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Face Recognition: Canonical Mechanisms at Multiple Timescales

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Adaptation is ubiquitous in the nervous system, and many possible computational roles have been discussed. A new functional imaging study suggests that, in face recognition, the learning of 'norm faces' and adaptation resulting in perceptual after-effects depend on the same mechanism.

Adaptation is a fundamental property of neurons, and many possible computational roles of adaptation in cortical processing have been discussed (for example [1]). Adaptation affects the perception of simple visual features, such as color or local motion, as well as higher visual processes, for example the recognition of faces [2,3]. It has been proposed that adaptation might be crucial for the statistically optimal neural encoding of stimuli [3,4]. According to a popular theory, faces might be represented in terms of their deviation from a 'norm face' representation, which is learned by averaging over many previously perceived faces. On the basis of a functional imaging study, Mattar *et al.* [5] propose in this issue of *Current Biology* that high-level adaptation effects for faces and the learning of norm faces might rely on the same underlying mechanism.

Historically, adaptation in vision has been studied extensively with respect to elementary stimulus properties, such as color or motion. A well-known example is the motion after-effect (the 'waterfall illusion'), a misperception where a static background is perceived as moving after extended exposure to motion in the opposite direction. More recent work has demonstrated that higher visual functions, such as face recognition, are also affected by adaptation [2,3,6].

In psychology, faces are often characterized as points in abstract *perceptual spaces* or face spaces [7]. The dimensions of such spaces are usually identified with features that change with facial identity or expression. Such a perceptual space is illustrated in Figure 1: it contains Asian and Caucasian faces (C1,C2;A1,A2), and its center is defined by an 'average' or '*norm face*' (N), which is typically derived by averaging the features of a large number of typical face pictures. According to a popular hypothesis ([8,9], but see [10]) faces might be encoded in terms of their position relative to this norm face in the perceptual space (*norm-referenced* or *norm-based encoding*). In Figure 1, the face C1 would thus be encoded by the length and the direction of the green arrow.

The right panel of Figure 1 shows a hypothetical neural circuit for the realization of norm-referenced encoding [11]. The circuit receives its input from lower-level shape-selective cortical areas (for example, corresponding to areas V4 or V2 in the macaque cortex) in terms of a feature vector $\mathbf{s}_t$ whose components signal the presence of specific shape features. The circuit consists of two modules (hypothetical classes of neurons). One of them, the 'norm neurons', just computes a moving average of all previous stimuli, resulting in an estimate $\mathbf{r}_t$ of the average input feature vector over the previous stimulus history. If the time scale of this computation is long enough to average over a large number of previous stimulus presentations, $\mathbf{r}_t$ is effectively an estimator of the expectation value of the input vector $\mathbf{s}_t$ over time. Typically, this vector corresponds closely to the feature vector of the norm face, since (by definition) this face is characterized by 'average' features.

The second module of the hypothetical circuit consists of 'face identity neurons' whose activity depends on the length and direction of the difference vector $\mathbf{d}_t = \mathbf{s}_t - \mathbf{r}_t$. This difference feature vector corresponds to the green arrow in the face space. The inset below the face identity neurons shows schematically the tuning curves of real face-selective neurons that have been measured in macaque area IT [12]. The response rate

changes as a function of the length of the difference vector $d_t = |\mathbf{d}_t|$. In addition such neurons are tuned for the direction of this vector. (In fact, the model in Figure 1 has been extended for the processing of real face images and accounts in detail for the electrophysiologically measured responses of single cells in area IT [11].)

Norm-referenced encoding provides an elegant explanation for several well-established phenomena in face perception, such as the 'caricature effect' [8]. The exaggeration of features in a face image relative to the norm face results in a facial caricature (as stimulus C1c in Figure 1). The identity of caricatures is typically easier to perceive than the one of the corresponding original face, consistent with the fact that the associated neural response modulation is larger (see inset Figure 1).

Another well-known phenomenon is the 'other-race effect' [13], which relates to the observation that Caucasians typically are much better in distinguishing Caucasian faces than Asian faces, and *vice versa*. This effect is easy to explain with norm-referenced encoding, as illustrated in Figure 2. The average face (red disc) of Caucasian observers is close to the Caucasian faces (C1 and C2), as the Caucasians meet many more Caucasians than Asians. Consequently, their average face is located in the region of the Caucasian faces in the face space. The opposite is true for Asian participants, whose norm face is close to the Asian faces (A1 and A2). For face pairs from the own ethnic group the distinction is easier than for faces of other ethnic groups because the angle between the corresponding difference vectors (solid green arrows) is larger than the one between the difference vectors belonging to the other race (dashed arrows). Psychophysical and imaging experiments suggest that the other-race effect can be modified by learning, where relevant plasticity processes require training with face pictures over hours, or even multiple days [14–16].

Interestingly, the neural mechanisms as sketched in Figure 1 might also be suitable to account also for high-level after-effects in face perception. In a classical adaptation experiment Leopold and colleagues showed their participants an *anti-face* for several seconds [2]. An anti-face for the face C1 is a stimulus that lies on the opposite side of the norm
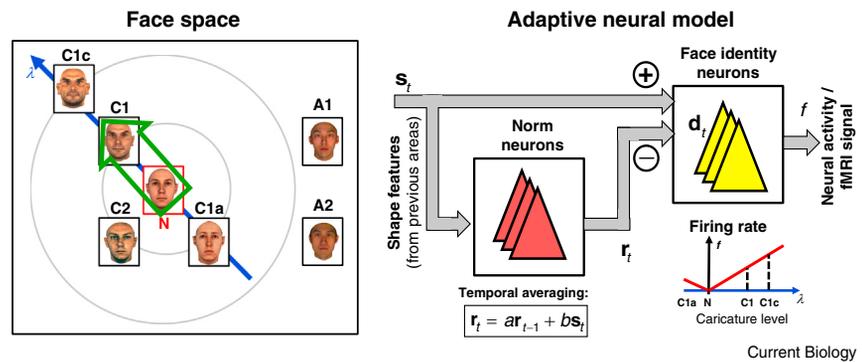
Figure 1. Face spaces and norm-referenced encoding.
The left panel shows a face space with Caucasian (C1,C2) and Asian faces (A1,A2), which is centered about the norm face N. C1c is a caricature and C1a an anti-face for face C1. The right panel illustrates a computational model for norm-referenced encoding. The 'norm neurons' compute a temporal average $\mathbf{r}_t$ of the input feature vectors $\mathbf{s}_t$ using the recursive equation in the inset. The activity of the 'face-identity neurons' depends on the length of the difference vector $\mathbf{d}_t = \mathbf{s}_t - \mathbf{r}_t$ (modified from [11].)

face (N) (see stimulus C1a in Figure 1). Unexpectedly, when they presented briefly the average face (N) as a test stimulus, their participants reported to see the face stimulus C1. Because of the similarity of this misperception with low-level after-effects, such as the motion after-effect, this phenomenon has been termed *high-level after-effect* [6].

This high-level after-effect can be explained with the model in Figure 1 if one assumes that the presentation of the stimulus C1a for a few seconds results in a shift of the norm representation (red disk) towards this adaptor. The subsequent presentation of the stimulus N results then in a difference vector (Figure 2; right panel) that is very similar to the one occurring during the presentation of the face C1 for the non-adapted system (left panel).

Motivated by the observation that the same computational mechanism can explain the learning of norm representations as well as high-level after-effects, Mattar *et al.* [5] propose that both phenomena might be accounted for by the same neural mechanisms. In order to support this hypothesis, they generated 27 example faces using a commercial face simulation program. For all pairs of these faces similarity judgments were assessed, and applying multi-dimensional scaling to them, a three-dimensional perceptual space was constructed, so that each face could be characterized as a vector $\mathbf{s}_t$ in this space. Consistent with the model discussed above, the authors assumed that the brain generates an internal estimate $\mathbf{r}_t$ that subsumes the previous

stimulus history by computation of a moving average. This average computation can be implemented by a simple recursive linear update equation $\mathbf{r}_t = a\,\mathbf{r}_{t-1} + b\,\mathbf{s}_t$. For adequate choice of the real constants a and b, this equation defines a moving average for which the importance of the previous input vectors $\mathbf{s}_t$ decays exponentially over time. In order to predict the measured fMRI signals, it was assumed that the neural signals depend on the length of the difference vector $\mathbf{d}_t = \mathbf{s}_t - \mathbf{r}_t$.

Participants observed the 27 test faces, performing an unrelated secondary task, while their brain activity (BOLD signal) was measured. The measured activity traces were fitted with the model predictions, varying the type and the parameters of the temporal integration model. As their main result, the authors found that the discussed simple linear prediction model, which defines a single timescale for the exponential decay, is sufficient for the accurate reproduction of the data. Models with more complex recursive update equations and ones with multiple exponential decays with different timescales did not provide better fits.

Fitting the model separately to different areas in the visual cortex, the authors observed in addition a characteristic variation of the timescale along the visual pathway. The range of time-scales was between 1 and 6 stimulus repetitions (corresponding to 1.5 to 9 seconds), and the time-scales in lower-level areas were faster than the ones higher up in the visual processing stream. This observation of a 'dynamic hierarchy' is consistent
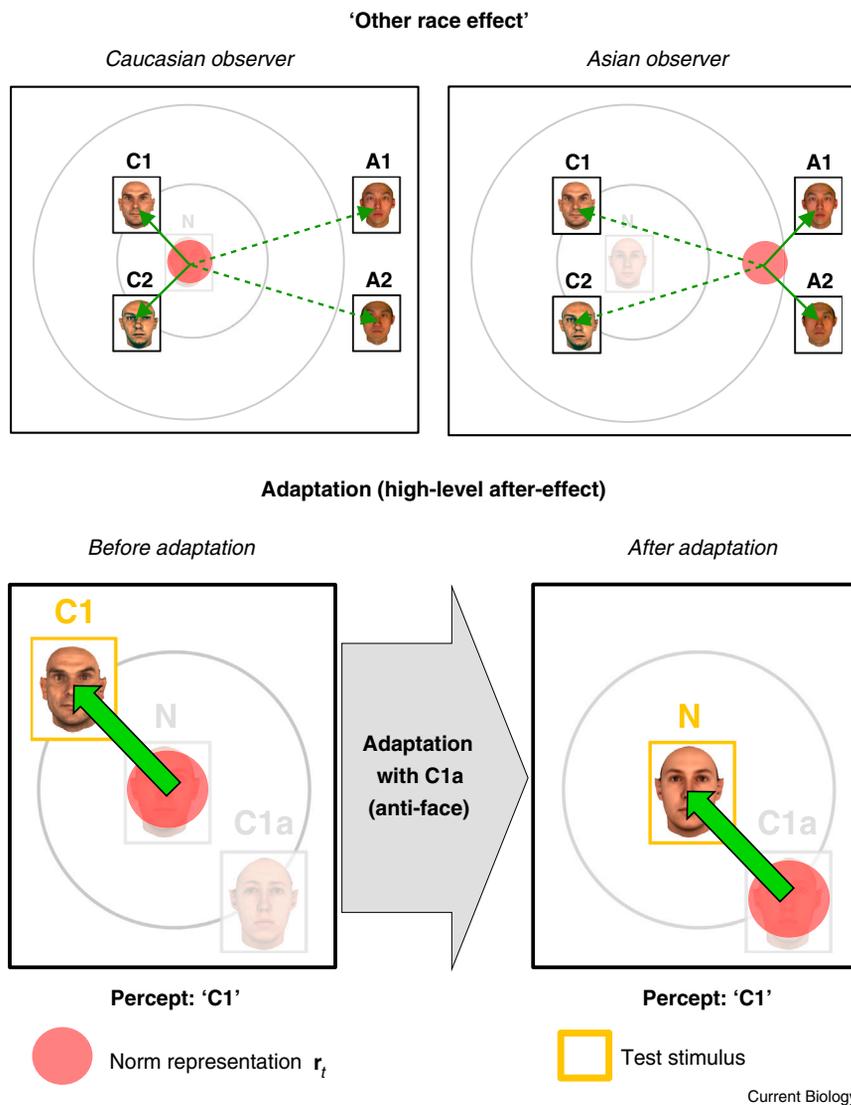
Figure 2. Explanation of the 'other-race effect' and high-level after-effects by norm-referenced encoding.
Top panel: The norm face is close to test faces from the own ethnic group. This makes the directions of the corresponding difference vectors (solid arrows) more dissimilar than the ones belonging to faces from the other race (dashed arrows). Bottom panel: After adaptation with the anti-face C1a the norm representation (red disc) wanders to this stimulus. Testing with the average face (N) creates then a difference vector (green arrow) that is very similar to the one that the original face C1 induces prior to adaptation (when the represented norm is still the stimulus N). After adaptation the stimulus N is thus misperceived as stimulus 'C1'.

with results from other studies, which observed such hierarchies at the level of single cells [17], or which claimed their relevance based on theoretical arguments [18].

The experiment by Mattar *et al.* [5] is inspiring in two ways. First, it motivates a discussion about possible common 'canonical' neural mechanisms that realize multiple, apparently different functions within the same basic circuit. Second, it contributes further evidence

for the existence of temporal hierarchies along the visual pathway.

The study has also some limitations that motivate future research. First, the hypothesis of a joint mechanism for norm learning and high-level after-effects relies on the argument that both processes happen on the same time-scale. Behavioral data show that high-level after-effects are associated with time constants in a range below 30 s [19] — in the range that was found by fitting the time-courses

of the fMRI signal. In contrast, learning processes for the modification of norm representations, which could explain changes of the other-race effect, are associated with much longer time-scales in the range of hours or even months [14–16]. Mattar *et al.* [5] speculate that such larger time-scales of adaptation might be present in higher cortical areas. However, the experimental demonstration of this fact is still missing and remains an interesting topic for future research.

Second, the measured fMRI signal averages the dynamic behavior of many neuron classes, which might operate on a variety of time-scales. Even though one time-scale accounts for the dynamics of the fMRI signal, the dynamics at the level of single neurons might thus be much more complex. Likely, single-cell physiology will be necessary for the clarification of this question.

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Zoology: Invertebrates that Parasitize Invertebrates

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The genome of an orthonectid, a group of highly modified parasitic invertebrates, is drastically reduced and compact, yet it shows the bilaterian gene toolkit. Phylogenetic analyses place the enigmatic orthonectids within Spiralia, although their exact placement remains uncertain.

"The most interesting question to be solved in the history of our parasites is whether these animals have remained normally at the planula-stage, or have retrograded to this primitive stage […] in consequence of parasitism" A. Giard, 1878 [1]

Invertebrate parasites are fascinating creatures that have inspired many of the most morbid characters in countless science fiction movies. Their life cycles can be extremely complicated, and adults and immature individuals can look radically different, especially when transitioning from free-living aquatic environments to intermediate or definitive hosts. When infecting vertebrates, such invertebrate parasites are often studied due to their potential economic and health impacts. However, when the invertebrates parasitize other invertebrates, they are often neglected. A report in this issue of *Current Biology* of the first genome of *Intoshia linei* [2], an orthonectid parasitizing ribbon worms in the genus *Lineus*, may be able to change our views on the evolution of these extreme parasites of invertebrates.

Orthonectids, with about 21 known species [3], live inside other invertebrates for most of their life cycle (Figure 1). Their simple morphology led earlier workers to think that they were closely related to ciliated protists or that they represented an intermediate step between protozoans and true animals or metazoans, hence their old name Mesozoa. They are rare parasites of a few marine animals, including acoels, brittle stars, molluscs, flatworms, ribbon worms and ascidians [4]. Orthonectids spend most of their lives as a trophic multinucleated plasmodial stage (a plasmodium is a cytoplasm that contains many nuclei, rather than being divided into individual cells each with a single nucleus) in their unfortunate hosts' tissues. The life cycle of only a few species has been well characterized [5,6]. A few hypertrophied cells develop from the plasmodia into small ciliated worm-like male and female adults (Figure 1A) that escape the host and swim free (Figure 1B). While the name Orthonectida may suggest a straightforward swimming behavior [3], they can exhibit complex movements, including spinning and bending [2]. These ephemeral adults lack digestive, circulatory or excretory systems, but are full of gametes surrounded by contractile cells of smooth muscle and a layer of ciliated cells. For the longest time, it was thought that they lacked a nervous system, until a recent study described a reduced nervous system using immunohistochemistry [7], which also helped to better characterize its muscular system. Yet both these systems are extremely simple: the whole muscular system consists of four longitudinal and 9–11 circular muscle cells, and its nervous system consists of six serotonin-like cells, and a total of 10–12 cells [7], although there is some variation [8].

When the ca. 1 mm long swimming female meets with a dwarf male in the water, they copulate briefly by uniting their genital pores. The fertilized eggs then develop into minute larvae that exit the female via the genital pore in search of a new victim. Once inside the host, the larva disintegrates, losing the ciliated cells first, and the inner cells scatter within the host's tissues to become new infective cells known as 'agametes' to