

People can identify the likely owner of heartbeats by looking at individuals' faces

Alejandro Galvez-Pol^{1,2*}, Salome Antoine², Charlotte Li², James M Kilner^{2*}

¹Psychology Department, University of the Balearic Islands, Palma de Mallorca 07122, Spain. ²Department of Clinical and Movement Neurosciences, Queen Square Institute of Neurology, University College London, London WC1N 3BG, UK. *Correspondence to: a.galvez-pol@uib.es, j.kilner@ucl.ac.uk.

Accepted article, cite as: Galvez-pol, A., Antoine, S., Li, C., & Kilner J. M. (2022). People can identify the likely owner of heartbeats by looking at individuals' faces. *Cortex*, <https://doi.org/10.1016/j.cortex.2022.03.003>

Abstract

For more than a century it has been proposed that visceral and vasomotor changes inside the body influence and reflect our experience of the world. For instance, cardiac rhythms (heartbeats and consequent heart rate) reflect psychophysiological processes that underlie our cognition and affective experience. Yet, considering that we usually infer what others do and feel through vision, whether people can identify the most likely owner of a given bodily rhythm by looking at someone's face remains unknown. To address this, we developed a novel two-alternative forced-choice task in which 120 participants watched videos showing two people side by side and visual feedback from one of the individuals' heartbeats in the centre. Participants' task was to select the owner of the depicted heartbeats. Across five experiments, one replication, and supplementary analyses, the results show that: i) humans can judge the most likely owner of a given sequence of heartbeats significantly above chance levels, ii) that performance in such a task decreases when the visual properties of the faces are altered (inverted, masked, static), and iii) that the difference between the heart rates of the individuals portrayed in our 2AFC task seems to contribute to participants' responses. While we did not disambiguate the type of information used by the participants (e.g., knowledge about appearance and health, visual cues from heartbeats), the current work represents the first step to investigate the possible ability to infer or perceive others' cardiac rhythms. Overall, our novel observations and easily adaptable paradigm may generate hypotheses worth examining in the study of human and social cognition.

Keywords: Face perception, mentalizing, inference, psychophysiological state, interoception, heartbeats

1. Introduction

For over a century it has been proposed that our experiences of the world originate from responses in the body that accompany the perception of external events (Cannon, 1927; Craig, 2002; James, 1884; Sherrington, 1906). While the study of what causes our phenomenological experience (body states, brain activity) continues to this day, recent studies have shown that perception and reasoning do vary as a function of internal bodily oscillations such as heartbeats (Al et al., 2020; Babo-Rebelo et al., 2016; Galvez-pol et al., 2022; Galvez-Pol et al., 2020; Garfinkel et al., 2014; Grund et al., 2022; Park et al., 2014; Quadt et al., 2018; Quigley et al., 2021). In turn, heartbeats also vary in terms of frequency (i.e., heart rate) and strength as a function of our psychophysiological state (Beauchaine & Bell, 2020; Thayer et al., 2012). These findings are often echoed in how people refer to their internal or ‘interoceptive’ bodily states to describe their own experiences ("*my heart skipped a beat*" or "*from the bottom of my heart*").

Although of considerable interest, most studies on the influence of cardiac rhythms upon cognition neglect levels of description beyond the individual. Yet, humans live in a highly social environment whereby dialectical attunement unfolds (Bolis & Schilbach, 2020). Namely, we signal our state and perceivers infer it (usually through exteroceptive visual information). Considering that we are highly social animals and that cardiac rhythms (i.e., heartbeats and heart rate) are both a reflection and modulator of our psychophysiological condition, a fundamental question is whether such important information could be inferred by others through vision. Accordingly, in this exploratory report we test whether people can identify the most likely owner of a given cardiac rhythm (i.e., a sequence of heartbeats). While this work does not directly inform about peoples’ ability to infer/perceive the heartbeats of others, it represents the first step to examine this possibility.

Although our report is exploratory rather than fully hypothesis-driven, the idea that people might be able to correctly select the owner of a given cardiac rhythm through vision is supported by findings in three different research fields. These findings show that transient and more stable aspects of facial features are associated with cardiovascular states. First, previous work has shown that it is possible to extract meaningful biological information from videos through the magnification of subtle visual cues (Lauridsen et al., 2019). Applying such a method has revealed small and transient variations in the redness of the face, as well as minute head and eye movements that are both concomitant to heartbeats (Wu et al., 2012). Second, studies in the social domain indicate that cardiac rhythms might play a role in socializing individuals and that according to their relationship and given situation, peoples’ cardiac rhythms may become synchronised (Ferrer & Helm, 2013; Fusaroli et al., 2016; Helm et al.,

2018; Konvalinka et al., 2011; Palumbo et al., 2017; Prochazkova et al., 2021; Reed et al., 2013). Third, studies in colour vision and emotion have shown that people are better at detecting subtle changes in colouration (e.g., redness) in faces than non-face stimuli (Tan & Stephen, 2013; Thorstenson et al., 2017), and that facial colour influences social and emotional judgments (Benitez-Quiroz et al., 2018; Thorstenson et al., 2017, 2019; Young et al., 2018), as well as more stable features such as others' health and fitness (Henderson et al., 2016; Perrett et al., 2020).

Taken together, the above research suggests that bodily changes, some locked to individual heartbeats and other concurrent to more stable cardiovascular states, could extend from inner to outer/superficial parts of the body. These in turn could be apprehended by others through vision. These studies do not imply that heartbeats can be directly perceived, but that others' cardiac rhythms could be inferred through transient and more stable visual cues. The main and first aim of this study was to test whether human participants can correctly identify which of two people a cardiac rhythm was recorded from.

2. Methods

2.1 Participants

We conducted an a priori power analysis using G*Power (Version 3.1; Faul et al., 2007) to determine the sample size required to detect a significant difference in performance compared to the chance level of 0.5. Our logic was that for any detected effect to be of behavioural/social significance, it should have a large effect size ($d=0.8$). We wanted to minimise the Type II as well as the Type I error rate, and therefore set the beta and alpha both at 0.05. A sample size of at least 23 participants was the minimal requirement for a power of 0.95 (i.e., beta .05), with an alpha of .05. Based on this analysis we recruited 24 participants in each experiment. Therefore, a total of 120 healthy (24 by 5 experiments) young adult participants (ages 18-46, 78 women) with normal or corrected-to-normal vision were recruited through the University College London (UCL) Institute of Psychology subject pool. All participants gave informed consent, volunteered to take part in the experiment. All participants completed their corresponding experiments, no exclusion criteria were established prior to data analysis, and all datasets were included for analyses. Ethical approval for the methods and procedures was obtained from the UCL research ethics committee.

2.2 Stimuli and apparatus

We filmed seven actors (four women) for two minutes looking straight ahead with a neutral expression (Fig. 1a). Each video was recorded with a high-definition camera (Panasonic HDC-TM900) at 25fps. The camera was placed in front of the actors at an approximate distance of 80cm and was mounted on a tripod at eye level. The videos were recorded from the shoulders to the top of the head. The actors were looking straight towards the camera, remaining still, with a neutral expression and direct gaze. Every person was filmed wearing a similar grey t-shirt and in front of the same dark background. Offline, these 2 min video recordings were edited into shorter videos of 10 seconds. Those videos in which the actor was moving the head or looking away from the camera were deleted. For each actor, 5 videos were randomly selected.

The electrocardiogram (ECG) of the actors was simultaneously recorded with the videos. The continuous ECG was recorded using the Active Two BioSemi system (BioSemi, Amsterdam, NL). The electrodes were placed over the right clavicle and left iliac crest according to Einthoven's triangular arrangement. Then, we proceed to identify the start of each heartbeat by detecting the R-peaks of the QRS complex. To this aim, we computed the local maxima of the ECG trace; *findpeaks* function with a minimum peak to peak distance of ~500 ms and a peak height of ~0.7 mV. We visually inspected the detection of the R-peaks returned by the algorithm and applied small adjustments when required. The actors' heart rate ranged from 67 to 85 bpm (mean = 74, SD = 7). See the Supplementary materials for IBI in ms of actors appearing by video.

We used the timepoints of the detected R-peaks to create visual feedback of the heartbeats occurring in each video. Specifically, we created a small square that changed in colouration from black to red with the start of each heartbeat. The duration of the red square (start of heartbeat) was 320ms (i.e., 8 frames of our 25 fps videos), after this, the square remained black until the beginning of the next heartbeat. The final video-montages were created by randomly selecting two videos of different actors and placing them side by side. Lastly, we inserted the small square depicting the heartbeats of one of the individuals on the bottom of the screen at the centre (Fig. 1b-c and Supp. Movie). All permutations of actor pairs, side of the screen, and visual feedback of the heartbeats resulted in 84 completely counterbalanced videos. For each actor there were 5 unique videos. To create the videos, all combinations of pairs of actors were used. So, each of the seven actors was paired with the remaining six (i.e., resulting in 42 video montages of actor pairs). These were then paired with one of the actor's heartbeats. This could either be the actor on the left or the right. For each

video montage, the video used (from the 5 available per actor) was randomly selected. This resulted in 84 unique videos. The same video montages were used in each experiment, yet the presentation order was randomized for each participant. In the experiments, we asked the participants to watch the videos and to indicate which person they thought the heartbeats had been recorded from (Fig. 1c).

In Experiment 1, we used the videos in their standard configuration (upright faces). In Experiment 2, we used the inverted version of the videos by flipping the videos through the vertical axis (i.e., upside-down, Fig. S1). In Experiment 3, we edited the videos of Experiment 1 to remove transient information about the individuals' cardiovascular dynamics (e.g., redness from the blood through the face). To do this, we generated facial masks based on the individuals' faces at 0.5 seconds after each video. These masks were created by editing the videos with Matlab R2016b. To create the mask the experimenter clicked on the area of the right cheek of the chosen frame of the video of each actor. All pixels with a similar colour (defined as within 100 pts of the RGB value of the chosen pixel) were found and were replaced with the colour value at the pixel for the middle frame. This produced a 'mask' of constant colouration across all frames for each pixel that included the neck, cheeks, forehead and chin, but excluded the eyes and mouth (Fig. S1d). This process was carried out for the 84 video pairs. This manipulation was not explained to the participants.

In Experiment 4 we conducted two different manipulations of the videos with the same participants. In the first part, we used still images of the videos by selecting the first frame in which both actors had their eyes open. This experiment aimed to remove information about the individuals' cardiovascular dynamics (e.g., variations of redness and ballistic movements). In the second part of Experiment 4, we replicated Experiment 1 by again using the dynamic videos in their usual configuration. Last, in experiment 5 we examined whether the task could be performed by learning to associate the rhythms of the depicted heartbeats with certain individuals. In other words, while participants progress in the experiment, they could learn the rhythms of the depicted heartbeats and associate these with the actors shown on the screen. This strategy does not involve subjects' judgement about others' cardiac rhythms but pairing concurrent stimuli. To rule out this possibility, we exchanged each actor appearing in the videos by a particular geometrical shape, i.e., each actor was consistently exchanged by a specific shape for all videos. These shapes were distinct from each other. Therefore, as with the actors, these shapes could be easily associated with the depicted heartbeats on the screen. This final experiment allowed us to examine if this was a strategy that participants could adopt (see all

the shapes together in Fig. S1e). Importantly, in all experiments, no feedback was given as to whether the participant had performed the trial correctly or not.

2.3 Procedure

The main task was designed to test whether people can identify which of two actors a cardiac rhythm was from by looking at their faces. The videos were presented using Matlab R2016b (The MathWorks Inc., Natick, MA, USA) through the Psychtoolbox-3 (Kleiner et al., 2007). All the participants were instructed to watch the whole videos and to indicate to whom the beating heart belonged. After each video, the screen turned black and showed two white arrows on the centre of the screen, one left and one right, which were separated by the word ‘Or’ (i.e., \leftarrow Or \rightarrow ; Fig 1c). The participants had to enter their choice, with no time limit, by pressing the left or arrow key of the keyboard. After they entered their response, the next video was played automatically. Before the start of the experiments, all participants completed 5 practice trials. If the task was understood and they had no further questions, they performed 84 trials in two blocks of 42 trials. The order of the 84 videos was randomised and was different for every participant.

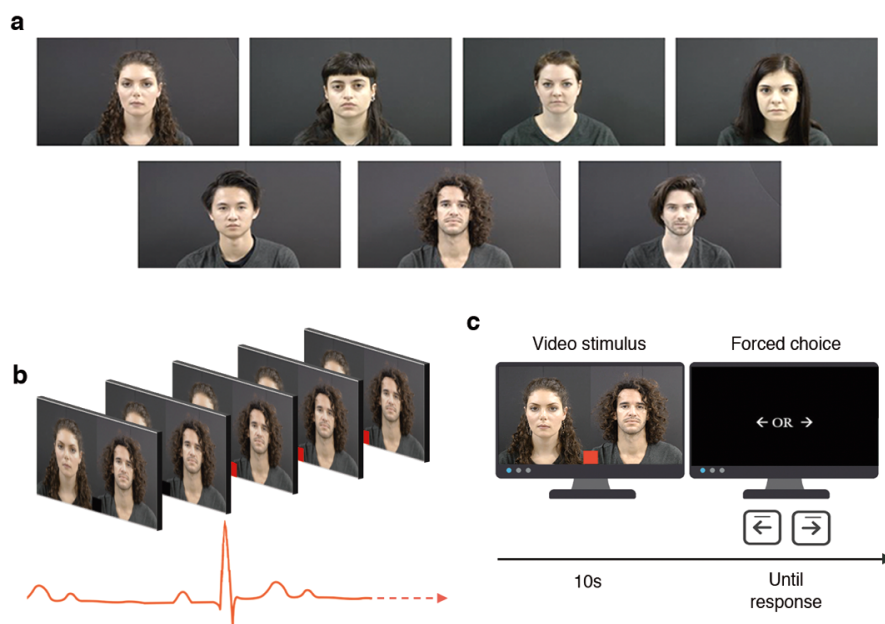


Figure 1. Recording of video stimuli and main experimental task. (a) Seven individuals were filmed in a neutral position and direct gaze (~2 min) while their ECG was also recorded. (b) Video-montages were created by randomly pairing two people side by side and placing visual feedback from one of the individuals' heartbeats [a small beating square changing in colouration according to the R-peak (contraction of the heart) in the ECG]. (c) After each video, participants indicated to whom the beating ‘heart’ belonged; the panel above depicts one trial; all actors consented to the use of their image in the experiments and study material; by the term ‘actors’ we just refer to the filmed individuals that appear in the videos.

2.4 Statistical analysis

In all experiments, we computed the participants' average performance as the proportion of correct responses. We compared such a proportion against the chance level (0.5) by computing a one-sample t-test. These results were plotted by using the Raincloud plots package in R (Allen et al., 2021). Accordingly, we report t and p-values, mean and standard deviations, 95% confidence intervals, effect sizes (Cohen's d), and Vovk-Sellke maximum p-ratios (VS-MPR). The latter computes a Bayes Factor approximation by using the p-value calibration introduced by Sellke et al., (2001), which estimates the maximum possible odds in favor of H_1 over H_0 .

We also compared the average proportion of correct responses across all experimental conditions. The p-values were adjusted for a comparison of 5 estimates using the Holm-Bonferroni method. Furthermore, we computed the average heartbeat interval for each one of the actors depicted in the videos. Then, we calculated the absolute difference between the average heartbeat intervals of the two actors shown in the videos. Next, we correlated this measure with the proportion of the participants that were correct for each video; this resulted in 84 values (one per video). In the subsequent analysis, a significant positive correlation denotes that videos with the greatest difference in heartbeat intervals are the easiest to correctly identify.

2.5 Data availability and transparency statement

We used in-house and standard code to create our video montages. The code and anonymised data are available in the corresponding Open Science Framework repository: <https://osf.io/zh3kt/>. Here we uploaded the performance for each experiment, the IBIs for the actors shown in each video, and the coded list of actors shown in each video. Regarding the videos, six of the seven actors consented the use of the video-montages in which they appeared only for research purposes. In order to comply with their consent, the video-montages of these actors are not publicly available but will be released on request on the sole condition that they are used for research purposes only. One of the actors did not agreed to the use of the actor's video-montages in further work. To comply legally and ethically with the subsequent consent, the corresponding video-montages cannot be shared. We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study (see Methods and Participants sections). No part of the study procedures or analyses was pre-registered before the research was conducted

3. Results

3.1 Experiments 1-3: Judging the most likely owner of given heartbeats is best when looking at dynamic natural faces.

In experiment 1, we tested the main research question of this study: whether humans can identify the likely owner of a given sequence of heartbeats. We asked 24 participants to watch the videos and to indicate in a 2AFC which person they thought the heartbeat had been recorded from. Twenty of the twenty-four participants had a mean proportion of correct responses above chance level (chance level was 0.5). The mean proportion of correct responses ranged from 0.452 to 0.738 and the mean across participants was 0.582 (SD = 0.068). This was significantly above chance [$t(23) = 5.895$; $p < 0.001$, 95% CI for mean difference [0.053, 0.111], $d = 1.203$, VS-MPR = 5796; Fig. 2a].

Having shown that participants were able to perform the task significantly above chance levels, we explored what visual information people could use to complete this task. It is assumed that people are highly experienced with viewing upright faces and that in such a canonical form, faces are processed as a whole with the use of well learnt configural information (Civile et al., 2019; Taubert et al., 2011; Yin, 1969). If the configural processing of faces supports the execution of our task, disrupting it should affect participants' performance. Instead, if the task can be accomplished by just extracting local features, no change in performance should be observed. Therefore, in Experiment 2, we repeated Experiment 1 in a new group of 24 participants but with the videos inverted. In this way, the visual information was kept constant while the configural processing of the faces was manipulated. In Experiment 2 the mean proportion of correct responses ranged from 0.381 to 0.655 with an average proportion of 0.54 correct responses (SD = 0.071). This was still significantly above chance levels [$t(23) = 2.753$, $p = 0.011$, 95% CI for mean difference [0.010, 0.070], $d = 0.562$, VS-MPR = 7.249].

The results of Experiment 2 demonstrated that altering the natural processing of faces disrupted to some extent participants' judgment. However, these results did not inform us about the visual cues that people used. Previous research has shown that the cardiac signal can be obtained from both the degree of facial redness, due to blood flow, and movements of the head as the blood was pumped into the head (Lauridsen et al., 2019; Wu et al., 2012). In Experiment 3 we tested whether removing any transient variance of facial redness in the videos could disrupt performance on the task (see methods and Supp. Fig. 1). To this end, we manipulated the videos so that the colour of the flesh of both actors remained constant throughout the video. We tested these videos in a third group of 24 participants. In Experiment 3 participants' mean

proportion of correct responses ranged from 0.44 to 0.702 with an average proportion of 0.55 correct responses ($SD = 0.069$). This was significantly above chance levels $t(23) = 3.628$, $p = 0.001$, 95% CI for mean difference $[0.022, 0.081]$, $d = 0.741$, $VS-MPR = 39.781$; Fig. 2a.

In the first three experiments we showed that although performance varied across the different experiments, participants were able to perform the task significantly above chance levels. One possibility is that rather than selecting the most likely owner of the depicted heartbeats by using transient visual cues in the videos, participants could be using prior beliefs about people's likely heart rates (e.g., based on the perception of age, sex, or health), and/or learning to associate the visual feedback of the heart with particular actors in the videos. To test this, we ran the fourth and fifth experiments.

3.2 Experiment 4-5: Top-down influences and replication of the current results

In Experiment 4 we ran two studies: a new manipulation and a direct replication of Experiment 1. In the new manipulation, we removed all dynamic information from the videos and presented just a still image of each actor. A new group of 24 participants performed both tasks. They always performed the STILL images task first. In Experiment 4 (Still) the average proportion of correct responses was 0.543 ($SD = 0.048$) and ranged from 0.452 to 0.643. Even though this performance was the lowest of these four experiments, the mean proportion of correct responses was significantly greater than chance [$t(23) = 4.348$, $p = 0.0002$, $d = 0.888$, 95% CI for mean difference $[0.023, 0.064]$, $VS-MPR = 186.344$]. This suggests that even with still images, our participants performed above chance level, probably by using prior knowledge about people's appearance, health, and supposed heart rate (Henderson et al., 2016; Perrett et al., 2020). In the second part of Experiment 4, the same participants performed the task with the dynamic videos in a direct replication of Experiment 1. Here, the mean proportion of correct responses was 0.602 ($SD = 0.066$), ranging from 0.476 to 0.762) and was significantly above chance [$t(23) = 7.532$, $p < 0.0001$, 95% CI for mean difference $[0.074, 0.130]$, $d = 1.537$, $VS-MPR = 194123.125$].

An alternative explanation for our results is the use of strategies that do not involve judging others' cardiac rhythms. For instance, our participants could learn to associate the rhythms of the depicted heartbeats with certain individuals (i.e., just learning to pair stimuli appearing together on the screen). To further investigate whether our results could be explained by this strategy, we ran a final control experiment. In Experiment 5 we created an analogous task in which we exchanged each actor appearing in the original videos by a particular geometrical shape (Supp. Fig.1). These shapes, as the people portrayed, were distinctive from

each other and could be easily named. In Experiment 5 the mean proportion of correct responses was 0.50 (SD = 0.062), ranging proportion from 0.381 to 0.631. Performance was not significantly different from chance $t(23) = 0.038$, $p = 0.969$, 95% CI for mean difference [-0.026, 0.027], $d = 0.008$, VS-MPR = 1; see Fig. 2a, Table 1, and Supp. Table 1 for summary statistics of all experiments.

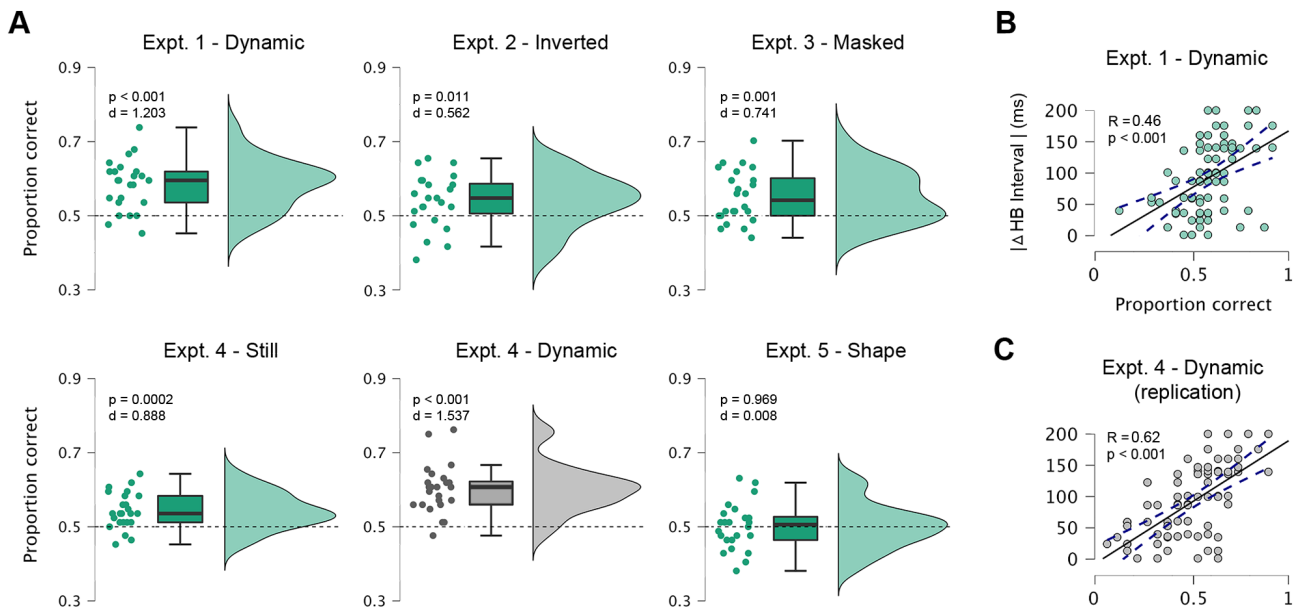


Figure 2. Participants' proportion of correct guesses. (a) In experiments 1-4 participants assigned the depicted heartbeat to the correct person significantly above chance level (0.5 depicted as a dashed line along the y-axis); greatest accuracy for the dynamic conditions (Expt.1 and 4-replication). Conversely, when exchanging each individual by a shape, accuracy did not differ from chance ($p = 0.969$, Expt. 5). (b-c) Pearson correlations between the difference of the portrayed individuals' heart rate (pairs in each video) and participants' accuracy. Video montages showing individuals with a greater difference between their heart rates were the easiest to correctly identify; the greatest correlation for the dynamic conditions (Expt.1 and 4). Lower correlations were found in the remaining conditions with absent correlation in Expt. 5 Shapes condition (Supp. Fig. 2).

3.3 Differences in participants' performance between experiments

To investigate differences in participants' performance as a function of the experimental manipulations, we compared the proportion of correct responses between conditions. To this end, we compared the pooled data from Expt. 1 and the second part of Expt. 4 (dynamic faces), as well as the corresponding data from the Inverted, Masked, Still, and Shape conditions (Expt.2-5). The comparison of all experimental conditions revealed that the accuracy in the dynamic condition was significantly greater than in the Inverted $t(115) = 3.191$, $p = 0.016$, CI for mean difference [0.007, 0.097], $d = 0.755$, the Still $t(115) = 3.008$, $p = 0.025$, 95% CI

[0.004, 0.094], $d = 0.791$, and the Shape experimental condition $t(115) = 5.634$, $p < 0.0001$, 95% CI [0.047, 0.136], $d = 1.390$. Yet, performance in the dynamic condition did not differ from that of the Masked condition $t(115) = 2.489$, $p = 0.084$, 95% CI for mean difference [-0.004, 0.085], $d = 0.594$. Interestingly, it is worth noting that participants in the Masked condition could still observe participants' subtle movements beyond the masked face, for instance in the neck area and due to respiration. See Table 1 for the comparison of participants' accuracy between experimental conditions

Table 1

Post Hoc comparison of participants' accuracy between experimental conditions

Condition	Inverted faces Expt. 2	Masked faces Expt. 3	Still faces Expt. 4a	Shape Expt. 5
Dynamic faces Expt. 1 and 4b	$d = 0.755$ $p = 0.016$	$d = 0.594$ $p = 0.084$	$d = 0.791$ $p = 0.025$	$d = 1.390$ $p < 0.0001$
Inverted faces Expt. 2		$d = -0.162$ $p = 1.000$	$d = -0.049$ $p = 1.000$	$d = 0.590$ $p = 0.145$
Masked faces Expt. 3			$d = 0.140$ $p = 1.000$	$d = 0.771$ $p = 0.051$
Still faces Expt. 4a				$d = 0.760$ $p = 0.122$

Note. The comparison of all experiments reveals that accuracy in the original dynamic conditions [Expt. 1 and the second part of 4 (replication)] was significantly greater than in the Inverted, Still, and Shape experimental conditions. This indicates greater performance during the natural perception of faces. d : effect size (Cohen's d); P -value adjusted for comparing a family of 5 estimates using Holm-Bonferroni method. See also Supp. Tables 2-3 for non-corrected P -values, as well as non-parametric Dunn's Post hoc comparisons. Also, analysis file in OSF repository.

3.4 Differences in the heart rates of displayed actors correlate with video difficulty

Up to this point, we were able to conclude that participants could select the most likely owner of the depicted heartbeats when looking at their face, and that performance was best when faces were perceived in their natural configuration (Fig. 2a, Table 1, and Supp. Table 1). While top-down processes may play a role (see Expt. 4), cues related to the physiological state of the perceived person could also support participants' performance. This idea is supported by an additional analysis in which we correlated the proportion of correct responses for each video according to the difference between the heartbeat intervals of the individuals portrayed. As seen in Fig. 2b-c, the greater the difference between the heart rates of the individuals in the dynamic conditions, the higher the accuracy for that particular video. This is true for all experiments except for Experiment 5 where no faces were displayed (Supp. Fig. 2). The

strongest correlation was found when using the original dynamic videos with no editing. The results of this analysis suggest that transient physiological signals might aid to select the most likely owner of the depicted heartbeats.

4. Discussion

People refer to inner bodily sensations when describing their intentions, emotions, and mental experiences. Increasingly research supports the influence of afferent signalling, such as heartbeats, upon cognition, movement, and perception (e.g., Galvez-pol et al., 2022, Al et al., 2020; Galvez-Pol et al., 2020, 2021; Garfinkel et al., 2020; Leganes-Fonteneau et al., 2020; Park et al., 2018). Although of considerable interest, these demonstrations usually adopt a rather individualistic perspective: physiological bodily signals serve ‘one’s purpose’. Yet, humans live in a highly social environment whereby a dialectical nature unfolds, namely, we signal our state and perceivers infer it. We explored the idea that particular physiological signals such as heartbeats, which relate and reflect one’s psychophysiological state (Beauchaine & Bell, 2020; Thayer et al., 2012), could be correctly attributed to individuals by looking at their faces. To test this, we developed a new paradigm that can be easily applied, replicated, and manipulated. This involved the use of video montages, showing two people side by side and visual feedback from one of the individuals’ heartbeats in the centre. Participants’ task was to judge the most likely owner of the depicted sequence of heartbeats. Across five experiments, including one replication, the findings indicate that our participants judged the most likely owner of the depicted sequence of heartbeats significantly above chance levels. The precise mechanism for this task needs further examination. Yet, we think that it could be achieved by using at least two sources of information: transient subtle visual cues that are locked to heartbeats (changes in coloration and motion), and more perpetual facial features such as perceived health, sex, fitness, and age (i.e., linking individuals’ appearance and cardiovascular functioning, e.g., expected heart rate).

Next, we highlight five aspects of this work that need to be considered: its biological significance, the finding that people can do the task above chance levels (even on the still faces; Expt. 4), the absence of learning effects on participants’ performance, limitations, and further work (e.g., testable hypotheses).

Biological significance. Faces transmit information that is used to reason and comprehend other people. Research in face perception often studies which personal information is readable from the face [e.g., identity, gender, emotion (Oruc et al., 2019; Tsao & Livingstone, 2008)].

Relatedly, studies in colour vision and perception of static faces have shown that people are better at detecting subtle changes in colouration on faces than non-face stimuli (Tan & Stephen, 2013; Thorstenson et al., 2017), and that changes in facial colouration (e.g., redness, yellowness) seem to support the discrimination of facial configurations (Benitez-Quiroz et al., 2018; Thorstenson et al., 2017, 2019; Young et al., 2018). Also, it is of interest that colour vision in primates seems tuned to discriminate spectral modulations on the skin of conspecifics, and that trichromat species (but not dichromats) seem more sensitive to variations in blood oxygen saturation and tend to be bare-faced (Changizi et al., 2006). This could allow discriminating socio-sexual signals, threat displays, and emotional states. All things considered, these studies suggest a link between visual information from faces and bodily signals, which are known to modulate and index one's psychophysiological state. Our results indicate that at least in the current 2AFC, participants could guess above chance levels the correct owner of a depicted sequence of heartbeats. Whether this possible ability provides perceivers with a better inference of others' thoughts and emotional states is a promising inquiry for future work.

Performance above chance level and absence of learning effects. There are at least three ways in which the participants could have accomplished the task: by learning to pair the depicted heartbeats with particular individuals; by inferring visual cues originating from physiological changes in the subjects portrayed (i.e., pumping of the blood evoking variations in redness and coupled pulsatile movement of the head/face/eyes); and lastly, by using prior knowledge about people's appearance, health, and heart rates.

We believe that our results cannot be explained by just learning to pair stimuli appearing together on the screen with the heart rate shown below. This seems unlikely as trial-to-trial feedback on performance was not given and the participants had no way of knowing if their choices were correct or not. However, as a control condition, we included Expt. 5, which eliminated the level of human-based characteristics while allowing participants to learn associations between the stimuli and the heart rate. In Expt. 5 the mean performance was not significantly different from the chance level. Therefore, we believe that our participants did try to select the most likely owner of the depicted heartbeats based on the human-based characteristics of the individuals portrayed.

Considering the novelty of our paradigm, we decided to reduce the complexity of our study by including video montages where the actors did not try to disclose any emotions, there was no context and no actions. Our results revealed that participants performed well above

chance level in the dynamic videos with more natural conditions (Expt.1 and 4; Table 1 and Supp. Table 1). Here nearly half of the participants reached a mean proportion between 60-70% correct responses. The implications of such an ability in more real-world scenarios require further examination. Interestingly, the additional analysis demonstrated that some video montages were more correctly selected than others and that this variance was related to differences between the heart rates of the individuals portrayed. This is consistent with the hypothesis that visual cues that are locked to heartbeats could support the performance of the task. Yet, an additional and more parsimonious explanation is that participants judged the health, fitness, sex, and/or age of the individuals portrayed. By using implicit or explicit knowledge about health and individuals' appearance, the participants could have guessed the actors' heart rate. Then, participants' responses could simply reflect the differential heart rate of the individuals portrayed.

In the current set of studies, performance above chance level could be accomplished by using the knowledge that we have about individuals' appearance and their heart rate. For instance, preceding studies have shown that impressions of health depend on face shape and skin colouration (Henderson et al., 2016; Perrett et al., 2020). Similarly, priors linking heart rate to factors such as sex, fitness, or health could come into play. By using these priors, our participants could have reached performance above chance level in Expt. 4 (Still condition). Yet, it is important to stress that this performance was still lower than in the dynamic conditions (Table 1, Supp. Table 1). The use of this knowledge by the participants requires further examination. Future studies may examine how reliable such priors are and how they are formed. Categorical associations reinforced by one's experiences and cultural consensus might influence the use of interoceptive knowledge about other people; see e.g., bodily maps of emotions and somatosensation (Nummenmaa et al., 2014; Palser et al., 2021).

4.1 Limitations

Here we consider the constraints of generality proposed by Simons et al., (2017). The videos used in this study showed young adults with neutral facial expressions, uniform background, clear skin pigmentation, minimal makeup and accessories, which were also judged by young adults (18-46yo) recruited through a university subject pool in the UK. In this context, it was not intended that most actors were from different countries, yet they were mostly white Europeans. Thus, we expect the results to generalize to situations in which participants observe similar video montages, as long as manipulation checks indicate the videos depict no emotion, intentions, or context. We believe the results will be reproducible with young adults from

similar subject pools serving as participants. However, we do not have enough evidence to state that our findings will occur outside of laboratory settings, nor to state which changes could be observed when either the recorded actors or participants are from different ethnic groups. Further research should exploit our easily testable paradigm to develop video-montages portraying individuals with different skin pigmentation and ages, as well as to collect additional variables such as RT. By doing so, strict and conceptual replications of the current work can be implemented, as well as the potential legitimacy of the present results can be attained. We have no reason to believe that the results depend on other characteristics of the participants, materials, or context.

Concerning the analysis, the current set of studies used 84 unique videos (i.e., each video is a unique pair of actor videos and cardiac rhythms of one of the actors). Therefore, there are no multiple repeats of each trial type and performance in each video depends on the combination of both actors and displayed heartbeat. This was by design to minimise any learning effects. Yet, this makes more difficult the recodification of the data in a way that can be analysed through statistical methods such as regressions and linear mixed models. Further work (see below section) could use paradigms with stimuli that allow analysing the data in more stringent manners such as computing both stimuli and participants as random factors (see e.g., Judd et al., 2012).

4.2 Further research

Considering that we are highly social animals and that cardiac rhythms reflect our psychophysiological state, a key question is whether such fundamental information could be inferred by others through vision. To approach this matter, we tested whether people could correctly identify which of two people of a cardiac rhythm was recorded. While this does not directly examine peoples' ability to infer/perceive others' heartbeats, the ensuing results are consistent with this idea.

Future work could examine this possible ability and the type of information required to accomplish it. In this regard, we did not disambiguate the type of information used by the participants, i.e., use of knowledge about stable features such as appearance and health, and/or the use of transient changes such as visual cues coupled to heartbeats. Across the six experiments, we manipulated the type of information available (i.e., stable and transient) and observed that participants managed to perform above chance level. This suggests that participants could accomplish the task by using, combining, or switching between the aforesaid approaches according to the demands of the task. In addition, this also indicates that our main

task (i.e., indicating to whom the depicted heart belongs to) is not optimal to disambiguate the type of information used by the participants. Therefore, the independent and/or interactive contribution of these potential sources of information remain to be examined.

To examine whether people guess others' heartbeats by perceiving transient cues locked to the cardiac cycle, researchers may adapt our paradigm by using the so-called tapping task and the method of constant stimuli. The idea behind this would be that participants can adjust a pulsatile signal to the heartbeats of the portrayed individuals, and/or that they can select whether the depicted heartbeats are synchronous (or asynchronous) to the heartbeats inferred from the actors' face (see Table 2). To examine whether people infer others' cardiac rhythms by using explicit knowledge based on appearance and expected heart rate, researchers could measure participants' knowledge or beliefs about heart rate and perceived health status (Table 2). In parallel, the creation of new stimuli could allow experiments in which participants' performance is tested under different conditions. For instance, perception of health from facial cues has been linked to skin colouration (yellowness), shape measures of adiposity, and affect in facial expressions (Henderson et al., 2016). Creating stimuli with a biometric profile of the portrayed individuals will support the design of experiments with various stimulus conditions.

In addition, irrespective of the source and its use, our work might tap into the broad construct of body awareness, including an exteroceptive visual channel of perception, and interoceptive sensations. People might learn to model others' physiological attributes based on their body awareness, which is constructed by both extero- and interoceptive processes. Future work should examine how people learn such models (e.g., about people's appearance and expected heart rate), as well as the impact of noticing bodily sensations (e.g., interoceptive sensibility; see Galvez-pol et al., 2021; Garfinkel et al., 2015; Murphy et al., 2019) in modelling and inferring others' physiological dynamics. Relatedly, previous studies found that the processing of facial stimuli varies with the ability to notice one's heartbeats (Georgiou et al., 2018; Pfeifer et al., 2017).

In this context, we hypothesize that inferring others' cardiac rhythms might also depend on the perceivers' sense, interpretation, and integration of signals originating from within the body (Table 2). Whether good interoceptors could exhibit better performance in our task is not clear. Yet, we can hypothesize based on two pieces of information: first, when considering atypical interoception, either low or amplified functioning are usually linked to a maladaptive valuation of stimulus processing (Bonaz et al., 2021; Khalsa et al., 2018). Second, the tendency to use one's emotional state when relating to others (i.e., emotional egocentricity bias) varies as a function of trait-like levels of interoceptive accuracy (von Mohr et al., 2021). Considering

these, we believe that amplified interoception might override the inference of other’s cardiac rhythms, alike the emotional egocentricity bias, but in the physiological domain.

Although in these initial studies we used actors with a neutral expression, we hope that this study can serve as a building block to examine further hypotheses that take into account emotional and contextual dimensions. For instance, by probing distinct facial configurations, adding external context, examining participants’ emotional granularity, scrutinising bodily memories, and bodily variables in observers and perceived people (Barrett et al., 2019; Galvez-Pol et al., 2020; Quigley et al., 2021). Last, we have considered the potential ability to infer others’ cardiac rhythms and how this could be accomplished. Eventually, researchers could examine the consequences of this possible ability. From the perceivers’ standpoint, being able to correctly infer others’ cardiac rhythms through the visual domain might allow a better inference of their thoughts and emotional state.

Table 2	
Outstanding questions and proposed paradigms	
Can people perceive the visual cues, such as colour changes or head/eye movement, that are locked to each heartbeat?	To test explicitly whether people can detect the visual signals that are time-locked to each heartbeat would require a different paradigm from that described here. Such studies could borrow methodological features from research into cardioception, where researchers have studied people's ability to feel their own heartbeats. Here we present three likely methods. 1) Tapping tasks : where participants press a key when they think that the heart of the actor beats. 2) Method of constant stimuli : here video montages showing one actor could be used, these videos appear multiple times, but the time of the depicted heartbeat would be delayed in different videos (e.g., +0, +300 ms, +600 ms from time of the actual R-peak). In these tasks, participants report whether they think the depicted heartbeats are synchronous with the actors’ heartbeats. The prediction would be that heartbeats that are less delayed are considered more synchronous. 3) Phase adjustment tasks : Here participants would change the phase of a depicted heartbeat until they think it is synchronous with the actors’ heartbeats.
Can others’ cardiac rhythms be estimated by using explicit knowledge about appearance and expected heart rate?	Measuring participants’ knowledge or beliefs about heart rate, e.g., inquiring about expected heart rate in different scenarios and perceived people, or directly asking participants to state what they believe is the heart rate of the actors portrayed. See e.g., Ring et al., (2015). Alternatively, the creation of stimuli with biometric information about the health of the individuals portrayed may support the design of experiments with different stimulus conditions. See e.g, Henderson et al., (2016).
Can others’ cardiac rhythms be detected/modulated by using our own implicit/explicit bodily sensations?	ECG recording: Using participants’ ECG and accelerated or decelerated versions of the real actors’ heartbeats depicted on the screen, it would be possible to estimate whether participants’ judgements of others’ heartbeats are biased towards their own heart rate and based on a more implicit processing Self-report questionnaires: examining explicit measures of interoception, body awareness, health, or social intelligence. This would allow profiling participants and to correlate their scores with the task of others’ cardiac inference to test the degree to which these metrics might drive or mediate estimates of other people’s heart rates (see e.g., Garfinkel et al., 2015).

5. Conclusions

The results of this study indicate that people can judge the most likely owner of a given sequence of heartbeats significantly above chance levels, that such a task is best performed when processing faces in their natural configuration, and that it is likely accomplished by using and/or switching between the use of visual bodily cues elicited with each heartbeat, and prior knowledge about the individuals' appearance and associated heart rate. The current set of studies represents the first step to examine whether people can infer/perceive the heartbeats of others. Accordingly, we have proposed various methods and experiments that could follow-up this work.

Acknowledgements: We would like to thank all those who participated in and helped to advance this study. **Funding:** This research was supported by the Leverhulme Trust – Grant code RPG-2016-120, United Kingdom (to J-M.K) and by the Autonomous Community of the Balearic Islands (CAIB), Postdoctoral grant Margalida Comas Ref PD/036/2019 (to A.G-P).

References

- Al, E., Iliopoulos, F., Forschack, N., Nierhaus, T., Grund, M., Motyka, P., Gaebler, M., Nikulin, V. V., & Villringer, A. (2020). Heart–brain interactions shape somatosensory perception and evoked potentials. *Proceedings of the National Academy of Sciences*, *117*(19), 10575–10584. <https://doi.org/10.1073/pnas.1915629117>
- Allen, M., Poggiali, D., Whitaker, K., Marshall, T. R., van Langen, J., & Kievit, R. A. (2021). Raincloud plots: a multi-platform tool for robust data visualization. *Wellcome Open Research*, *4*, 63. <https://doi.org/10.12688/wellcomeopenres.15191.2>
- Babo-Rebelo, M., Richter, C. G., & Tallon-Baudry, C. (2016). Neural Responses to Heartbeats in the Default Network Encode the Self in Spontaneous Thoughts. *Journal of Neuroscience*, *36*(30), 7829–7840. <https://doi.org/10.1523/JNEUROSCI.0262-16.2016>
- Barrett, L. F., Adolphs, R., Marsella, S., Martinez, A. M., & Pollak, S. D. (2019). Emotional Expressions Reconsidered: Challenges to Inferring Emotion From Human Facial Movements. *Psychological Science in the Public Interest*, *20*(1), 1–68. <https://doi.org/10.1177/1529100619832930>
- Beauchaine, T. P., & Bell, Z. E. (2020). Respiratory sinus arrhythmia as a transdiagnostic biomarker of emotion dysregulation. *The Oxford Handbook of Emotion Dysregulation*, 153–166.

- Benitez-Quiroz, C. F., Srinivasan, R., & Martinez, A. M. (2018). Facial color is an efficient mechanism to visually transmit emotion. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(14), 3581–3586. <https://doi.org/10.1073/pnas.1716084115>
- Bolis, D., & Schilbach, L. (2020). “through others we become ourselves”: The dialectics of predictive coding and active inference. *Behavioral and Brain Sciences*, 1–5. <https://doi.org/10.1017/S0140525X19002917>
- Bonaz, B., Lane, R. D., Oshinsky, M. L., Kenny, P. J., Sinha, R., Mayer, E. A., & Critchley, H. D. (2021). Diseases, Disorders, and Comorbidities of Interoception. *Trends in Neurosciences*, *44*(1), 39–51. <https://doi.org/10.1016/j.tins.2020.09.009>
- Cannon, W. B. (1927). The James-Lange theory of emotions: a critical examination and an alternative theory. *American Journal of Psychology*, *39*. <https://doi.org/10.2307/1422695>
- Changizi, M. A., Zhang, Q., & Shimojo, S. (2006). Bare skin, blood and the evolution of primate colour vision. *Biology Letters*, *2*(2), 217–221. <https://doi.org/10.1098/rsbl.2006.0440>
- Civile, C., Obhi, S. S., & McLaren, I. P. L. (2019). The role of experience-based perceptual learning in the face inversion effect. *Vision Research*, *157*, 84–88. <https://doi.org/10.1016/j.visres.2018.02.010>
- Craig, A. D. (2002). How do you feel? Interoception: the sense of the physiological condition of the body. *Nature Reviews Neuroscience*, *3*(8), 655–666. <https://doi.org/https://doi.org/10.1038/nrn894>
- Ferrer, E., & Helm, J. L. (2013). Dynamical systems modeling of physiological coregulation in dyadic interactions. *International Journal of Psychophysiology*, *88*(3), 296–308. <https://doi.org/10.1016/j.ijpsycho.2012.10.013>
- Fusaroli, R., Bjørndahl, J. S., Roepstorff, A., & Tylén, K. (2016). A heart for interaction: Shared physiological dynamics and behavioral coordination in a collective, creative construction task. *Journal of Experimental Psychology: Human Perception and Performance*, *42*(9), 1297–1310. <https://doi.org/10.1037/xhp0000207>
- Galvez-Pol, A., Forster, B., & Calvo-Merino, B. (2020). Beyond action observation: Neurobehavioral mechanisms of memory for visually perceived bodies and actions. *Neuroscience & Biobehavioral Reviews*, *116*, 508–518. <https://doi.org/10.1016/j.neubiorev.2020.06.014>
- Galvez-Pol, A., McConnell, R., & Kilner, J. M. (2020). Active sampling in visual search is coupled to the cardiac cycle. *Cognition*, *196*(April 2019), 104149. <https://doi.org/10.1016/j.cognition.2019.104149>
- Galvez-Pol, A., Nadal, M., & Kilner, J. M. (2021). Emotional representations of space vary as a function of peoples’ affect and interoceptive sensibility. *Scientific Reports*, *11*(1), 16150. <https://doi.org/10.1038/s41598-021-95081-9>
- Galvez-pol, A., Pavandeep, V., Villacampa, J., & Kilner, J. M. (2022). Active sampling during tactile

- discrimination is modulated by the cardiac cycle. *BioRxiv*.
<https://doi.org/https://doi.org/10.1101/2022.02.10.479959>
- Garfinkel, S N, Minati, L., Gray, M. A., Seth, A. K., Dolan, R. J., & Critchley, H. D. (2014). Fear from the heart: sensitivity to fear stimuli depends on individual heartbeats. *The Journal of Neuroscience*, *34*(19), 6573–6582. <https://doi.org/10.1523/JNEUROSCI.3507-13.2014>
- Garfinkel, S N., Gould van Praag, C. D., Engels, M., Watson, D., Silva, M., Evans, S. L., Duka, T., & Critchley, H. D. (2020). Interoceptive cardiac signals selectively enhance fear memories. *Journal of Experimental Psychology: General*, *44*(0), 1–39. <https://doi.org/10.1037/xge0000967>
- Garfinkel, S N., Seth, A. K., Barrett, A. B., Suzuki, K., & Critchley, H. D. (2015). Knowing your own heart: Distinguishing interoceptive accuracy from interoceptive awareness. *Biological Psychology*, *104*, 65–74. <https://doi.org/10.1016/j.biopsycho.2014.11.004>
- Georgiou, E., Mai, S., Fernandez, K. C., & Pollatos, O. (2018). I see neither your Fear, nor your Sadness – Interoception in adolescents. *Consciousness and Cognition*, *60*, 52–61. <https://doi.org/10.1016/j.concog.2018.02.011>
- Grund, M., Al, E., Pabst, M., Dabbagh, A., Stephani, T., Nierhaus, T., Gaebler, M., & Villringer, A. (2022). Respiration, Heartbeat, and Conscious Tactile Perception. *The Journal of Neuroscience*, *42*(4), 643–656. <https://doi.org/10.1523/JNEUROSCI.0592-21.2021>
- Helm, J. L., Miller, J. G., Kahle, S., Troxel, N. R., & Hastings, P. D. (2018). On Measuring and Modeling Physiological Synchrony in Dyads. *Multivariate Behavioral Research*, *53*(4), 521–543. <https://doi.org/10.1080/00273171.2018.1459292>
- Henderson, A. J., Holzleitner, I. J., Talamas, S. N., & Perrett, D. I. (2016). Perception of health from facial cues. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1693), 0–2. <https://doi.org/10.1098/rstb.2015.0380>
- James, W. 1884. (1884). What Is an Emotion? *Mind*, *34*, 188–205.
- Judd, C. M., Westfall, J., & Kenny, D. A. (2012). Treating stimuli as a random factor in social psychology: A new and comprehensive solution to a pervasive but largely ignored problem. *Journal of Personality and Social Psychology*, *103*(1), 54–69. <https://doi.org/10.1037/a0028347>
- Khalsa, S. S., Adolphs, R., Cameron, O. G., Critchley, H. D., Davenport, P. W., Feinstein, J. S., Feusner, J. D., Garfinkel, S. N., Lane, R. D., Mehling, W. E., Meuret, A. E., Nemeroff, C. B., Oppenheimer, S., Petzschner, F. H., Pollatos, O., Rhudy, J. L., Schramm, L. P., Simmons, W. K., Stein, M. B., ... Zucker, N. (2018). Interoception and Mental Health: A Roadmap. *Biological Psychiatry: Cognitive Neuroscience*

- and Neuroimaging*, 3(6), 501–513. <https://doi.org/10.1016/j.bpsc.2017.12.004>
- Kleiner, M., Brainard, D. H., Pelli, D. G., Broussard, C., Wolf, T., & Niehorster, D. (2007). What's new in Psychtoolbox-3? *Perception*, 36, S14. <https://doi.org/10.1068/v070821>
- Konvalinka, I., Xygalatas, D., Bulbulia, J., Schjødt, U., Jegindø, E. M., Wallot, S., Van Orden, G., & Roepstorff, A. (2011). Synchronized arousal between performers and related spectators in a fire-walking ritual. *Proceedings of the National Academy of Sciences of the United States of America*, 108(20), 8514–8519. <https://doi.org/10.1073/pnas.1016955108>
- Lauridsen, H., Gonzales, S., Hedwig, D., Perrin, K. L., Williams, C. J. A., Wrege, P. H., Bertelsen, M. F., Pedersen, M., & Butcher, J. T. (2019). Extracting physiological information in experimental biology via Eulerian video magnification. *BMC Biology*, 17(1), 103.
- Leganes-Fonteneau, M., Buckman, J. F., Suzuki, K., Pawlak, A., & Bates, M. E. (2020). More than meets the heart: systolic amplification of different emotional faces is task dependent. *Cognition and Emotion*, 1–9. <https://doi.org/10.1080/02699931.2020.1832050>
- Murphy, J., Catmur, C., & Bird, G. (2019). Classifying individual differences in interoception: Implications for the measurement of interoceptive awareness. *Psychonomic Bulletin and Review*, 26(5), 1467–1471. <https://doi.org/10.3758/s13423-019-01632-7>
- Nummenmaa, L., Glerean, E., Hari, R., & Hietanen, J. K. (2014). Bodily maps of emotions. *Proceedings of the National Academy of Sciences of the United States of America*, 111(2), 646–651. <https://doi.org/10.1073/pnas.1321664111>
- Oruc, I., Balas, B., & Landy, M. S. (2019). Face perception: A brief journey through recent discoveries and current directions. *Vision Research*, 157, 1–9. <https://doi.org/10.1016/j.visres.2019.06.005>
- Palser, E. R., Galvez-Pol, A., Palmer, C. E., Hannah, R., Fotopoulou, A., Pellicano, E., & Kilner, J. M. (2021). Reduced differentiation of emotion-associated bodily sensations in autism. *Autism*. <https://doi.org/10.1177/1362361320987950>
- Palumbo, R. V., Marraccini, M. E., Weyandt, L. L., Wilder-Smith, O., McGee, H. A., Liu, S., & Goodwin, M. S. (2017). Interpersonal Autonomic Physiology: A Systematic Review of the Literature. *Personality and Social Psychology Review*, 21(2), 99–141. <https://doi.org/10.1177/1088868316628405>
- Park, H. D., Bernasconi, F., Salomon, R., Tallon-Baudry, C., Spinelli, L., Seeck, M., Schaller, K., & Blanke, O. (2018). Neural Sources and Underlying Mechanisms of Neural Responses to Heartbeats, and their Role in Bodily Self-consciousness: An Intracranial EEG Study. *Cerebral Cortex*, 28(7), 2351–2364. <https://doi.org/10.1093/cercor/bhx136>

- Park, H. D., Correia, S., Ducorps, A., & Tallon-Baudry, C. (2014). Spontaneous fluctuations in neural responses to heartbeats predict visual detection. *Nature Neuroscience*, *17*(4), 612–618.
<https://doi.org/10.1038/nn.3671>
- Park, H. D., & Tallon-Baudry, C. (2014). The neural subjective frame: From bodily signals to perceptual consciousness. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1641), 1–9.
<https://doi.org/10.1098/rstb.2013.0208>
- Perrett, D. I., Talamas, S. N., Cairns, P., & Henderson, A. J. (2020). Skin Color Cues to Human Health: Carotenoids, Aerobic Fitness, and Body Fat. *Frontiers in Psychology*, *11*, 1–14.
<https://doi.org/10.3389/fpsyg.2020.00392>
- Pfeifer, G., Garfinkel, S. N., Gould van Praag, C. D., Sahota, K., Betka, S., & Critchley, H. D. (2017). Feedback from the heart: Emotional learning and memory is controlled by cardiac cycle, interoceptive accuracy and personality. *Biological Psychology*, *126*, 19–29. <https://doi.org/10.1016/j.biopsycho.2017.04.001>
- Prochazkova, E., Sjak-Shie, E., Behrens, F., Lindh, D., & Kret, M. E. (2021). Physiological synchrony is associated with attraction in a blind date setting. *Nature Human Behaviour*.
<https://doi.org/10.1038/s41562-021-01197-3>
- Quadt, L., Critchley, H. D., & Garfinkel, S. N. (2018). The neurobiology of interoception in health and disease. *Annals of the New York Academy of Sciences*, *1428*(1), 112–128. <https://doi.org/10.1111/nyas.13915>
- Quigley, K. S., Kanoski, S., Grill, W. M., Barrett, L. F., & Tsakiris, M. (2021). Functions of Interoception: From Energy Regulation to Experience of the Self. *Trends in Neurosciences*, *44*(1), 29–38.
<https://doi.org/10.1016/j.tins.2020.09.008>
- Reed, R. G., Randall, A. K., Post, J. H., & Butler, E. A. (2013). Partner influence and in-phase versus anti-phase physiological linkage in romantic couples. *International Journal of Psychophysiology*, *88*(3), 309–316.
<https://doi.org/10.1016/j.ijpsycho.2012.08.009>
- Ring, C., Brener, J., Knapp, K., & Mailloux, J. (2015). Effects of heartbeat feedback on beliefs about heart rate and heartbeat counting: A cautionary tale about interoceptive awareness. *Biological Psychology*, *104*, 193–198. <https://doi.org/10.1016/j.biopsycho.2014.12.010>
- Sellke, T., Bayarri, M. J., & Berger, J. O. (2001). Calibration of p Values for Testing Precise Null Hypotheses
 Published by : Taylor & Francis , Ltd . on behalf of the American Statistical Association Stable URL :
<http://www.jstor.org/stable/2685531> Calibration of p Values for Testing Precise Null Hypothe. *The American Statistician*, *55*(1), 62–71.
- Sherrington, C. (1906). *The integrative action of the nervous system*. New Haven, CT: Yale University Press.

- Simons, D. J., Shoda, Y., & Lindsay, D. S. (2017). Constraints on Generality (COG): A Proposed Addition to All Empirical Papers. *Perspectives on Psychological Science*, *12*(6), 1123–1128.
<https://doi.org/10.1177/1745691617708630>
- Tan, K. W., & Stephen, I. D. (2013). Colour detection thresholds in faces and colour patches. *Perception*, *42*(7), 733–741. <https://doi.org/10.1068/p7499>
- Taubert, J., Athorp, D., Aagten-Murphy, D., & Alais, D. (2011). The role of holistic processing in face perception: Evidence from the face inversion effect. *Vision Research*, *51*(11), 1273–1278.
<https://doi.org/10.1016/j.visres.2011.04.002>
- Thayer, J. F., Åhs, F., Fredrikson, M., Sollers III, J. J., & Wager, T. D. (2012). A meta-analysis of heart rate variability and neuroimaging studies: Implications for heart rate variability as a marker of stress and health. *Neuroscience and Biobehavioral Reviews*, *36*(2), 747–756.
<https://doi.org/10.1016/j.neubiorev.2011.11.009>
- Thorstenson, C. A., Pazda, A. D., & Elliot, A. J. (2017). Subjective perception of color differences is greater for faces than non-faces. *Social Cognition*, *35*(3), 299–312.
- Thorstenson, C. A., Pazda, A. D., Young, S. G., & Elliot, A. J. (2019). Face color facilitates the disambiguation of confusing emotion expressions: Toward a social functional account of face color in emotion communication. *Emotion*, *19*(5), 799–807. <https://doi.org/10.1037/emo0000485>
- Tsao, D. Y., & Livingstone, M. S. (2008). Mechanisms of face perception. *Annual Review of Neuroscience*, *31*, 411–437. <https://doi.org/10.1146/annurev.neuro.30.051606.094238>
- von Mohr, M., Finotti, G., Villani, V., & Tsakiris, M. (2021). Taking the pulse of social cognition: Cardiac afferent activity and interoceptive accuracy modulate emotional egocentricity bias. *Cortex*, *145*, 327–340.
<https://doi.org/10.1016/j.cortex.2021.10.004>
- Wu, H. Y., Rubinstein, M., Shih, E., Guttag, J., Durand, F., & Freeman, W. (2012). Eulerian video magnification for revealing subtle changes in the world. *ACM Transactions on Graphics*, *31*(4).
- Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, *81*(1), 141–145.
<https://doi.org/10.1037/h0027474>
- Young, S. G., Thorstenson, C. A., & Pazda, A. D. (2018). Facial redness, expression, and masculinity influence perceptions of anger and health. *Cognition and Emotion*, *32*(1), 49–60.
<https://doi.org/10.1080/02699931.2016.1273201>