

Contents lists available at ScienceDirect

Behavioural Brain Research



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

Observers predict actions from facial emotional expressions during real-time social interactions

Leon O.H. Kroczek^{a,*}, Angelika Lingnau^b, Valentin Schwind^{c,d}, Christian Wolff^d, Andreas Mühlberger^a

^a Department of Psychology, Clinical Psychology and Psychotherapy, University of Regensburg, Regensburg, Germany

^b Department of Psychology, Cognitive Neuroscience, University of Regensburg, Regensburg, Germany

^c Human Computer Interaction, University of Applied Sciences in Frankfurt a. M., Frankfurt a. M, Germany

^d Department of Media Informatics, University of Regensburg, Regensburg, Germany

ARTICLE INFO

Keywords: Psychophysiology Social cognition Virtual reality Action Emotion Heart rate Skin conductance response

ABSTRACT

In face-to-face social interactions, emotional expressions provide insights into the mental state of an interactive partner. This information can be crucial to infer action intentions and react towards another person's actions. Here we investigate how facial emotional expressions impact subjective experience and physiological and behavioral responses to social actions during real-time interactions. Thirty-two participants interacted with virtual agents while fully immersed in Virtual Reality. Agents displayed an angry or happy facial expression before they directed an appetitive (fist bump) or aversive (punch) social action towards the participant. Participants responded to these actions, either by reciprocating the fist bump or by defending the punch. For all interactions, subjective experience was measured using ratings. In addition, physiological responses (electrodermal activity, electrocardiogram) and participants' response times were recorded. Aversive actions were judged to be more arousing and less pleasant relative to appetitive actions. In addition, angry expressions increased heart rate relative to happy expressions. Crucially, interaction effects between facial emotional expression and action were observed. Angry expressions reduced pleasantness stronger for appetitive compared to aversive actions. Furthermore, skin conductance responses to aversive actions were increased for happy compared to angry expressions and reaction times were faster to aversive compared to appetitive actions when agents showed an angry expression. These results indicate that observers used facial emotional expression to generate expectations for particular actions. Consequently, the present study demonstrates that observers integrate information from facial emotional expressions with actions during social interactions.

1. Introduction

Social actions – like greeting someone with a handshake, congratulating with a tap on the shoulder, comforting with touch, or defending oneself with a push or a punch – are a fundamental part of real-life human interactions. Every day we experience numerous social encounters with different agents in various (emotional) contexts and with a range of different communicative goals. Importantly, in each of these encounters, people need to coordinate social actions between themselves and their interaction partner in a fast and adaptive manner [1-3]. Being able to infer another person's intention even before an action has been completed allows one to prepare an adaptive response. This may help to keep social interactions in synchrony, e.g. by reciprocating a handshake, or to get a time advantage in preparing a defense, e.g. when an attack needs to be parried [4]. Typically, observers are fast and accurate in inferring other agents' intentions both when actions are directed towards persons or towards objects [5-7]. This raises the question of which mechanisms underlie the inference of action intentions during social interactions. According to the emotion as social information model [8] emotional expressions play an important role in this regard as they allow observers to draw inferences about another person's state and intentions which then inform the observer's behavior and ultimately allows for coordinated social interactions [9]. Returning to the examples from above, when a stranger approaches one with a smile on the face, one might infer that this person has an affiliative intention and one might prepare for a handshake. By contrast, when a

https://doi.org/10.1016/j.bbr.2024.115126

Received 30 October 2023; Received in revised form 7 June 2024; Accepted 19 June 2024 Available online 29 June 2024 0166-4328/© 2024 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

^{*} Correspondence to: Universitätsstr. 31, Regensburg 93053, Germany. *E-mail address:* leon.kroczek@ur.de (L.O.H. Kroczek).

stranger approaches with an angry expression, one might infer that this person has the intention to attack and therefore prepare a defense. The emotion as social information model therefore suggests an interplay between a person's emotional expressions and upcoming actions. However, while it has been demonstrated that emotional expression allow to draw inferences about other persons [10,11], it is less clear whether such inferences are also used to directly predict upcoming behavior in face-to-face social interactions.

Previous research has demonstrated that observers exploit a wide range of multimodal cues to infer intentions. These cues include action kinematics [12], preshaping of the hand [13], but also body posture [14], gaze [13,15], and facial expressions [16]. In addition, observers use contextual information related to the situation, identity, and gender of the interactive partner [17-19]. There is also increasing evidence that observers use facial expressions to understand another person's social intention [20,21]. However, while there is evidence that the processing of action intentions relies on a range of different sources of information, it remains unclear whether social cues can directly impact the processing of actions and the preparation of responses in direct social interactions.

Facial emotional expressions are highly salient non-verbal communicative cues that are omnipresent in interpersonal encounters [22]. Not only do facial emotions allow to infer the mental state of the interactive partner but they can also be predictive with respect to upcoming social actions [23]. As an example, Kroczek et al. [16] recently demonstrated that observing an angry facial expression biased participants' action judgements towards aversive actions (i.e. punches), especially when actions were hard to recognize. These data suggest that observers use facial emotional expressions to infer action intentions. Furthermore, these data suggest that angry facial expressions are evaluated to be congruent to aversive punch actions while happy facial expressions are congruent with appetitive fist bump actions. Such congruency information can be beneficial in preparing adaptive responses [24]. Interestingly, such a predictive relation between facial emotional expressions and actions could also be demonstrated in the context of sports, where emotional facial expressions of professional baseball players influenced observers' predictions regarding players' accuracy, speed and difficulty of a throw, i.e. players with happy expressions were expected to throw more accurately than players with worried expressions, while players with angry expressions were expected to throw faster and more difficult shots [25]. However, it remains an open question whether such findings generalize to situations outside professional sports in everyday social encounters. Importantly, recent theoretical accounts have highlighted predictive coding in social interactions [26,27] where interactive partners continuously generate predictions about each other in order to infer the other person's mental state.

It has to be noted that most previous studies investigated the processing of action intentions in the absence of interactive behavior by simply letting participants passively observe actions (cf. isolation paradigms, [28]. This approach has been criticized because live reciprocal interactions and passive observation of social stimuli may rely on fundamentally different processes [26,27,29,30]. Evidence for this claim comes from behavioral studies, which found different patterns of social attention depending on whether another person was shown on a computer screen or was actually present in the same room [31]. Moreover, neuroimaging studies revealed increased neural activation in the so-called mentalizing network during the processing of social signals within a real social interactive scenario compared to passive observation [29,32,33]. These findings suggest that non-interactive paradigms may only reveal an incomplete picture of social interactive processing and have inspired a call for a second-person neuroscience approach [34].

This is especially relevant as appetitive or aversive outcomes of social actions only come into play when there is an interaction between persons. In order to investigate such claims it is important to study online interactive paradigms that require an interactive partner, not only to observe but also to react upon actions of another person [26,29, **35-37**]. Thus, studying real-time social interactions may be advantageous for understanding mechanisms related to the processing of social action intentions.

The goal of the present study was to investigate whether persons use facial emotional expressions to predict upcoming actions and how this influences evaluative, physiological, and behavioral responses to social actions. For this reason, we implemented a novel Virtual Reality (VR) paradigm using a Cave Automatic Virtual Environment (CAVE) system where participants interacted with virtual agents (one female, one male). As experimental manipulations, virtual agents first displayed a facial emotional expression (happy vs. angry) and then performed an action towards the participants (fist bump vs. punch). Participants were instructed to react to this action by using a congruent action (reciprocal fist bump vs. defend punch), thereby moving their hand to the position of the hand of the virtual agent. Continuous tracking of participants' hand movements allowed for action-contingent reactions once participants had reached the target position. Importantly, this Virtual Reality set-up allowed to present social interactions with high experimental control while key features of naturalistic social interactions could be maintained. These features included the presentation of virtual agents within the participant's peripersonal space, the use of action-specific hand movements as responses rather than button presses, as well as the presentation of action-specific reactions that were contingent on participants actions. In addition, the CAVE system allowed participants to see their own (real) body while interacting with virtual agents via hand movement. Note, however, that Virtual Reality systems using head-mounted displays also allow to present user's hands via real-time tracking and visual rendering [38].

We obtained ratings of arousal, valence, and realism after each interaction to characterize subjective experiences. In addition, physiological parameters (electrodermal activity, EDA, heart rate, HR, measured via electrocardiogram, ECG) were continuously recorded during interactions and response times (RTs) of action responses were measured as a behavioral index. In line with previous findings, angry facial expression were thought to result in preferential processing and a stronger activation of the fear-avoidance system resulting in increased unpleasantness and physiological responses in social interactions [20, 39]. In the present study we expected that the interplay between an agent's facial emotional expression and a subsequent action would affect the evaluation of social interactions as well as physiological responses to social actions, i.e. that subjective experience and physiological responses would differ depending on whether an angry or happy facial emotional expression was paired with an aversive or appetitive action. On a behavioral level we expected that this interplay would result in facilitated actions that are congruent with respect to the preceding facial emotional expression compared to actions that are incongruent.

2. Materials and methods

2.1. Participants

Thirty-three healthy students participated in the study (23 female, $M_{Age} = 22.20$ years, $SD_{Age} = 2.84$, range_{Age} = 18 – 30 years). All participants had normal or corrected-to-normal vision and did not report any mental or neurological disorder. One participant was excluded from analysis of HR data due to excessive artifacts in the ECG data. Another participant was excluded from the RT analysis due to technical problems with RT measurement. A sensitivity analysis using MorePower (v 6.0.4, [40] for a repeated measures ANOVA with a 2×2 design and a power of.80 revealed that the study was able to find interaction effects with minimum effect size of $\eta_p^2 = .21$, i.e. large effects. This is in line with a previous, non-interactive study that found large emotional bias effects of facial emotional expressions on action intention processing (range η_p^2 from 0.17 to 0.42, [16]. The study was reviewed and approved by the ethics board of the University of Regensburg and the study was conducted according to the approved procedures. The study is in line with

L.O.H. Kroczek et al.

the Declaration of Helsinki. All participants gave written informed consent.

2.2. Study design

We used an *Emotion (2)* x *Action (2)* within-subject design. Participants engaged in short face-to-face interactions with virtual agents (female or male). During these interactions, we manipulated the facial emotional expression that was displayed by the virtual agent (independent variable *Emotion*: angry vs. happy) and the action that was performed by the virtual agent (independent variable *Action*: fist bump vs. punch). Agents always displayed the emotional facial expression first and then performed the action. To investigate the interplay of emotion and action, we measured participants' subjective experience in terms of ratings of arousal, valence, and realism, as well as physiological responses with respect to heart rate and skin conductance and the reaction times of participants' responses towards the actions of the virtual agents.

2.3. Apparatus and stimulus material

The present experiment was conducted in Virtual Reality using a CAVE system with a size of 3.6 m x 2.4 m x 2.5 m. Participants wore 3D shutter glasses with attached motion tracker targets (Advance Realtime Tracking GmbH). Virtual Reality was projected on the four surrounding walls and the floor of the CAVE (Barco F50 WQX6A projectors with a resolution of 2560 by 1600 pixels). An additional motion tracker target (Advance Realtime Tracking GmbH) was rendered using the Unreal 4 game engine (v 4.22, Epic Games Inc.) in a cluster of ten computers (i7–4790k, GeForce 1080, 16 GB RAM). Sounds were presented via a surround sound system (Yamaha HTR-3066).

The experiment included a full virtual room, two virtual agents as well as action animations of fist bump and punch actions. Video stimuli showing the same room, agents, and animations have been implemented in a previous study [16]. An empty room with an elevator door at the front wall served as the virtual environment (see Fig. 1). Two virtual agents (one male and one female) were created using Daz3D (Daz3D Inc.), based on the standard Genesis 8 models (https://www.daz3d.com /genesis8) with black clothes and standard geometry-based hair. Animated actions (fist bump or punch) were created for both agents. Animations were based on movement recordings from one male and one female actor using tracking of optical markers (for further details regarding the procedure, see [16]). Finally, three different exemplars per action were created during post-processing by inducing slight variations with respect to the end position (vertical and horizontal offset) of each action. All animations were exported into the Unreal Engine. As action animations were recorded from real actions, punches were performed faster than fist bump action (movement time fist bump; M =1.05 s, SD = 0.039 s, movement time punch: M = 0.738 s, SD = 0.023). This difference lies in the nature of the actions.

Physiological measures included electrocardiogram and electrodermal activity. For ECG recordings, three electrodes were attached to the chest of the participants with one electrode at the sternum, a reference electrode at the left, lower coastal arch and a ground electrode at the right, lower coastal arch. For EDA recordings, two 6 mm Ag/AgCl electrodes were attached to the thenar site of the palm of the left hand [41]. All physiological data were recorded at 1000 Hz using a V-Amp amplifier (BrainProducts, Gilching, Germany) connected to a recording PC. In order to allow free movements inside the CAVE system, participants carried the amplifier inside a backpack during the experiment. Data were recorded with BrainVision Recorder software (BrainProducts, Gilching, Germany) and streamed using the Lab Streaming Layer (LSL,



Fig. 1. Schematic illustration of the experimental trial structure. Upper row shows trial procedure in Virtual Reality, bottom row shows participant inside the CAVE system at corresponding time points. At trial start, an elevator door opened and revealed a virtual agent (first column). Next, the agent displayed either a happy or angry facial emotional expression and then approached (second column) the participant until a final position was reached (third column). 2000 ms after reaching this position, the virtual agent initiated either a punch or fist bump action (fourth and fifth column respectively). Participants had to react towards this action with a congruent response, either by defending the punch (fourth column, bottom row) or by reciprocating the fist bump (fifth column, bottom row).

[42].

In addition, participant's head position and the position of the right hand was tracked at 60 Hz (DTrack 2 software, Advance Realtime Tracking GmbH) and recorded using LSL.

2.4. Procedure

Upon arrival at the laboratory participants were informed about experimental procedures, gave written informed consent, and filled in questionnaires to assess anxiety and social cognition and to screen participants for clinically relevant symptoms. These questionnaires included demographic information (age, sex, occupation), social anxiety (Social Phobia Inventory; [43]), positive and negative affect (PANAS, [44]), general anxiety (State-Trait Anxiety Inventory), as well as sensitivity to reward and punishment [45]. In addition, the "reading the mind in the eyes" test was conducted [46] to screen for difficulties in reading social intentions from gaze.

Then, electrodes were attached at the chest (ECG) and left hand (EDA) of the participant. In addition, a motion tracker target was attached to the right hand of the participants, and they were given 3D shutter glasses. Finally, participants were led into the CAVE system where the empty virtual room was displayed.

After entering the CAVE, participants were allowed to explore the environment for 2 minutes and were then asked to stand on a marked starting position. The starting position was located at the center of the CAVE and was oriented so that participants would face the elevator door, which was projected on the long wall of the CAVE (distance from the starting position to the elevator door in VR was approx 3.5 m).

Once participants were standing correctly oriented on the starting position, the experiment was started. The experiment consisted of 24 trials with an identical trial structure (see Fig. 1). Trial order was pseudo-randomized with no more than three repetitions of emotion, action, or agent gender. Every trial started with the opening of the elevator door, with the agent standing behind the door. Agents were always facing the participant with their gaze focused on the participant. After 2000 ms, the agents started to display a facial emotional expression (happy condition: smile; angry condition: frown). The agent maintained this emotional expression throughout the trial. Another 2500 ms after the onset of the facial expression, the agent moved to a position in front of the participant (0.75 m distance to participants' starting position, walking duration 2500 ms). Agents were in a neutral body posture with both hands in a resting position, hanging loosely next to the legs. The agent remained in this position for another 2000 ms and then initiated the action with the right hand (fist bump or punch). Importantly, the action was stopped at the apex position of the movement and participants had to react towards the action by moving their right hand to the hand position of the virtual agent. Participants were instructed to show congruent actions, i.e., to respond with a fist bump when the agent performed a fist bump and to defend the punch when the agent performed a punch. No instructions were given regarding response speed and accuracy. Once participants reached the target position (defined as a sphere with a radius of 15 cm centered around the position of the agent hand), a clapping sound was played from the loudspeakers and the virtual agent retracted the hand to the resting position. The agent then turned around and left the room through the door.

After the agent had left, ratings were obtained for arousal, valence, and realism by auditory presentation of the rating questions. Participants gave an oral response which was noted by the experimenter. Arousal ratings were obtained by asking "How high was your arousal?" (0 = no arousal, 100 = very high arousal), valence ratings were obtained by asking "How unpleasant did you feel?" (0 = very pleasant, 100 = very unpleasant), and realism ratings were obtained by asking "How realistic was the situation?" (0 = completely unrealistic, 100 = completely realistic). Following the ratings, the next trial started.

The Virtual Reality experiment had a total duration of approximately 25 minutes. After the last trial had been presented, participants were led

outside the CAVE and filled in further questionnaires including a second state anxiety inventory, as well as questionnaires related to presence (Multimodal Presence Scale [47], Igroup Presence Questionnaire [48], and simulator sickness [49].

2.5. Data processing and statistical analyses

Physiological and behavioral data were preprocessed using custom scripts in MATLAB (v 8.6, MathWorks, Natik, USA). For ECG data, the Pan-Tompkins algorithm was applied to identify R-peaks in the continuous signal [50]. One participant had to be excluded from analysis because R-peaks could not be identified reliably. Next, segments with a length of 16 s timelocked to the onset of the emotion of the virtual agent including a 2 s pre-stimulus interval were extracted. Segments were manually checked for incorrectly identified R-peaks and R-peaks were corrected if necessary. Then, intervals between R-peaks (RR) were calculated and converted to heart rate. To obtain event-related measures, heart rate was interpolated and sampled at 1000 Hz. Segments were baseline corrected by subtracting the average heart rate in the 2 s period before the emotion onset. For statistical analysis, HR data was averaged in segments of 1 s length.

For EDA, data were low-pass filtered using a first order butterworth filter with a cut-off frequency of 1 Hz and then log-transformed to account for the non-normal distribution [41]. Analogous to ECG analysis, segments of 16 s length were extracted time-locked to emotion onset including a 2 s pre-stimulus interval. Segments were baseline corrected using the 2 s pre-stimulus interval. For statistical analysis, skin conductance response (SCR) amplitudes were further averaged in 16 non-overlapping time windows of 1 s length.

Reaction times (RTs) were calculated as the time difference between the time point when the virtual agents reached the apex position of the action and the time point when participants reached the hand position of the virtual agent. We chose apex position as a start of RT measurement because action animations of fist bump and punch were of different length (see above). Trials were rejected when participants responded later than 2 seconds after the agent had completed the action (mean number of rejected trials = 1.78 trials, SD = 1.86).

All data were averaged across trials into four experimental conditions (Emotion x Action: Happy – Fist bump, Happy – Punch, Angry – Fist bump, and Angry – Punch) and then exported for further analyses. Statistical analyses were conducted in the R environment [51]. For rating variables, we conducted repeated-measures ANOVAs with the within-subject factors *Emotion* and *Action*. For the windowed time-series data of EDA and HR responses, we conducted repeated-measures ANOVAs with the within-subject factors *Time Window, Emotion*, and *Action*. Finally, RT data were analyzed by investigating a congruency effect for each action comparing congruent and incongruent emotion-action pair. For these analyses a repeated-measures ANOVAs with the within-subject factors *Action* and *Congruency* was conducted. Data of the questionnaires were not included in the analysis but are available in the data repository.

Post-hoc t-tests were conducted to follow up on significant effects with the Holm method [52] applied to correct for multiple comparisons. Assumptions of normality were assessed by Shapiro-Wilk tests (p > .05). All analyses were conducted with Type-I errors set to alpha = 5 %.

2.6. Open science statement

Study procedures, hypotheses, and analyses were not pre-registered prior to data acquisition. Anonymized raw data and analysis scripts are publicly available in an online repository (https://osf.io/q4cru/).

3. Results

3.1. Experience: ratings

3.1.1. Arousal

A repeated measures ANOVA with Arousal ratings as dependent variable (see Fig. 2, left panel) revealed a main effect of *Emotion*, *F*(1,32) = 14.16, p < .001, $\eta_p^2 = .31$, and a main effect of *Action F*(1,32) = 8.52, p = .006, $\eta_p^2 = .21$, but no interaction effect between *Emotion* and *Action*, *F*(1,32) = 0.36, p = .553, $\eta_p^2 = .01$. Arousal was rated significantly higher for angry (M = 35.0, SD = 18.4) compared to happy facial expressions (M = 28.6, SD = 15.2) as well as for punch (M = 34.8, SD = 18.0) compared to fist bump actions (M = 29.8, SD = 16.0).

3.1.2. Valence

For valence ratings (Fig. 2, middle panel), we obtained a main effect of *Emotion*, F(1,32) = 41.19, p < .001, $\eta_p^2 = .56$, a main effect of *Action*, *F* (1,32) = 50.42, p < .001, $\eta_p^2 = .61$, as well as a significant interaction between *Emotion* and *Action*, F(1,32) = 26.38, p < .001, $\eta_p^2 = 0.45$. Posthoc t-tests (Holm corrected) revealed that happy expressions with fist bump actions were rated as more pleasant compared to other combinations of facial expression and action (Angry-Fist bump: t(32) = -7.18, p <.001, d = -1.25; Angry-Punch: t(32) = -8.52, p <.001, d = 1.48: Happy-Punch: t(32) = -7.33, p < .001, d = -1.28), while angry expressions paired with punch actions were rated as more unpleasant compared to other combinations of facial expression and action (Angry-Fist bump: *t*(32) = 4.57, *p* <.001, *d* = 0.80; Happy-Punch: *t*(32) = 3.77, *p* =.001, d = 0.66). Interestingly, the effect of emotion (i.e. the difference between happy and angry expressions) was significantly stronger when agents performed fist bump actions compared to punch actions, t(32) =-5.14, p < .001, d = -0.89.

In sum, the analysis of valence ratings revealed that happy expressions with fist bump actions were evaluated as most pleasant, while angry expressions with punch actions were evaluated as most unpleasant. Furthermore, facial emotions had a stronger modulatory effect on appetitive fist bump actions compared to aversive punch actions.

3.1.3. Realism

For realism ratings (Fig. 2, right panel), results showed a main effect of *Emotion*, *F*(1,32) = 15.02, *p* <.001, η_p^2 =.32, a main effect of *Action*, *F* (1,32) = 9.93, *p* =.004, η_p^2 =.24, as well as a significant interaction between *Emotion* and *Action*, *F*(1,32) = 23.63, *p* <.001, η_p^2 =.43. Post-hoc

t-tests revealed that fist bumps with a happy expression were rated as more realistic than fist bumps with an angry expression, t(32) = 5.85, p<.001, d=1.02. In contrast, punch actions were rated as more realistic when performed with an angry expression compared to a happy expression, t(32) = 2.77, p = .018, d= 0.48. However, fist bumps with happy expressions were rated as even more realistic than punches with angry expression, t(32) = 4.33, p < .001, d = 0.75. Furthermore, the effect of facial expressions was stronger for fist bump actions compared to punch actions, t(32) = 4.86, p < .001, d = 0.85. In other words, the combination of congruent pairs of facial expression and action was rated as more realistic than incongruent pairs of facial expression and action. However, appetitive face-action pairs were more realistic than aversive face-action pairs.

3.2. Physiology

3.2.1. Heart rate

Changes in heart rate following the display of the facial emotional expression (Fig. 3) were analyzed throughout the interaction with the virtual agent using a 2 \times 2 x 16 repeated measures ANOVA with the factors Emotion, Action and Time Window. There was a significant main effect of *Emotion*, F(1,31) = 8.446, p = .007, $\eta_p^2 = .21$, a significant main effect of Time Window, F(16,465) = 17.215, p <.001, , η_p^2 =.36 (ϵ = 0.28), and a significant interaction of Emotion and Time Window, F $(15,465) = 3.65, p = .007, \eta_p^2 = .11$ ($\varepsilon = 0.27$). There was no significant effect involving the factor Action (all F < 1). The main effect of Time Window was driven by a general heart deceleration at the onset of the action in the time window from 7 to 8 seconds compared to the preceding time window from 6 to 7 seconds, t(32) = -3.92, p = .005, and a consecutive heart acceleration in the time window from 10 to 11 seconds compared to the preceding time window from 9 to 10 seconds, t(32) = 5.58, p < .001. With respect to the interaction effect between Emotion and Time Window, a follow-up analyses revealed that angry compared to happy facial expressions increased heart rate from 5 to 9 seconds post emotion onset, Fs(1,31) = 4.63-11.04, ps = .002 $-.039, \eta s_p^2 = .13 - .28.$

3.2.2. Skin conductance responses

SCR amplitude following the onset of facial emotional expression was analyzed using a $2 \times 2 \times 16$ repeated measures ANOVA including the factors *Emotion, Action,* and *Time Window*. As can be seen in Fig. 4, a typical SCR peak was observed following the action of the virtual agent.



Fig. 2. Subjective experience as a function of facial emotional expression and action of the virtual agent. Ratings on a scale from 0 to 100 reflect arousal (left), valence (middle), and realism (right). Box plots are superimposed with individual data points.



Fig. 3. Effect of facial emotional expression on heart rate following the onset of the facial emotion. Time windows with significant differences between angry and happy facial expressions are highlighted in grey. Shaded areas around the lines reflect the standard error of the mean (SEM).



Fig. 4. SCR following the onset of the emotional expression. Data from angry (left) and happy (right) facial expression conditions are shown in separate graphs. Actions of the virtual agent are color-coded (fist bump = blue, punch = red). Time windows with significant differences between punch and fist bump conditions are highlighted in grey. Shaded areas reflect SEM.

The statistical analysis revealed a main effect of *Action*, F(1,32) = 5.99, p = .020, $\eta_p^2 = .16$, a main effect of *Time Window*, F(15,480) = 21.41, p < .091, $\eta_p^2 = .40$ ($\varepsilon = 0.10$), an interaction of *Action* and *Time Window*, F(15,480) = 15.57, p < .001, $\eta_p^2 = .33$ ($\varepsilon = 0.15$), as well as an interaction of *Emotion*, *Action* and *Time Window*, F(15,480) = 3.12, p = .049, $\eta_p^2 = .09$ ($\varepsilon = 0.14$). No other effects were significant.

Follow-up analyses revealed a main effect of action with increased SCR for punch compared to fist bump actions in time windows from 10 – 14 seconds post emotion onset, Fs(1,32) = 12.06-26.83, ps <.001, $\eta s_p^2 = .27$ –.46, and a significant interaction effect of *Emotion* and *Action* from 11 to 14 seconds post emotion onset, Fs(1,32) = 4.40 - 5.87, ps =.021 -.044, $\eta s_p^2 = .12 -.16$. In the window of the significant *Emotion* by *Action*

interaction (11–14 s post emotion onset), post-hoc tests showed an increased SCR when punch actions had been preceded by a happy compared to an angry facial expression, t(32) = 3.54, p = .005, d = 0.62, but there was no difference between angry and happy expressions for fist bump actions, t(32) = 0.76, p = .455, d = 0.13.

In summary, SCR to punch actions was increased when agents were displaying a happy compared to an angry facial expression, while SCRs to fist bump actions did not differ between facial emotions.

3.3. Behavior: reaction times

A 2 ×2 repeated-measures ANOVA on reaction times with respect to Congruency and Action revealed a significant main effect of *Congruency*, F(1,31) = 9.68, p = .004, $\eta_p^2 = .24$, but no main effect for *Action*, F(1,31) = 3.79, p = .061, $\eta_p^2 = .11$, and no interaction between *Congruency* and *Action*, F(1,31) = 0.09, p = .761, $\eta_p^2 < .01$. A simple effects analysis (two-sided) demonstrated that participants responded faster to congruent compared to incongruent emotion-action pairs both for fist bump actions, t(31) = -2.60, p = .014, d = -0.64, and punch action, t(32) = -2.16, p = .038, d = -0.38 (see Fig. 5). The data show that congruency of emotion-action pairs influenced behavioral responses to actions.

4. Discussion

Facial emotional expressions modulate the evaluation of face-to-face interactions and influence physiological and behavioral responses to social actions. In the present study we implemented an interactive Virtual Reality paradigm where participants responded to social actions of virtual agents. Virtual agents displayed either an angry or happy facial expression while directing aversive punch or appetitive fist bump actions towards the participant. The observed main effects of facial emotional expression and action on valence and arousal ratings are in line with previous findings [53,54], i.e. angry expressions and aversive actions were perceived as more arousing and less pleasant than happy expressions and appetitive actions. Interestingly, we also found that the interplay between actions and accompanying facial expressions modulated pleasantness of interactions: fist bumps paired with a smile were perceived as pleasant, while the same fist bumps paired with angry expressions were perceived as unpleasant (even to a similar degree as punch actions). Furthermore, realism of interactions was evaluated on the basis of the congruency between the facial expression and the action. Congruent facial expression-action pairs (i.e., both facial expression and action aversive or appetitive) were rated as more realistic compared to incongruent pairs (i.e., facial expression aversive and action appetitive or vice versa). These results suggest that observers integrate information from facial expressions and actions. Interestingly, physiological



parameters were differently affected by facial expressions and actions. Heart rate showed a general effect of facial expression with an increase for angry compared to happy facial expression that was most prominent shortly before and during action initiation of the virtual agent. By contrast, skin conductance responses were affected by the interaction between facial emotional expressions and actions: SCRs to aversive punch actions were increased when agents displayed a happy compared to an angry facial expression, while SCRs to appetitive fist bump actions did not differ between facial expressions. Finally, facial emotional expressions also influenced behavioral responses, i.e. reaction time. Participants responded faster to actions which were congruent to the preceding facial emotional expressions compared to actions which were incongruent to the preceding facial emotional expression. Taken together, the present findings shed light on the interplay of facial emotional expressions and actions in social interactions. Our data are compatible with the view that observers use facial emotional expressions to generate expectations for actions and that these expectations affect the evaluation of social interactions as well as physiological and behavioral responses.

Previous studies have highlighted facial expressions as communicative cues that allow to infer mental states of others [22,55]. Thereby observers can predict upcoming behavior, thus allowing for adaptive responses in social interactions [4]. The emotion as social information model [8,9] suggests that observers use emotional expressions to draw inferences on another person's intentions and prepare adaptive responses. In line with this model, the present results suggest that observers use facial emotional expression to build expectations regarding aversive or appetitive actions. This is demonstrated by increased SCRs to aversive punch actions when punches were following a happy compared to an angry facial expression. This suggests that aversive actions were unexpected for happy facial expression and the mismatch between facial emotional expression and action was indexed by a heightened physiological response [56]. There was, however, no increased response for unexpected appetitive actions (fist bump actions following angry expressions). These findings might suggest that unexpected punch actions evoked an additional defensive response while fist bump actions may only have evoked an orienting response. This could be explained by differences in salience and threat immanence between fist bump and punch actions, as costs of an unexpected fist bump actions are lower than the costs of an unexpected punch action [57,58]. This is in line with the anger-superiority effect according to which threatening stimuli are preferentially processed due to their relevance for survival [39,59]. Alternatively, the results can be described from a Bayesian predictive coding perspective where the brain generates predictions which are then compared against sensory input [60-62]. These predictions are built on prior beliefs and can be updated when new information becomes available. In the present experiment, persons may have stronger priors for appetitive compared to aversive actions because appetitive actions are much more common (see also [16]). Facial emotional expressions might change the likelihood of aversive or appetitive actions, however, due to strong prior beliefs, fist bump actions may be expected even when an angry facial expression is observed (cf. [63]). In contrast, beliefs about aversive actions may be less strong, resulting in a greater influence of facial emotional expressions. Future studies should test whether explicit manipulation of prior beliefs about actions, for example by varying contextual information, results in mismatch responses also for appetitive actions. Overall, the findings suggest that facial emotional expression influence action inferences in social interactions.

The results of the present study further suggest an adaptive role of facial emotional expressions in interpersonal behavior. We found increased heart rate responses for angry compared to happy facial expressions in a time-window prior and during the action initiation. Thus, observers showed increased physiological activation to the aversive facial expressions. One might speculate that the expectation of an aversive action increased sympathetic activity in order to prepare the organism towards a threatening action [64,65]. Heightened sympathetic

activity during the observation of the action might be beneficial in generating an adaptive response. It should be noted, however, as we did not jitter the interval between facial expression and action, we cannot rule out the possibility that the effect of facial expression would occur with a timing of 5-9 seconds regardless of the onset of the action. This should be tested in future experiments. Interestingly, while we found a typical heart rate orienting response in form of a rapid deceleration following the onset of the action [56,64], we also observed increased rather than decreased heart rate for angry relative to happy facial expressions. Decelerated heart rate has been reported as a physiological response to threatening stimuli [66]. The observed acceleration in the present study may be explained by our study design, which allowed participants to actively react towards a threat action rather than to just passively observe it. As a consequence, given the option to react, heart rate increases might facilitate action responding in terms of a fight-or-flight response [65,67]. Importantly, the claim that anticipatory increases in heart rate are conditional on having the option to defend oneself needs to be confirmed in experiments that manipulate whether participants do have an active response option against a threat. In addition, one might manipulate whether a given response option is effective in preventing a negative outcome. Based on the present study one might expect increases in heart rate only in conditions in which an effective response option is available.

The present findings also demonstrate a behavioral benefit for using information from facial emotional expressions in response preparation, as faster responses were observed for congruent compared to incongruent face-action pairs. Therefore the decoding of social intentions via facial expressions may allow for smooth interpersonal coordination [9] and thus may constitute an adaptive mechanism in real-time social interactions. In addition to cues from kinematics [68], gaze [15,32], and body posture [14,69], facial emotional expressions may therefore provide important information for upcoming actions. Interestingly, previous research has shown that persons adapt their movement patterns in communicative compared to individual settings [12,70]. One could ask whether similar mechanism might come into play with respect to facial emotional expressions differently in cooperative compared to competitive settings or when interacting with a familiar or unfamiliar person.

Finally, our data suggest that inferred intentions have a strong impact on the evaluation of social actions that may even override the valence of the actual performed action. Pleasantness of appetitive fist bump actions strongly differed between facial expressions, suggesting that the inferred intention influenced experience to a greater degree than the actual performed action. Facial expressions have been related to impression formation [71]. With respect to the current study, expectations based on facial expressions might be processed as true social intentions, thus altering the meaning of a given action. For the experience of punch actions, however, the influence of facial expressions was less prominent. Thus, angry expressions can render an appetitive action as unpleasant, but happy expression cannot render an aversive action as pleasant to the same degree. One might speculate that fist bump actions may be less unequivocal with respect to being aversive/appetitive and thus be more affected by inferred intentions from facial expressions. In line with this interpretation, Kroczek et al. [16] found that angry facial emotions biased observers towards aversive punch actions in a perception task using video clips of the same stimuli as in the present study. Importantly, this bias was strongest when actions were ambiguous. Furthermore, realism ratings regarding expression-action pairs showed that congruent pairs (both aversive/appetitive) were perceived as more realistic than incongruent pairs (one aversive, one appetitive). This suggests that observers integrated action expectations based on facial expressions with the actual performed actions. Note, however, that ratings can be only seen as indirect evidence for action expectations, as participants rated valence and realism only after the full interaction had been presented and consequently might have based their evaluations on post-hoc processing. Together, these findings highlight the role of facial expressions in the evaluation of actions in social interactions.

The current study used an interactive Virtual Reality paradigm to study social interactions. Yet, there are some limitations that need to be acknowledged. To present participants with naturalistic social scenarios that allow to measure physiological variables and prevent habituation we adopted an experimental procedure with rather long trial durations but a small number of trials in total. Therefore, the number of total conditions was limited, resulting in only two types of actions, facial emotional expressions, and only two virtual agents. This does not reflect the everyday range of social interactions. Including a more diverse range of actions would allow to test whether the observed effects are limited to extreme cases of social interactions (e.g. attack) or do also account for less extreme forms of aversive interactions (e.g. taking something away). Furthermore, due to the low number of trials no subgroup analysis was conducted and we cannot make claims about effects of agent gender [72]. Future studies should therefore be conducted that increase variability with respect to facial emotional expressions, actions, and virtual agents. To increase trial numbers, future studies might also rely on "minimal interactive paradigms" where participants interact with varying agents without an extended approach phase.

Another limitation is related to generalizability of the paradigm. While the study aimed at presenting naturalistic social encounters, it should be noted that due to the standardized and repeated presentation of the same two actions, the ecological validity of the paradigm may have been reduced, as real-life greetings and punches typically do not happen in a row of 24 repetitions. While this constraint should be considered when generalizing results to real-world situations, it is important to note that the present study included several features of face-to-face social interactions that go far beyond static presentation of social stimuli on a computer screen, e.g. the presentation of real-life sized 3D persons in peri-personal space, responding via natural actions, and contingent reactions of the virtual agents. However, it is an ongoing challenge to study social behavior both with a high degree of experimental control and ecological validity. The development of more plausible and unobtrusive interactive settings [73] might help to solve this challenge in future studies. The present study can thus be seen as a starting point to investigate the interplay of facial emotional expressions and actions in an interactive paradigm.

In conclusion, the present study implemented a real-time interactive paradigm in Virtual Reality to investigate the influence of facial emotional expressions on social actions. Facial emotions had an impact on the evaluation of social actions and influenced physiological and behavioral responses. Consequently, facial emotional expressions are important cues in social interactions that allow to infer action intentions of an interactive partner and to generate adaptive responses.

Ethics statement

The study was reviewed and approved by the ethics board of the University of Regensburg and the study was conducted according to the approved procedures. The study is in line with the Declaration of Helsinki. All participants gave written informed consent.

Funding

This study was supported by the "UR Fellows" program of the University of Regensburg. AL is supported by a Heisenberg Professorship (Li 2840/2–1) from the German Research Foundation.

CRediT authorship contribution statement

Andreas Mühlberger: Writing – review & editing, Supervision, Funding acquisition, Conceptualization. Christian Wolff: Writing – review & editing, Funding acquisition, Conceptualization. Valentin Schwind: Writing – review & editing, Software, Resources, Funding acquisition. Angelika Lingnau: Writing – review & editing, Supervision, Funding acquisition, Conceptualization. Leon O.H. Kroczek: Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Conflict of Interest

The authors declare no competing interests.

Data availability

Anonymized raw data and analysis scripts are publicly available in an online repository (https://osf.io/q4cru/).

Acknowledgements

We are thankful to Andreas Ruider for technical support and Julia Veitenhansl and Kevin Weber for data collection.

References

- A. Curioni, C. Vesper, G. Knoblich, N. Sebanz, Reciprocal information flow and role distribution support joint action coordination, Cognition 187 (February)) (2019) 21–31, https://doi.org/10.1016/j.cognition.2019.02.006.
- [2] E.G. McMahon, L. Isik, Seeing social interactions, Trends Cogn. Sci. (2023) S1364661323002486, https://doi.org/10.1016/j.tics.2023.09.001.
- [3] N. Sebanz, H. Bekkering, G. Knoblich, Joint action: Bodies and minds moving together, Trends Cogn. Sci. 10 (2) (2006) 70–76, https://doi.org/10.1016/j. tics.2005.12.009.
- [4] N. Sebanz, G. Knoblich, Prediction in Joint Action: What, When, and Where, Top. Cogn. Sci. 1 (2) (2009) 353–367, https://doi.org/10.1111/j.1756-8765.2009.01024.x.
- [5] C.D. Frith, U. Frith, How we predict what other people are going to do, Brain Res. 1079 (1) (2006) 36–46, https://doi.org/10.1016/j.brainres.2005.12.126.
- [6] E.G. McMahon, C.Y. Zheng, F. Pereira, R. Gonzalez, L.G. Ungerleider, M. Vaziri-Pashkam, Subtle predictive movements reveal actions regardless of social context, J. Vis. 19 (7) (2019) 16, https://doi.org/10.1167/19.7.16.
- [7] L. Sartori, C. Becchio, U. Castiello, Cues to intention: The role of movement information, Cognition 119 (2) (2011) 242–252, https://doi.org/10.1016/j. cognition.2011.01.014.
- [8] G.A. Van Kleef, How Emotions Regulate Social Life: The Emotions as Social Information (EASI) Model, Curr. Dir. Psychol. Sci. 18 (3) (2009) 184–188, https:// doi.org/10.1111/j.1467-8721.2009.01633.x.
- [9] J. Lange, M.W. Heerdink, G.A. Van Kleef, Reading emotions, reading people: Emotion perception and inferences drawn from perceived emotions, Curr. Opin. Psychol. 43 (2022) 85–90, https://doi.org/10.1016/j.copsyc.2021.06.008.
- [10] T.M. Erle, K. Schmid, S.H. Goslar, J.D. Martin, Emojis as social information in digital communication, Emotion 22 (7) (2022) 1529–1543, https://doi.org/ 10.1037/emo0000992.
- [11] E.A. Van Doorn, G.A. Van Kleef, J. Van Der Pligt, Deriving meaning from others' emotions: Attribution, appraisal, and the use of emotions as social information, Front. Psychol. 6 (2015), https://doi.org/10.3389/fpsyg.2015.01077.
- [12] C. Becchio, L. Sartori, M. Bulgheroni, U. Castiello, Both your intention and mine are reflected in the kinematics of my reach-to-grasp movement, Cognition 106 (2) (2008) 894–912, https://doi.org/10.1016/j.cognition.2007.05.004.
- [13] E. Ambrosini, M. Costantini, C. Sinigaglia, Grasping with the eyes, J. Neurophysiol. 106 (3) (2011) 1437–1442, https://doi.org/10.1152/jn.00118.2011.
- [14] B. De Gelder, Towards the neurobiology of emotional body language, Nat. Rev. Neurosci. 7 (3) (2006) 242–249, https://doi.org/10.1038/nrn1872.
- [15] E. Ambrosini, G. Pezzulo, M. Costantini, The eye in hand: Predicting others' behavior by integrating multiple sources of information, J. Neurophysiol. 113 (7) (2015) 2271–2279, https://doi.org/10.1152/jn.00464.2014.
- [16] L.O.H. Kroczek, A. Lingnau, V. Schwind, C. Wolff, A. Mühlberger, Angry facial expressions bias towards aversive actions, PLOS ONE 16 (9) (2021) e0256912, https://doi.org/10.1371/journal.pone.0256912.
- [17] P. Bach, K.C. Schenke, Predictive social perception: Towards a unifying framework from action observation to person knowledge, Soc. Personal. Psychol. Compass 11 (7) (2017) 1–17, https://doi.org/10.1111/spc3.12312.
- [18] Y. Ferstl, H. Bülthoff, Rosa, S. De, Action recognition is sensitive to the identity of the actor, Cognition 166 (2017) 201–206, https://doi.org/10.1016/j. cognition.2017.05.036.
- [19] S. Krüger, A.N. Sokolov, P. Enck, I. Krägeloh-Mann, M.A. Pavlova, Emotion through locomotion: Gender impact, PLoS ONE 8 (11) (2013), https://doi.org/ 10.1371/journal.pone.0081716.
- [20] A.A. Marsh, N. Ambady, R.E. Kleck, The Effects of Fear and Anger Facial Expressions on Approach- and Avoidance-Related Behaviors, Emotion 5 (1) (2005) 119–124, https://doi.org/10.1037/1528-3542.5.1.119.
- [21] J.L. Tracy, D. Randles, C.M. Steckler, The nonverbal communication of emotions, Curr. Opin. Behav. Sci. 3 (2015) 25–30, https://doi.org/10.1016/j. cobeha.2015.01.001.

- [22] C.D. Frith, Role of facial expressions in social interactions, Philos. Trans. R. Soc. B: Biol. Sci. 364 (1535) (2009) 3453–3458, https://doi.org/10.1098/rstb.2009.0142.
- [23] R.E. Jack, P.G. Schyns, The Human Face as a Dynamic Tool for Social Communication, Curr. Biol. 25 (14) (2015) R621–R634, https://doi.org/10.1016/ j.cub.2015.05.052.
- [24] G. Csibra, G. Gergely, Obsessed with goals': Functions and mechanisms of teleological interpretation of actions in humans, Acta Psychol. 124 (1) (2007) 60–78, https://doi.org/10.1016/j.actpsy.2006.09.007.
- [25] A. Cheshin, M.W. Heerdink, J.J. Kossakowski, G.A. Van Kleef, Pitching Emotions: The Interpersonal Effects of Emotions in Professional Baseball, Front. Psychol. 7 (2016), https://doi.org/10.3389/fpsyg.2016.00178.
- [26] D. Bolis, G. Dumas, L. Schilbach, Interpersonal attunement in social interactions: From collective psychophysiology to inter- personalized psychiatry and beyond, Philos. Trans. R. Soc. B: Biol. Sci. 378 (1870) (2023) 20210365, https://doi.org/ 10.1098/rstb.2021.0365.
- [27] K. Lehmann, D. Bolis, K.J. Friston, L. Schilbach, M.J.D. Ramstead, P. Kanske, An Active-Inference Approach to Second-Person Neuroscience, Perspect. Psychol. Sci. (2023) 1–21, https://doi.org/10.1177/17456916231188000.
- [28] C. Becchio, L. Sartori, U. Castiello, Toward you: The social side of actions, Curr. Dir. Psychol. Sci. 19 (3) (2010) 183–188, https://doi.org/10.1177/ 0963721410370131
- [29] E. Redcay, L. Schilbach, Using second-person neuroscience to elucidate the mechanisms of social interaction, Nat. Rev. Neurosci. 20 (8) (2019) 495–505, https://doi.org/10.1038/s41583-019-0179-4.
- [30] E.F. Risko, K. Laidlaw, M. Freeth, T. Foulsham, A. Kingstone, Social attention with real versus reel stimuli: Toward an empirical approach to concerns about ecological validity, Front. Hum. Neurosci. 6 (2012), https://doi.org/10.3389/ fnhum.2012.00143.
- [31] K.E.W. Laidlaw, T. Foulsham, G. Kuhn, A. Kingstone, Potential social interactions are important to social attention, Proc. Natl. Acad. Sci. 108 (14) (2011) 5548–5553, https://doi.org/10.1073/pnas.1017022108.
- [32] A. Cavallo, O. Lungu, C. Becchio, C. Ansuini, A. Rustichini, L. Fadiga, When gaze opens the channel for communication: Integrative role of IFG and MPFC, NeuroImage 119 (2015) 63–69, https://doi.org/10.1016/j. neuroimage.2015.06.025.
- [33] E. Redcay, D. Dodell-Feder, M.J. Pearrow, P.L. Mavros, M. Kleiner, J.D.E. Gabrieli, R. Saxe, Live face-to-face interaction during fMRI: A new tool for social cognitive neuroscience, NeuroImage 50 (4) (2010) 1639–1647, https://doi.org/10.1016/j. neuroimage.2010.01.052.
- [34] L. Schilbach, B. Timmermans, V. Reddy, A. Costall, G. Bente, T. Schlicht, K. Vogeley, A second-person neuroscience in interaction, Behav. Brain Sci. 36 (4) (2013) 441–462, https://doi.org/10.1017/S0140525X12002452.
- [35] L.O.H. Kroczek, A. Mühlberger, Returning a smile: Initiating a social interaction with a facial emotional expression influences the evaluation of the expression received in return, Biol. Psychol. 175 (2022) 108453, https://doi.org/10.1016/j. biopsycho.2022.108453.
- [36] X. Pan, A.F. de C. Hamilton, Why and how to use virtual reality to study human social interaction: The challenges of exploring a new research landscape, Br. J. Psychol. 109 (3) (2018) 395–417, https://doi.org/10.1111/bjop.12290.
- [37] L. Schilbach, S.B. Eickhoff, E. Cieslik, N.J. Shah, G.R. Fink, K. Vogeley, Eyes on me: An fMRI study of the effects of social gaze on action control, Soc. Cogn. Affect. Neurosci. 6 (4) (2011) 393–403, https://doi.org/10.1093/scan/nsq067.
- [38] V. Schwind, P. Knierim, C. Tasci, P. Franczak, N. Haas, N. Henze, These are not my hands!": Effect of Gender on the Perception of Avatar Hands in Virtual Reality, Proc. 2017 CHI Conf. Hum. Factors Comput. Syst. (2017) 1577–1582, https://doi. org/10.1145/3025453.3025602.
- [39] A. Öhman, D. Lundqvist, F. Esteves, The face in the crowd revisited: A threat advantage with schematic stimuli, J. Personal. Soc. Psychol. 80 (3) (2001) 381–396, https://doi.org/10.1037/0022-3514.80.3.381.
- [40] J.I.D. Campbell, V.A.T. Thompson, MorePower 6.0 for ANOVA with relational confidence intervals and Bayesian analysis, Behav. Res. Methods 44 (2012) 1255–1265, https://doi.org/10.3758/s13428-012-0186-0.
- [41] W. Boucsein, D.C. Fowles, S. Grimnes, G. Ben-Shakhar, W.T. Roth, M.E. Dawson, D. L. Filion, Publication recommendations for electrodermal measurements, Psychophysiology 49 (8) (2012) 1017–1034, https://doi.org/10.1111/j.1469-8986.2012.01384.x.
- [42] C. Kothe, Lab Streaming Layer. (LSL) (2014).
- [43] Z. Sosic, U. Gieler, U. Stangier, Screening for social phobia in medical in- and outpatients with the German version of the Social Phobia Inventory (SPIN), J. Anxiety Disord. 22 (5) (2008) 849–859, https://doi.org/10.1016/j. janxdis.2007.08.011.
- [44] D. Watson, L.A. Clark, A. Tellegen, Development and validation of brief measures of positive and negative affect: The PANAS scales, J. Personal. Soc. Psychol. 54 (6) (1988) 1063–1070, https://doi.org/10.1037/0022-3514.54.6.1063.
- [45] R. Torrubia, C. Avila, J. Molto, X. Caseras, The sensitivity to punishment and sensitivity to reward questionnaire, Personal. Individ. Differ. 31 (1) (2001) 837–862.
- [46] S. Baron-Cohen, S. Wheelwright, J. Hill, Y. Raste, I. Plumb, The "Reading the Mind in the Eyes" Test revised version: A study with normal adults, and adults with Asperger syndrome or high-functioning autism, J. Child Psychol. Psychiatry Allied Discip. 42 (2) (2001) 241–251, https://doi.org/10.1017/S0021963001006643.
- [47] G. Makransky, L. Lilleholt, A. Aaby, Development and validation of the Multimodal Presence Scale for virtual reality environments: A confirmatory factor analysis and item response theory approach, Comput. Hum. Behav. 72 (2017) 276–285, https:// doi.org/10.1016/j.chb.2017.02.066.

- [48] T. Schubert, F. Friedmann, H. Regenbrecht, The Experience of Presence: Factor Analytic Insights, Presence.: Teleoperators Virtual Environ. 10 (3) (2001) 266–281, https://doi.org/10.1162/105474601300343603.
- [49] R.S. Kennedy, N.E. Lane, K.S. Berbaum, M.G. Lilienthal, Simulator Sickness Questionnaire: An Enhanced Method for Quantifying Simulator Sickness, Int. J. Aviat. Psychol. 3 (3) (1993) 203–220, https://doi.org/10.1207/ s15327108ijap0303_3.
- [50] J. Pan, W.J. Tompkins, A Real-Time QRS Detection Algorithm, *IEEE Trans. Biomed. Eng.*, *BME 32* (3) (1985) 230–236, https://doi.org/10.1109/TBME.1985.325532.
- [51] R. Core Team, R: A Lang. Environ. Stat. Comput. 3.3.2 (2016).
 [52] S. Holm, A simple sequentially rejective multiple test procedure, Scand. J. Stat. 6 (2) (1979) 65–70.
- [53] A. Di Crosta, P. La Malva, C. Manna, A. Marin, R. Palumbo, M.C. Verrocchio, M. Cortini, N. Mammarella, A. Di Domenico, The Chieti Affective Action Videos database, a resource for the study of emotions in psychology, Sci. Data 7 (1) (2020) 32, https://doi.org/10.1038/s41597-020-0366-1.
- [54] F. Schrammel, S. Pannasch, S. Graupner, A. Mojzisch, B.M. Velichkovsky, Virtual friend or threat? The effects of facial expression and gaze interaction on psychophysiological responses and emotional experience, Psychophysiology 46 (5) (2009) 922–931, https://doi.org/10.1111/j.1469-8986.2009.00831.x.
- [55] C.D. Frith, U. Frith, Mechanisms of Social Cognition, Annu. Rev. Psychol. 63 (2012) 287–313, https://doi.org/10.1146/annurev-psych-120710-100449.
- [56] M.M. Bradley, Natural selective attention: Orienting and emotion, Psychophysiology 46 (1) (2009) 1–11, https://doi.org/10.1111/j.1469-8986.2008.00702.x.
- [57] M. Codispoti, M. Bradley, P. Lang, Affective reaction to briefly presented pictures. Psychophysiol Psychophysiol 38 (2001) 474–478.
- [58] A. Flykt, F. Esteves, A. Öhman, Skin conductance responses to masked conditioned stimuli: Phylogenetic/ontogenetic factors versus direction of threat? Biol. Psychol. 74 (3) (2007) 328–336, https://doi.org/10.1016/j.biopsycho.2006.08.004.
- [59] G. Horstmann, A. Bauland, Search asymmetries with real faces: Testing the angersuperiority effect, Emotion 6 (2) (2006) 193–207, https://doi.org/10.1037/1528-3542.6.2.193.
- [60] A. Bubic, D.Y. von Cramon, R.I. Schubotz, Prediction, cognition and the brain, Front. Hum. Neurosci. 4 (March)) (2010) 25, https://doi.org/10.3389/ fnhum.2010.00025.
- [61] A. Clark, Whatever next? Predictive brains, situated agents, and the future of cognitive science, Behav. Brain Sci. 36 (3) (2013) 181–204, https://doi.org/ 10.1017/S0140525X12000477.

- [62] J.M. Kilner, K.J. Friston, C.D. Frith, Predictive coding: An account of the mirror neuron system, Cogn. Process. 8 (3) (2007) 159–166, https://doi.org/10.1007/ s10339-007-0170-2.
- [63] E.V.C. Friedrich, I.C. Zillekens, A.L. Biel, D. O'Leary, E.V. Seegenschmiedt, J. Singer, L. Schilbach, P. Sauseng, Seeing a Bayesian ghost: Sensorimotor activation leads to an illusory social perception, iScience 25 (4) (2022) 104068, https://doi.org/10.1016/j.isci.2022.104068.
- [64] M.M. Bradley, A. Keil, P.J. Lang, Orienting and emotional perception: Facilitation, attenuation, and interference, Front. Psychol. 3 (NOV)) (2012) 1–6, https://doi. org/10.3389/fpsyg.2012.00493.
- [65] A. Löw, P.J. Lang, J.C. Smith, M.M. Bradley, Both predator and prey: Emotional arousal in threat and reward, Psychol. Sci. 19 (9) (2008) 865–873, https://doi.org/ 10.1111/j.1467-9280.2008.02170.x.
- [66] M.A. Hagenaars, M. Oitzl, K. Roelofs, Updating freeze: Aligning animal and human research, Neurosci. Biobehav. Rev. 47 (2014) 165–176, https://doi.org/10.1016/j. neubiorev.2014.07.021.
- [67] K. Roelofs, Freeze for action: Neurobiological mechanisms in animal and human freezing, Philos. Trans. R. Soc. B: Biol. Sci. 372 (1718) (2017), https://doi.org/ 10.1098/rstb.2016.0206.
- [68] A. Cavallo, A. Koul, C. Ansuini, F. Capozzi, C. Becchio, Decoding intentions from movement kinematics, Sci. Rep. 6 (1) (2016) 37036, https://doi.org/10.1038/ srep37036.
- [69] B. de Gelder, M. Poyo Solanas, A computational neuroethology perspective on body and expression perception, Trends Cogn. Sci. 25 (9) (2021) 744–756, https:// doi.org/10.1016/j.tics.2021.05.010.
- [70] L. Sartori, C. Becchio, B.G. Bara, U. Castiello, Does the intention to communicate affect action kinematics? Conscious. Cogn. 18 (3) (2009) 766–772, https://doi. org/10.1016/j.concog.2009.06.004.
- [71] A. Todorov, P. Mende-Siedlecki, R. Dotsch, Social judgments from faces, Curr. Opin. Neurobiol. 23 (3) (2013) 373–380, https://doi.org/10.1016/j. conb.2012.12.010.
- [72] J. Reichenberger, M. Pfaller, D. Forster, J. Gerczuk, Y. Shiban, A. Mühlberger, Men scare me more: Gender differences in social fear conditioning in virtual reality, Front. Psychol. 10 (JULY)) (2019) 1–20, https://doi.org/10.3389/ fpsyg.2019.01617.
- [73] J.M. Lahnakoski, P.A.G. Forbes, C. Mccall, L. Schilbach, Unobtrusive Track. Interpers. Orient. Distance Predicts Subj. Qual. Soc. Interact. (2020).