

# Learning to Discriminate Face Views

Taiyong Bi, Nihong Chen, Qiuje Weng, Dongjun He and Fang Fang

*J Neurophysiol* 104:3305-3311, 2010. First published 14 July 2010; doi:10.1152/jn.00286.2010

## You might find this additional info useful...

---

This article cites 56 articles, 21 of which can be accessed free at:

<http://jn.physiology.org/content/104/6/3305.full.html#ref-list-1>

Updated information and services including high resolution figures, can be found at:

<http://jn.physiology.org/content/104/6/3305.full.html>

Additional material and information about *Journal of Neurophysiology* can be found at:

<http://www.the-aps.org/publications/jn>

---

This information is current as of December 15, 2010.

# Learning to Discriminate Face Views

**Taiyong Bi,\* Nihong Chen,\* Qiujie Weng,\* Dongjun He, and Fang Fang**

*Department of Psychology and Key Laboratory of Machine Perception (Ministry of Education), Peking University, Beijing, China*

Submitted 22 March 2010; accepted in final form 7 July 2010

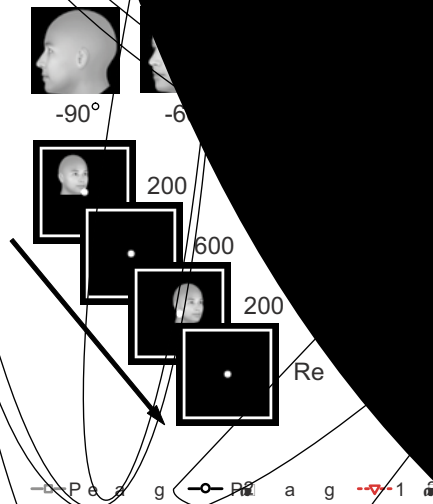
**Bi T, Chen N, Weng Q, He D, Fang F.** Learning to discriminate face views. *J Neurobiol* 104: 3305–3311, 2010. First published July 14, 2010; doi:10.1152/jn.00286.2010. Although perceptual learning of simple visual features has been studied extensively and intensively for many years, we still know little about the mechanisms of perceptual learning of complex object recognition. In a series of seven experi-

models were generated by (facegen.com/). No hair was rendered on the default average face (Fig. 1A) in the texture gamma correction was set to 2. In most experiments except *e e imen 5*, stimuli were rendered with two face images: Jim and which were a face/anti-face pair developed by the Biological Cybernetics (Leopold et al. 2001). used in *e e imen 5* and our previous study like paperclip model (Fig. 2F) was rendered (Fig. 7). It was also used in a study by Fang

generated by projecting a 3D stimulus model onto the monitor plane with the rotation angles. Both left and right rotations were of 0.2°. The stimuli (except those in 10% of visual angle. They were presented on a 21" monitor, with a spatial resolution of 1024x768 pixels and a refresh rate of 100 Hz. Subjects viewed the stimuli from a distance of 57 cm. Their head position was stabilized by a chin rest. Throughout the experiments, a small white dot presented at the

daily training sessions to discrimination of 30°, either left tilted or right tilted. Each session (~1 h) consisted of 25 trials (Leopold and Pelli 1983). In a trial, 30 stimuli were presented for 200 ms and their temporal order was randomized (Fig. 1B). Their temporal order

could affect face from 19 to 23



Threshold( $^\circ$ )

Face view



averaged as a measure of subjects' discrimination performance and plotted as a function of orientation. Note that subjects were randomly selected to be trained at either  $-30^\circ$  or  $+30^\circ$ . Because training at the two orientations induced a similar learning effect, for the sake of presentation simplicity, the discrimination performance functions for subjects trained at  $-30^\circ$  were flipped horizontally and averaged together with the functions for subjects trained at  $+30^\circ$ . Subjects' performance improvement at an orientation was calculated as (pretraining threshold - posttraining threshold)/pretraining threshold  $\times$  100%. To measure the time course of the training effect (learning curve), discrimination thresholds from 25 QUEST staircases in a daily training session were averaged and plotted as a function of training day. Learning curves were fitted with a power function (Jeter et al. 2009).

To quantify the transfer of training between the trained and the test stimuli, transfer index was defined as the ratio of performance improvement with the test stimulus and that with the trained stimulus. Performance improvement with the trained stimulus over eight daily training sessions was calculated as (1st day threshold - 8th day threshold)/1st day threshold  $\times$  100%. The test stimulus here had the same orientation as the trained stimulus. Paired *t*-test and independent-samples *t*-test were carried out for within-subject comparisons and between-subject comparisons, respectively.

## RESULTS

### Perceptual learning in face view discrimination

In *experiment 1*, we first measured subjects' face view discrimination thresholds at seven orientations of  $-90^\circ$ ,  $-60^\circ$ ,  $-30^\circ$ ,  $0^\circ$ ,  $30^\circ$ ,  $60^\circ$ , and  $90^\circ$  (Fig. 1, A and B). Subjects practiced for 8,000 trials during eight daily training sessions on face view discrimination at the orientation of  $30^\circ$ . Throughout the training course, their discrimination thresholds gradually decreased, which resulted in a 36% performance improvement (Fig. 1C). After training, we measured thresholds at the seven orientations again.

Before training, subjects had a significant lower threshold (better performance) at  $0^\circ$  than the thresholds at other orientations [all ( $n$ )  $>$  4.7,  $P <$  0.01; gray line in Fig. 1D], which is consistent with the claim that 3D symmetric shapes are discriminated more efficiently than asymmetric ones (Liu and Kersten 2003). After training, the threshold at  $30^\circ$  was comparable to that at  $0^\circ$  [ $(n) = 0.45$ ,  $P = 0.67$ ] and was significantly lower than those at other orientations [all ( $n$ )  $>$  4.4,  $P <$  0.01; black line in Fig. 1D]. We calculated the percent improvement in discrimination performance after training. The improvement at the trained orientation of  $30^\circ$  was 44%, which was significantly higher than those (about or  $<$ 10%) at other orientations [black line in Fig. 1E; all ( $n$ )  $>$  4.7,  $P <$  0.01]. These results suggest an orientation-specific perceptual learning in face view discrimination.

To examine the persistence of the learning effect, we measured the discrimination thresholds 1 and 6 mo after training (red and green lines in Fig. 1D). Relative to the performance before training, the percent improvements in discrimination performance at the trained orientation of  $30^\circ$  was 34% 1 mo after training and 33% 6 mo after training (red and green lines in Fig. 1E). This means that the learning effect was long-lasting, and 75% of the effect was kept after a half-year break. It is noteworthy that the learning effect persisted in an orientation-specific manner. The improvements at the untrained orientations were around or  $<$ 10%, which were significantly

lower than the improvement at  $30^\circ$  [all ( $n$ )  $>$  3.5,  $P <$  0.01, except the marginal significance at  $90^\circ$  6 mo after training, ( $n) = 2.1$ ,  $P = 0.077$ ]. The long-lasting orientation-specific perceptual learning in face view discrimination was quite robust and consistent across individual subjects.

### Transfer of the face learning effect

*Experiment 2* were designed to study the transfer of training from trained stimuli to test stimuli. The test stimuli were always faces. The trained stimuli shared more or less properties with the test stimuli. Similar to *experiment 1*, subjects underwent eight daily training sessions to discriminate views of the trained stimulus at the orientation of  $30^\circ$ . Before and after training, we measured subjects' face view discrimination thresholds with the test stimulus at the seven orientations of  $-90^\circ$ ,  $-60^\circ$ ,  $-30^\circ$ ,  $0^\circ$ ,  $30^\circ$ ,  $60^\circ$ , and  $90^\circ$ .

*Experiment 2* studied how a size change from the trained stimulus to the test stimulus could affect the transfer of learning (Fig. 2A). The area of the test stimulus was four times that of the trained stimulus. The 8-day training resulted in a 31% improvement in discrimination performance with the trained stimulus at the orientation of  $30^\circ$ . Relative to the performance before training, the improvement after training with the test stimulus at  $30^\circ$  was 33%, significantly higher than the improvements at the untrained orientations [all ( $n$ )  $>$  2.5,  $P <$  0.05].

*Experiment 3* investigated the effect of face part change on the transfer of learning. The trained and the test stimuli were mutually exclusive, and they constituted a complete face (Fig. 2B). Throughout the training course, subjects' discrimination thresholds gradually decreased, which resulted in a 38% performance improvement with the trained face. Relative to the pretraining performance, the improvement after training with the test face at  $30^\circ$  was 41%, significantly higher than the improvements at the untrained orientations [all ( $n$ )  $>$  3.1,  $P <$  0.05].

In *experiment 4*, the trained face was presented in the lower visual field, and the test face was presented in either the lower or the upper visual fields (Fig. 2C). The objective of the experiment was twofold. First, *experiment 1* showed that face view learning could take place around the fixation point. Here we examined if the learning could occur at a more eccentric area, e.g., the lower or the upper visual field. Second, we were interested in the effect of visual field change on the transfer of learning. Similar to *experiment 1*, eight training sessions in the lower visual field led to a 27% performance improvement. Before and after training, we measured face view discrimination thresholds in both the lower and the upper visual fields. Subjects' performance improvements at the trained orientation were 33 and 32% in the lower and the upper visual fields, respectively, both of which were orientation specific [lower visual field: all ( $n$ )  $>$  2.6,  $P <$  0.05, dotted line; upper visual field: all ( $n$ )  $>$  3.3,  $P <$  0.05, solid line].

*Experiment 5* examined the effect of face identity change on the transfer of learning (within-category transfer). The trained face was Anti-Jim and the test face was Jim (Fig. 2D). They were a face/anti-face pair, which lay at the two ends of a face identity trajectory (Leopold et al. 2001). After eight daily training sessions, subjects' performance with the trained face improved by 37%. We also found that the learning transfer was

orientation specific because the improvement with the test stimulus at 30° was 41%, significantly higher than those at the untrained orientations [all (6) > 2.5,  $P < 0.05$ ].

In *e e imen 6* and *7*, the test stimulus was a face and the trained stimuli were an inverted face (Fig. 2E) and an M-like paperclip (Fig. 2F). Here we examined how face inversion and object category change affected the learning transfer. Similar to the training effect with an upright face, training with the inverted face and the paperclip at the orientation of 30° also improved subjects' discrimination performance by 36 and 45%, respectively. However, compared with *e e imen 2 5*, the performance improvements with the test face at 30° were weak (13 and 22%). These improvements were not orientation-specific because there was no significant difference between the trained orientation and the untrained orientations [inverted face: all (6) < 1.9,  $P > 0.12$ ; paperclip: all (7) < 2.3;  $P > 0.07$ ].

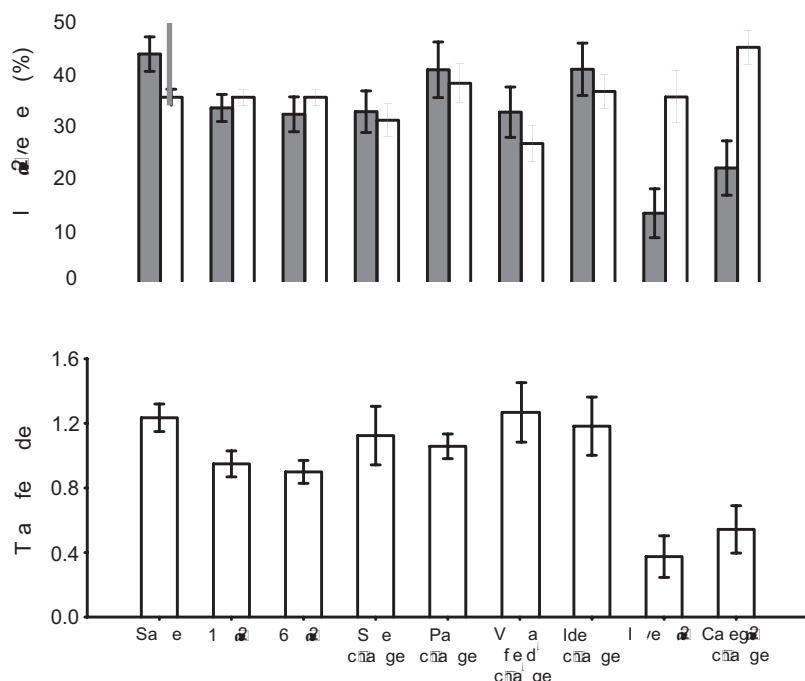
To quantify the transfer of training between the trained and the test stimuli, the transfer index was calculated as the ratio of performance improvement with the test stimulus and that with the trained stimulus (Fig. 3). A large index means that a large amount of the training effect has been transferred to the test stimulus; in other words, the performance improvement with the test stimulus can be largely attributed to the training effect. The transfer indices in *e e imen 1 5* were 1.23, 1.12, 1.06, 1.27, and 1.18. There was no significant difference among them [ $F(6,50) = 1.176$ ,  $P = 0.336$ ]. Note that, in *e e imen 1*, the test and the trained stimuli were the same. These results suggest a complete transfer from the trained stimulus to the test stimulus in *e e imen 2 5*. Why are the indices larger than 1? This is because the threshold measurement before training also led to some learning effect. The transfer indices in *e e imen 6* and *7* were 0.37 and 0.54, respectively. There was no significant difference between them ( $F = 0.85$ ,  $P = 0.41$ ). However, they were significantly lower than the indices in

*e e imen 1 5* [ $F(8,65) = 5.616$ ,  $P < 0.001$ ], which suggests a partial or weak transfer in *e e imen 6* and *7*.

## DISCUSSION

We see faces from various viewing angles every day. Face view perception informs us not only about a person's identity but also about his/her social attention. Even from a small face view change, we could infer changes in their current goals and intentions (Nummenmaa and Calder 2009). Can our ability of face view perception (discrimination) be improved with training? In this study, a series of seven experiments was conducted to address this question and to investigate the characteristics of perceptual learning of face view discrimination. *E e imen 1* showed that training led to a significant improvement in sensitivity to face view orientation. The improvement was highly specific to the trained orientation and lasted up to 6 mo. In *e e imen 2 5*, we found that the orientation-specific learning effect completely transferred across changes in face size, visual field, and face identity. A complete transfer also occurred between two partial face images that were mutually exclusive but constituted a complete face. However, the transfers were weak between an upright face and an inverted face and between a paperclip object and a face, as shown in *e e imen 6* and *7*. It should be noted that, in most experiments, only one face stimulus was used. These conclusions can be further strengthened if more face stimuli were used.

Face view learning exhibited two important characteristics of perceptual learning: specificity and persistence (Liu 1999; Sasaki et al. 2010). Training at 30° had a very weak effect on the discrimination performance at other orientations, even at 0° and 60°. It could be argued that subjects' view sensitivity at 0° (cardinal orientation) was already very high, leaving little room for improvement. To rule out the explanation, we trained two subjects using the same procedure as that for 30°. The training



resulted in a 48% performance improvement at 0°, comparable to the training effect at 30°. It has been reported that some face neurons in STS responded symmetrically to left and right views (De Souza et al. 2005). This would predict that training at 30° should also lead to a higher performance improvement at -30° than at 0, ±60, and ±90°. However, we did not find such an effect, which indicates that training might have a very weak or little influence on these STS neurons. The benefits of perceptual learning with visual features are usually long-lasting, persisting for up to 2 yr (Karni and Sagi 1993). In high-level vision, training effects with a shape/object identification task could last 1 mo (Furmanski and Engel 2000; Sigman and Gilbert 2000). Here, we expanded these results by showing that the orientation-specific face view learning could last ≤6 mo.

Using a visual search or identification task, past studies indicated that face/shape recognition is subject to perceptual learning (Furmanski and Engel 2000; Golcu and Gilbert 2009; Hussain et al. 2009; Sigman and Gilbert 2000). However, few of them studied the characteristics of high-level visual perceptual learning as comprehensively as this study. There are two similar findings in previous studies and ours. One is the complete transfer across a change in face size, in agreement with the finding that object learning was insensitive to image size (Furmanski and Engel 2000). The other is the weak transfer from an upright face to its vertical inversion. Hussain et al. (2009) also found that face identification training was largely specific to the in-plane orientations of trained faces. Both studies suggest that the neural codings of upright faces and inverted faces are quite different. However, a significant contrast between past studies and ours is whether learning was restricted to the area where the stimulus was trained. Our study showed a complete transfer from the lower visual field to the upper visual field. Such a transfer between visual fields was not found in other studies (Cox and DiCarlo 2008; Dill and Fahle 1997; Nazir and O'Regan 1990). Two noteworthy points can explain the discrepancy. First, in these studies, subjects were trained to identify simple shapes that can be coded by retinotopic areas (e.g., V2 and V4; Hedge and Van Essen 2007). Second, these shapes were trained at a fixed position in the visual field. The face stimuli in our study were randomly presented in a small area, which might subserve the spatial transfer of the learning effect.

Where does face view learning occur in the visual cortex? In the human visual cortex, there are three face-selective areas: OFA, STS, and FFA (Fang et al. 2007; Haxby et al. 2000), which are the possible loci of the learning. Also, a recent study (Sigman et al. 2005) suggested that retinotopic areas played an important role in high-level visual perceptual learning with a shape identification task. By measuring the transfer of learning from the trained face to other visual stimuli more or less resembling it, we can infer where face view learning took place in the visual system and what was learned during training. First, the complete transfers across changes in face size, face part, and visual field could rule out early retinotopic areas and OFA. Because the receptive fields of neurons in early retinotopic areas are small (Smith et al. 2001), they are sensitive to stimulus changes in size, local feature, and position in the visual field. Although OFA is at a higher position in the visual processing hierarchy than early retinotopic areas, it is still retinotopically organized (see a review by Wandell et al. 2007) and is sensitive to changes in face part (Pitcher et al. 2007). Thus the properties of early retinotopic areas and OFA do not support the

complete transfers we observed. Second, the complete transfer of the learning from a face to its anti-face suggests that the learning effect is identity invariant, which resonates with the finding that most view-selective face neurons in macaque STS are not sensitive to identity (Perrett et al. 1992). Using fMRI adaptation, Fang et al. (2007) showed that both STS and FFA in human visual cortex could encode face views. However, Grill-Spector et al. (2004) showed that FFA, but not STS, is selective for face identity. Thus STS is more likely to be the cortical locus of face view learning than FFA. Third, the weak transfers from the trained face to its in-plane inversion and to the paperclip object can rule out an alternative explanation that the face view discrimination learning is a general 3D orientation discrimination learning and takes place at cortical areas coding 3D orientation. Hinkle and Connor (2002) reported that some neurons in macaque area V4 carry robust signals for 3D orientation defined by binocular disparity. Although the orientation of the face views was not defined by disparity, the finding by Hinkle and Connor does suggest the alternative explanation for our observation. A key prediction of this 3D orientation learning explanation is that it should not depend on the object representation in the visual system, as long as the trained and the test stimuli are in the same 3D orientation. In our study, however, only weak transfers were observed, even though both the inverted face and the paperclip object as the trained stimuli (Bi et al. 2009; Fang and He 2005) have the same orientation as the test face. Taken together, converging evidence suggests that training on face view discrimination resulted in a large amount of plastic changes at a level of higher visual processing where size-, position-, and identity-invariant face views are represented.

Our results suggest that what was learned by the visual system during training is the improved ability of computing face orientation from the configural information of face views, rather than the configural information itself or face parts. Another recent study, on the other hand, suggests that objects are learned in a parts-based manner (Golcu and Gilbert 2009). This superficial contradiction can be easily explained. In the study of Golcu and Gilbert, objects were composed of three line segments, each of which could provide diagnostic information for accomplishing object recognition. In our study, although local features in face views could provide more or less information about face orientation, it might be more reliable to extract the orientation from the configural information, especially when the face views were randomly presented in a small area. Indeed, both studies support the claim that perceptual learning drives the visual system to extract the regularities of the environment and develop optimal strategies for visual information processing (Gilbert et al. 2001).

Visual perceptual learning studies have led to an increasing understanding of plasticity in the adult visual system. This study developed a powerful experimental protocol to study high-level visual perceptual learning and shown the characteristics of face view learning. It is time to use brain imaging and single-unit methods to study the neural mechanisms of face view learning and therefore open the window into one of the central questions in vision sciences—plastic object representation in the visual system.

#### ACKNOWLEDGMENTS

We thank S. He for helpful discussions and D. Leopold for providing the face images with different identities.



## GRANTS

This work was supported by the National Natural Science Foundation of China (Projects 30870762, 90920012, and 30925014) and the Ministry of Science and Technology of China (2010CB833903).

## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

## REFERENCES

- Andrews TJ, Ewbank MP.** Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. *NeuroImage* 23: 905–913, 2004.
- Baker CI, Behrmann M, Olson CR.** Impact of learning on representation of parts and wholes in monkey inferotemporal cortex. *Neuroscience* 151: 1210–1216, 2002.
- Ball K, Sekuler R.** Direction-specific improvement in motion discrimination. *Visual Neuroscience* 27: 953–965, 1987.
- Berardi N, Fiorentini A.** Interhemispheric transfer of visual information in humans: spatial characteristics. *Journal of Physiology* 384: 633–647, 1987.
- Bi T, Su J, Chen J, Fang F.** The role of gaze direction in face viewpoint aftereffect. *Visual Neuroscience* 49: 2322–2327, 2009.
- Cox DD, DiCarlo JJ.** Does learned shape selectivity in inferior temporal cortex automatically generalize across retinal position? *Journal of Neuroscience* 28: 10045–10055, 2008.
- De Souza WC, Eifuku S, Tamura R, Nishijo H, Ono T.** Differential characteristics of face neuron responses within the anterior superior temporal sulcus of macaques. *Journal of Neuroscience* 25: 1252–1266, 2005.
- Desimone R, Albright TD, Gross CG, Bruce C.** Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience* 4: 2051–2062, 1984.
- Dill M, Fahle M.** The role of visual field position in pattern discrimination learning. *Proceedings of the Royal Society London B Biological Sciences* 264: 1031–1036, 1997.
- Fahle M.** Perceptual learning: specificity versus generalization. *Cognitive Brain Research* 15: 154–160, 2005.
- Fahle M, Edelman S.** Long-term learning in Vernier acuity: effects of stimulus orientation, range and of feedback. *Visual Neuroscience* 33: 397–412, 1993.
- Fahle M, Poggio T.** *Perceptual Learning*. Cambridge, MA: MIT Press, 2002.
- Fang F, He S.** Viewer-centered object representation in the human visual system revealed by viewpoint aftereffects. *NeuroImage* 45: 793–800, 2005.
- Fang F, Ijichi K, He S.** Transfer of the face viewpoint aftereffect from adaptation to different and inverted faces. *Visual Neuroscience* 7: 1–9, 2007a.
- Fang F, Murray SO, He S.** Duration-dependent fMRI adaptation and distributed viewer-centered face representation in human visual cortex. *Cerebral Cortex* 17: 1402–1411, 2007b.
- Fendick M, Westheimer G.** Effects of practice and the separation of test targets on foveal and peripheral stereoacuity. *Visual Neuroscience* 23: 145–150, 1983.
- Freedman DJ, Riesenhuber MP, Miller EK.** Experience-dependent sharpening of visual shape selectivity in inferior temporal cortex. *Cerebral Cortex* 16: 1631–1644, 2006.
- Furmanski CS, Engel SA.** Perceptual learning in object recognition: object specificity and size invariance. *Visual Neuroscience* 40: 473–484, 2000.
- Furmanski CS, Schluppeck D, Engel SA.** Learning strengthens the response of primary visual cortex to simple patterns. *Cerebral Cortex* 14: 573–578, 2004.
- Ghose G, Yang T, Maunsell J.** Physiological correlates of perceptual learning in monkey V1 and V2. *Journal of Neuroscience* 22: 1867–1888, 2002.
- Gilbert CD, Sigman M, Crist RE.** The neural basis of perceptual learning. *Neuron* 31: 681–697, 2001.
- Golcu D, Gilbert CD.** Perceptual learning of object shape. *Journal of Neuroscience* 29: 13621–13629, 2009.
- Gold J, Bennett PJ, Sekuler AB.** Signal but not noise changes with perceptual learning. *Neuron* 40: 176–178, 1999.
- Grill-Spector K, Knouf N, Kanwisher N.** The fusiform face area subserves face perception, not generic within-category identification. *Neuroscience* 124: 555–562, 2004.
- Grill-Spector K, Kushnir T, Hendler T, Malach R.** The dynamics of object-selective activation correlate with recognition performance in humans. *Neuroscience* 135: 837–843, 2000.
- Haxby JV, Hoffman EA, Gobbini MI.** The distributed human neural system for face perception. *Trends in Cognitive Sciences* 4: 223–233, 2000.
- Hegde J, Van Essen DC.** A comparative study of shape representation in macaque visual areas V2 and V4. *Cerebral Cortex* 17: 1100–1116, 2007.
- Hinkle DA, Connor CE.** Three-dimensional orientation tuning in macaque area V4. *Neuroscience* 117: 665–670, 2002.
- Hussain Z, Sekuler AB, Bennett PJ.** Perceptual learning modifies inversion effects for faces and textures. *Visual Neuroscience* 49: 2273–2284, 2009.
- Ito M, Tamura H, Fujita I, Tanaka K.** Size and position invariance of neuronal responses in monkey inferotemporal cortex. *Journal of Neuroscience* 15: 218–226, 1995.
- Jeter PE, Doshier BA, Petrov A, Lu Z.** Task precision at transfer determines specificity of perceptual learning. *Visual Neuroscience* 9: 11–13, 2009.
- Karni A, Sagi D.** Where practice makes perfect in texture discrimination: evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences USA* 88: 4966–4970, 1991.
- Karni A, Sagi D.** The time course of learning a visual skill. *Neuron* 14: 250–252, 1993.
- Kourtzi Z, Betts LR, Sarkheil P, Welchman AE.** Distributed neural plasticity for shape learning in the human visual cortex. *PLOS Biology* 3: e204, 2005.
- Leopold D, O'Toole A, Vetter T, Blanz V.** Prototype-referenced shape encoding revealed by high-level aftereffects. *Neuroscience* 104: 89–94, 2001.
- Liu Z.** Perceptual learning in motion discrimination that generalizes across motion directions. *Proceedings of the National Academy of Sciences USA* 96: 14085–14087, 1999.
- Liu Z, Kersten D.** Three-dimensional symmetric shapes are discriminated more efficiently than asymmetric ones. *Journal of the Optical Society of America A* 20: 1331–1340, 2003.
- Nazir TA, O'Regan JK.** Some results on translation invariance in the human visual system. *Spa Vision* 5: 81–100, 1990.
- Nummenmaa L, Calder AJ.** Neural mechanisms of social attention. *Trends in Cognitive Sciences* 13: 135–143, 2009.
- Op de Beeck HP, Baker CI, DiCarlo JJ, Kanwisher NG.** Discrimination training alters object representations in human extrastriate cortex. *Journal of Neuroscience* 26: 13025–13036, 2006.
- Perrett DI, Hietanen JK, Oram MW, Benson PJ, Rolls ET.** Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society London B Biological Sciences* 335: 23–30, 1992.
- Perrett DI, Oram MW, Harries MH, Bevan R, Hietanen JK, Benson PJ, Thomas S.** Viewer-centered and object-centered coding of heads in the macaque temporal cortex. *Experimental Brain Research* 86: 159–173, 1991.
- Perrett DI, Smith PAJ, Potter DD, Mistlin AJ, Head AS, Milner AD.** Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society London B Biological Sciences* 223: 293–317, 1985.
- Pitcher D, Walsh V, Yovel G, Duchaine B.** TMS evidence for the involvement of the right occipital face area in early face processing. *Cerebral Cortex* 17: 1568–1573, 2007.
- Pourtois G, Rauss KS, Vuilleumier P, Schwartz S.** Effects of perceptual learning on primary visual cortex activity in humans. *Visual Neuroscience* 48: 55–62, 2008.
- Sasaki Y, Nanez JE, Watanabe T.** Advances in visual perceptual learning and plasticity. *Neuroscience* 166: 53–60, 2010.
- Schoups A, Vogels R, Orban GA.** Human perceptual learning in identifying the oblique orientation: retinotopy, orientation specificity and monocularly. *Journal of Physiology* 483: 797–810, 1995.
- Schoups A, Vogels R, Qian N, Orban G.** Practising orientation identification improves orientation coding in V1 neurons. *Neuron* 41: 549–553, 2001.
- Schwartz S, Maquet P, Frith C.** Neural correlates of perceptual learning: A functional MRI study of visual texture discrimination. *Proceedings of the National Academy of Sciences USA* 99: 17137–17142, 2002.
- Sigala N, Logothetis NK.** Visual categorization shapes feature selectivity in the primate temporal cortex. *Neuron* 45: 318–320, 2002.
- Sigman M, Gilbert CD.** Learning to find a shape. *Neuroscience* 103: 264–269, 2000.
- Sigman M, Pan H, Yang Y, Stern E, Silbersweig D, Gilbert CD.** Top-down reorganization of activity in the visual pathway after learning a shape identification task. *Neuron* 46: 823–835, 2005.
- Smith AT, Singh KD, Williams AL, Greenlee MW.** Estimating receptive field size from fMRI data in human striate and extrastriate visual cortex. *Cerebral Cortex* 11: 1182–1190, 2001.
- Tarr MJ, Gauthier I.** FFA: a flexible fusiform area for subordinate-level visual processing automatized by expertise. *Neuroscience* 115: 764–769, 2000.
- Wandell BA, Dumoulin SO, Brewer AA.** Visual field maps in human cortex. *Neuron* 56: 366–383, 2007.
- Watson AB, Pelli DG.** QUEST: A Bayesian adaptive psychometric method. *Perceptual Psychology* 33: 113–120, 1983.
- Yu C, Klein SA, Levi DM.** Perceptual learning in contrast discrimination and the (minimal) role of context. *Visual Neuroscience* 4: 169–182, 2004.