

LETTERS

Norm-based face encoding by single neurons in the monkey inferotemporal cortex

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The rich and immediate perception of a familiar face, including its identity, expression and even intent, is one of the most impressive shared faculties of human and non-human primate brains. Many visually responsive neurons in the inferotemporal cortex of macaque monkeys respond selectively to faces^{1–4}, sometimes to only one or a few individuals^{5–7}, while showing little sensitivity to scale and other details of the retinal image^{8,9}. Here we show that face-responsive neurons in the macaque monkey anterior inferotemporal cortex are tuned to a fundamental dimension of face perception. Using a norm-based caricaturization framework previously developed for human psychophysics^{10–12}, we varied the identity information present in photo-realistic human faces¹³, and found that neurons of the anterior inferotemporal cortex were most often tuned around the average, identity-ambiguous face. These observations are consistent with face-selective responses in this area being shaped by a figural comparison, reflecting structural differences between an incoming face and an internal reference or norm. As such, these findings link the tuning of neurons in the inferotemporal cortex to psychological models of face identity perception.

Previous work showing that face recognition benefits from caricaturization—that is, the exaggeration of distinguishing features^{10,14–16}—has led to the conceptualization of a multidimensional ‘face space’ (see cartoon in Fig. 1a), within which each point represents an individual face and the average of all faces resides at the centre¹⁷. We focused on stimuli along four face-space trajectories branching away from the average face (sometimes termed the ‘norm’ or ‘prototype’ face) towards increasing identity levels. This radial axis, sometimes termed an axis of caricaturization or identity trajectory, has been studied extensively, and is thought to play an important role in face perception^{10–12,18,19}. Also shown are faces separated tangentially, morphed directly between faces of different identities. The construction of photo-realistic faces along radial and tangential trajectories in a face space were generated with a ‘morphable face model’, which interpolates between three-dimensional laser scans of human heads¹³. A recent study using these stimuli found that equal increments along the caricaturization axes in a face space defined by such a morphable model translated directly to equal perceptual increments¹². These data are shown for humans in Fig. 1b, and are compared directly to similar data from one of the monkeys used in this study (N97). This monkey recognized human faces in a manner similar to human subjects (albeit with a slightly diminished performance), and experienced a face-identity after-effect in the same way as human subjects²⁰ (see also Supplementary Fig. 2).

To test whether the psychological representation of the caricaturization axes was reflected in the firing of single neurons in the

inferotemporal cortex, we performed extracellular microelectrode recordings in two monkeys (see Methods) that were presented with a large number of faces corresponding to different positions in face space. The faces were presented in a pseudorandom sequence. The microelectrodes were situated in the anterior inferotemporal cortex (AIT) region (see Supplementary Fig. 3), an area known to contain neurons that respond selectively to face and other complex patterns. Each day, the monkey was presented with faces from four different axes of caricaturization, corresponding to four different individuals. Different sets of faces were used for the two monkeys. One of the animals, C99, was additionally tested with faces modulated along tangential directions of face space (see dotted line in Fig. 1a), corresponding to morphs between different face identities. A total of 250 face-responsive units were monitored, with 209 tested with a complete set of faces for our evaluation. Despite several differences in the training and testing, and in the electrophysiological procedures (see Methods), the results were similar in both animals.

The main finding was a striking tendency for neurons to show tuning that appeared centred about the average face. For a large proportion of neurons, this entailed monotonic trends in firing for

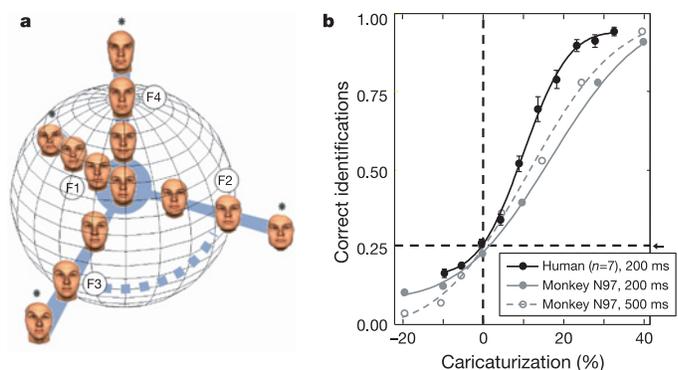


Figure 1 | Face space and behavioural data. **a**, Each identity trajectory (F1–F4) intersects in the centre, at the average face (0% identity). Identity levels change from the average through to the full identity (100%) faces, to the caricatures (160% shown, asterisks). Other face identities in this study (for example, between F2 and F3, dotted blue line), lay on the tangential trajectories. **b**, Behavioural performance of monkey N97 in the recognition task, shown for two different face presentation durations and compared to seven humans (mean \pm s.e.m.) performing the same task (with 500-ms presentations). Chance performance for correctly recognizing a face out of four learned identities was 0.25 (horizontal dashed line). Vertical dashed line corresponds to zero identity level.

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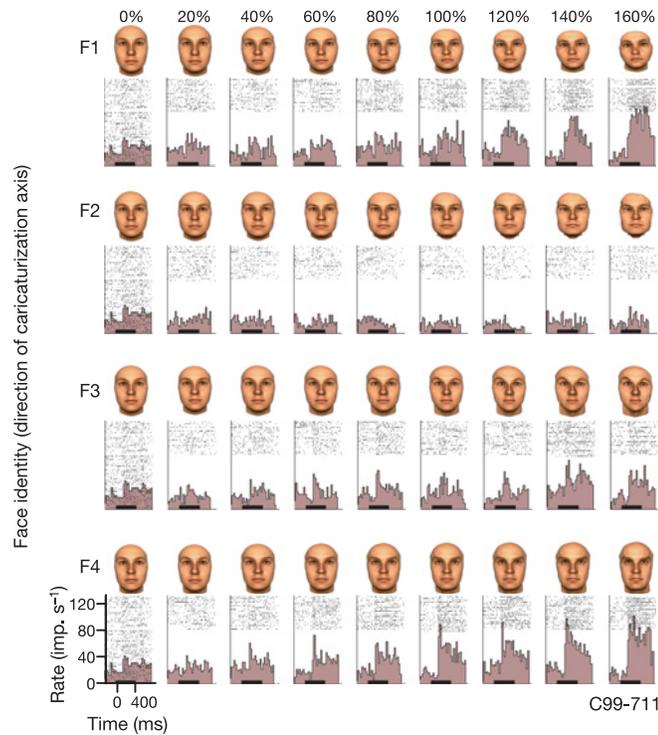


Figure 2 | Responses of a single neuron (C99-117) to faces along axes of caricaturization. Each panel corresponds to the rasters and peristimulus time histogram in response to a 400-ms presentation of the face stimulus (dark bar); see panel at bottom left for axis information (imp., impulse). Rows represent each radial axis in face space for faces F1–F4, from the average face (left, identical in all cases) through to the full identity face (100%), to the caricatures (right).

increasing levels of caricaturization, for two or more of the face trajectories. The example in Fig. 2 shows a typical result, for four faces modulated at nine caricaturization values ranging from 0% (average face) through to 100% (full identity) and up to 160% (caricature). This neuron, like many we observed, showed a roughly linear increase in the discharge of action potentials as a function of face identity. It was able to reliably discriminate between extremely subtle differences in the successive faces along the radial dimension, even for identity levels well above the recognition threshold suggested by the behavioural data. Additional examples are represented in a more succinct form in Fig. 3, as coloured spheres emanating from a central sphere (the average face), with the geometry illustrated in Fig. 1a. More traditional tuning curves for a large number of individual neuron examples for both monkeys are provided in Supplementary Figs 4 and 5, further demonstrating the apparently special role of the average face in the firing of AIT neurons. Interestingly, neurons with extreme near-linear tuning appeared to be clustered²¹, and were typically encountered within the same recording session. The examples in Fig. 3a are the responses of four neurons collected from four different electrodes within an estimated 250 μm of each other in the same session.

Across the population, each of the four face identities elicited similar, near-linear changes in response magnitude as a function of caricaturization level for both monkeys (Fig. 4a). We next asked for how many of the four identities, on average, did the neurons show monotonic trends with the identity level, and whether or not these trends had a tendency to go in the same direction. To address this question, we first rank-ordered the responses to the four identities for each neuron, and then computed the average normalized rank-ordered profile (Fig. 4b). The results show that, on average, between two and three of the four faces showed significant monotonic activity changes in the same direction with increasing identity levels. Note

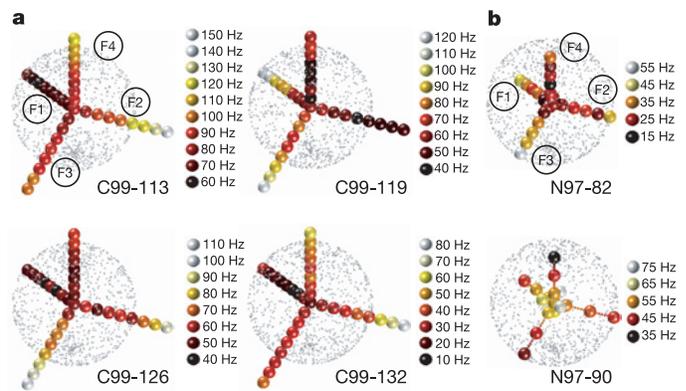


Figure 3 | Response magnitudes for different caricaturization levels of all four faces. Each tetrahedron corresponds to the responses of a single AIT neuron for monkey C99 (a) and N97 (b). Labels below (for example, C99-113) are identifiers for each neuron from monkey C99 and N97. Each sphere comprising the tetrahedra is coloured according to the neuron's mean spike rate following 8–12 presentations of the face at that caricaturization level. The four neurons in a were collected on nearby electrodes during the same session.

that in the case of monkey N97, which was presented a negative caricaturization level (–10%), there is a response minimum at the average face, revealing that both positive and negative deviations from the average face in either direction leads, at the population level, to increased responses. Systematic trends in the data were not observed when the data sets were randomly reordered (see Supplementary Fig. 6).

Finally, in monkey C99, we presented faces along tangential directions in face space, corresponding to morphs between different facial identities. Several representative examples of responses to both radial and tangential morphs are shown in Fig. 5a, in the same representation as in Fig. 3. These examples illustrate the diversity of tuning we observed along the tangential direction, and further show the tendency towards monotonic trends in the radial (caricaturization) axes. In addition, traditional tuning curves along the tangential direction, between all combinations of face identities, are shown for four examples in Supplementary Fig. 7, which demonstrates the high variability in the population. The overall tangential tuning, averaged for the entire population of 87 neurons, is shown in Fig. 5b. Note that the data panels are sorted in order, from the face that gave the lowest response (R1) to that which gave the highest response (R4). The population responses reveal that the tuning was, on average, also largely monotonic between faces. All these monotonic trends were significant, and were no longer present after reshuffling (Supplementary Fig. 8).

These findings, taken together, demonstrate that the axis of caricaturization, known to be a meaningful perceptual dimension in face recognition, is also a primary determinant of the firing of face-selective neurons in the inferotemporal cortex. The special role of the average face in shaping the tuning of neurons in this area may reflect the brain's plasticity in capturing the natural variation in facial characteristics. Considerable electrophysiological evidence suggests that the tuning in area AIT can be shaped by relevant statistics of the visual input^{22–24}, and it is therefore likely that the tuning we observed was a result of exposure to this particular stimulus set. It is also difficult to disentangle the tuning of these cells from factors such as stimulus familiarity²⁵ or response certainty, though the similar results obtained for the two monkeys argues against this playing a major role in the neural responses. Furthermore, neural responses to the identity-ambiguous average face were only minimally correlated with identity reported from trial to trial, reaching significance in only 15/84 neurons where such analysis was possible (monkey N97, one-way analysis of variance, $P < 0.05$). It therefore appears that,

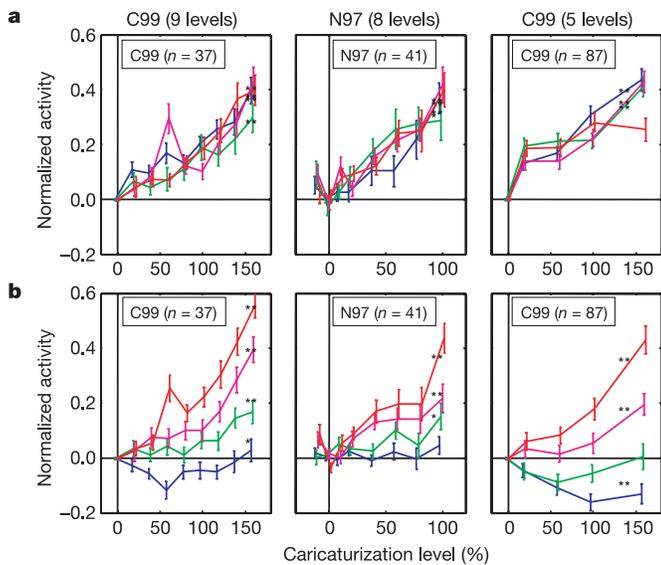


Figure 4 | Population responses as a function of the caricaturization level. **a**, Population responses for each monkey (C99 participated in some sessions with five levels and some with nine) for all four of the faces used, which were different for the two animals. **b**, Faces were rank-ordered, from the one that elicited maximum response to the one that elicited minimum response for each neuron, and then averaged for each monkey. Normalized responses were averaged separately for each rank and caricaturization level. Asterisks indicate a significant deviation from a constant trend ($*P = 0.05$; $**P = 0.01$; error bars, s.e.m.; see Methods and Supplementary Information for details).

once tuning for faces in AIT has been established, neural responses are determined primarily by the physical structure of each face stimulus. Interestingly, a recent electrophysiological study demonstrated that neurons tuned for different shapes tend to show their maximum responses for the extreme values of those shapes²⁶, suggesting that the brain may exploit a norm-based approach for a wide range of visual stimuli and tasks.

We conclude that the face-selective responses reported in the present study may represent the outcome of an internal, comparative process, perhaps expressed over multiple stages of visual processing that may allow the brain to decipher subtle differences in the shape and configuration of facial features that form the basis of face recognition. In this context, it is interesting to consider that norm-based processing may contribute to the visual system's robustness to stimulus transformations encountered in normal vision. Common transformations such as changes in scale and viewing angle, facial expression or even age need not be applied and learned for each facial identity, but might instead be applied to the normalizing pattern to which incoming faces are compared, saving both the time required to learn invariant representations of each face, as well as the corresponding storage capacity in the brain. Norm-based mechanisms, having adapted to our precise needs in face recognition, may also help explain why our face recognition is so immediate and effortless, and why at the same time we have such poor intuitive insight into how we accomplish this task.

METHODS

Subjects and task. Two monkeys (*Macaca mulatta*), N97 and C99, were used in this study, each trained on a different set of faces. Although both animals had viewed the faces extensively (that is, had been trained on them for several weeks), by the time of testing only monkey N97 (male) was required to explicitly learn and respond to the face identity. Specifically, this monkey was trained in a four alternative forced-choice procedure to report, with two bidirectional levers, which of the four identities had been presented. This monkey's performance reached near perfect with roughly 40% face identity, which was slightly worse than that of humans tested with the same stimuli¹² (see Fig. 1b, and Supplementary

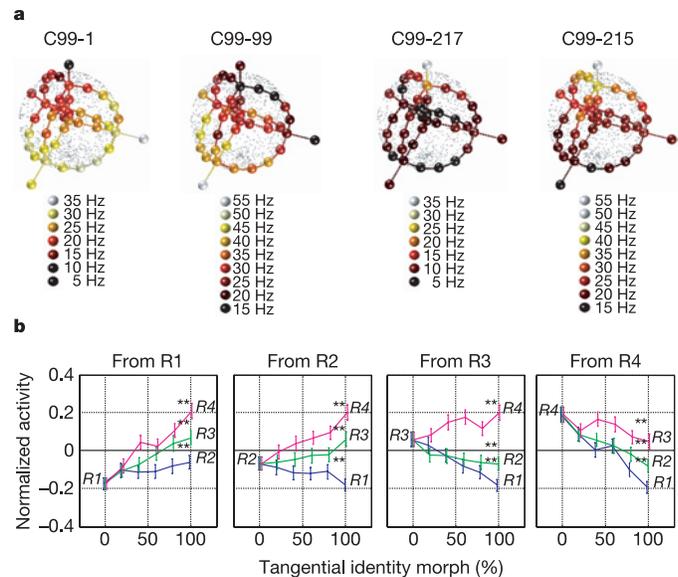


Figure 5 | Responses to radial and tangential morphs. **a**, Tetrahedron representation as in Fig. 3, but now with tangential directions included. The four tetrahedrons correspond to four examples from C99 collected in different recording sessions. **b**, Rank-ordered population responses along the tangential morph trajectories (for details see Methods). On each panel, three curves trace each of the trajectories away from a given face, from that yielding the minimum response (R1) to that leading the maximum response (R4) (conventions same as in Fig. 4).

Fig. 2). In contrast, monkey C99 (male) was not trained to respond to the identity of the test faces.

Daily testing proceeded as follows. Upon hearing a brief tone, the monkey was required to fixate a small point that appeared in the centre of the screen. After 500 ms, the test face appeared and remained on the screen for 400 ms before disappearing. The fixation requirements were minimal, with the trial aborting only if the animal's gaze was not directed towards the face at all. Monkeys received apple juice as a reward, with between 800 and 1,200 trials collected in a typical recording session. Monkey C99 was rewarded as long as it fixated throughout the entire trial, whereas monkey N97 was rewarded on a variable reward schedule for correct responses (for more details, see ref. 20).

The stimuli were generated using a morphable face model¹³, which was based on the Face Database of the Max Planck Institute for Biological Cybernetics in Tübingen, Germany (<http://faces.kyb.tuebingen.mpg.de/index.php>)¹³. Each day, the spiking of single units was monitored as the monkey was presented with between 16 and 41 different faces in pseudorandom order, at least 8 times each and often more than 20 times each. For additional details on stimuli, electrophysiological procedures and surgical procedures, see Supplementary Information.

Analysis. Data were analysed using custom software written in Matlab (Mathworks Inc.). Tuning curves were computed using the mean discharge rate of well-isolated single neurons, in a time interval from 120 to 370 ms following stimulus onset. For the population analysis, the tuning curves for each neuron were first normalized by subtracting the response to the average face, and then dividing by the maximum response elicited by any face. For further details, see Supplementary Information.

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