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Cortical representations of bodies and faces are strongest in commonly experienced configurations

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Faces and bodies are perhaps the most salient and evolutionarily important visual stimuli. Using human functional imaging, we found that the strength of face and body representations depends on long-term experience. Representations were strongest for stimuli in their typical combinations of visual field and side (for example, left field, right body), although all conditions were simply reflections and translations of one another. Thus, high-level representations reflect the statistics with which stimuli occur.

In natural viewing, observers typically fixate faces[1], and, consequently, the right side of the observed body often lands in the left visual field and the left side lands in the right visual field. We investigated whether this natural experience modulates the strength of face and body part representations in extrastriate cortex (extrastriate body area, EBA[2]; fusiform face area, FFA[3]). Although prior studies have shown that training modulates responsiveness and selectivity for categories of visual stimuli[4–8], we focused primarily on the strength of discrimination across simple affine transformations of otherwise identical stimuli in the absence of explicit training.

In an event-related functional magnetic resonance imaging (fMRI) experiment (**Supplementary Methods**), 18 participants saw allocentric views of five body parts (shoulder, elbow, hand, knee and foot) and half-faces (**Fig. 1** and **Supplementary Methods**). All participants gave written informed consent, approved by the National Institutes of Health Institutional Review Board. We chose allocentric views because prior studies have shown that right EBA responds more to allocentric than to egocentric body views[9,10]. We manipulated both side of body (left, right) and field of presentation (left, right) by reflecting and translating the stimuli, respectively. We independently localized EBA and FFA, which were both larger and more consistent in the right than in the left hemisphere (**Supplementary Data 1**); we focused on the data from the right hemisphere (rEBA and rFFA).

The average response magnitude in each region of interest (ROI) showed little differentiation between conditions (**Supplementary Data 2**), and we used a split-half correlation method to investigate discrimination for faces and body parts[11] (**Supplementary Methods**). For each pair of conditions, we calculated the similarity of the response patterns in EBA and FFA across independent halves of the data (**Supplementary Data 3** and **4**).

For each combination of field and side, we compared the within-condition correlation (for example, hand to hand) to the between-condition correlations (for example, hand to leg, hand to shoulder, etc.) (**Fig. 2a**,**b**). Greater within-condition than between-condition correlation indicates that the response pattern can be used to discriminate between conditions. We calculated an average discrimination index by subtracting the average between-condition correlations from the within-condition correlations for each condition (**Supplementary Data 5**). Given the category-selectivity of the ROIs, we examined half-faces and body parts separately.

For discrimination between body parts in rEBA, we observed significant discrimination indices ($P < 0.05$; **Fig. 2c**) only for right body parts in the left visual field and for left body parts in the right visual field. Notably, these combinations of field and side correspond to the commonly experienced configurations. This effect of experience also gave rise to a significant interaction between field and side ($F_{1,17} = 11.848$,

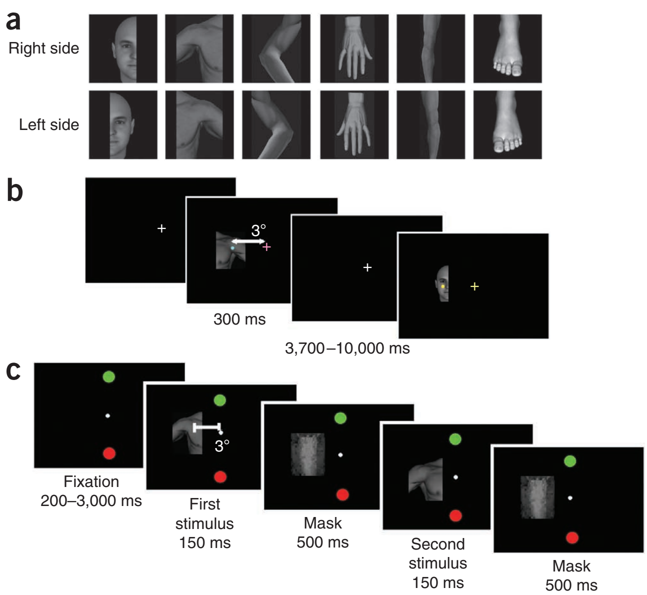

Figure 1 Experimental design. (**a**) Sample stimuli from right (top row) or left side (bottom row) of the body. Left and right side stimuli are mirror images. (**b**) fMRI experiment. On each trial, participants indicated whether the color of the fixation cross matched that of a small circle placed on top of each stimulus (average accuracy, 94%). (**c**) Behavioral experiment. The same stimuli, sizes and locations were used as in the fMRI experiment. On each trial, participants viewed two masked presentations of exemplars from a given stimulus type and made an eye movement to the either the green or red target to indicate whether the exemplars were the same or different, respectively.

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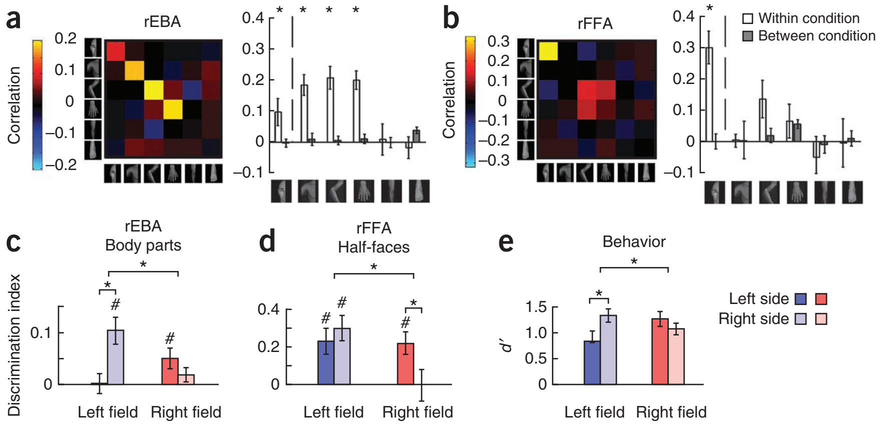

Figure 2 Discrimination of body parts and half-faces. (**a**,**b**) Similarity matrices and summary plots for the right side of the body in the left visual field in rEBA (**a**) and rFFA (**b**). Each element in the similarity matrices shows the correlation between two conditions. The within-condition correlations (white bars) are plotted against the average between-condition correlations (gray bars) for each condition. Discrimination indices were calculated as the difference between these bars. Error bars indicate the between-subjects s.e. $^*P < 0.05$. (**c**–**e**) Interaction of field and side for discrimination indices in rEBA (**c**) and rFFA (**d**) and for behavioral performance (**e**). Error bars indicate the between-subjects s.e. # indicates significant difference from zero ($P < 0.05$) and thus significant discrimination.

$P < 0.003$). This specific pattern of the interaction (**Fig. 2c**) was observed in 11 of 18 participants. In contrast, for body parts in rFFA, we observed no significant discrimination indices ($P > 0.16$) and no significant effects involving field or side ($P > 0.8$) (**Supplementary Data 6**). A direct comparison of rEBA and rFFA revealed stronger discrimination for body parts in rEBA than rFFA ($F_{1,13} = 10.59$, $P < 0.006$). The same pattern of results was observed even when voxel numbers were matched between the regions (**Supplementary Data 7**). Thus, in rEBA, but not rFFA, there is discrimination for body parts, confirming prior suggestions that EBA contains representations of individual body parts[12,13], but only for the commonly experienced configurations.

Notably, discrimination was not equal for all body parts (**Fig. 2a** and **Supplementary Data 8**). In particular, for right body parts in the left visual field, we observed stronger discrimination for upper compared with lower body parts (main effect of body part, $F_{4,68} = 8.533$, $P < 0.0001$). Furthermore, planned comparisons revealed significant discrimination for shoulder ($t_{1,17} = 3.916$, $P < 0.0005$), elbow ($t_{1,17} = 4.917$, $P < 0.0001$) and hand ($t_{1,17} = 4.946$, $P < 0.0001$) but not knee or foot (both $P > 0.07$). Thus, we observed the strongest discrimination for body parts closest to the face, consistent with a long-term effect of preferential fixation of faces.

For half-faces in rFFA, we observed significant discrimination ($P < 0.0001$) for faces from body parts (**Fig. 2d**) in all combinations of field and side except for right half-faces in the right visual field ($P > 0.49$). Similar to the discrimination pattern for body parts in rEBA, discrimination was strongest for right half-faces in the left visual field and left half-faces in the right visual field, leading to a significant interaction between field and side ($F_{1,13} = 6.185$, $P < 0.027$). In contrast, in rEBA, there were no significant effects ($P > 0.65$) and overall discrimination of half-faces from body parts was stronger in rFFA than in rEBA ($F_{1,13} = 13.376$, $P < 0.003$).

Thus, for body parts in rEBA and half-faces in rFFA, discrimination was stronger for the commonly experienced combination of field and side (see **Supplementary Data 9** for other face- and body-selective ROIs; see **Supplementary Data 10** for data from early visual cortex and analysis of low-level stimulus differences).

To confirm that the strength of face and body part representations was contingent on field and side, we conducted a separate behavioral experiment (**Fig. 1c**) in which 13 new participants performed a within body part or half-face discrimination in a delayed match-to-sample task (**Supplementary Methods**). Participants d' scores revealed the same interaction of field and side ($F_{1,12} = 10.34$, $P < 0.007$) as was observed for body parts in rEBA and half-faces in rFFA (**Fig. 2e** and **Supplementary Data 11**). This finding indicates that the effect of field and side observed in the response patterns of rEBA and rFFA effects behavioral discrimination.

In conclusion, we found that the strength and distinctiveness of visual representations in both body- and face-selective cortex is determined by long-term natural visual experience. How the effect of field and side that we observed for allocentric body views relates to egocentric body views[9,10], to the putative mirror neuron system, and to body representations in parietal cortex[14,15] will need to be addressed by future work. Notably, our findings extend prior evidence for the role of experience in shaping the selectivity of high-level visual cortex[4–8] and suggest that representations in these regions directly capture the statistics with which complex stimuli occur.

Note: Supplementary information is available on the Nature Neuroscience website.

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AUTHOR CONTRIBUTIONS

A.W.-Y.C., D.J.K., S.T. and C.I.B. designed the fMRI study. A.W.-Y.C., D.J.K. and S.T. collected and analyzed the fMRI data. A.W.-Y.C., D.J.K., J.A. and C.I.B. designed the behavioral study. J.A. collected and analyzed the behavioral data with help from A.W.-Y.C., D.J.K. and C.I.B. A.W.-Y.C., D.J.K. and C.I.B. wrote the paper with contributions from S.T. and J.A.

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1. Cerf, M., Harel, J., Einhauser, W. & Koch, C. in *Advances in Neural Information Processing Systems* (eds Platt, J.C., Koller, D., Singer, Y. & Roweis, S.) (MIT Press, Cambridge, Massachusetts, 2008).
2. Peelen, M.V. & Downing, P.E. *Nat. Rev. Neurosci.* **8**, 636–648 (2007).
3. Kanwisher, N. & Yovel, G. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **361**, 2109–2128 (2006).
4. Harley, E.M. *et al. Cereb. Cortex* **19**, 2746–2754 (2009).
5. Gauthier, I., Skudlarski, P., Gore, J.C. & Anderson, A.W. *Nat. Neurosci.* **3**, 191–197 (2000).
6. Baker, C.I. *et al. Proc. Natl. Acad. Sci. USA* **104**, 9087–9092 (2007).
7. Gauthier, I., Tarr, M.J., Anderson, A.W., Skudlarski, P. & Gore, J.C. *Nat. Neurosci.* **2**, 568–573 (1999).
8. Op de Beeck, H.P., Baker, C.I., DiCarlo, J.J. & Kanwisher, N.G. *J. Neurosci.* **26**, 13025–13036 (2006).
9. Chan, A.W., Peelen, M.V. & Downing, P.E. *Neuroreport* **15**, 2407–2410 (2004).
10. Saxe, R., Jamal, N. & Powell, L. *Cereb. Cortex* **16**, 178–182 (2006).
11. Haxby, J.V. *et al. Science* **293**, 2425–2430 (2001).
12. Taylor, J.C., Wiggett, A.J. & Downing, P.E. *J. Neurophysiol.* **98**, 1626–1633 (2007).
13. Urgesi, C., Calvo-Merino, B., Haggard, P. & Aglioti, S.M. *J. Neurosci.* **27**, 8023–8030 (2007).
14. Shmuelof, L. & Zohary, E. *J. Neurosci.* **26**, 9736–9742 (2006).
15. Shmuelof, L. & Zohary, E. *Nat. Neurosci.* **11**, 1267–1269 (2008).