



Unique contributions of perceptual and conceptual humanness to object representations in the human brain

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A B S T R A C T

The human brain is able to quickly and accurately identify objects in a dynamic visual world. Objects evoke different patterns of neural activity in the visual system, which reflect object category memberships. However, the underlying dimensions of object representations in the brain remain unclear. Recent research suggests that objects similarity to humans is one of the main dimensions used by the brain to organise objects, but the nature of the human-similarity features driving this organisation are still unknown. Here, we investigate the relative contributions of perceptual and conceptual features of humanness to the representational organisation of objects in the human visual system. We collected behavioural judgements of human-similarity of various objects, which were compared with time-resolved neuroimaging responses to the same objects. The behavioural judgement tasks targeted either perceptual or conceptual humanness features to determine their respective contribution to perceived human-similarity. Behavioural and neuroimaging data revealed significant and unique contributions of both perceptual and conceptual features of humanness, each explaining unique variance in neuroimaging data. Furthermore, our results showed distinct spatio-temporal dynamics in the processing of conceptual and perceptual humanness features, with later and more lateralised brain responses to conceptual features. This study highlights the critical importance of social requirements in information processing and organisation in the human brain.

1. Introduction

Successful object recognition is critically important for a wide array of human activities, from selecting food and tools to recognising faces and interacting with others. Objects encountered every day, including those never seen before, are recognised by the human brain within hundred milliseconds, enabling timely decision-making and flexible behavioural responses. To understand how the human brain achieves such performance, it is necessary to elucidate how object representations emerge from the retinal input and are organised in the visual system. Object recognition is achieved in the “ventral visual stream”, a hierarchically structured pathway from striate cortex to the ventral temporal cortex, which responds selectively to different object categories. The organisation of object representations in ventral temporal cortex underpins how humans make sense of the world and adapt to their environment. While previous research has revealed distinct representations for several object categories, such as animals (Caramazza and Shelton, 1998; Cichy et al., 2014), body parts (Downing et al., 2001; Downing and Peelen, 2016), tools, and faces (Kanwisher et al., 1997), it remains unclear what drives the organisation of these object representations in the human visual system. The representational organisation of objects can be construed as a multi-dimensional space where individual dimensions code for different object features (Bao et al., 2020; Clarke, 2015; Hebart et al., 2020; Huth et al., 2012; Mitchell et al., 2008).

Growing evidence suggests that humanness features are one of the driving forces of such representational organisation, which is believed to

have developed through evolution to support effective interaction with others and the survival of the specie (cf. Caramazza and Shelton, 1998). Previous research has revealed a continuum of biological classes in the ventral temporal cortex where object representations are distributed in the visual system, with inanimate objects on one side, and animate objects on the other, with humans and non-human primates standing out from other animate objects (Connolly et al., 2012; Sha et al., 2015). Recent research also showed that the presence of faces or face-like features, as well as the attributed capacity to think or feel like a human, further explain the representational organisation of objects in the ventral temporal cortex (Contini et al., 2020; Proklova and Goodale, 2022; Ritchie et al., 2021; Thorat et al., 2019), which has been argued to reflect the importance of conceptual (i.e., agency) features of humanness (Contini et al., 2020; Gobbini et al., 2007; Proklova and Goodale, 2022; Thorat et al., 2019). As such, humanness seems to be an important dimension of object representations in the ventral temporal cortex, but it remains unclear whether it represents either perceptual features (e.g., faces or limbs), conceptual features (e.g., agency/intelligence), or both.

The respective contribution of conceptual features of humanness (i.e., thinks or feels like a human) and perceptual features of humanness (i.e., looks like a human) to the representational organisation of objects in the human visual system remains an open question because these two levels have not been fully disentangled yet. Judgements of object agency used in previous research might not necessarily reflect the contribution of conceptual features but rather that of perceptual features such as human face-like or body-like shapes, as object shape has been shown to play a large role in object representations (Bracci et al., 2019;

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Bracci and Op de Beeck, 2016; Grootswagers et al., 2019b; Long et al., 2018; Proklova et al., 2016, 2019). Moreover, humanness has commonly been measured using rating scales (e.g., Contini et al. 2020) which may not reveal subtle differences between objects. Here we address these issues by testing separately the contribution of perceptual and conceptual features of humanness to the organisation of object representations in the human visual system, using a two-alternative forced choice task. Instructions were manipulated to guide behavioural choices towards specific features, in contrast to related previous work that used very different tasks to measure the different features (e.g., Thorat et al. 2019), which limits the ability to draw direct comparisons. We collected human-similarity judgements of 200 various object images from 191 participants and compared them using representational similarity analysis (RSA; Kriegeskorte et al., 2008) to their corresponding neural representations recorded from 16 participants with Electroencephalography (EEG). Presented with randomly paired objects, the 191 participants in our behavioural judgement task were divided into three groups and asked either (i) “which object is more similar to a human?”, (ii) “which object looks more similar to a human?”, or (iii) “which object thinks/feels more similar to a human?”, in order to test the respective contribution of overall humanness, perceptual humanness, and conceptual humanness in object representations.

2. Methods

We used a previously published stimulus set and corresponding EEG data, obtained from <https://osf.io/a7knv/> (Grootswagers et al., 2019a). For the current study, we collected humanness scores in three online behavioural experiments. Data and analysis code for the current study are available on <https://osf.io/3ed8f/>.

2.1. Participants

Participants were 191 undergraduate students at Western Sydney University (50 male, 140 female, 1 non-binary) between the ages of 17 and 64 ($M = 22.74$, $SD = 8.85$). Participants were recruited through the Western Sydney University online research participation platform (SONA) and received course credit for their participation. Of the participants, 14 were left-handed and 177 were right-handed. 47 participants were non-native English speakers and 144 participants were native English speakers. Prior to commencing this study, participants were presented with an information statement summarising the project and the requirements of the task and provided informed consent. All aspects of the study were approved by the Western Sydney University Human Research Ethics Committee.

2.2. Visual stimuli

This study used a previously published stimulus set (Grootswagers et al., 2019a). The stimulus set consisted of 200 images of animate and inanimate objects (Fig. 1). Stimuli were grouped into two high level categories; 100 animate objects and 100 inanimate objects. These two categories were further divided into five animate subcategories (i.e., mammal, human, insect, aquatic, bird) and five inanimate subcategories (i.e., clothing, fruits, furniture, plants, tools). Within the subcategories, stimuli were further separated into 50 different objects (e.g., cow, kangaroo) with four different images per object (Fig. 1). This stimulus set was chosen as it contains a large number of objects that could be associated with a wide range of humanness judgements.

2.3. Behavioural data

The behavioural experiments used in this study sought explicit judgements of human-similarity in response to pairs of stimuli. The behavioural experiments were conducted online, and were programmed

in JavaScript (De Leeuw, 2015), allowing it to be run in a web-browser. The experiments were hosted on the Pavlovia.org platform (Peirce et al., 2019), and ran on the participant's own computer (cf. Grootswagers, 2020). The experimenters had no direct interaction with participants. After providing informed consent, participants commenced the behavioural survey and were prompted to enter their age, gender, handedness and native language. Next, they received written instructions with one example trial to indicate how they should respond.

For each participant, we randomly selected one image out of the four image exemplars belonging to each object (see Fig. 1), resulting in 50 images. A total of 1225 image pairs (all combinations of 50 images) were presented in random order. Participants were asked to decide which of the two images in a pair was most similar to a human and were asked to go with their first, instinctive response. Image pairs were presented in random order for 200 ms, after which the prompt remained on the screen until participants indicated their response, using the ‘F’ key on their keyboard to select the image on the left side and the ‘J’ key to select the image on the right. Testing pairs of images made it possible to go beyond the dichotomous responses often observed when using rating scales (Contini et al., 2020) and obtain a finer degree of humanness scores for all images. Every 100 pairs, the experiment paused, and participants were given the opportunity to take a break for as long as they required. The entire session lasted approximately 30 min, after which participants were shown a debrief statement and were redirected to receive course credit on SONA.

There were three different experiment versions. Participants were not aware of a difference between the three versions and could only participate in one. Each experiment version presented stimuli in the manner described above, however, a different question was asked in each version to emphasize participants to either focus on overall humanness (“which of these stimuli is more similar to a human?”, $n = 63$), perceptual humanness (“which of these stimuli looks more similar to a human?”, $n = 63$), or conceptual humanness (“which of these stimuli thinks or feels more similar to a human?”, $n = 65$) of the objects. The mean humanness response for each group of participants was calculated by how often a stimulus was selected as more similar to a human when compared with all other stimuli. That is, a score of 1 meant the stimulus was selected as more similar to a human in 100% of the paired comparisons. Therefore, the ‘most human’ stimuli had the highest values on a scale of 0 to 1.

2.4. EEG data

We made use of previously published EEG data (Grootswagers et al., 2019a). Relevant aspects of this study are described here but we refer the reader to the original article for further detailed methods (Grootswagers et al., 2019a). EEG data were collected from 16 adult participants. The 200 images were presented in random order in rapid serial visual presentation (RSVP) sequences at a rate of 5 images per second (5 Hz, 200 ms each). A total of 40 sequences were presented, yielding 40 presentations for each of the 200 stimuli. 64-channel EEG recordings were filtered (0.1–100 Hz), downsampled (250 Hz), and epoched at time points from 100 ms before stimulus onset up to 996 ms after stimulus onset. These procedures were the same as in the original study (Grootswagers et al., 2019a).

2.5. Analyses

We used Representational Similarity Analysis (Kriegeskorte et al., 2008) to compare the EEG data to the behavioural data. This approach involves constructing Representational Dissimilarity Matrices (RDMs) that capture the structure of dissimilarities between the responses to each pair of stimuli. We used the mean pairwise decoding accuracies between each stimulus pair computed using regularised ($\lambda=0.01$) linear discriminant analysis classifiers (this was the same procedure as Grootswagers et al., 2019a) and represented them in an EEG-RDM

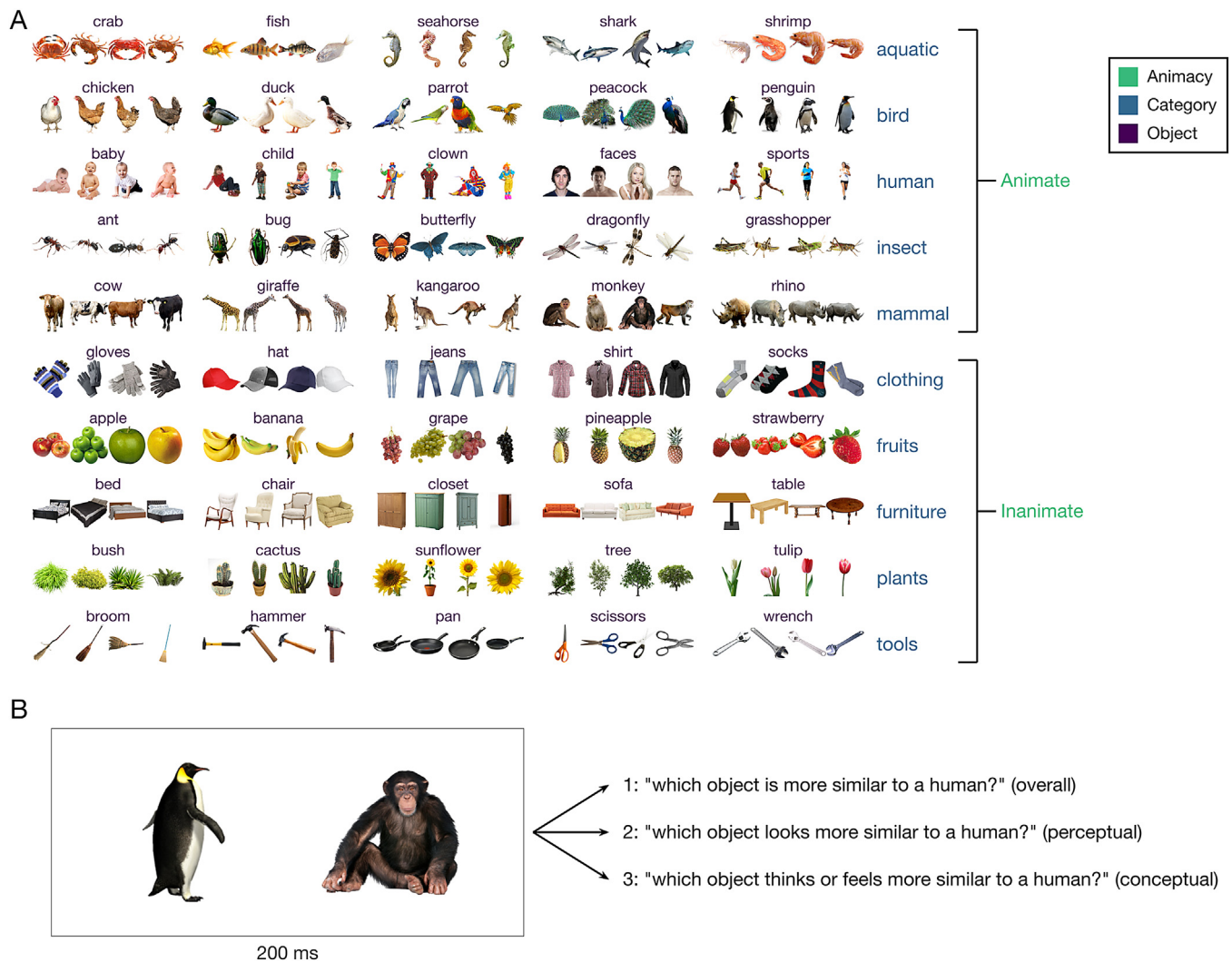


Fig. 1. Stimulus set and task. **A:** The stimulus set was divided into animate and inanimate objects, with 5 subcategories each, and further divided into 5 objects with 4 associated image exemplars. **B:** In each trial, participants were presented with a pair of stimuli for 200 ms, after which they had to select the stimulus with the highest human-similarity. Participants were randomly assigned one of the three questions, probing the different dimensions of humanness.

(Grootswagers et al., 2017; Kriegeskorte et al., 2008) for each subject, at each time point. Behavioural RDMs were constructed by taking the difference between humanness scores for each pair of images, so that the RDM reflects the dissimilarity in the humanness-rating of a pair of images. To measure the shared and unique variance between the three questions (i.e., perceptual/conceptual/overall), we computed the correlation and partial correlation between the three behavioural RDMs. We then assessed the shared and unique variance between each question and the EEG-RDMs, by computing the time-varying correlations between each of the 16 subject's EEG-RDM and the overall behavioural RDM for each question (i.e., perceptual/conceptual/overall), resulting in 3×16 time-varying correlations. For comparison to previous results, we also included the categorical RDMs that model theoretical categorical object organisations (obtained from Grootswagers et al. 2019a).

To measure the unique contributions of the perceptual aspects of humanness, we computed the time-varying partial correlation between the perceptual RDM and the EEG-RDMs while controlling for the correlation between the conceptual RDM and the EEG-RDMs. To measure the unique contributions of the conceptual aspects of humanness, we computed the partial correlation between the conceptual RDM and the EEG-RDMs while controlling for the correlation between the perceptual RDM and the EEG-RDMs. We computed the partial correlations using all objects in the stimulus set, but also separately for animate and inanimate

objects, to examine whether these two superordinate categories showed similar effects. The partial correlations made it possible to test how variance of overall humanness is explained by each feature (perceptual or conceptual) while controlling for the contribution of the other one (conceptual or perceptual, respectively). This differs from the regression approach taken in previous work on the same dataset (Grootswagers et al., 2019a), where the goal was to examine unique contributions of all models, in contrast to our current goal of comparing the relative contribution of two particular models.

We also examined the spatio-temporal dynamics of the above-zero correlations. This was done in two ways. First, we performed a channel searchlight, where we performed the same analysis as described above separately for each EEG channel plus its four closest neighbours, resulting in a channel-by-time map of correlations. Secondly, we performed the same analysis described above, but separately using only EEG channels located above each hemisphere (excluding the channels on the mid-line), resulting in time-varying correlations for each hemisphere.

2.6. Statistical inference

We used Bayesian statistics to determine the evidence for the alternative hypothesis of non-zero correlations (across the 16 participants) and the null hypothesis of no correlation for each point in

time (Dienes, 2011; Kass and Raftery, 1995; Rouder et al., 2009a; Teichmann et al., 2022; Wagenmakers, 2007), using the Bayes Factor R package (Morey and Rouder, 2018). The prior for the null hypothesis was set at zero. For the alternative hypothesis we used a half-Cauchy prior centred around zero, with the default prior width of 1 (Rouder et al., 2009b; Wetzels et al., 2011) and a null-interval (0 to 0.5) to treat small effects sizes as null (Morey and Rouder, 2011). Bayes Factors were computed separately for each time point, and for each question (i.e., perceptual/conceptual/overall). We interpreted Bayes Factors smaller than 1/10 as strong evidence for the null hypothesis, and Bayes Factors larger than 10 as strong evidence for the alternative hypothesis (Wetzels et al., 2011). Bayes Factors that fall in between this range in-

dicate insufficient evidence for either hypothesis. In addition, we computed frequentist statistics to complement the Bayes Factors. At each time point, we computed the p-value for non-zero correlation at the group level using a one-tailed t-test, and the resulting p-values were corrected for multiple comparisons across time points using the False Discovery Rate (Benjamini and Hochberg, 1995).

3. Results

Human-similarity behavioural judgements and EEG data revealed that perceptual and conceptual features of humanness both contribute to the representational organisation of objects in the human visual sys-

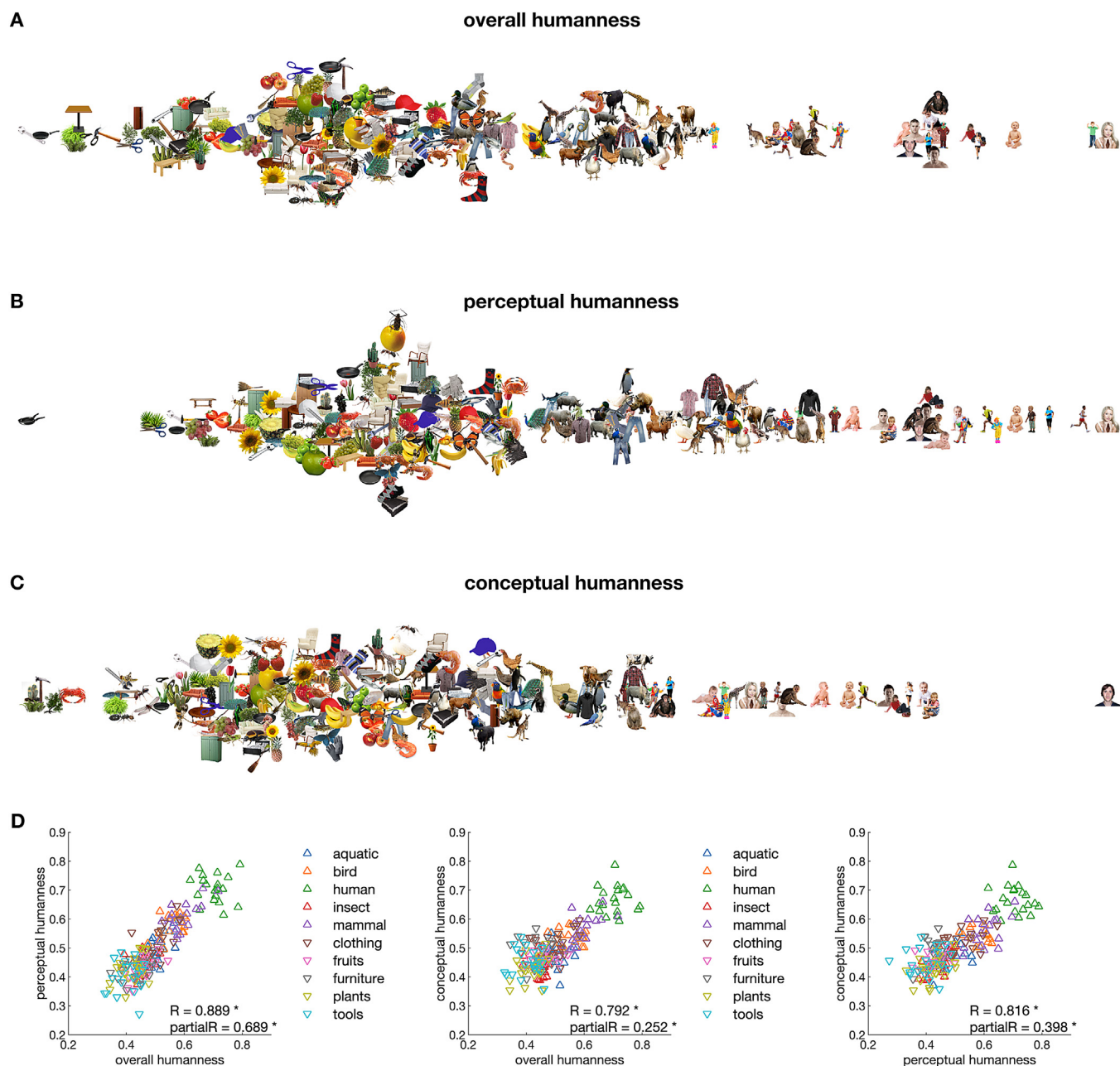


Fig. 2. Human-similarity behavioural judgements for all humanness dimensions. A–C: The mean ‘humanness’ response for each condition was calculated by how often a stimulus was selected as ‘more similar to a human’ when compared with all other stimuli. For each question, the horizontal location of each image reflects its humanness score with higher scores on the right. The vertical separation of images is only included for visualisation purposes. D: Scatter plots to directly compare the humanness-responses for all stimuli on all dimension-pairs. Correlations and the partial correlations (controlling for the left-out dimension) are shown in the plots with asterisks indicating significant relationships ($p < .05$). Together, these results show that the different ways of operationalising humanness led to different responses to human similarity.

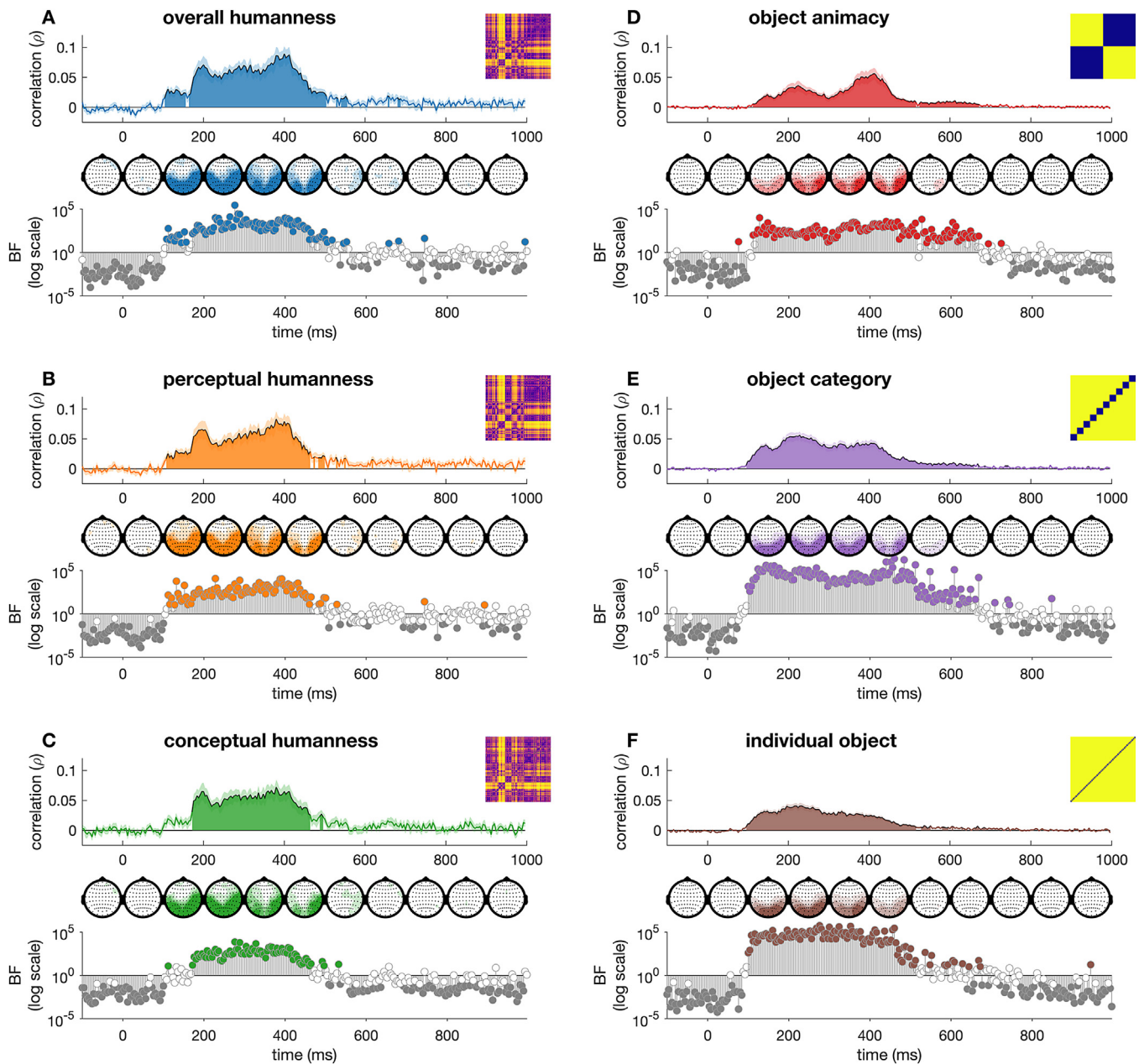


Fig. 3. EEG-behaviour correlations for all models. Plots show the correlation over time for the different humanness features (A-C), and theoretical category models for comparison (D-F). The corresponding model RDMs are shown in the inset. Light shaded areas show standard error across EEG participants ($n = 16$). Filled areas show time windows where the correlation was significantly above zero ($p < .05$, FDR-corrected). Shown below each plot are the corresponding scalp topographies averaged into 100 ms windows. The bottom rows of each group show the Bayes Factors (BF) at each time point on a log scale, with $BF < 1/10$ marked in grey and $BF > 10$ highlighted with coloured circles. These plots show that the models derived from the three humanness dimensions all correlated with the EEG data and outperformed the categorical models, with notably different temporal dynamics for the conceptual humanness model (C).

tem. Our results show that perceptual and conceptual features explain unique variance in the behavioural judgement of overall humanness and EEG data, and involve different neural processes evidenced by distinct EEG spatio-temporal patterns.

3.1. Human-similarity behavioural judgements

Participants' judgement responses for all stimuli on the three different dimensions of humanness (overall/perceptual/conceptual) transformed into the humanness score, which defined how often a stimulus was selected as more similar to a human when compared with all other stimuli, are represented in Fig. 2. It is important to note that not all participants were presented with all combinations of the stimuli, which in

combination with the online setting of the experiment may have led to a few unintuitive individual stimulus locations in these plots. Although the humanness scores for the different dimensions were strongly correlated, significant partial correlations with overall humanness were found for both perceptual (partial $\rho = 0.69$, $p < .05$) and conceptual dimensions (partial $\rho = 0.25$, $p < .05$), showing that the different questions asked to participants captured different information and variance of overall humanness.

3.2. EEG-behaviour correlations

Correlations between representational dissimilarity matrixes (RDMs) of EEG and behavioural judgement data, which enabled direct com-

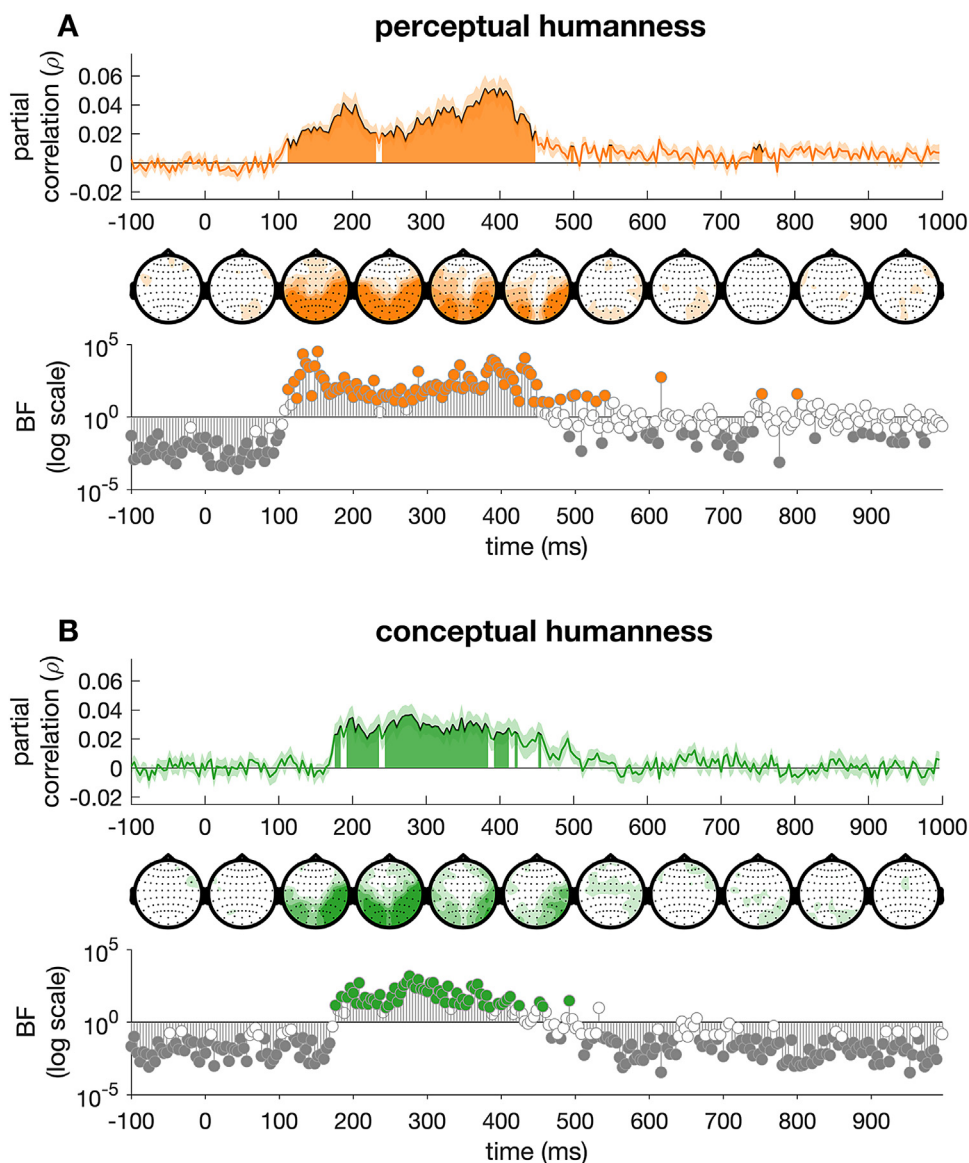


Fig. 4. EEG-behaviour partial correlations for perceptual and conceptual humanness. Plots show the partial correlation over time, controlled for the other dimension. Shaded area shows standard error across EEG participants ($n = 16$). Filled areas show time windows where the correlation was significantly above zero ($p < .05$, FDR-corrected). Shown below each plot are the corresponding scalp topographies averaged into 100 ms windows. The bottom rows of each group show the Bayes Factors (BF) at each time point on a log scale, with $BF < 1/10$ marked in grey and $BF > 10$ highlighted with coloured circles. These plots show that the perceptual (A) and conceptual (B) models explained unique variance in the EEG data, but with an earlier onset for the perceptual model.

comparisons of these two levels (Kriegeskorte et al., 2008), revealed that both perceptual and conceptual features of humanness contribute to the organisation of object representations in the visual system with distinct brain processing. Fig. 3 shows the correlation results between the EEG-RDMs (time-varying pairwise decoding accuracies for each stimulus pair and each participant) and the behavioural model RDMs (humanness-rating dissimilarity for each stimulus pair) in panels A-C, and the theoretical model RDMs (subcategories in the stimulus set: animacy, category, and object) in panels D-F. All models were significantly correlated with EEG-RDMs starting within 200 ms after stimulus presentation, showing that all dimensions of humanness (overall/perceptual/conceptual) and levels in the stimulus set (animacy/category/object) were represented in EEG data.

The unique contributions of perceptual and conceptual models were confirmed by time-varying partial correlations between each model and the EEG-RDMs, which enabled to control for the contribution of the other model. The results showed that both perceptual and conceptual features explained unique variance in the EEG data (Fig. 4), and had different temporal dynamics, with conceptual features contributing to brain's dynamic object representation later (starting ~ 200 ms) than perceptual features (starting ~ 100 ms). Notably, the perceptual model showed a rise from around 100 ms to a local peak at 200 ms, which

is consistent with the temporal dynamics of information processing in the visual hierarchy (e.g., Carlson et al. 2013; Cichy et al. 2014), which was largely absent for the conceptual model. The channel searchlight results also suggested an important role of the right hemisphere compared to the left hemisphere in the processing of the conceptual features of humanness, as indicated by stronger correlations in the right hemisphere.

This hemispheric asymmetry was confirmed by partial correlation analysis performed using data from EEG channels located above the right and left hemisphere separately, as seen in Fig. 5. While perceptual humanness partial correlations were present in data from both hemispheres (Fig. 5A-C), partial correlations for conceptual humanness were only present in the right hemisphere (Fig. 5E, F), and nearly absent in the left hemisphere (Fig. 5D). Although it is important to note that channels above one hemisphere can still record activity from the other hemisphere, these results do suggest conceptual features of humanness are predominantly coded in the right hemisphere.

Partial correlations between EEG-RDMs and behaviour conducted separately for inanimate and animate objects indicated that the unique contributions of perceptual and conceptual models occurred for both superordinate categories of stimuli, as shown in Fig. 6. The results within each superordinate category are similar in their temporal dynamics

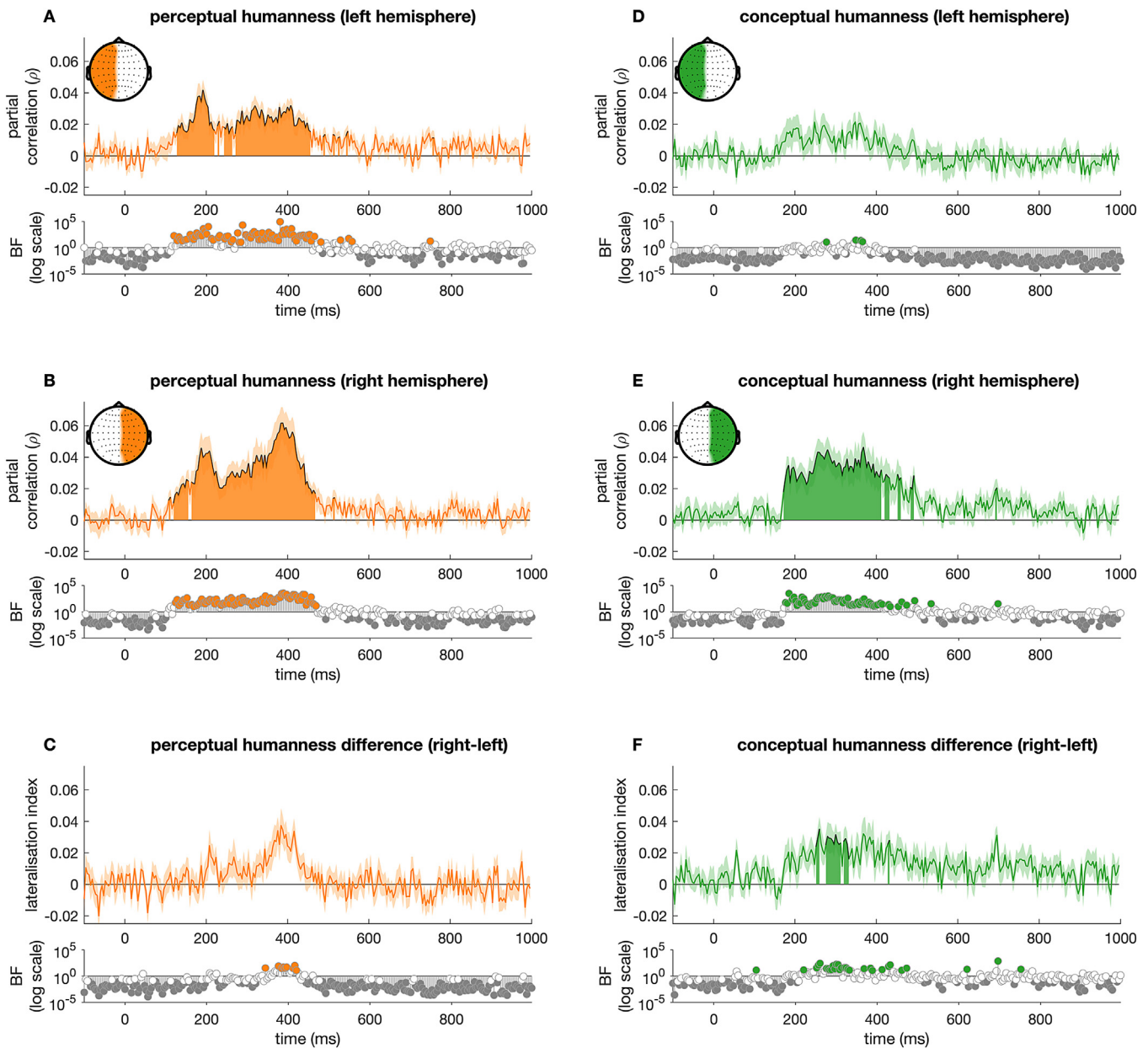


Fig. 5. Lateralisation effects for EEG-behaviour partial correlations for perceptual and conceptual humanness. Plots show the partial correlation over time for the perceptual and conceptual dimensions, controlled for the other dimension, using data from channels located above the right and left hemisphere separately, as highlighted in topographical maps. Shaded area shows standard error across EEG participants ($n = 16$). Filled areas show time windows where the correlation was significantly above zero ($p < .05$, FDR-corrected). Shown below each plot are the corresponding Bayes Factors (BF) at each time point on a log scale, with $BF < 1/10$ marked in grey and $BF > 10$ highlighted with coloured circles. These plots show that the perceptual model (A-C) correlated with both hemispheres, but that partial correlations for the conceptual model (D-F) were only apparent in the right hemisphere.

(e.g., earlier onset for perceptual) to the results for all objects together (Fig. 4). They also suggest that the main contribution for inanimate objects may have come from perceptual humanness, with conceptual humanness as the main contribution for the animate objects.

4. Discussion

In this study, we investigated the contribution of the perceptual and conceptual features of humanness to the organisation of object representations in the human visual system. Human-similarity judgements were collected from participants focusing either on perceptual features, conceptual features, or overall humanness through asking different questions. Human-similarity judgements were subsequently

compared to human neural object representations obtained from EEG recordings.

The results revealed that both perceptual and conceptual features of humanness contribute to the multi-dimensional organisation of object representations in the human brain. Behavioural human-similarity judgement data showed that the two types of features explain unique variance in the overall judgement of humanness. Representational similarity analysis, which enabled testing the variance explained in EEG data by human-similarity judgement data, confirmed an important role of overall humanness, explaining greater variance in EEG data than theoretical categorical models such as object animacy and category (Contini et al., 2020). More importantly, this analysis also revealed a significant and distinct contribution of both perceptual and concep-

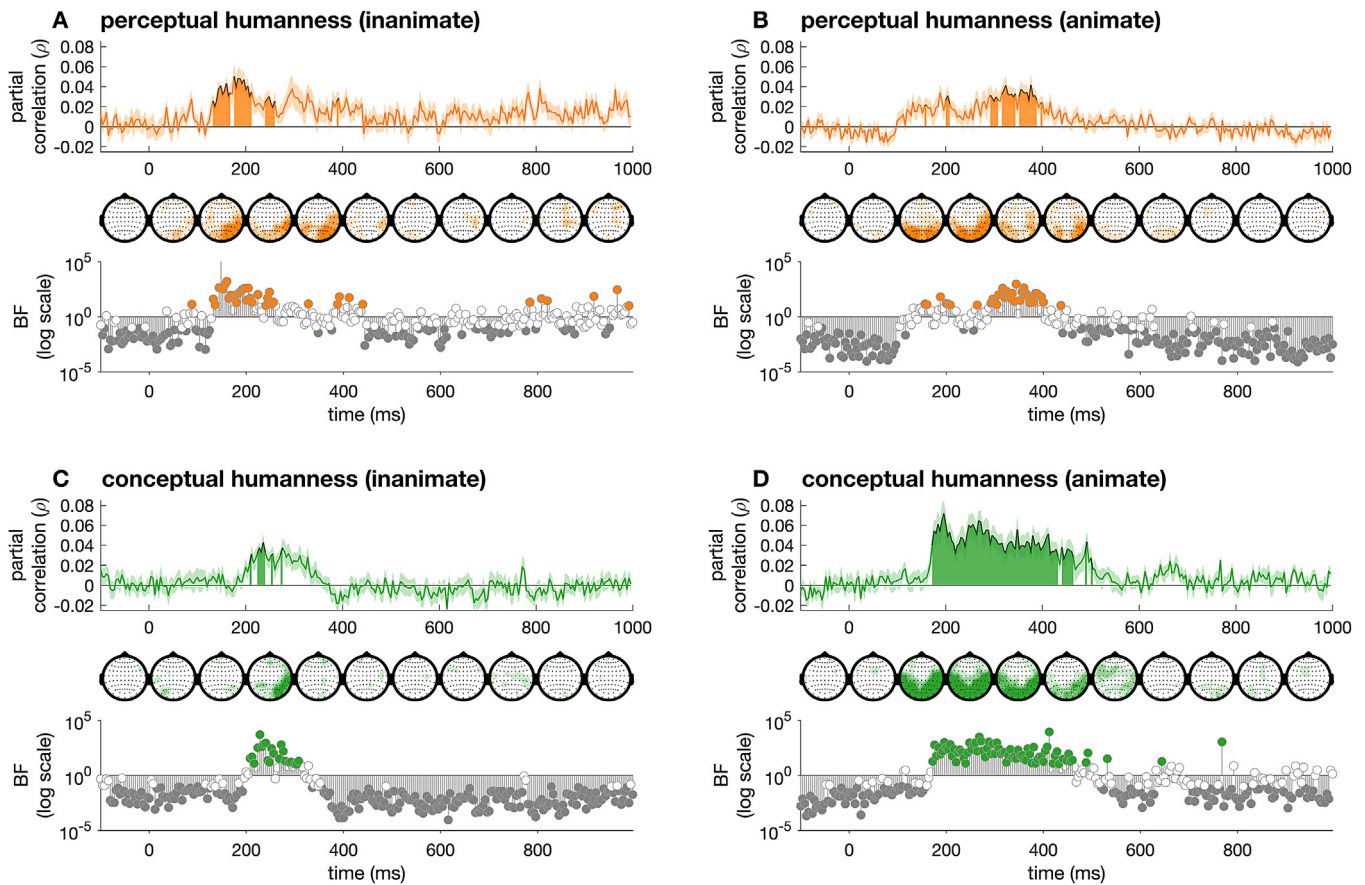


Fig. 6. EEG-behaviour partial correlations for perceptual and conceptual humanness separately for inanimate and animate objects. Plots show the partial correlation over time, controlled for the other dimension. Shaded area shows standard error across EEG participants ($n = 16$). Filled areas show time windows where the correlation was significantly above zero ($p < .05$, FDR-corrected). Shown below each plot are the corresponding scalp topographies averaged into 100 ms windows. The bottom rows of each group show the Bayes Factors (BF) at each time point on a log scale, with $BF < 1/10$ marked in grey and $BF > 10$ highlighted with coloured circles. These plots show that the perceptual (A-B) and conceptual (C-D) models explained unique variance in the EEG data for both inanimate (left column) and animate (right column) objects.

tual features of humanness, each explaining unique variance in EEG data. This is particularly remarkable considering that EEG data were obtained from a previous study, which involved different participants and was not purposely designed to test humanness (Grootswagers et al., 2019a). This not only addresses the persistent question to what extent results from object studies generalise to different stimulus sets (cf. Grootswagers and Robinson, 2021), but also builds on previous research by showing that objects are organised in the human visual system not only according to their conceptual (agency) human-like features (e.g., Connolly et al. 2012, Gobbini et al. 2007, Martin and Weisberg 2003, Sha et al. 2015) but also perceptual human-like features. Our results corroborate results from previous studies that measured perceptual similarity with a different task (e.g., visual search; Proklova et al. 2016, Thorat et al. 2019), and show that changing the instructions while observers perform the same behavioural paradigm effectively guided their choices towards perceptual or conceptual features. We also found that the “humanness” dimension is present in both animate and inanimate objects, which is particularly noteworthy given that inanimate objects do not exhibit any of the features of the animate objects that could account for humanness such as face presence, perceived intelligence, or autonomous movement. Future work can explore this further, perhaps with more ambiguous stimuli that blur the boundaries between animate and inanimate (e.g., clouds or waves as in Shatek et al. 2021) or on large datasets that contain a bigger variety of objects (Grootswagers et al., 2022; Hebart et al., 2019).

The results also showed distinct temporal dynamics in the processing of conceptual and perceptual features of humanness. Humanness ratings based on perceptual features explained unique variance in EEG data earlier than those based on conceptual features. Perceptual feature information was evident from around 100 ms and rising to an initial peak around 200 ms which is consistent with the temporal profile of the visual system hierarchy that progresses from encoding simple (e.g., edges and orientations) to complex (e.g., shapes and textures) features (e.g., Carlson et al. 2013, Cichy et al. 2014). This earlier contribution of perceptual humanness features to the representational organisation of objects in the visual system is in line with previous research that showed that the brain processes perceptual features (e.g., shape) earlier than conceptual features (e.g., category) in general (Contini et al., 2020; Grootswagers et al., 2019b, 2019a). It is also in accordance with functional Magnetic Resonance Imaging (fMRI) research showing that the ventral temporal cortex, which responds later than lower level perceptual areas (Cichy et al., 2016, 2014), represents perceptual category information as well as agency concepts (Thorat et al., 2019). These results show that top-down processes, modulated here by asking different questions in the human-similarity judgement task, can induce a shift in observers’ focus toward earlier or later features, which translates into actual decision-making.

Furthermore, the results revealed distinct spatial distributions for the processing of conceptual and perceptual features of humanness in the human brain. Although the results revealed that objects were gener-

ally represented to greater extent in the right hemisphere than the left hemisphere, this hemispheric asymmetry was found to be stronger for conceptual features than perceptual features. This asymmetry observed for all dimensions is generally consistent with overall neural responses to objects being stronger in the right hemisphere (e.g., [Quek and Peelen 2020](#)), especially for faces ([Kanwisher et al., 1997](#); [Puce et al., 1995](#)) and bodies ([Downing et al., 2006, 2001](#)). Our results suggest that the processing of conceptual humanness features of the objects drives this asymmetry stronger than the processing of perceptual humanness features, which were more symmetrically distributed. This asymmetry also seemed stronger for the inanimate objects, for which the results were almost entirely right lateralised.

Our results raise questions about when and why these two dimensions of humanness would have become significant and distinct driving forces of the organisation of object representations in the human brain. While it is plausible that a human-focused object dimension may have developed under evolutionary pressures, such as enabling effective interactions with others, the origin of the perceptual and conceptual dimensions of humanness as revealed here remains an open question. It is possible that new objects created by humans (e.g., clothes, toys, robots) challenged the effectiveness of a visual system organised around a purely perceptual dimension of humanness. For example, clothes are shaped like human body parts but do not exhibit human-like agency. It can be seen in [Fig. 2](#) that judgements for this category of objects were strongly influenced by whether participants were requested to base their human-similarity judgements on perceptual or conceptual features. Likewise, computers, robots, and other autonomous agents often do not look like humans, but increasingly think and act like humans thanks to artificial intelligence. These objects could be challenging the conceptual definition of humanness in our daily lives. More research would be needed to address these questions and to better understand the development of perceptual and conceptual humanness dimensions, as well as other potentially important dimensions that shape the representational organisation of objects in the human brain.

In conclusion, our results highlight unique contributions of perceptual and conceptual human-similarity in neural object representations. The two types of features involve distinct neural processing, with a later and more lateralised contribution of conceptual humanness than perceptual humanness. This study provides new evidence for a multi-faceted object representation and highlights that knowledge organisation in the human brain is shaped in part by social requirements.

Stimuli and data can be found at [10.17605/OSF.IO/A7KNV](https://doi.org/10.17605/OSF.IO/A7KNV) and [10.17605/OSF.IO/3ED8F](https://doi.org/10.17605/OSF.IO/3ED8F)

Credit authorship contribution statement

Tijl Grootswagers: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Visualization, Supervision, Project administration, Funding acquisition. **Harriet McKay:** Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – review & editing, Project administration. **Manuel Varlet:** Conceptualization, Methodology, Formal analysis, Writing – review & editing, Supervision, Project administration, Funding acquisition.

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References

- Bao, P., She, L., McGill, M., Tsao, D.Y., 2020. A map of object space in primate inferotemporal cortex. *Nature* 1–6. doi:[10.1038/s41586-020-2350-5](https://doi.org/10.1038/s41586-020-2350-5).
 Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B Methodol.* 57, 289–300.

- Bracci, S., Op de Beeck, H.P., 2016. Dissociations and associations between shape and category representations in the two visual pathways. *J. Neurosci.* 36, 432–444. doi:[10.1523/JNEUROSCI.2314-15.2016](https://doi.org/10.1523/JNEUROSCI.2314-15.2016).
 Bracci, S., Ritchie, J.B., Kalfas, I., Op de Beeck, H., 2019. The ventral visual pathway represents animal appearance over animacy, unlike human behavior and deep neural networks. *J. Neurosci.* 1714–1718. doi:[10.1523/JNEUROSCI.1714-18.2019](https://doi.org/10.1523/JNEUROSCI.1714-18.2019).
 Caramazza, A., Shelton, J.R., 1998. Domain-Specific knowledge systems in the brain: the animate-inanimate distinction. *J. Cogn. Neurosci.* 10, 1–34. doi:[10.1162/089992998563752](https://doi.org/10.1162/089992998563752).
 Carlson, T.A., Tovar, D.A., Alink, A., Kriegeskorte, N., 2013. Representational dynamics of object vision: the first 1000 ms. *J. Vis.* 13, 1. doi:[10.1167/13.10.1](https://doi.org/10.1167/13.10.1).
 Cichy, R.M., Pantazis, D., Oliva, A., 2016. Similarity-Based fusion of MEG and fMRI reveals spatio-temporal dynamics in human cortex during visual object recognition. *Cereb. Cortex* 26, 3563–3579. doi:[10.1093/cercor/bhw135](https://doi.org/10.1093/cercor/bhw135).
 Cichy, R.M., Pantazis, D., Oliva, A., 2014. Resolving human object recognition in space and time. *Nat. Neurosci.* 17, 455–462. doi:[10.1038/nn.3635](https://doi.org/10.1038/nn.3635).
 Clarke, A., 2015. Dynamic information processing states revealed through neurocognitive models of object semantics. *Lang. Cogn. Neurosci.* 30, 409–419. doi:[10.1080/23273798.2014.970652](https://doi.org/10.1080/23273798.2014.970652).
 Connolly, A.C., Guntupalli, J.S., Gors, J., Hanke, M., Halchenko, Y.O., Wu, Y.C., Abdi, H., Haxby, J.V., 2012. The representation of biological classes in the human brain. *J. Neurosci.* 32, 2608–2618. doi:[10.1523/JNEUROSCI.5547-11.2012](https://doi.org/10.1523/JNEUROSCI.5547-11.2012).
 Contini, E.W., Goddard, E., Grootswagers, T., Williams, M., Carlson, T., 2020. A humanness dimension to visual object coding in the brain. *Neuroimage* 221, 117139. doi:[10.1016/j.neuroimage.2020.117139](https://doi.org/10.1016/j.neuroimage.2020.117139).
 De Leeuw, J.R., 2015. jsPsych: a javascript library for creating behavioral experiments in a web browser. *Behav. Res. Methods* 47, 1–12.
 Dienes, Z., 2011. Bayesian versus orthodox statistics: which side are you on? *Perspect. Psychol. Sci.* 6, 274–290. doi:[10.1177/1745691611406920](https://doi.org/10.1177/1745691611406920).
 Downing, P.E., Chan, A.W.Y., Peelen, M.V., Dodds, C.M., Kanwisher, N., 2006. Domain specificity in visual cortex. *Cereb. Cortex* 16, 1453–1461. doi:[10.1093/cercor/bhj086](https://doi.org/10.1093/cercor/bhj086).
 Downing, P.E., Jiang, Y., Shuman, M., Kanwisher, N., 2001. A cortical area selective for visual processing of the human body. *Science* 293, 2470–2473. doi:[10.1126/science.1063414](https://doi.org/10.1126/science.1063414).
 Downing, P.E., Peelen, M.V., 2016. Body selectivity in occipitotemporal cortex: causal evidence. *Neuropsychologia* 83, 138–148. doi:[10.1016/j.neuropsychologia.2015.05.033](https://doi.org/10.1016/j.neuropsychologia.2015.05.033), Special Issue: Functional Selectivity In Perceptual And Cognitive Systems - A Tribute To Shlomo Bentin (1946–2012).
 Gobbi, M.I., Koralek, A.C., Bryan, R.E., Montgomery, K.J., Haxby, J.V., 2007. Two takes on the social brain: a comparison of theory of mind tasks. *J. Cogn. Neurosci.* 19, 1803–1814. doi:[10.1162/jocn.2007.19.11.1803](https://doi.org/10.1162/jocn.2007.19.11.1803).
 Grootswagers, T., 2020. A primer on running human behavioural experiments online. *Behav. Res. Methods* doi:[10.3758/s13428-020-01395-3](https://doi.org/10.3758/s13428-020-01395-3).
 Grootswagers, T., Robinson, A.K., 2021. Overfitting the literature to one set of stimuli and data. *Front. Hum. Neurosci.* 15. doi:[10.3389/fnhum.2021.682661](https://doi.org/10.3389/fnhum.2021.682661).
 Grootswagers, T., Robinson, A.K., Carlson, T.A., 2019a. The representational dynamics of visual objects in rapid serial visual processing streams. *Neuroimage* 188, 668–679. doi:[10.1016/j.neuroimage.2018.12.046](https://doi.org/10.1016/j.neuroimage.2018.12.046).
 Grootswagers, T., Robinson, A.K., Shatek, S.M., Carlson, T.A., 2019b. Untangling featural and conceptual object representations. *Neuroimage* 202, 116083. doi:[10.1016/j.neuroimage.2019.116083](https://doi.org/10.1016/j.neuroimage.2019.116083).
 Grootswagers, T., Wardle, S.G., Carlson, T.A., 2017. Decoding dynamic brain patterns from evoked responses: a tutorial on multivariate pattern analysis applied to time series neuroimaging data. *J. Cogn. Neurosci.* 29, 677–697. doi:[10.1162/jocn_a.01068](https://doi.org/10.1162/jocn_a.01068).
 Grootswagers, T., Zhou, I., Robinson, A.K., Hebart, M.N., Carlson, T.A., 2022. Human EEG recordings for 1,854 concepts presented in rapid serial visual presentation streams. *Sci. Data* 9, 3. doi:[10.1038/s41597-021-01102-7](https://doi.org/10.1038/s41597-021-01102-7).
 Hebart, M.N., Dickter, A.H., Kidder, A., Kwok, W.Y., Corriveau, A., Wicklin, C.V., Baker, C.I., 2019. THINGS: a database of 1,854 object concepts and more than 26,000 naturalistic object images. *PLoS One* 14, e0223792. doi:[10.1371/journal.pone.0223792](https://doi.org/10.1371/journal.pone.0223792).
 Hebart, M.N., Zheng, C.Y., Pereira, F., Baker, C.I., 2020. Revealing the multidimensional mental representations of natural objects underlying human similarity judgements. *Nat. Hum. Behav.* 4, 1173–1185. doi:[10.1038/s41562-020-00951-3](https://doi.org/10.1038/s41562-020-00951-3).
 Huth, A.G., Nishimoto, S., Vu, A.T., Gallant, J.L., 2012. A continuous semantic space describes the representation of thousands of object and action categories across the human brain. *Neuron* 76, 1210–1224. doi:[10.1016/j.neuron.2012.10.014](https://doi.org/10.1016/j.neuron.2012.10.014).
 Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17, 4302–4311. doi:[10.1523/JNEUROSCI.17-11-04302.1997](https://doi.org/10.1523/JNEUROSCI.17-11-04302.1997).
 Kass, R.E., Raftery, A.E., 1995. Bayes factors. *J. Am. Stat. Assoc.* 90, 773–795.
 Kriegeskorte, N., Mur, M., Bandettini, P.A., 2008. Representational similarity analysis - connecting the branches of systems neuroscience. *Front. Syst. Neurosci.* 2, 4. doi:[10.3389/neuro.06.004.2008](https://doi.org/10.3389/neuro.06.004.2008).
 Long, B., Yu, C.P., Konkle, T., 2018. Mid-level visual features underlie the high-level categorical organization of the ventral stream. *Proc. Natl. Acad. Sci.* doi:[10.1073/pnas.1719616115](https://doi.org/10.1073/pnas.1719616115), 201719616.
 Martin, A., Weisberg, J., 2003. Neural foundations for understanding social and mechanical concepts. *Cogn. Neuropsychol.* 20, 575–587. doi:[10.1080/02643290342000005](https://doi.org/10.1080/02643290342000005).
 Mitchell, T.M., Shinkareva, S.V., Carlson, A., Chang, K.M., Malave, V.L., Mason, R.A., Just, M.A., 2008. Predicting human brain activity associated with the meanings of nouns. *Science* 320, 1191–1195. doi:[10.1126/science.1152876](https://doi.org/10.1126/science.1152876).
 Morey, R.D., Rouder, J.N., 2018. BayesFactor: Computation of Bayes Factors for Common Designs. R package v0.9.12. URL: <http://CRAN.R-project.org/package=BayesFactor>.
 Morey, R.D., Rouder, J.N., 2011. Bayes factor approaches for testing interval null hypotheses. *Psychol. Methods* 16, 406.

- Peirce, J., Gray, J.R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., Kastman, E., Lindeløv, J.K., 2019. PsychoPy2: experiments in behavior made easy. *Behav. Res. Methods* 51, 195–203. doi:[10.3758/s13428-018-01193-y](https://doi.org/10.3758/s13428-018-01193-y).
- Proklova, D., Goodale, M.A., 2022. The role of animal faces in the animate-inanimate distinction in the ventral temporal cortex. *Neuropsychologia* 169, 108192. doi:[10.1016/j.neuropsychologia.2022.108192](https://doi.org/10.1016/j.neuropsychologia.2022.108192).
- Proklova, D., Kaiser, D., Peelen, M.V., 2019. MEG sensor patterns reflect perceptual but not categorical similarity of animate and inanimate objects. *Neuroimage* 193, 167–177. doi:[10.1016/j.neuroimage.2019.03.028](https://doi.org/10.1016/j.neuroimage.2019.03.028).
- Proklova, D., Kaiser, D., Peelen, M.V., 2016. Disentangling representations of object shape and object category in human visual cortex: the animate-inanimate distinction. *J. Cogn. Neurosci.* 1–13. doi:[10.1162/jocn_a_00924](https://doi.org/10.1162/jocn_a_00924).
- Puce, A., Allison, T., Gore, J.C., McCarthy, G., 1995. Face-sensitive regions in human extrastriate cortex studied by functional MRI. *J. Neurophysiol.* 74, 1192–1199. doi:[10.1152/jn.1995.74.3.1192](https://doi.org/10.1152/jn.1995.74.3.1192).
- Quek, G.L., Peelen, M.V., 2020. Contextual and spatial associations between objects interactively modulate visual processing. *Cereb. Cortex* 30, 6391–6404. doi:[10.1093/cercor/bhaa197](https://doi.org/10.1093/cercor/bhaa197).
- Ritchie, J.B., Zeman, A.A., Bosmans, J., Sun, S., Verhaegen, K., op de Beeck, H.P., 2021. Untangling the animacy organization of occipitotemporal cortex. *J. Neurosci.* 41, 7103–7119. doi:[10.1523/JNEUROSCI.2628-20.2021](https://doi.org/10.1523/JNEUROSCI.2628-20.2021).
- Rouder, J.N., Speckman, P.L., Sun, D., Morey, R.D., Iverson, G., 2009a. Bayesian t tests for accepting and rejecting the null hypothesis. *Psychon. Bull. Rev.* 16, 225–237.
- Rouder, J.N., Speckman, P.L., Sun, D., Morey, R.D., Iverson, G., 2009b. Bayesian t tests for accepting and rejecting the null hypothesis. *Psychon. Bull. Rev.* 16, 225–237.
- Sha, L., Haxby, J.V., Abdi, H., Guntupalli, J.S., Oosterhof, N.N., Halchenko, Y.O., Connolly, A.C., 2015. The animacy continuum in the human ventral vision pathway. *J. Cogn. Neurosci.* 27, 665–678. doi:[10.1162/jocn_a_00733](https://doi.org/10.1162/jocn_a_00733).
- Shatek, S.M., Robinson, A.K., Grootswagers, T., Carlson, T.A., 2021. Capacity for movement is an organisational principle in object representations. *PsyArXiv*, 3x2qh. doi:[10.31234/osf.io/3x2qh](https://doi.org/10.31234/osf.io/3x2qh).
- Teichmann, L., Moerel, D., Baker, C., Grootswagers, T., 2022. An empirically-driven guide on using Bayes factors for M/EEG decoding. *Aperture Neuro* 1, 1–10. <https://www.doi.org/10.52294/82179f90-eeb9-4933-adbe-c2a454577289>.
- Thorat, S., Proklova, D., Peelen, M.V., 2019. The nature of the animacy organization in human ventral temporal cortex. *eLife* 8, e47142. doi:[10.7554/eLife.47142](https://doi.org/10.7554/eLife.47142).
- Wagenmakers, E.J., 2007. A practical solution to the pervasive problems of p values. *Psychon. Bull. Rev.* 14, 779–804. doi:[10.3758/BF03194105](https://doi.org/10.3758/BF03194105).
- Wetzels, R., Matzke, D., Lee, M.D., Rouder, J.N., Iverson, G.J., Wagenmakers, E.J., 2011. Statistical evidence in experimental psychology: an empirical comparison using 855 t tests. *Perspect. Psychol. Sci.* 6, 291–298. doi:[10.1177/1745691611406923](https://doi.org/10.1177/1745691611406923).