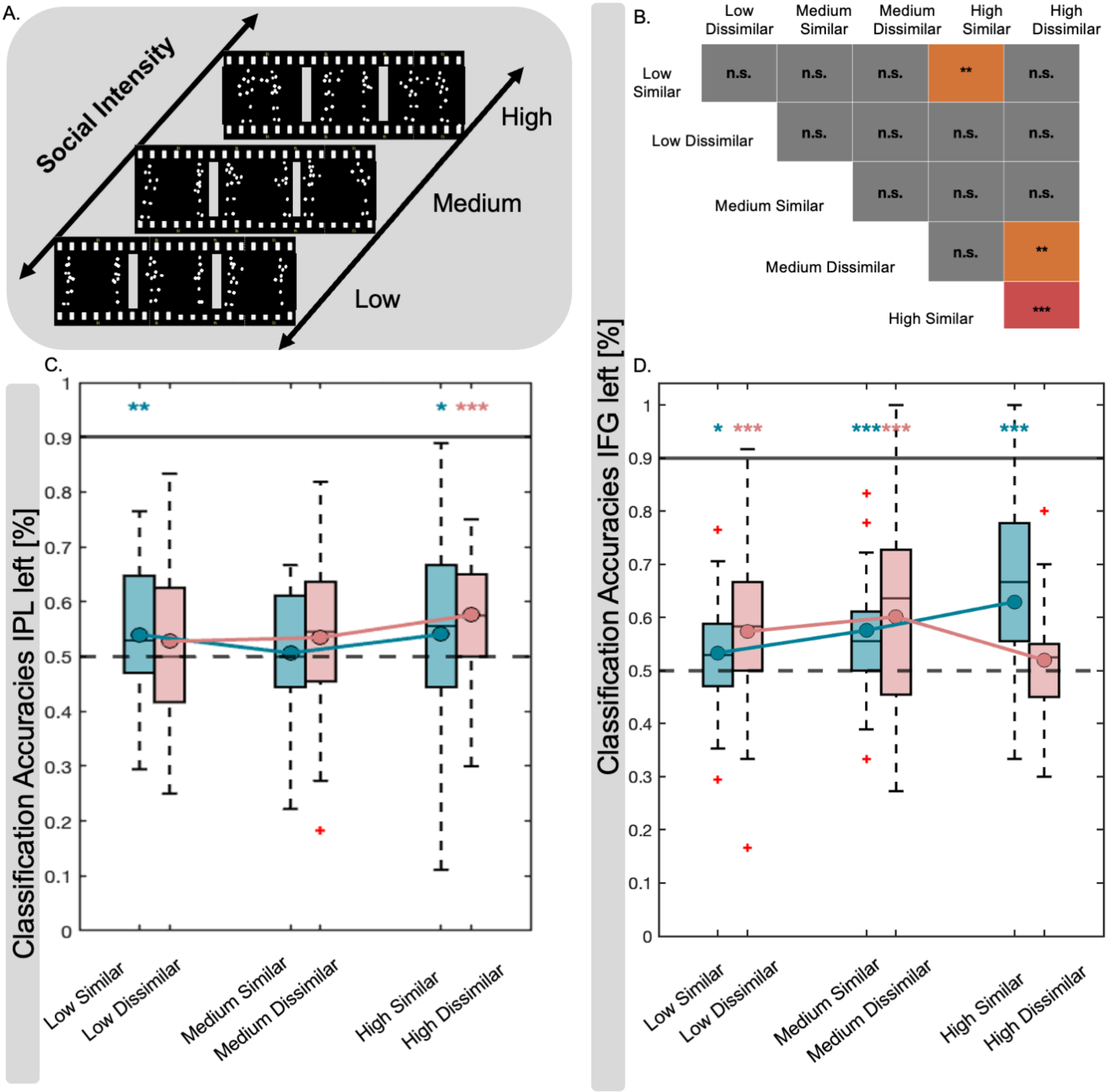


Figure 2. Affective judgments, classification pipeline, and ROI results.

(A) Mean affective-intensity ratings for *similar* versus *dissimilar* movements (± SEM). **(B)** Classification pipeline: A linear support-vector machine was trained separately on trials from each movement similarity group using cross-validation. **(C)** Mean BOLD signal change for similar versus dissimilar movements in the inferior frontal gyrus (IFG) and inferior parietal lobule (IPL) of both hemispheres. **(D)** Box plots for decoding accuracy (% correct) for similar and dissimilar movements in left and right IFG/IPL plotted against chance performance (colored asterisks at 50 %) and their respective differences (black asterisk). Asterisks denote significance (*p* < .05, **p* < .01, ***p* < .001, FDR-corrected).



	Low Dissimilar	Medium Similar	Medium Dissimilar	High Similar	High Dissimilar
Low Similar	n.s.	n.s.	n.s.	**	n.s.
Low Dissimilar		n.s.	n.s.	n.s.	n.s.
Medium Similar			n.s.	n.s.	n.s.
Medium Dissimilar				n.s.	**
High Similar					***

Figure 3. Influence of social intensity on affective intention decoding based on movement similarities

(A) Gradient of affective intensity. **(B)** Decoding accuracies for similar and dissimilar movements within the IPL. Chance level performance is marked by colored asterisks tested against 50%. **(C)** Pairwise comparisons between classifiers within the IFG. Color indicates significance level (black = not significant, orange = *p* < .01, red = *p* < .001) based on two-sided signed-ranks tests across subjects with false discovery rate (FDR) controlled at .05. **(D)** Decoding accuracies for similar and dissimilar movements within the IFG. Box plots show decoding accuracy (% correct) for similar and dissimilar movements in the left IFG and IPL. Chance-level performance is indicated by colored asterisks at 50%. Significant differences are shown by asterisks: * = p < .05, ** p = < .01, *** p = .001.

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