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#### 1

### Decoding face recognition abilities in the human brain

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### 18 Significance

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The ability to robustly recognise faces is crucial to our success as social beings. Yet, we still 20 know very little about the brain mechanisms allowing some individuals to excel at face 21 recognition. This study builds on a sizeable neural dataset measuring the brain activity of 22 individuals with extraordinary face recognition abilities-super-recognisers-to tackle this 23 challenge. Using state-of-the-art computational methods, we show robust prediction of face 24 recognition abilities in single individuals from a mere second of brain activity, and reveal 25 specific brain computations supporting individual differences in face recognition ability. Doing 26 so, we provide direct empirical evidence for an association between semantic computations 27 28 and face recognition abilities in the human brain-a key component of prominent face recognition models. 29

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## 31 Abstract

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Why are some individuals better at recognising faces? Uncovering the neural mechanisms supporting face recognition ability has proven elusive. To tackle this challenge, we used a multi-modal data-driven approach combining neuroimaging, computational modelling, and behavioural tests. We recorded the high-density electroencephalographic brain activity of individuals with extraordinary face recognition abilities—super-recognisers—and typical recognisers in response to diverse visual stimuli. Using multivariate pattern analyses, we

decoded face recognition abilities from 1 second of brain activity with up to 80% accuracy. To 1 2 better understand the mechanisms subtending this decoding, we compared representations in 3 the brains of our participants with those in artificial neural network models of vision and 4 semantics, as well as with those involved in human judgments of shape and meaning similarity. Compared to typical recognisers, we found stronger associations between early 5 6 brain representations of super-recognisers and mid-level representations of vision models as 7 well as shape similarity judgments. Moreover, we found stronger associations between late 8 brain representations of super-recognisers and representations of the artificial semantic model as well as meaning similarity judgments. Overall, these results indicate that important 9 individual variations in brain processing, including neural computations extending beyond 10 11 purely visual processes, support differences in face recognition abilities. They provide the first empirical evidence for an association between semantic computations and face recognition 12 abilities. We believe that such multi-modal data-driven approaches will likely play a critical role 13 in further revealing the complex nature of idiosyncratic face recognition in the human brain. 14

#### 15

#### 16 Introduction

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The ability to robustly recognise the faces of our colleagues, friends and family members is 18 paramount to our success as social beings. Our brains complete this feat with apparent ease 19 and speed, in a series of computations unfolding within tens of milliseconds in a wide brain 20 network comprising the inferior occipital gyrus, the fusiform gyrus, the superior temporal 21 22 sulcus, and more anterior areas such as the anterior temporal lobe (1-3). Accumulating neuropsychological and behavioural evidence indicates that not all individuals, however, are 23 equally competent at recognising faces in their surroundings (4). Developmental 24 prosopagnosics show a great difficulty at this task despite an absence of brain injury (5). In 25 26 contrast, super-recognisers exhibit remarkable abilities for processing facial identity, and can recognize individuals even after little exposure several years before (6-8). The specific nature 27 of the neural processes responsible for these individual differences remains largely unknown. 28 29 So far, individual differences studies have used univariate techniques to investigate facespecific aspects of brain processing. This revealed that contrasts between responses to faces 30 compared to non-faces, measured by the N170 event-related potential component or by the 31 blood oxygen level dependent signals in regions of interest, are modulated by ability (9-15). 32 33 However, univariate and contrast approaches are limited in their capacity to reveal the precise 34 nature of the underlying brain computations (16–19).

Here, we tackled this challenge with a data-driven approach. We examined the functional differences between the brains of super-recognisers and typical recognisers using decoding and representational similarity analyses (RSA; (18, 20–23)) applied to high-density electrophysiological (EEG) signals and artificial neural network models. We recruited 33 participants, including 16 super-recognisers, i.e., individuals better than the 98th percentile on a battery of face recognition tests (8); **Fig. 1a**). We measured EEG in more than 100,000 trials while participants performed a one-back task. The objects depicted in the stimuli belonged to 1 multiple visual categories including face images of different sexes, emotions, and identities, as

- 2 well as images of man-made and non-face natural objects (e.g., a computer, a plant), animals
- 3 (e.g., a giraffe, a monkey), and scenes (e.g., a city, a dining room; **Fig. 1b**).
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- 5

#### Results

#### 6 Behavioural results

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8 All participants' face recognition ability was assessed using the Cambridge Face Memory Test long-form (CFMT+, (8). Scores on the CFMT+ ranged from 50 to 85 in the typical recognisers 9 group (MTRs=70.00; SD=9.09), and from 92 to 100 in the experimental super-recogniser group 10 (Msrs=95.38, SD=2.68; difference between groups : t(31)=10.6958, p<.00001 see Fig. 1a). 11 The main experimental task was a one-back task (Fig. 1b). Accuracy was significantly greater 12 for the super-recognisers (MsRs=.8649, SD=.0626) than for the typical recognisers 13 (MTRs=.7591, SD=.096; t(30)=3.6131, p=.0011). This was also true when analysing separately 14 face (Msrs= .8677, SD=.0590; Mrrs=.7385, SD=.1048; t(30)=4.2180, p=.00020) and non-face 15 trials (Msrs=.8619, SD=.0750; Mrrs=.7798, SD=.1000; t(30)=2.6000, p=.0143). Furthermore, 16 accuracy in the one-back task was positively correlated with scores on the CFMT+ (r=.68, 17 p<.001; RT was marginally associated with CFMT+, r=.37, p=.04). We observed a significant 18 difference in response times between the two groups for face stimuli (MsRs=0.6222 ms, 19 20 SD=.1386 ms; MTRs= 0.6817 ms, SD=.0660 ms; p = 0.0258) but not for non-face stimuli  $(M_{SRs}=0.6262 \text{ ms}, \text{SD}=.1401 \text{ ms}; M_{TRs}=0.6739 \text{ ms}, \text{SD}=.0643 \text{ ms}; p = .0801).$ 21

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## Discriminating super-recognisers and typical recognisers from 1 second of brain activity

With this sizable and category-rich dataset, we first attempted to classify a participant as either 25 26 a super- or a typical recogniser based solely on their brain activity. More specifically, we trained Fisher linear discriminants to predict group membership from single, 1-second trials of 27 EEG patterns (in a moving searchlight of five neighbouring electrodes; Fig. 2b). We observed 28 up to ~80% cross-validated decoding performance, peaking over electrodes in the right 29 hemisphere. This performance is impressive given that the noise ceiling imposed on our 30 classification by the test-retest reliability of the CFMT+ (8, 24), the gold-standard test used to 31 identify super-recogniser individuals, is ~93% (SD=2.28%; see Supplementary material). To 32 reveal the time course of these functional differences, we applied the same decoding 33 procedure to each 4-ms interval of EEG recordings. Group-membership predictions attained 34 35 statistical significance (p<.001, permutation tests, Fig. 2a) from about 65 ms to at least 1 s 36 after stimulus onset, peaking around 135 ms, within the N170 window (25, 26).

Notably, similar results were obtained following the presentation of both face *and* nonface visual stimuli (**Fig. 2a**; **see also Figure S1**). This did not result from face representations stored in short-term memory from one-back trials. Indeed, we repeated our decoding analysis for non-face trials either preceded by face trials or by non-face trials, and found significant

decoding of group membership in both cases (Figure S1). In addition, we successfully cross-1 2 decoded group membership from a model trained on face EEG activity and applied to non-face EEG activity (see Figure S2). The decoding of group-membership could be based on various 3 4 features. Some of these features are directly related to brain representations for object and face recognition, and these aspects are further explored in subsequent sections of this article. 5 6 On the other hand, there could be additional contributing features that are not directly linked to 7 object and face recognition. For instance, differences in motor responses between the two 8 subject groups might explain these results to some extent. However, excluding the 10% of trials with a motor response did not affect decoding accuracy (Figure S2). Additionally, the 9 decoding model might have relied on potential noise differences between the two subject 10 11 groups. Nevertheless, our analysis did not reveal any evidence supporting such differences in the cross-participant similarity of the Representational Dissimilarity Matrices (RDMs) for both 12 groups (see section Linking neural representations with computational models of vision; 13 Figure S3). 14

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#### 16 Predicting individual recognition ability from 1 second of brain activity

An ongoing debate in individual differences research is whether the observed effects emerge from qualitative or quantitative changes in the supporting brain mechanisms (27–35). The decoding results presented up to this point might give the impression that face recognition ability is supported by qualitative differences in brain mechanisms. However, these results were obtained with dichotomous classification models applied, by design, to the brains of individuals from a bimodal distribution of ability scores (e.g. (32).

- To better assess the nature of the relationship between neural representations and ability in 23 the general population, we thus performed a new decoding analysis on the typical recognisers 24 25 only, using a continuous regression model. Specifically, we used cross-validated fractional ridge regression (36) to predict individual CFMT+ face recognition ability scores from single-26 trial EEG data. This showed essentially similar results to the previous dichotomic decoding 27 results: performance was above statistical threshold (p<.01, FDR-corrected) from about 80 ms 28 29 to at least 1 s, peaking around 135 ms following stimulus onset for both face and non-face stimuli (Fig. 2c, peak-rhoface=.4149 at 133 ms, peak-rhonon-face=.4899 at 141 ms). This accurate 30 decoding of individual scores from EEG patterns is compatible with a quantitative account of 31 variations in brain mechanisms across individuals differing in face recognition abilities. 32 33 Altogether, these decoding results provide evidence for important, quantitative and temporally 34 extended variations in the brain activity supporting face recognition abilities. This extended decoding suggests effects of individual ability across multiple successive processing stages. 35
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#### 37 Linking neural representations with computational models of vision

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Decoding time courses, however, offer limited insights on the level of brain computations (37,
38). To better characterise the visual brain computations covarying with face recognition
ability, we compared, using representational similarity analysis (20–22, 39), the brain

representations of our participants to that of convolutional neural networks (CNNs) trained to
 categorise objects (40–42). These CNNs process visual features of gradually higher
 complexity and abstraction along their layers (42), from low-level (e.g., orientation, edges) to
 high-level features (e.g., objects and object parts).

The brain representations were characterised by computing representational dissimilarity 5 6 matrices (RDMs) for each participant and for each 4-ms time interval. These brain RDMs were 7 derived using the cross-validated decoding performance of a linear discriminant model, where 8 brain activity was decoded for every pair of stimuli at a given time interval (43, 44); see Figure 9 **S4** for the group-average RDMs and time course of key categorical distinctions). The visual model representations were characterised by computing RDMs from the layers of the CNNs, 10 11 using Pearson correlations of the unit activations across all pairs of stimuli. Compared to typical participants, we found that the brain RDMs of super-recognisers showed larger mutual 12 information (45) with the layer RDMs of CNNs that represent mid-level features (e.g., 13 combinations of edges, contour, shape, texture; (42, 46) between 133 and 165 ms (Fig. 3a, 14 p < .05, cluster-test; see also **Figure S5** for similar results with unconstrained analyses; 15 16 supplementary analyses on specific category conditions in the RDMs are shown on Figure **S6**). These results indicate that mid-level representations of an object-trained CNN matched 17 the representations of super-recognisers more closely than those of typical participants. We 18 replicated these results using a face-trained CNN (e.g., (47-49), VGGface (50), which possess 19 20 mid-level representations similar to those of object-trained CNN (see Figure S7; p<.05, cluster-test). The stronger association between brain representational geometries of the super-21 recognisers with computational models of vision could be explained by a marked difference in 22 signal to noise between the two groups of participants. To control for this potential confound, 23 we computed the cross-participant similarity of the RDMs in both groups (see Figure S3). If 24 25 the signal to noise was larger in the super-recognisers, we would expect larger crossparticipant similarity of the RDMs, however, we observed no significant difference between the 26 27 two groups.

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#### 29 Linking neural representations with computational model of semantics

The finding that ability decoding was significant as late as 1 s after stimulus onset hints 31 that brain computations beyond what is typically construed as pure visual processing also 32 33 differ as a function of face recognition ability. To test this hypothesis, we asked five new participants to write captions describing the images presented during our experiment (e.g., "A 34 city seen through a forest."), and used a deep averaging network (Google Universal Sentence 35 Encoder, GUSE; (51) to transform these captions into embeddings (points in a caption space). 36 37 GUSE has been trained to predict semantic textual similarity from human judgments, and its 38 embeddings generalise to an array of other semantic judgement tasks (51). We then compared 39 the RDMs computed from this semantic model to the brain RDMs of both typical- and super-40 recognisers. Importantly, both this comparison, and the one comparing brain and visual models, excluded the information shared between the semantic and visual models (but see 41

Figure S8 for similar results with unconstrained analyses). We found larger mutual information with these semantic representations in the brains of super-recognisers than in those of typical recognisers in a late window between 598 and 727 ms (Fig. 3b, *p*<.05, cluster-test). Supplementary analyses on specific stimulus categories of the RDMs (Figure S9) suggest that these results emerged mainly from the face-vs-face and face-vs-non-face stimuli pair conditions.

## Linking neural representations with behavioural representations for shape and semantic similarity judgements

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Our findings so far suggest that mid-level visual and semantic brain processes both support 11 individual differences in face recognition abilities. We looked for further support for these 12 conclusions using RDMs derived from a behavioural experiment. A group of 32 new human 13 participants were submitted to two multiple arrangement tasks (52-54) in which they were 14 asked to evaluate the shape similarities of all pairs of the 49 visual stimuli used in the main 15 experiment, and the meaning similarities of all pairs of the 49 mean sentence captions 16 17 produced by five human participants to describe these images and used for the semantic model (see section Linking neural representations with computational model of semantics). 18 More specifically, participants arranged the images/sentences inside a white circular arena 19 according to the task instructions using simple drag and drop operations (see Fig. 4). We 20 computed the mutual information between the mean RDMs extracted from each of these tasks 21 22 and the time-resolved brain RDMs of super- and typical recognisers as well as the same while 23 excluding the information shared with the other task. Results indicated only a small trend for shape representations being enhanced around mid-latencies in super-recognisers relative to 24 typical recognisers which did not survive cluster correction (p<.01, uncorrected;  $p_{MI}$  = .1259; 25 26  $p_{CMI} = .2098$ ; cluster-corrected; see Fig. 4). Meaning representations were enhanced in late latencies in super-recognisers compared to typical recognisers (sentence meaning : 635-787 27 ms p < .05, cluster-corrected; see Fig. 4). These results confirm that semantic representations 28 29 at relatively late latencies and, to a lesser degree, shape representations at mid latencies are enhanced in the brains of super-recognisers. 30

#### Discussion

34 Using a data-driven approach combining neuroimaging, computational models, and 35 behavioural tests, we characterised the computations modulated by variations in face recognition ability in the human brain. We recorded high-density electroencephalographic 36 (EEG) responses to face and non-face stimuli in super-recognisers and typical recognisers. 37 Using multivariate analysis, we reliably decoded group membership as well as recognition 38 abilities of single individuals from a single second of brain activity. We then characterised the 39 neural computations underlying these individual differences by comparing human brain activity 40 with representations from artificial neural network models of vision and semantics using 41

representational similarity analysis. Furthermore, we compared the brain activity with similarity 1 2 judgments derived from additional human participants engaged in two tasks. In the first task, 3 participants judged our visual stimuli on the similarity of their shape, while in the second task, participants judged sentence captions describing these stimuli on the similarity of their 4 meaning. These sets of comparisons revealed two main findings. First, we found higher 5 similarity between early brain representations of super-recognisers and mid-level 6 7 representations of vision models as well as, to a lesser degree, shape similarity judgments. 8 Second, this approach revealed higher similarity between late brain representations of superrecognisers and representations of an artificial semantic model as well as sentence caption 9 similarity judgments. To our knowledge, this is the first demonstration of a link between face 10 11 recognition ability and brain computations beyond high-level vision. Overall, these findings revealed specific computations supporting our individual ability to recognise faces, and 12 suggest widespread variations in brain processes related to this crucial ability. 13

We achieved robust decoding of face recognition ability when examining EEG responses to face *and* non-face stimuli. This is consistent with several neuropsychological (30, 55–59) and brain imaging findings (12, 29, 60, 61) showing face and non-face processing effects in individuals across the spectrum of face recognition ability ((19, 62); but see (13, 63–65)).

The decoding we observed for face and non-face stimuli peaked at right occipito-temporal 18 19 electrodes, in the temporal window around the N170 component (25). At that time, the 20 representations in the brains of our participants differed most with respect to the mid-layer representations of artificial models of vision. These layers have been previously linked to 21 processing in human infero-temporal cortex (hIT; (42, 66–68) and functionally to mid-level 22 feature representations such as combinations of edges and parts of objects (42, 46). Such 23 associations with the N170, however, do not mean that this component is exclusively involved 24 in these mid-level processes. Rather, it suggests that other visual computations, including the 25 high-level visual computations usually associated with the N170, do not differ substantially 26 between super-recognisers and typical recognisers. The fact that these mid-level features are 27 mostly shared between face and non-face stimuli could explain at least partly the high 28 29 decoding performance observed for both classes of stimuli. They suggest that a mid-level visual processing is enhanced in SRs leading to improved processing of faces and objects. 30

Crucially, we found that face recognition ability is also associated with semantic computations 31 that extend beyond basic-level visual categorisation in a late time-window around the P600 32 33 component (69–71). Recent studies using computational techniques have shown that word representations derived from models of natural language processing explain significant 34 variance in the visual ventral stream (18, 72–74). The current study goes beyond this recent 35 work in two ways. First, our use of human sentence description and sentence encoders to 36 37 characterise semantic (caption-level) computations provides a more abstract description of 38 brain representations. Second, and most importantly, our work revealed a link between 39 semantic brain computations and individual differences in face recognition ability. An 40 association between semantic processes and face recognition ability had been posited in models of face recognition (1, 75) but, to our knowledge, it had never been shown empirically 41

1 before.

Overall, thus, our findings suggest important differences in perceptual and semantic 2 representations in individuals with outstanding ability to recognise faces. The higher similarity 3 4 with computational models of vision indicate that super-recognisers have more efficient midlevel representations. These enhanced representations suggest that part-based information 5 about faces and objects, putatively emerging from mid-level occipito-temporal regions (76), is 6 7 richer in individuals with strong face recognition abilities (77). Furthermore, our findings show that the more similar the brain representations of an individual are to task-optimised 8 computational models of semantics, the better they are at recognising faces. These enhanced 9 late semantic representations, for example, might emerge from enhanced subordinate-level 10 information about objects and faces (78, 79). 11

- Our approach of decoding group membership to reveal electrophysiological differences 12 between super-recognisers and typical recognisers, followed by representational similarity 13 analysis with computational models of vision and language, enabled revealing potential 14 mechanisms underlying enhanced recognition ability. Other possible differences between our 15 participants might also contribute to our ability to decode their brain signals. Differences in top-16 17 down (i.e. attention) mechanisms, better ability to memorise images more generally, or both, could also lead to enhanced representations. Interestingly, we could decode from both face 18 and nonface categories, and across categories (training with face trials and testing on non-face 19 20 trials) suggesting that the mechanisms subtending the enhanced abilities of super-recognisers
- 21 are not restricted to faces (4), (56).
- Furthermore, while our decoding approach indicates that important differences in brain processing emerge from early (80 ms) to late (~1s) processing windows, our RSA modelling approach only explained part of these processing windows. Specifically, while broad visual (~150 ms), face-specific (~430 ms), and semantic representations (~600 ms) were found to differ in super-recognisers using this computational approach, it still remains to be shown what specific representations are critical in differentiating the best face recognisers during early (<150 ms) and very late (>800 ms) windows of processing.
- In conclusion, our results offer a stepping stone for a better understanding of face recognition 29 idiosyncrasies in the human brain. Indeed, with the development of novel and better artificial 30 models simulating an increasing variety of cognitive processes, and with the technological 31 advances allowing the processing of increasingly larger neuroimaging datasets, the approach 32 described here provides a new and promising way to tackle the link between individual 33 differences in human behaviour and specific computations in the brain. In addition, this 34 decoding approach may provide quick and accurate alternatives to standardised behavioural 35 tests assessing face recognition ability, for example in the context of security settings that 36 benefit from strong face processing skills among their personnel (such as police agencies, 37 border patrol, etc.). It could also be used in a closed-loop training procedure designed to 38 39 improve face recognition ability (80).

## 40 Methods

41 Participants

A total of 33 participants were recruited for this study. The first group consisted of 16
 individuals with exceptional ability in face recognition — super-recognisers. The second group
 was composed of 17 neurotypical controls. These sample sizes were chosen according to the

effect sizes described in previous multivariate object recognition studies (43, 44, 54). The data
from one super-recogniser was excluded due to faulty EEG recordings. No participant had a
history of psychiatric diagnostic or neurological disorder. All had normal or corrected to normal

4 vision. This study was approved by the Ethics and Research Committee of the University of

5 Birmingham, and informed consent was obtained from all participants.

Sixteen previously known super-recognisers were tested in the current study (30-44 years old, 6 10 female). Eight of these (SR1-SR8) were identified by Prof. Josh Davis from the University of 7 Greenwich using an online test battery comprising a total of six face cognition tasks (6) and 8 tested at the University of Birmingham. The remaining eight (SR-9 to SR-16) were identified 9 using three challenging face cognition tests (7) and were tested at the University of Fribourg. 10 The behavioural test scores for all participants are provided in **Tables S1 and S2.** Across SR 11 cohorts, the Cambridge Face Memory Test long-form (CFMT+; (8) was used as the measure 12 of face identity processing ability. A score greater than 90 (i.e., 2 SD above average) is 13 typically considered the threshold for super-recognition (8, 56, 81). Our 16 super-recognisers 14 all scored above 92 (M=95.31; SD=2.68). A score of 92 corresponds to the 99<sup>th</sup> percentile 15 according to our estimation from a group of 332 participants from the general population 16 17 recruited in three independent studies (77, 82, 83).

An additional 17 typical recognisers (20-37 years old, 11 female) were recruited and tested on campus at the University of Fribourg (n=10) and the University of Birmingham (n=7). Their CFMT+ scores ranged from 50 to 85 (M=70.00; SD=9.08). Neither the average nor the distribution of this sample differed significantly from those of the 332 participants from the general population mentioned above (see **Fig. 1a**; t(346)=1.3065, *p*=0.1922; two-sample Kolmogorov-Smirnov test; D(346)=0.2545, *p*=0.2372).

- 24 Tasks
- 25 **CFMT+**

All participants were administered the CFMT long-form, or CFMT+ (8). In the CFMT+, participants are required to memorise a series of face identities, and to subsequently identify the newly learned faces among three faces. It includes a total of 102 trials of increasing difficulty. The duration of this test is about 15 minutes. EEG was not recorded while participants completed this test.

#### 31 One-back task

Stimuli. The stimuli used in this study consisted of 49 images of faces, animals (e.g., giraffe, 32 monkey, puppy), plants, objects (e.g., car, computer monitor, flower, banana), and scenes 33 (e.g., city landscape, kitchen, bedroom). The 24 faces (13 identities, 8 males, and 8 neutral, 8 34 happy, 8 fearful expressions) were sampled from the Radboud Face dataset (84). The main 35 facial features were aligned across faces using Procrustes transformations. Each face image 36 was revealed through an ellipsoid mask that excluded non-facial cues. The non-face images 37 38 were sampled from the stimulus set of Kiani et al. (85). All stimuli were converted to 250 x 250 pixels (8x8 deg of visual angle) greyscale images. The mean luminance and the luminance 39 standard deviation of these stimuli were equalised using the SHINE toolbox (86). 40

**Procedure.** We measured high-density electroencephalographic (EEG; sampling rate = 1024) 1 2 Hz; 128-channel BioSemi ActiveTwo headset) activity while participants performed ~3200 trials of a one-back task in two recording sessions separated by at least one day and by a maximum 3 of two weeks (Fig. 1b). Participants were asked to press a computer keyboard key on trials 4 5 where the current image was identical to the previous one. Repetitions occurred with a 0.1 6 probability. They were asked to respond as quickly and accurately as possible. Feedback was 7 done in the form of a change in colour of the fixation point (red or green) after a repetition trial (which happened on a .1 probability basis). This was done to help participants pay attention 8 during the task. Target trials were not excluded from the analyses. A trial unravelled as follows: 9 a white fixation point was presented on a grey background for 500 ms (with a jitter of  $\pm$  50 ms); 10 followed by a stimulus presented on a grey background for 600 ms; and, finally, by a white 11 12 fixation point on a grey background for 500 ms. Participants had a maximum of 1100 ms following stimulus onset to respond. This interval, as well as the 200 ms preceding stimulus 13 onset, constituted the epoch selected for our EEG analyses. In total, our participants 14 completed 105.600 one-back trials which constituted ~32 hours of EEG epochs. 15

**Shape and sentence meaning multiple arrangements tasks.** Thirty two new neurotypical participants took part in two multiple arrangements tasks (22, 87) in counterbalanced orders. In two of the tasks, they were asked to evaluate the shape or function similarities of the 49 stimuli used in the main experiment while, in the other task, they were instructed to judge the meaning similarities of sentence captions describing these stimuli (see Semantic Caption-level Deep Averaging Neural Network RDM for more information about these sentence captions).

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More specifically, participants were asked to arrange stimuli or sentence captions on a 23 computer screen inside a white circular arena by using computer mouse drag and drop 24 operations. During the shape/function (vs. meaning) multiple arrangement task, they were 25 instructed to place the displayed visual stimuli (vs. sentence captions) in such a way that their 26 27 pairwise distances match their shape/function (vs. meaning) similarities as much as possible (Fig. 4). On the first trial of each task, participants arranged all 49 items. On subsequent trials, 28 a subset of these items was selected based on an adaptive procedure aimed at minimising 29 30 uncertainty for all possible pairs of items (e.g. items that initially were placed very close to each other) and at better approximating the high-dimensional perceptual representational space 31 (87). This procedure was repeated until the task timed out (20 min). 32 33

We computed one RDM per task per participant. Three participants were excluded from the final sample because their RDMs differed from the mean RDMs by more than two standard deviations. Finally, we averaged the remaining individual RDMs within each task.

## 37 Analyses

All reported analyses were performed independently for each EEG recording session and then
 averaged. Analyses were completed using custom code written in MATLAB (MathWorks) and
 Python.

## 41 EEG preprocessing

42 EEG data was preprocessed using FieldTrip (88): continuous raw data was first re-referenced

1 relative to Cz, filtered with a band-pass filter [0.01-80 Hz], segmented into trial epochs from -

2 200 ms to 1100 ms relative to stimulus onset, and down-sampled at 256 Hz.

#### 3 Decoding analyses

4 Whole-brain analyses. To predict group-membership from EEG brain activity, we trained 5 Fisher linear discriminant classifiers to predict participants' group membership based on raw EEG topographies, using all 128 channels of single-trial EEG data as features. Notably, here, 6 the decoding is made on an *across-participants* basis. This was done across all trials of either 7 face or non-face condition, for each of the two sessions separately (~26,000 observations per 8 condition, per session, 5-fold cross-validation, 5 repetitions; (89, 90). The number of trials were 9 matched across participants. This process was repeated over all EEG time samples 10 separately, starting from -200 ms and ending 1100 ms after stimulus onset, creating decoding 11 accuracy time courses. The Area Under the Curve (AUC) was used to assess sensitivity. 12 Decoding time courses were averaged across the two EEG sessions. The resulting evidence 13 indicates when super-recognisers can be categorised from brain activity when processing 14 15 faces (blue) and non-face stimuli (grey), as shown in Figure 2a. Additional control decoding analyses investigating effects of one-back trials on the predictions are shown in Figure S1. 16 These trials required that our participant compared their representations of the presented 17 image and the one stored in short-term memory. This showed similar findings, with one 18 notable difference being that the face-face discrimination condition was the one that obtained 19 20 peak decoding accuracy.

Searchlight analysis. We conducted a searchlight analysis decoding EEG signals from all subsets of five neighbouring channels to characterise the scalp topographies of group-membership AUC. This searchlight analysis was done either using the entire EEG time series of a trial (0-1100 ms; Fig. 2b, leftmost topographies), or using 60 ms temporal windows (centred on 135 ms, 350 ms, 560 ms, and 775 ms; Fig. 2b rightmost topographies). We ran additional control searchlight decoding procedures investigating the effect of one-back trials (Figure S1).

Regression analysis. We used fractional ridge regression models (36) to predict individual 28 29 face recognition ability scores (CFMT+) among the typical recognisers from EEG patterns across time. We trained our model on subsets of 60% of the EEG patterns. We chose the 30 alpha hyperparameter with the best coefficient of determination among 20 alpha 31 32 hyperparameters ranging linearly from 0.001 to 0.99 applied on a 30% validation set. The decoding performance was assessed using the Spearman correlation between the CFMT+ 33 scores and predictions from the overall best model (applied on the remaining 10% of EEG 34 patterns). This process was repeated 10 times and the Spearman correlations were averaged. 35 Significance was assessed using a permutation test (see Group comparisons and inferential 36 statistics section). 37

#### 38 Representational Similarity Analysis of brain and computational models

We compared our participants' brain representations to those from visual and semantic (caption-level) artificial neural networks using Representational Similarity Analysis (RSA; (20– 22, 39). **Brain Representational Dissimilarity Matrices.** For every participant, we trained a Fisher linear discriminant to distinguish pairs of stimuli from every 4-ms intervals of EEG response (on all 128 channels) to these stimuli from -200 to 1100 ms after stimulus onset (91, 92). Crossvalidated AUC served as pairwise classification dissimilarity metric. By repeating this process for all possible pairs (1176 for our 49 stimuli), we obtained a representational dissimilarity matrix (RDM). RDMs are shown for selected time points in **Figure S4**.

Visual Convolutional Neural Networks RDMs. We used a pre-trained AlexNet (40) as one 8 model of the visual computations along the ventral stream (42). Our 49 stimuli were input to 9 AlexNet. Layer-wise RDMs were constructed comparing the unit activation patterns for each 10 pair of images using Pearson correlations. Similarly, we computed laver-wise RDMs from 11 12 another well-known CNN, VGG-16 (see Figure S5). Following previous studies using this model (93, 94), we averaged the convolutional layer RDMs situated between each max pooling 13 layers and the layers' input into five aggregated convolutional RDMs (e.g. conv1-1 & conv1-2 14 into RDM-conv1); this facilitated the comparison of our results with the five convolutional layers 15 16 of AlexNet.

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Semantic Caption-level Deep Averaging Neural Network RDM. We asked five new 18 participants to provide a sentence caption describing each stimulus (e.g., "a city seen from the 19 other side of the forest", see Fig. 1d) using the Meadows online platform (www.meadows-20 21 research.com). The sentence captions were input in Google's universal sentence encoder (GUSE; (51) resulting in 512 dimensional sentence embeddings for each stimulus. We then 22 computed the dissimilarities (cosine distances) between the sentence embeddings across all 23 pairs of captions, resulting in a semantic caption-level RDM for each participant. The average 24 25 RDM was used for further analyses.

- 26 Comparing brain representations with computational models
- 27

We compared our participants' brain RDMs to those from the vision (Fig. 3a) and semantic (Fig. 3b) models described in the previous section using Conditional Mutual Information (45), which measures the statistical dependence between two variables (e.g. mutual information l(x;y)), removing the effect from a third variable (i.e. l(x;y|z)). Additional comparisons using unconstrained Mutual Information between brain RDMs and both models are shown in **Figure S5 and S8.** 

- 34 Group comparison and inferential statistics
- 35

Comparison of Conditional Mutual Information time courses. Time courses of CMI were 36 compared between the super-recognisers and typical recognisers using independent samples 37 t-tests and a Monte Carlo procedure at a *p-value* of .05, as implemented in the Fieldtrip 38 Toolbox (88). Family-wise errors were controlled for using cluster-based corrections, with 39 maximum cluster size as cluster-level statistic and an arbitrary t threshold for cluster statistic of 40 [-1.96, 1.96] for the comparison of brain and semantic (excluding CNN) and for the comparison 41 of brain and CNN (excluding semantic) time courses. The standard error is shown for all 42 curves as colour-shaded areas (Fig. 3). Analyses with MI (brain; CNN) and MI (brain; 43 semantic) were completed in an identical manner. 44

**Time course of group-membership decoding.** Significance was assessed using nonparametric permutation tests. We simulated the null hypothesis by training the linear classifier to identify shuffled group-membership labels from the experimental EEG patterns. This process was repeated 1000 times for each time point and each one of the two sessions. We then compared the real, experimental decoding value at each time point to its corresponding null distribution, and rejected the null hypothesis if the decoding value was greater than the prescribed critical value at a p < .001 level.

8

9 Time course of individual ability decoding using ridge regression. Significance was again assessed using non-parametric permutation testing. The ridge regression analysis predicted 10 cross-validated CFMT+ scores from single trial EEG patterns, and goodness of fit is reported 11 12 using Spearman's correlation between the predicted and observed CFMT+ scores. Under the null hypothesis that all participants elicited comparable EEG response patterns, irrespective of 13 their CFMT+ score, the face recognition ability scores are exchangeable. We simulated this 14 null hypothesis by repeating the ridge regression model training using randomly shuffled 15 CFMT+ scores. The predicted CFMT+ scores were then correlated to the empirical, observed 16 CFMT+ scores using Spearman's correlation, and this was repeated 1000 times for each time 17 point. We finally compared the real, experimental correlation value with its corresponding null 18 distribution at each time point, and rejected the null hypothesis if the correlation value was 19 greater than the prescribed critical value at a p < .01 level. 20

21

## 22 Data availability

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High-density EEG data associated with this article is available on The Open Science Framework (<u>https://osf.io/pky28/</u>).

#### 26

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28

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## 41 Author contributions

#### 42 (CRediT standardised author statement)

S.F-S.: Conceptualisation, methodology, software, formal analysis, investigation, data curation,
 writing - original draft, visualisation, supervision, project administration, funding acquisition.
 M.R.: Investigation, resources, project administration, writing - review and editing. E.B.:

investigation, project administration. M.Z.: investigation. J.W.: funding acquisition, writing review and editing. A-R.R.: Investigation. R.C.: Resources. F.G.: Methodology, writing original draft, supervision, funding acquisition. I.C.: Supervision, methodology, software,
resources, formal analysis, writing - original draft, project administration, funding acquisition.

5

## 6 Competing interests

7

8 The authors declare no competing interests.

9

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- 2627 Figure captions
- 28

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- Figure 1. Experimental procedure. a) The histogram shows the Cambridge Face Memory Test longform (CFMT+, (8)) scores of super-recognisers (yellow bars), typical recognisers (black bars), and an additional 332 neurotypical observers from three independent studies for comparison (77, 82, 83). b) Participants engaged in a one-back task while their brain activity was recorded with high-density electroencephalography. The objects depicted in the stimuli belonged to various categories, such as faces, objects, and scenes. Note that the face drawings shown here are an anonymised substitute to the experimental face stimuli presented to our participants.
- Figure 2. Decoding interindividual recognition ability variations from EEG activity. a) Trial-by-trial group-membership predictions (super-recogniser or typical recogniser) were computed from EEG

patterns, for each 4-ms interval, while participants processed face (blue trace) or non-face stimuli (grey 1 2 trace). Significant decoding performance occurred as early as 65 ms, peaked in the N170 window, and 3 lasted for the remainder of the EEG epochs (p<.001). **b**) Topographies were obtained using searchlight 4 decoding analyses, either concatenating all time points (left topographies) or for selected time-windows 5 (right topographies). Concatenating all time points resulted in peak classification performance of 77.3% 6 over right occipito-temporal electrodes for face and 77.5% over right occipito-temporal electrodes for 7 non-face conditions. In the N170 window, we observed a peak classification performance of 74.8% over 8 right-temporal electrodes for face, and 72.1% over left-temporal electrodes for non-face conditions. c) 9 We decoded the CFMT+ scores of the typical recognisers using fractional ridge regression. This 10 yielded similar results with significant decoding as early as 75 ms, peaking around the N170 time window (peak-rhorace=.4149, peak-rhonon-face=.4899), and lasted for the remainder of the EEG epochs 11 12 (p<.01, 1K permutations, 10 repetitions).

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Figure 3. Comparison of super- and typical-recogniser brain representations with those of 14 artificial neural networks of visual and semantic processing. a) Representational dissimilarity 15 matrices (RDM) were computed from convolutional neural networks (CNN; (40, 41) of vision, human 16 brain activity, and a deep neural network of caption classification and sentence semantics (51). To 17 18 characterise the CNN RDMs, we computed the pairwise similarity between unit activation patterns for each image independently in each CNN layer. The caption-level RDMs were derived from human 19 20 caption descriptions of the images transformed into sentence embeddings. Brain RDMs were computed using cross-validated decoding performance between the EEG topographies from each pair of stimuli at 21 22 every 4 ms time-point. Mutual information (45) between the model RDMs and the brain RDMs was 23 assessed, for every participant, at each 4 ms step from stimulus onset. b) Mutual information between brain RDMs and AlexNet RDMs (removing shared mutual information between brain and semantic 24 25 model) is shown for typical- (grey solid curve) and super-recognisers (pink solid curve). We found 26 greater similarity with mid-level visual representations (layer 4 and 5 shown, but similar results were found for mid-layers of VGG16, another popular CNN model; see Figure S5) in the brains of super-27 28 recognisers (black line indicates significant contrasts, p<.05, cluster-corrected) between 133 ms and 29 165 ms. Similar results were observed when comparing brains and CNN models without removing the shared mutual information between brains and the semantic (caption-level) model (Figure S5). c) 30 Mutual Information with the semantic model (excluding shared mutual information between brain and 31 AlexNet) differed for typical- and super-recognisers in a later time window centred around 650 ms (cyan 32 curve; super > typical, p < .05, cluster-corrected). Again, similar results were observed when comparing 33 34 brains and the semantic model without removing the shared mutual information between the brain and CNN model (see Figure S8). 35

Figure 4. Linking neural representations with behavioural representations for shape, function, 36 37 and semantic similarity judgements. a) Mutual information between brain RDMs and the mean RDM built from shape similarity judgements (first column) and sentence meaning similarity judgements 38 39 (second column) is shown for typical- (grey curves) and super-recognisers (coloured curves). Greater similarity with shape information in the brains of super-recognisers (p<.01, uncorrected; p-corrected<sub>M</sub> = 40 41 .1259) and greater similarity with sentence meaning information for super-recognisers (p<.01, 42 uncorrected; p-corrected<sub>M</sub> = 0.0819) only reached significance before cluster corrections. The shaded areas of all curves represent the standard error. b) Conditional Mutual information between brain RDMs 43 and the mean RDM built from similarity judgements of shape & of sentence captions meaning 44 (removing shared mutual information between brain and sentence caption meaning RDM for shape 45 46 similarity, and vice versa) is shown in typical- and super-recognisers. We found greater similarity with 47 sentence meaning in the brains of super-recognisers between 635 ms and 787 ms (black line indicates 48 significant contrasts, p<.05, cluster-corrected), in agreement with our comparisons with the artificial 1 semantic model (fig. 3b). Greater similarity with shape information in the brains of super-recognisers

2 only reached significance before cluster corrections (p<01, uncorrected; pcorrected\_cm = .2098).









