

UC San Diego

UC San Diego Electronic Theses and Dissertations

Title

Selectivity of face processing mechanisms

Permalink

<https://escholarship.org/uc/item/89j5x09g>

Author

Ng, Minna

Publication Date

2007

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA, SAN DIEGO

Selectivity of Face Processing Mechanisms

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy

in

Psychology

by

Minna Ng

Committee in charge:

Professor Stuart Anstis. Chair
Professor Geoffrey M. Boynton
Professor Seana Coulson
Professor Karen R. Dobkins
Professor Donald I. A. MacLeod

2007

The dissertation of Minna Ng is approved, and it
is acceptable in quality and form for publication on
microfilm:

Chair

University of California, San Diego

2007

DEDICATION

*To Boon Kin, Goretti & Kenley Ng;
to Agnes, Simon & Pearly Lee;
to Paul Chan.*

TABLE OF CONTENTS

Signature Page.....	iii
Dedication.....	iv
Table of Contents.....	v
List of Figures and Tables.....	vi
Acknowledgments.....	vii
Vita.....	x
Abstract.....	xii
Chapter 1. General Introduction.....	1
Chapter 2. A Psychophysical Study of Selectivity for the Face Properties of Gender and Ethnicity.....	16
Chapter 3. An fMRI Adaptation Study of Brain Regions Selective for Face Properties.....	32
Chapter 4. A Psychophysical Study of the Effect of Face Adaptation on Search, Detection, and Discrimination.....	58
Chapter 5. Conclusions.....	93

LIST OF FIGURES AND TABLE

Figure 2.1: Experimental design and example psychometric function.....	27
Figure 2.2: Adaptation effect predictions.....	28
Figure 2.3: Adaptation results and predictions.....	29
Table 3.1: Brain areas showing significant BOLD responses for each subject by condition.....	50
Figure 3.1: Example BOLD responses described by slow or transient time-courses.....	51
Figure 3.2: Coherence maps based on the slow time-course.....	52
Figure 3.3: Coherence maps based on the transient time-course.....	53
Figure 3.4: Correlation coefficients between conditions.....	54
Figure 4.1: Design for experiment 1: RSVP.....	83
Figure 4.2: Design for experiment 2: spatial search.....	84
Figure 4.3: Design for experiment 3: discrimination.....	85
Figure 4.4: Results for experiment 2A: four-face display spatial search.....	86
Figure 4.5: Results for experiment 2B: two-face display spatial search.....	87
Figure 4.6: Results for experiment 3: discrimination.....	88

ACKNOWLEDGMENTS

Who would have thought that I would have a dissertation to my name? Certainly not me. If it were not for the encouragement of Dean Marilyn Chernin and the incredibly supportive faculty advisors of the Student Life Department at Kingsborough Community College, my education would have been completed after earning an Associates of Arts Degree, in Liberal Arts. But to my continued good fortune, I received instruction, and direction, from the best biology teachers at City College of the City University of New York: Michael Laverde and Shubha Govind.

Good fortune continued after graduation; Gero Miesenböck needed a research technician that could recognize a female fruitfly from a male fruitfly, and I had mastered this skill! The years I spent in his lab opened my eyes to opportunities that I never knew existed. I cannot thank him enough for his belief in me.

I would like to thank all the members of my dissertation committee: Stuart Anstis, Geoffrey M. Boynton, Seana Coulson, Karen Dobkins, Donald I.A. MacLeod, and my honorary member, Ione Fine. I am eternally grateful for the unique contribution each one of you had in shaping my graduate career. Thank you for entertaining all my questions, however small, crazy or confused they might have been. Thank you for your support, encouragement, and humor throughout this journey; and for always having your doors open to me. Having such an incredibly talented and inspiring committee humbles me, and reminds me how lucky I have been these last several years.

Geoff, thank you for putting the “whos” in my head and for generating such a great lab environment to work in. Ione, thank you for all the things you have done for me.

What immediately comes to mind when I think of you is your compassion, generosity, amazing strength, and psychic abilities. Thank you for your example. You are an incredible role model!

I would also like to extend a special thanks to several faculty members that have made a significant impact on my graduate training: Michael Gorman, Marni Bartlett, Garrison Cottrell, and Michael M. Webster.

For their mentorship, collaborations, friendship, and never-ending supply of snacks (particular in the wee hours of the night), I must thank my wonderful lab family: A. Cyrus Arman, Vivian M. Ciaramitaro, Robert O. Duncan, Edward M. Hubbard, Sara Mednick, Kate Murray, John T. Serences, Margaret R. Tarampi, and August S. Tuan. And for the special friendships I made outside of the lab – Elizabeth Allman, M. Colin Ard, Sarah-Jane Kim, Francois Klam, Julie Onton, Amira A. Rezec, Anja Schlak, Liane Lane Wardlow – I am deeply grateful. Last, but not least, Greg D. Field, I thank you from the bottom of my heart.

Chapter 2, in part, and Chapter 3, in full, has been published as: Ng, M., Ciaramitaro, V.M., Anstis, S.A., Boynton, G.M., Fine, I. (2006), Selectivity for the configural cues that identify the gender, ethnicity, and identity of faces in human cortex. *Proc of National Academy of Sciences*, 103(51): 19552-19557. Permission to reprint these chapters was granted by all co-authors. The dissertation author was the primary investigator and author of this paper.

Chapter 2, in part, and Chapter 4, in full, is in preparation for resubmission to *Journal of Vision* as: Ng, M., Boynton, G.M., Fine, I., Face adaptation does not improve search or discrimination tasks. Permission to reprint these chapters was granted by all co-

authors. The dissertation author was the primary investigator and author of this manuscript.

VITA

Born February 18, 1975, New York, New York

Education

2007 Ph.D. in Psychology
University of California, San Diego

2004 M.A. in Psychology
University of California, San Diego

1998 B.S. in Biological Sciences
City College, City University of New York, New York

Teaching Experience

2002 - 2006 Teaching Assistant, Department of Psychology, UCSD
Introduction to Statistics (2006)
Sensation and Perception (2005)
Cognitive Psychology (2004)
Judgment & Decision Making (2003)
Biological Foundations of Psychology (2003)
Introduction to Psychology (2002)

2007 Associate Lecturer, Department of Psychology, UCSD
Physiological Psychology

University Service

2004 Graduate Admission Representative
2003 Colloquium Representative

Workshops

2006 (Nov) Neuroscience of Facilities for the Aging and People with Alzheimer's
2006 (Jun/Jul) Cold Spring Harbor Summer Course: Computational Vision
2004 (Jun/Jul) Cognitive Neuroscience Summer Institute at Dartmouth University

Awards

2003 Travel Award - Psychology Department, UCSD
2004 Travel Award - Psychology Department, UCSD
2003 - 2005 National Science Foundation Interdisciplinary Graduate Education
Research Training Fellowship

Publications

- Ng, M., Boynton, G.M., Fine, I. (2007) Face adaptation does not improve performance on search or discrimination tasks. *Journal of Vision* (submitted).
- Ng, M., Ciaramitaro, V.M., Anstis, S., Boynton, G.M., Fine, I. (2006) Selectivity for cues to gender, ethnicity, and individuals in human visual cortex. *PNAS* 103(51):19552-57.
- Zemelman, B.V., Lee, G.A., Ng, M., Miesenböck, G. (2002) Selective Photostimulation of Genetically ChARGed Neurons. *Neuron*. 33:15-22.
- Ng, M., Roorda, R.D., Lima, S.Q., Zemelman, B.V., Miesenböck, G. (2002) Transmission of Olfactory Information Between Three Populations of Neurons in the Antennal Lobe of the Fly. *Neuron*. 36:463-74.

Presentations

- Ng, M., Kaping, D., Webster, M., Anstis, S., Boynton, G.M., Fine, I. (2003) Selective Tuning of Face Perception. Third Annual Meeting of Vision Sciences Society, Sarasota, FL.
- Ng, M., Ciaramitaro, V.M., Fine, I., Boynton, G.M., Fine, I. (2004) Selective Tuning of Face Perception. Fourth Annual Meeting of Vision Sciences Society, Sarasota, FL.
- Ng, M., Ciaramitaro, V.M., Anstis, S., Boynton, G.M., Fine, I. (2004) Neural Basis of Gender and Ethnicity. Society for Neurosciences, San Diego, CA.
- Ng, M., Ciaramitaro, V.M., Anstis, S., Boynton, G.M., Fine, I. (2005) Neural Basis of Gender, Ethnicity, and Individuals. Society for Neurosciences Adaptation Symposium, Washington, D.C.
- Ng, M., Boynton, G.M., Fine, I. (2007) Face Adaptation Does Not Improve Performance on Search or Discrimination. Sixth Annual Meeting of Vision Sciences Society, Sarasota, FL.

Memberships

- | | |
|----------------|---------------------------|
| 2002 - Present | Vision Sciences Society |
| 2003 - Present | Society for Neurosciences |

ABSTRACT OF THE DISSERTATION

Selectivity of Face Processing Mechanisms

by

Minna Ng

Doctor of Philosophy in Psychology
University of California, San Diego, 2007

Professor Stuart Anstis, Chair

Face perception is the specialized ability to process information about faces. This skill is developed early in life; and as adults, we are experts at categorizing, searching and discriminating individual faces. In this dissertation, we investigated mechanisms selective for processing important facial properties - gender, ethnicity, and individual identity - using a combination of psychophysical and fMRI adaptation method. In Chapter 2, we found that there exist both singly (selective for either gender *or* ethnicity) and jointly (selective for both gender *and* ethnicity) tuned mechanisms. Using a functional magnetic resonance imaging (fMRI) adaptation paradigm in Chapter 3, we identified cortical regions selective for the gender, ethnicity and identity of individual faces. Finally, in Chapter 4, we examined whether our face adaptation technique on performance in search and discrimination tasks, and found that adaptation had no discernible effects on performance on these tasks.

Chapter 1

General Introduction

Face perception is a specialized ability for processing facial information. Electrophysiology and neuroimaging studies have discovered a neural basis for face processing within specialized regions of extrastriate cortex. Recently, investigators have begun to use perceptual and functional imaging adaptation paradigms to examine important attributes of face perception. Here, we use adaptation to examine selectivity for facial properties, such as the tuning of gender and ethnicity (described in Chapter 2), and to identify brain regions highly selective for facial gender, ethnicity and identity (described in Chapter 3). While the exact mechanism underlying these perceptual and fMRI adaptation effects remain unclear, especially in the case of face processing, we, and others, have repeatedly shown its robust effects. In Chapter 4, we carried out experiments examining the perceptual consequences of face adaptation on RSVP, spatial search and discrimination tasks. The failure of adaptation to affect performance on these tasks suggests that adaptation might affect different underlying mechanisms than those that underlie the previous tasks in Chapter 2.

Sensitivity to facial properties of gender and ethnicity

Certain facial attributes tend to be more salient than others. For example, when looking at an unfamiliar face, its gender and ethnicity are immediately noticeable, more so than almost any other feature. When preparing 'mug books' for identification of suspects, a standard law enforcement guide advocates grouping photos of individuals that are similar in ethnicity, age and gender, as eye-witnesses rely strongly on these facial properties (Technical Working Group for Eyewitness Evidence, 1999). Similarly, for preschool children, gender is the most salient characteristic for face categorization; ethnicity and age are also salient, but the presence or absence of eyeglasses is extremely non-salient (McGraw, Durm, & Durnam, 1989). My goal in this thesis was to examine how the cues of gender and ethnicity are processed, using adaptation (both psychophysical and fMRI) as a tool.

Adaptation: “the psychophysicist’s electrode”

In physiology, when neurons are stimulated intensely for a period of time, they become less responsive due to fatigue or habituation (Maffei, Fiorentini, & Bisti, 1973; Movshon & Lennie, 1979). Psychophysicists have borrowed this adaptation technique, calling it the “psychophysicist’s electrode” (Frisby, 1980), since adaptation allows psychophysicists to examine the influence of sub-populations of neurons, by isolating and temporarily diminishing the contribution of specific neural populations (Clifford & Rhodes, 2005). Psychophysical adaptation paradigms have been used extensively to examine the selectivity of neural tuning in low-level mechanisms sensitive to visual attributes such as motion, color, orientation and luminance (Gibson & Radner, 1937;

Mather, Verstraten, & Anstis, 1998). Adaptation can also be used to examine how selectivity to more than one property interacts (Lovegrove & Over, 1972; Stromeyer & Dawson, 1978; Webster & Mollon, 1993; Webster & Mollon, 1995; Webster, Malkoc, Bilson, & Webster, 2002). The classic McCollough effect used an adaptation paradigm to demonstrate that orientation and color are jointly tuned properties (McCollough, 1965). When subjects adapted to red vertical gratings and green horizontal gratings, gray gratings looked pinkish when horizontal, but looked greenish when vertical. The McCollough contingent after-effect is attributed to the selective adaptation of neurons that respond not just to color or to orientation, but to both color and orientation (Stromeyer, Khoo, & Muggeridge, 1978).

In Chapter 2, we describe experiments that use psychophysical adaptation to examine selectivity for gender and ethnicity.

Effects of adaptation on detection and discrimination tasks

A simplistic explanation for these observations is that adaptation either reduces the responsivity of mechanisms tuned for the adapting category, or shifts their selectivity away from the category boundary (Grill-Spector & Malach, 2001). Changes such as these should have perceptual consequences beyond a category shift.

Consistent with the notion that adaptation is capable of changing the detectability of stimuli, some early studies examining the effects of adaptation on low-level features have found increased detection thresholds after adaptation to orientation (Blakemore & Nachmias, 1971; Barlow, Macleod, & van Meeteren, 1976; Regan & Beverly, 1985; Clifford, Wyatt, Arnold, Smith, & Wenderoth, 2001), spatial frequency (Blakemore &

Campbell, 1969) and speed (Clifford & Wenderoth, 1999). In the color domain, adaptation has been observed to have selective effects on color detection thresholds, and these selective effects have been used to examine the selectivity of chromatic mechanisms (Thornton & Pugh, 1983; Macleod, & von der Twer, 2003). However, for many tasks and stimuli, adaptation can have little or no effect on detection thresholds.

Several groups have found that orientation adaptation affects orientation discrimination (Regan & Beverly, 1985; Clifford, Wyatt, Arnold, Smith, & Wenderoth, 2001; Dragoi, Sharma, Miller, & Sur, 2002), with discrimination thresholds tending to be smaller after adaptation when the test stimulus has an orientation similar to or orthogonal to the adapting stimulus, and higher for gratings 7.5-20 degrees away from the adapting stimulus (though see (Westheimer & Gee, 2002)).

In the color domain, the selective effects of adaptation on color discrimination thresholds provide a well-established tool for examining the selectivity of chromatic mechanisms (Thornton & Pugh, 1983). Indeed, it has been suggested that our exquisite ability to make fine discrimination judgments for chromatically neutral stimuli may be a result of adapting to the statistics of natural scenes, where most stimuli are remarkably chromatically unsaturated (Macleod, & von der Twer, 2003).

Some studies have also demonstrated adaptation effects on discrimination in other domains. For example, under certain regimes, lightness and contrast adaptation are capable of affecting contrast discrimination (Barlow, 1969; Abbonizio, Langley, & Clifford, 2002; Greenlee & Heitger, 1988); although as described in the Discussion of Chapter 4, these adaptation effects are by no means universal (Maatanen & Koenderink,

1991; Ross, Speed, & Morgan, 1993; Foley & Chen, 1997; Abbonizio, Langley, & Clifford, 2002).

Finally, it has also been shown that adaptation can affect search. McDermott et al. (McDermott, Mulligan, Bebis, & Webster, 2006; Webster, Raker, & Malkoc, 1998) examined subjects' ability to detect a target ellipse of variable color presented at a random location on a dense background of ellipses that varied along either the LvsM or SvsLM cardinal axes. Observers adapted by viewing a rapid succession of backgrounds drawn from one color axis, and then searched for a target on a background from the same or different color axis. Targets were located more quickly on the background axis that observers were pre-exposed to, confirming that this exposure can improve search efficiency for stimuli that differ from the background.

In Chapter 4 we tested search in a rapid serial visual presentation, a spatial search paradigm and a discrimination task. We found no effects of adaptation on performance in any of these tasks suggesting that in the case of face processing adaptation might affect different underlying mechanisms than those that underlie these other types of task.

Psychophysical Adaptation to faces

Recently, adaptation has been used to study higher level visual processing of faces, and certain facial attributes (Webster & MacLin, 1999; Leopold, O'Toole, Vetter, & Blanz, 2001; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Webster, Kaping, Mizokami, & Duhamel, 2004). For example, Rhodes and colleagues used an adaptation paradigm to demonstrate selectivity of facial attractiveness (Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003). Adaptation to an unattractive face rendered a moderately

attractive face significantly more attractive. In a similar paradigm, Leopold and colleagues demonstrated the existence of mechanisms tuned for the identity of particular faces (Leopold, O'Toole, Vetter, & Blanz, 2001). Adaptation to an individual face shifted the apparent perception of subsequently presented faces along a trajectory passing through the adapting face and an “average” face. Webster and colleagues, the first to develop the face adaptation technique (Webster & MacLin, 1999), showed that adaptation to a set of female faces made previously neutral face appear male (Webster, Kaping, Mizokami, & Duhamel, 2004). This is consistent with neurons tuned to “femaleness” becoming less responsive as a consequence of adaptation. Face-selective adaptation does not seem to be mediated by low-level mechanisms. Unlike adaptation effects thought to be mediated by low-level neurons, face-selective adaptation transfers across size, retinal position, and orientation, albeit to a lesser degree (Webster & MacLin, 1999; Zhao & Chubb, 2001; Watson & Clifford, 2003).

Face processing occurs in specialized cortical areas

Numerous clinical (Damasio, Damasio, & Van Hoesen, 1982; Farah, Levinson, & Klein, 1995) and neuroimaging (Sergent, Ohta, & MacDonald, 1992; Sergent & Signoret, 1992; Puce, Allison, Gore, & McCarthy, 1995; Kanwisher, McDermott, & Chun, 1997; Grill-Spector, Knouf, & Kanwisher, 2004) studies have associated face processing with specialized regions in the human occipital and ventral temporal extrastriate cortex. Electrophysiology recordings on the surface of human inferior extrastriate visual cortex (Fried, MacDonald, & Wilson, 1997; Fried, Cameron, Yashar, Fong, & Morrow, 2002) and analogous regions of the non-human primate inferior temporal cortex find neuronal

selectivity for faces (Perrett, Rolls, & Caan, 1982; Desimone, Albright, Gross, & Bruce, 1984; Rolls, 1984; Rolls & Baylis, 1986; Abbott, Rolls, & Tovee, 1996; Tsao, Freiwald, Tootell, & Livingstone, 2006).

More recently, a conjunction of human fMRI and monkey neurophysiology studies have also begun to suggest segregated cortical representations for independent attributes of faces, such as identity, expression, and gender (Perrett et al., 1984; Kreiman, Koch, & Fried, 2000; Puce, Allison, Gore, & McCarthy, 1995; Rolls, 1984; Baylis, Rolls, & Leonard, 1985; Hasselmo, Rolls, & Baylis, 1989; Allison, McCarthy, Nobre, Puce, & Belger, 1994).

FMRI adaptation for faces

Adaptation also has consequences for the fMRI signal; repeated presentations of a visual stimulus decreases the fMRI signal over time. While the neuronal mechanisms underlying this repetition effect are not yet clear (Sawamura, Orban, & Vogels, 2006), the working hypothesis is that the decreased fMRI signal reflects adaptation of a neuronal population response (Grill-Spector & Malach, 2001).

The brain area showing such a decrease is therefore thought to contain neurons selective for the visual stimulus. For example, Winston and colleagues showed that rapidly repeating a particular facial identity for a fraction of a second decreased activity in the fusiform cortex (Winston, Henson, Fine-Goulden, & Dolan, 2004). This suggested that there were neurons selectively activated to a facial identity within this cortical area. The Winston study also found decreased fMRI responses in an area anterior to the STS (superior temporal sulcus; Winston, Henson, Fine-Goulden, & Dolan, 2004) associated

with a change in facial expression. The area that processed facial identity corresponded to the fusiform “face area” (FFA), an area that shows a greater fMRI response to faces than to non-face stimuli (Kanwisher, McDermott, & Chun 1997). Importantly, the FFA was not localized using an adaptation paradigm, and the STS activation would not have been observed without using fMRI adaptation. Thus, fMRI adaptation helped identify brain regions that otherwise would not be revealed (Grill-Spector & Malach, 2001; Avidan, Hasson, Hendler, Zohary, & Malach, 2002). In Chapter 3, I will describe how we used an fMRI adaptation paradigm to reveal selective face processing within brain areas that traditional methods failed to identify. We will show how adaptation revealed brain areas that were not sensitive to generic face stimuli, but were instead showed selectivity for gender, ethnicity and identity, suggesting that these contained neurons showing selective responses to particular types of face.

Summary

This dissertation focuses on using adaptation to study the tuning of face-selective mechanisms. In Chapter 2 of this dissertation, I will describe how we extended the face adaptation paradigm used by Webster and colleagues (Webster, Kaping, Mizokami, & Duhamel, 2004) to examine tuning for gender and ethnicity (Asian and Caucasian) in face-selective mechanisms. We investigated whether face-selective mechanisms are *singly* tuned, i.e. selective for either gender or ethnicity, but not both, or *jointly* tuned, i.e. selective for both gender and ethnicity, or whether both types of tuning (both *single* and *joint*) co-exist.

Having found psychophysical evidence for mechanisms selective for gender and ethnicity, we sought to investigate where in the visual cortex these attributes are processed. In Chapter 3, I will describe how we used an fMRI adaptation paradigm, analogous to the one used in the psychophysics study in Chapter 2, to find the location of areas showing selective tuning for ethnicity and gender. In addition, we also examined where individual identity was processed. We were interested in whether gender and ethnicity were processed in similar regions of visual cortex, and to what extent these regions fell within cortical areas traditionally associated with face processing (Kanwisher, McDermott, & Chun, 1997).

Chapter 2 describes perceptual shifts in facial category (i.e. female to male) as a result of adaptation. Chapter 3 examines reductions in fMRI response as a result of adaptation. A simplistic explanation for the effects of adaptation in Chapters 2 and 3 is that adaptation either reduces the responsivity of mechanisms tuned for the adapting category, or shifts their selectivity away from the category boundary (Grill-Spector & Malach, 2001). As described in the General Introduction, changes such as these should have perceptual consequences beyond a category shift. Chapter 4 describes a set of experiments that show that face adaptation (to the properties of ethnicity and gender) does not affect performance on either visual search or face discrimination tasks.

REFERENCES

- Abbonizio, G., Langley, K., & Clifford, C. W. (2002). Contrast adaptation may enhance contrast discrimination. *Spat Vis*, 16(1), 45-58.
- Abbott, L. F., Rolls, E. T., & Tovee, M. J. (1996). Representational capacity of face coding in monkeys. *Cereb Cortex*, 6(3), 498-505.
- Allison, T., McCarthy, G., Nobre, A., Puce, A., & Belger, A. (1994). Human extrastriate visual cortex and the perception of faces, words, numbers, and colors. *Cereb Cortex*, 4(5), 544-554.
- Avidan, G., Hasson, U., Hendler, T., Zohary, E., & Malach, R. (2002). Analysis of the neuronal selectivity underlying low fMRI signals. *Curr Biol*, 12(12), 964-972.
- Baylis, G. C., Rolls, E. T., & Leonard, C. M. (1985). Selectivity between faces in the responses of a population of neurons in the cortex in the superior temporal sulcus of the monkey. *Brain Res*, 342(1), 91-102.
- Barlow, H. B., Macleod, D. I., & van Meeteren, A. (1976). Adaptation to gratings: no compensatory advantages found. *Vision Res*, 16(10), 1043-45.
- Blakemore, C., & Campbell, F. W. (1969). Adaptation to spatial stimuli. *J Physiol*, 200(1), 11P-3P.
- Blakemore, C., & Nachmias, J. (1971). The orientation specificity of two visual after-effects. *J Physiol*, 213(1), 157-74.
- Clifford, C. W., & Wenderoth, P. (1999). Adaptation to temporal modulation can enhance differential speed sensitivity. *Vision Res*, 39(26), 4324-32.
- Clifford, C. W., Wyatt, A. M., Arnold, D. H., Smith, S. T., & Wenderoth, P. (2001). Orthogonal adaptation improves orientation discrimination. *Vision Res*, 41(2), 151-59.
- Clifford, C. W. G. & Rhodes, G. (2005). *Fitting the Mind to the World: Adaptation and After-Effects in High-Level Vision (Advances in Visual Cognition)*. Oxford University Press, USA.
- Damasio, A. R., Damasio, H., & Van Hoesen, G. W. (1982). Prosopagnosia: anatomic basis and behavioral mechanisms. *Neurology*, 32(4), 331-341.

- Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *J Neurosci*, 4(8), 2051-2062.
- Dragoi, V., Sharma, J., Miller, E. K., & Sur, M. (2002). Dynamics of neuronal sensitivity in visual cortex and local feature discrimination. *Nat Neurosci*, 5(9), 883-91.
- Farah, M. J., Levinson, K. L., & Klein, K. L. (1995). Face perception and within-category discrimination in prosopagnosia. *Neuropsychologia*, 33(6), 661-674.
- Foley, J. M., & Chen, C. C. (1997). Analysis of the effect of pattern adaptation on pattern pedestal effects: a two-process model. *Vision Res*, 37(19), 2779-88.
- Fried, I., Cameron, K. A., Yashar, S., Fong, R., & Morrow, J. W. (2002). Inhibitory and excitatory responses of single neurons in the human medial temporal lobe during recognition of faces and objects. *Cereb Cortex*, 12(6), 575-584.
- Fried, I., MacDonald, K. A., & Wilson, C. L. (1997). Single neuron activity in human hippocampus and amygdala during recognition of faces and objects. *Neuron*, 18(5), 753-765.
- Frisby, J. P. (1980). *Seeing. Illusion, Brain and Mind*. Oxford Univ. Press.
- Gibson, J. J. & Radner, M. (1937). Adaptation, after-effect, and contrast in the perception of tilted lines. I. Quantitative studies. *J Exp Psychol*, 20, 453-467.
- Greenlee, M. W., & Heitger, F. (1988). The functional role of contrast adaptation. *Vision Res*, 28(7), 791-97.
- Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nat Neurosci*, 7(5), 555-562.
- Grill-Spector, K. & Malach, R. (2001). fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol (Amst)*, 107(1-3), 293-321.
- Hasselmo, M. E., Rolls, E. T., & Baylis, G. C. (1989). The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. *Behav Brain Res*, 32(3), 203-218.

- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J Neurosci*, *17*(11), 4302-4311.
- Kreiman, G., Koch, C., & Fried, I. (2000). Category-specific visual responses of single neurons in the human medial temporal lobe. *Nat Neurosci*, *3*(9), 946-953.
- Leopold, D. A., O'Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nat Neurosci*, *4*(1), 89-94.
- Lovegrove, W. J. & Over, R. (1972). Color adaptation of spatial frequency detectors in the human visual system. *Science*, *176*(34), 541-543.
- Maatanen, L. M., & Koenderink, J. J. (1991). Contrast adaptation and contrast gain control. *Experimental Brain Research*, *87*, 205-12.
- Macleod, D. I., & von der Twert, T. (2003). The Pleistochrome: optimal opponent codes for natural colours. In R. Mausfeld, & D. Heyer (Eds.), *Colour Perception: Mind and the Physical World* Oxford University Press, USA.
- Maffei, L., Fiorentini, A., & Bisti, S. (1973). Neural correlate of perceptual adaptation to gratings. *Science*, *182*(116), 1036-1038.
- Mather, G., Verstraten, F., & Anstis, S. (1998). *The Motion Aftereffect: A Modern Perspective*. The MIT Press.
- McCollough, C. (1965). Color adaptation of edge-detectors in the human visual system. *Science*, *149*(3688), 1115-1116.
- McDermott, K., Mulligan, J. B., Bebis, G., & Webster, M. A. (2006). Visual search and eye movements in novel and familiar contexts. *Proc SPIE*, 6057.
- McGraw, K. O., Durm, M. W., & Durnam, M. R. (1989). The relative salience of sex, race, age, and glasses in children's social perception. *J Genet Psychol*, *150*(3), 251-267.
- Perrett, D. I., Rolls, E. T., & Caan, W. (1982). Visual neurones responsive to faces in the monkey temporal cortex. *Exp Brain Res*, *47*(3), 329-342.

- Perrett, D. I., Smith, P. A., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., et al. (1984). Neurons responsive to faces in the temporal cortex: studies of functional organization, sensitivity to identity and relation to perception. *Hum Neurobiol*, 3(4), 197-208.
- Puce, A., Allison, T., Gore, J. C., & McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *J Neurophysiol*, 74(3), 1192-1199.
- Regan, D., & Beverly, K. I. Postadaptation orientation discrimination. *Journal of the Optical Society of America A*, 2(2), 147-55.
- Rhodes, G., Jeffery, L., Watson, T. L., Clifford, C. W., & Nakayama, K. (2003). Fitting the mind to the world: face adaptation and attractiveness aftereffects. *Psychol Sci*, 14(6), 558-66.
- Rolls, E. T. (1984). Neurons in the cortex of the temporal lobe and in the amygdala of the monkey with responses selective for faces. *Hum Neurobiol*, 3(4), 209-222.
- Rolls, E. T. & Baylis, G. C. (1986). Size and contrast have only small effects on the responses to faces of neurons in the cortex of the superior temporal sulcus of the monkey. *Exp Brain Res*, 65(1), 38-48.
- Ross, J., Speed, H. D., & Morgan, M. J. (1993). The effects of adaptation and masking on incremental thresholds for contrast. *Vision Res*, 33(15), 2051-56.
- Sawamura, H., Orban, G. A., & Vogels, R. (2006). Selectivity of neuronal adaptation does not match response selectivity: a single-cell study of the fMRI adaptation paradigm. *Neuron*, 49(2), 307-318.
- Sergent, J., Ohta, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain*, 115 Pt 1, 15-36.
- Stromeyer, C. F. & Dawson, B. M. (1978). Form-colour aftereffects: selectivity to local luminance contrast. *Perception*, 7(4), 407-415.
- Stromeyer, C. F., Khoo, M. C., & Muggeridge, D. (1978). Detection of red and green flashes: evidence for cancellation and facilitation. *Sens Processes*, 2(3), 248-271.
- Technical Working Group for Eyewitness Evidence, National Institutes of Justice (U.S.). (1999). Eyewitness evidence: a guide for law enforcement. Washington, D.C..

- Thornton, J. E., & Pugh, E. N. J. (1983). Red/Green color opponency at detection threshold. *Science*, 219(4581), 191-93.
- Tsao, D. Y., Freiwald, W. A., Tootell, R. B., & Livingstone, M. S. (2006). A cortical region consisting entirely of face-selective cells. *Science*, 311(5761), 670-674.
- Watson, T. L. & Clifford, C. W. G. (2003). Pulling faces: an investigation of the face-distortion aftereffect. *Perception*. 32(9), 1109-16.
- Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, 428(6982), 557-61.
- Webster, M. A., & MacLin, O. H. (1999). Figural aftereffects in the perception of faces. *Psychon Bull Rev*, 6(4), 647-53.
- Webster, M. A. & Mollon, J. D. (1993). Contrast adaptation dissociates different measures of luminous efficiency. *J Opt Soc Am A*, 10(6), 1332-1340.
- Webster, M. A. & Mollon, J. D. (1995). Colour constancy influenced by contrast adaptation. *Nature*, 373(6516), 694-698.
- Webster, M. A., Malkoc, G., Bilson, A. C., & Webster, S. M. (2002). Color contrast and contextual influences on color appearance. *J Vis*, 2(6), 505-519.
- Webster, M. A., Raker, V. E., & Malkoc, G. (1998). Visual search and natural color distributions. *Human Vision and Electronic Imaging III*, 3299, 198-509.
- Westheimer, G., & Gee, A. (2002). Orthogonal adaptation and orientation discrimination. *Vision Res*, 42(20), 2339-43.
- Winston, J. S., Henson, R. N., Fine-Goulden, M. R., & Dolan, R. J. (2004). fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. *J Neurophysiol*, 92(3), 1830-1839.
- Zhao, L. & Chubb, C. (2001). The size-tuning of the face-distortion after-effect. *Vision Res*, 41(23), 2979-2994.

Chapter 2

A Psychophysical Study of Selectivity for the Face Properties of Gender and Ethnicity

ABSTRACT

Face-selective neurons in monkeys are highly selective for emotion and gender. Also, the perception of human faces shows adaptation for configuration, gender, ethnicity, expression and identity. Are the mechanisms mediating face perception jointly tuned (i.e. selective for both gender and ethnicity) or are they singly tuned (i.e. selective for gender or ethnicity, but not for both)? The perceptual change in the appearance (male of female/Asian or Caucasian) of morphed face images varying in either ethnicity (Asian or Caucasian) or gender was measured before and after adaptation to female Caucasian, male-Caucasian faces, female-Asian faces, or male-Asian faces. The point along the morph continuum that is seen as belonging to either category (e.g. male or female) is the subjective midpoint. Results across three adaptation conditions suggest that there exist both singly and jointly tuned face-selective mechanisms.

INTRODUCTION

Webster and colleagues recently showed that adaptation to a set of female faces made a previously neutral face appear male (Webster, Kaping, Mizokami, & Duhamel, 2004). This is consistent with neurons tuned to “femaleness” becoming less responsive as a consequence of adaptation. This adaptation effect is analogous to the waterfall illusion, in which adaptation to upward motion makes a stationary pattern appear to move downward (Movshon & Lennie, 1979; Mather, Verstraten, & Anstis, 1998).

In this study, we replicated the face adaptation experiment by Webster and colleagues (Webster, Kaping, Mizokami, & Duhamel, 2004) demonstrating a shift in categorical perception as a result of adaptation. We then extended the paradigm to include two other adaptation conditions. Comparing the pattern of adaptation across these three adaptation conditions, we examined whether face-selective mechanisms are singly tuned, i.e. selective for either gender or ethnicity, but not both, or are jointly tuned, i.e. selective for both gender and ethnicity.

METHODS

1. Subjects

A total of 70 subjects gave informed consent to participate in these experiments, which were approved by the internal review boards either at The Salk Institute for Biological Studies, or University of California, San Diego. All subjects, ages 18-30 years of age, had normal or corrected-to-normal vision. Subjects received either money or

course credit for their participation. One of the six subjects was not included in data analysis because he failed to show adaptation in the control condition (local adaptation).

2. Stimuli

Frontal-view gray-scale face images of Asian (A), Caucasian (C), male (M), and female (F) faces of neutral-expression were taken from the Ekman 1976 face set and the Cohn-Kanade AU-Coded Facial Expression Database; others were photographs of students and staff of UCSD and The Salk Institute. The un-morphed face image set contained 88 exemplars, 22 faces for each category.

Morph images were created by morphing a pair of face images (MorphMan, version 4.0; STOIK Imaging, Moscow, Russia) varying (for example) from male to female. Each morph continuum contained 50 images ranging from fully male to fully female. 10 morph continuums were created for each morphing dimension (e.g. 10 sets of Asian male-female morphs, 10 sets of Caucasian male-female morphs, and so on).

3. Setup

Subjects maintained a viewing distance of 57 cm and images were presented on a Sony computer monitor using MATLAB and the Psychophysics toolbox (Brainard, 1997) on a Dell desktop computer. Stimuli therefore subtended 6.8 degrees of visual angle in Experiments 1, 2 & 4, and 4.1 degrees of visual angle in Experiment 3.

4. Procedure

Subjects performed a 2AFC classification on each morphed face image with a keypress. Each subject was tested in 4 conditions over 8 testing sessions: (1) baseline –

no adaptation, (2) local adaptation, (3) remote adaptation, (4) contingent adaptation. Each testing session was separated by at least one day. In a given session, subjects either judged whether the face images appeared Asian or Caucasian (for A/C morphs), or male or female (for M/F morphs). Subjects were given as much time as they needed and were instructed to maintain central fixation throughout the testing session.

4.1. Local adaptation

This was a replication of the Webster study (Webster, Kaping, Mizokami, & Duhamel, 2004). Subjects were adapted to, for example, MA faces and were then tested with one of two possible morph continuums: (a) a gender (male or female) judgment for Asian faces morphed between male and female, or (b) an ethnicity judgment for male faces morphed between Asian and Caucasian. In both cases, one end-point of the continuum was always male Asian – exactly the same as the adapting face category while the other end-point of the morphs shared one feature (ethnicity or gender) with the adapting face category. Shifts in the subjective midpoint were expected regardless of whether mechanisms are singly or jointly tuned for ethnicity and gender (Figure 2.1 a-b).

4.2. Remote adaptation

For example, a subject adapted to MA faces was then tested with two possible morph continuums: (a) a gender judgment for Caucasian faces morphed between male and female or (b) an ethnicity judgment for female faces morphed between Asian and Caucasian. In both cases, one of the end-points of the continuum shared one feature (ethnicity or gender) with the adapting face category while the other end-point of the continuum did not share any feature with the adapting face. Shifts in the subjective

midpoint were expected if mechanisms were singly tuned, but not if they were jointly tuned (Figure 2.1 c-d).

4.3. Contingent adaptation

Subjects were adapted to two face categories in alternation. For example, observers might be adapted to both MA and FC faces. The adaptation face categories were always “opposites”, i.e. did not share any features with each other. Observers were then tested with two possible morph continuums: (a) a gender judgment for either Caucasian or Asian faces morphed between male and female, or (b) an ethnicity judgment for either female or male faces morphed between Asian and Caucasian. In this case, every morph end-point shared one feature with each of the adapting face categories. Shifts in the subjective midpoint were expected if mechanisms were jointly tuned, but not if they were singly tuned (Figure 2.1 e-f).

All possible combinations of adapting and test categories were tested in a counterbalanced and randomized design. Each testing session was separated by at least one day. In a given session, subjects judged whether the face images appeared Asian or Caucasian (for A/C morphs), or male or female (for M/F morphs). Subjects were given as much time as they needed to make each judgment.

Sessions 1 and 2 were baseline tests that measured responses to gender and ethnicity judgments without adaptation (the order of conditions was randomized across subjects). The remaining 6 sessions were adaptation conditions tested in random order. In

each adaptation session, observers were pre-adapted for three minutes, and were then “topped-up” with a 12 sec re-adaptation period after each trial (Figure 2.1 a).

During adaptation, subjects viewed a series of faces (1 sec/image) while maintaining fixation, from one or two of the 4 face categories (FA, FC, MA, MC). In the local and remote adaptation conditions, subjects were adapted with faces drawn from one category; while in the contingent adaptation condition, subjects were adapted to two categories. To equalize the amount of adaptation for a given category over time, in both local and remote adaptation conditions we used a blank screen as the ‘second category’. There were 96 trials per session and each session lasted approximately 40 minutes.

Responses were averaged across all possible morphs and a psychometric function (cumulative normal) was fit to each subject’s responses. See Figure 1b for an example; the x-axis represents the morph continuum and the y-axis represents the percentage of time the subject responded that the morph face image appeared Asian. We interpolated the psychometric function to find the morph that was seen as being Asian 50% of the time (and Caucasian the other 50% of the time). This point in the psychometric function is referred to as the subjective mid-point.

Changes in the categorical boundary were then quantified by measuring shifts in the subjective mid-point away from the adaptor category. After adapting to a MA face, for example, we expected to see a shift in the subjective midpoint when observers are asked to judge the gender of a morph varying between male and female Asians. To quantify the shift in the subjective midpoint, we measured the difference between the pre- and post-adaptation subjective midpoints along the y-axis since the x-axis (morph continuum) is not necessarily linear. For instance, the change from morph step 10 to 20

may not equal the change from step 20 to 30. We dealt with this by measuring the difference between the pre- and post-adaptation subjective midpoints along the y-axis rather than the x-axis. We interpolated the post-adaptation psychometric function to find the morph that was reported as appearing Asian 50% of the time (and Caucasian the other 50% of the time) – in Figure 2.1b this morph number is 32. We then found the percentage of time that morph 32 was reported as appearing Asian before adaptation (the baseline condition). In Figure 2.1b, morph 32 was reported as appearing Asian 97% of the time before adaptation. We calculated the shift in the subjective midpoint as being 47% - the difference between 97% and 50%. This shift along the y-axis can be thought of as being a measure of the shift in subjective “Asianess” of a given morph as a function of adaptation. These shifts along the y-axis were averaged over multiple replications of the same experimental condition for each subject. We measured the shift in this subjective midpoint under local, remote, and contingent adaptation conditions.

The predicted pattern of results across all three adaptation conditions is shown in Figure 2.2. If mechanisms are singly tuned, then adaptation effects are expected under local and remote adaptation. If mechanisms are jointly tuned, then adaptation effects are expected under local and contingent adaptation.

RESULTS

The mean adaptation effect for all 5 subjects is shown in Figure 2.3. We found significant adaptation effects for all subjects under all three adaptation conditions ($p < 0.05$). The average adaptation effect across all subjects for local, remote and

contingent adaptation was 21.54% (SEM \pm 3.47), 16.96% (SEM \pm 3.86), 11.74% (SEM \pm 2.77), respectively.

Adaptation effects averaged across subjects were also significant (local: $t(94)=12.8586$, $p<.0001$; remote $t(100)=11.2775$, $p<.0001$; contingent: $t(296)=8.3715$, $p<.0001$). As might be expected, we found greater adaptation in the local condition than in the remote or the contingent condition, though this result was only significant for the contingent condition (Tukey-Kramer, $p<0.05$). There was also greater adaptation in the remote condition than the contingent condition (Tukey-Kramer, $p<0.05$). These results are consistent with the a model in which the local adaptation effect is driven by both singly and jointly tuned mechanisms, adaptation in the remote condition is driven by singly tuned mechanisms, and adaptation in the contingent condition is determined by jointly tuned mechanisms. The presence of adaptation under all three conditions therefore, implies the existence of both singly and jointly tuned mechanisms.

DISCUSSION

We used a face adaptation technique developed by Webster and colleagues (2004) to examine the tuning properties of face-selective mechanisms (Webster, Kaping, Mizokami, & Duhamel, 2004). We tested observers in three adaptation conditions under which singly tuned and jointly tuned mechanisms would be expected to yield different patterns of adaptation. Our results suggest the existence of both singly and jointly tuned mechanisms selective for gender and ethnicity (Asian and Caucasian).

As described above, we would expect to see adaptation in the local adaptation condition regardless of whether or not mechanisms were singly or jointly tuned. We did

see significant local adaptation effects in 5 of the 6 observers (the sixth did not show adaptation effects under any condition). We would only expect to see contingent adaptation if there are jointly tuned mechanisms. We found that, of the 5 observers who showed adaptation effects, all five did show significant adaptation effects in the contingent condition. If there are singly tuned mechanisms, we would expect to see remote adaptation. Again, of the 5 observers who showed adaptation effects, all five showed remote adaptation effects.

Until now, we have described “femaleness” and “Asianness” as being a single dimension. However the quality of “femaleness” or “Asianness” does not consist of a single feature. Rather, femaleness is represented by a variety of cues that are fairly unreliable individually, but tend to be highly correlated with each other within female faces (rounder cheeks, larger eyes, etc.). According to visual coding theories (Barlow, 1991; Barlow, & Földiák, 1989), adaptation does not adapt individual mechanisms tuned for each of the individual underlying cues, but rather results in adaptation to the conjunction of these features along axes whose orientations best de-correlate these features. Thus visual coding provides an alternative explanation for why we see opponent coding and adaptation effects for dimensions such as gender and ethnicity, even though these qualities are clearly delineated by a complex multiplicity of cues (Barlow, 1991; Barlow, & Földiák, 1989). For a more complete description of how visual coding models might apply to our results see the Discussion of Chapter 4.

It still remains to be seen whether this joint selectivity is restricted to the properties of gender and ethnicity. Both of these properties do not vary over time for a given face, and there are fairly limited numbers of relatively disjoint “features” to encode

– the number of genders is limited to male vs. female and there are only a limited number of distinguishable ethnicities. One promising area of future research will be to see whether other more continuous properties of faces, such as expression and attractiveness will show this same joint tuning.

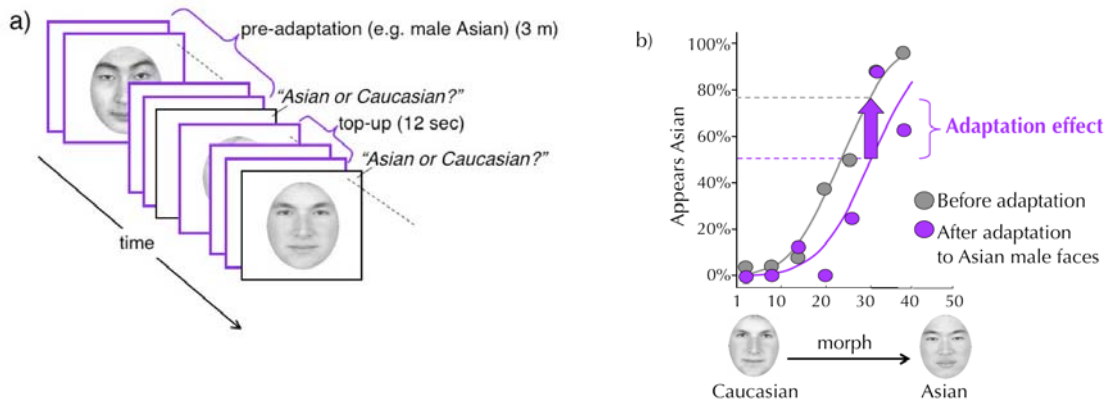


Figure 2.1. Experimental design and example psychometric function. a) Subjects performed a 2-AFC classification of morphed face images. There was no initial adaptation period and blanks replaced face images during the top up in the baseline conditions. b) The x-axis represents the morph continuum; the y-axis represents the percentage of time that subject 1 responded that the face appeared Asian. We measured the shift in the psychometric function along the y-axis by interpolating (black dotted line) the post-adaptation psychometric function to find the morph (No. 31) that was seen as Asian on 50% of the trials; and then interpolated again (vertical arrow) to find that the percentage of trials this morph was seen as Asian before adaptation was 79% (gray dotted line); this yields a 29% adaptation effect.

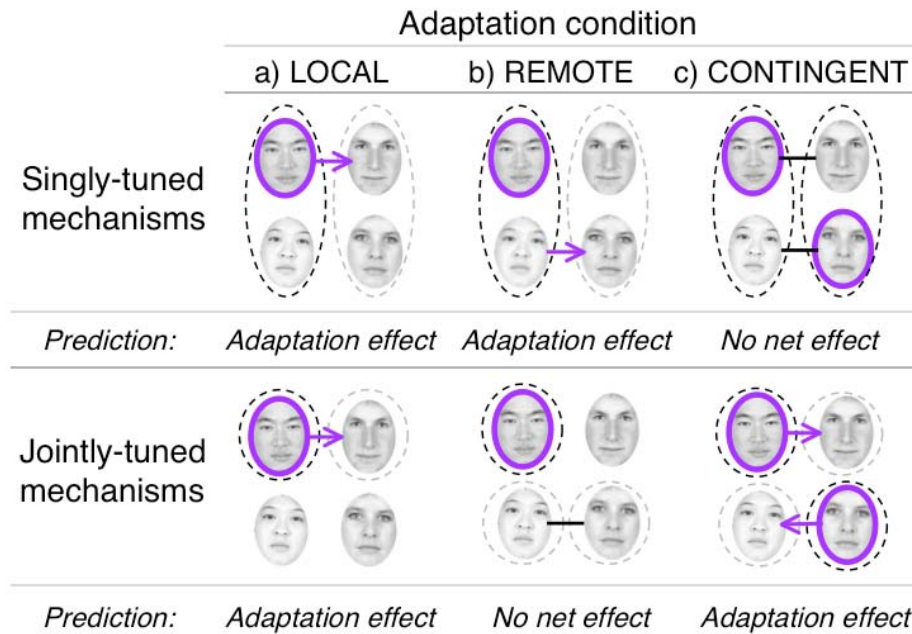


Figure 2.2. Adaptation effect predictions. For all conditions, a single example is described in which subjects were first adapted to MA faces (purple circle). Dashed circles represent the mechanisms that would be expected to mediate performance in the task; only those mechanisms involved in the task are shown. a, Local adaptation for singly-tuned mechanisms. Subjects discriminated the ethnicity of A/C male morphs. Mechanisms selective for Asian faces would be adapted (black dashed circle) while mechanisms selective for Caucasian faces would be un-adapted (gray dashed circle). We predict adaptation effects (arrow). b, Local adaptation for jointly-tuned mechanisms. Mechanisms selective for MA faces would be adapted while mechanisms selective for MC faces would be un-adapted; thus, we predict an adaptation effect. c, Remote adaptation for singly-tuned mechanisms. Subjects discriminated the ethnicity of A/C female morphs. Singly tuned mechanisms mediating ethnicity discrimination are unselective for gender. Adaptation to MA faces would therefore transfer to ethnicity discriminations on female faces. d, Remote adaptation for jointly-tuned mechanisms. Both mechanisms selective for FA and FC faces would remain un-adapted; thus, we predict no net effect (line). e, Contingent adaptation for singly-tuned mechanisms. Subjects were adapted to FC faces randomly alternating with MA faces. Subjects then made ethnicity discriminations on A/C male morphs and A/C female morphs. For singly tuned mechanisms, mechanisms selective for both Asian and Caucasian faces would be adapted, resulting in no net effect. f, Contingent adaptation for jointly-tuned mechanisms. Mechanisms selective for FA and FC faces would remain un-adapted, resulting in an adaptation effect.

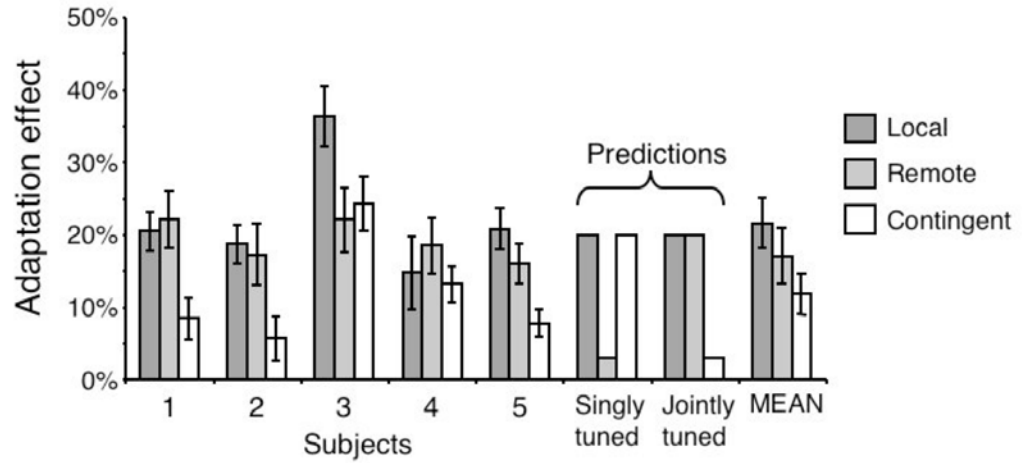


Figure 2.3. Adaptation results and predictions. Categorical boundary shifts were found in all subjects in all adaptation conditions. Error bars for individual subjects are calculated across all repeats within a condition. The error bar for the mean response is calculated across subjects.

ACKNOWLEDGMENTS

Chapter 2 of this dissertation, “Psychophysical Study of Selective Mechanisms for Face Properties”, contains work that has been published in:

Ng, M., Ciaramitaro, V. M., Anstis, S. A., Boynton, G. M., Fine, I. (2006). Selectivity for the configural cues that identify the gender, ethnicity, and identity of faces in human cortex. *Proc Nat Ac Sci* 103(51):19552-57.

and in the following submitted manuscript:

Ng, M., Boynton, G. M., Fine, I. (2007). Face adaptation does not improve performance on search or discrimination tasks. *Journal of Vision*.

Permission to include work from these manuscripts was granted by the co-authors.

REFERENCES

- Barlow, H. B. (1991). A theory about the functional role and synaptic mechanism of after-effects. In C. Blakemore (Ed.), *Vision: Coding and Efficiency* (pp. 363-75). Cambridge: Cambridge University Press.
- Barlow, H. B., & Földiák, P. (1989). Adaptation and decorrelation in the cortex. In *The computing neuron* (pp. 54-72). Boston: Addison-Wesley Longman Publishing Co., Inc.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spat Vis*, 10(4), 433-436.
- Mather, G., Verstraten, F., & Anstis, S. (1998). *The Motion Aftereffect: A Modern Perspective*. The MIT Press.
- Movshon, J. A. & Lennie, P. (1979). Pattern-selective adaptation in visual cortical neurones. *Nature*, 278(5707), 850-852.
- Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, 428(6982), 557-61.

Chapter 3

An fMRI Adaptation Study of Brain Regions Selective for Face Properties

ABSTRACT

We used functional magnetic resonance (fMRI) adaptation to examine how and where the visual configural cues underlying identification of facial ethnicity, gender and identity are processed. We found that the cortical regions showing selectivity to these cues are distributed widely across inferior occipital cortex, fusiform areas, and the cingulate gyrus. These regions were not co-localized with areas activated by traditional face area localizer scans. Traditional face area localizer scans isolate regions defined by stronger fMRI responses to a random series of face images than to a series of non-face images. Because these scans present a random assortment of face images, they presumably produce the strongest responses within regions containing neurons that are face-sensitive, but not highly tuned for face type. These selective neurons might be expected to show only weak selective adaptation effects. In contrast, the largest responses to our selective adaptation paradigm would be expected within areas containing more selectively tuned neurons that might only show a sparse collective response to a series of random faces. Many aspects of face processing (e.g. prosopagnosia, recognition, configural vs. featural processing) are likely to rely heavily on regions containing high proportions of neurons that show selective tuning for faces.

INTRODUCTION

In the previous study (Chapter 2), we found mechanisms selective for both gender and ethnicity using psychophysical face adaptation (Webster, Kaping, Mizokami, & Duhamel, 2004). As described below (Discussion), in recent years, there has been increasing interest in using fMRI adaptation techniques to investigate the selectivity of neural tuning within face processing areas (Loffler, Yourganov, Wilkinson, & Wilson, 2005; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Winston, Henson, Fine-Goulden, & Dolan, 2004).

In the current study, we used an fMRI adaptation paradigm analogous to the psychophysical paradigm described in Chapter 2 to further examine how and where conjunctions of configural cues to ethnicity, gender and identity are processed in the human visual system. We were interested in whether these cues were processed in similar regions of visual cortex, and to what extent these regions fall within cortical areas traditionally associated with face processing.

METHODS

1. Participants

Four subjects (2 females and 2 males; 23-29 yrs. old, mean age: 25.3) gave informed consent to participate in this experiment, which was approved by the institutional review board of the Salk Institute for Biological Studies. Each subject

participated in six scanning sessions. fMRI data were acquired several weeks after the completion of the psychophysical experiment.

2. Stimuli

Face images were frontal-view grayscale face images used in the study described in Chapter 2. There were 11 exemplars of each face type and images were presented at a rate of 1 sec/image (similar to the psychophysical study in Chapter 2). Object images included 22 exemplars each of cars, houses, and phase-scrambled faces. The images subtended approximately 6.7 degrees of visual angle (as compared to 7.1 degrees of visual angle in the psychophysical experiments in Chapter 2).

3. Apparatus

Functional imaging was conducted at the Center for Functional Magnetic Resonance Imaging at the University of California, San Diego (UCSD). A GE 3T scanner system and standard 8-channel head coil was used to collect the functional data; a Siemens 1.5T scanner was used to collect an anatomical reference volume which was used to align functional data across multiple scanning sessions using standard alignment techniques (Teo, Sapiro, & Wandell, 1997b).

In all sessions, subjects lay in a supine position stabilized by a bite bar, which was fastened to the MR table. In functional scans, visual stimuli were projected from a computer laptop by an NEC projector on to a screen near the subject's head. Subjects viewed the reflected stimuli on an angled mirror fixed above the eyes.

4. Adaptation scans

Only one scanning session (one condition) was conducted in a day, in order to avoid subject fatigue and minimize carry-over adaptation across sessions. The effect of any residual adaptation remaining from adaptation on a previous day would only reduce the magnitude of measured adaptation.

Prior to BOLD signal measurement, subjects were pre-adapted for 4 min to faces from the adaptor set, while lying in the scanner. We then immediately measured BOLD responses using an uneven block design, which alternated between the adaptor set (24 sec) and the non-adapted set (8 sec). This was repeated for 6 1/2 cycles for a total scan time of 208 sec. The first half cycle was discarded to avoid magnetic saturation effects; so analyzed data consisted of 6 cycles. The transition between pre-adaptation and measurement was invisible to the observer, except for a change in scanner noise.

4.1. Contingent Adaptation

We carried out 2 sessions; each consisting of 6 repeated scans, to measure contingent adaptation to a combination of gender and ethnicity cues. In one session, the adaptor set consisted of MA and FC faces, and the non-adapted set consisted of FA and MC faces. In the second session (carried out on a different day), the faces in the adaptor set would consist of MC and FA faces and the non-adapted faces would consist of MA and FC faces. The order of these sessions was randomly counterbalanced across subjects, and the order in which face images were presented was randomized both within and across scans. In total, we obtained 48 contingent condition scans (2 sessions x 6 repetitions x 4 subjects).

4.2. Individual Adaptation

To measure adaptation to individual faces, we arbitrarily assigned each face to either the adaptor or non-adapt sets. The same adapting set was used throughout a given session to maximize adaptation effects. This condition was equivalent to the identity specific adaptation demonstrated psychophysically by Leopold et al. (Leopold, O'Toole, Vetter, & Blanz, 2001; also see (Loffler, Yourganov, Wilkinson, & Wilson, 2005)). In total, we obtained 24 individual condition scans (6 repetitions x 4 subjects).

4.3. Configural Adaptation

To test the extent to which any adaptation observed in the contingent condition was due to general configural similarities within faces, we adapted 3 of our 4 subjects to Asian and Caucasian hermaphrodites (morphs between males and females), and measured adaptation effects for Eurasian males and females (morphs between Asian and Caucasian), and vice versa. If mechanisms are preferentially tuned along the cardinal directions of M/F, and A/C, then, analogous to experiments that have been carried out examining chromatic tuning (Krauskopf, Williams, & Heeley, 1982), we would expect to see weaker effects when adapting “off-axis”.

We carried out 2 scanning sessions, each consisting of 6 repeated scans. In one session, the adaptor set contained male Eurasian and female Eurasian faces, and the non-adapted set consisted of hermaphrodite Caucasian and hermaphrodite Asian faces. In the second session (carried out on a different day), the adaptor set was hermaphrodite Caucasian and Asian face images, and the non-adapted set consisted of male and female

Eurasian faces. The order of sessions was randomly counterbalanced across subjects. In total, we obtained 48 scans for the configural condition (2 sessions x 6 repetitions x 4 subjects).

4.4. Faces vs. non-face localizer scans

We ran the following three localizers: (1) faces vs. houses, (2) faces vs. cars, and (3) faces vs. phase-scrambled faces. We used an even block design that alternated between a variety of faces for 16 seconds, and, for example, a variety of car images for 16 seconds; this was repeated for 6 1/2 cycles for a total of 208 seconds of scan time. Analyzed data consisted of 6 cycles since the first half cycle was discarded to avoid magnetic saturation effects. Each localizer was run twice for a total of twelve scans per localizer condition. All six localizer scans were completed in a single session. In total, we obtained 24 localizer scans (2 repetitions x 3 localizer conditions x 4 subjects).

5. Analysis

Segmentation, flattening, and inflation of cortical surfaces were carried out using customized Matlab software (Sereno, McDonald, & Allman, 1994; Engel, Glover, & Wandell, 1997). Linear trends were subtracted from the fMRI time course of each voxel and the activity of each voxel across each scan was divided by the mean activity to convert BOLD response to percentage signal change (Boynton, Engel, Glover, & Heeger, 1996). There were, necessarily, slight differences in slice prescriptions across scans. Occipital and temporal areas were always included, but the extent of parietal coverage

varied slightly across sessions. Each session's data was registered to an anatomical image collected in a separate scanning session, and for each subject only those voxels for which we collected data in every session were included in further analyses.

The fMRI response of each voxel was then fit with an estimate of the hemodynamic response function. In the case of the adaptation scans, a canonical hemodynamic impulse response function was convolved with the uneven block-design (Teo, Sapiro, & Wandell, 1997a) and coherence values were calculated between the response of each voxel and the estimated BOLD responses for the best fitting delay.

In the case of the localizer scans, the impulse response function was convolved with the even block design and coherence values were calculated between the response of each voxel and the estimated BOLD responses for the best fitting delay for responses in phase with the face stimuli. Voxels that responded out of phase with the non-face stimuli were assigned a negative coherence value. We then averaged coherence and delay values for each voxel across every repetition of each condition.

RESULTS

Face selective adaptation responses were measured in three conditions. In all adaptation scans, prior to BOLD signal measurement, subjects were pre-adapted to an adaptor face set while lying in the scanner. Immediately following pre-adaptation, we measured BOLD responses using an uneven block design that alternated between presenting the adaptor set for 24 seconds, and the non-adapted set for 8 seconds.

The contingent adaptation condition was analogous to the psychophysical experiment described in Chapter 2. The adaptor set contained MA and FC faces; the non-adapted set contained FA and MC faces, or vice versa. In the individual adaptation condition, we arbitrarily assigned faces to the adaptor or non-adapted sets. In the configural adaptation condition, we adapted subjects to Asian and Caucasian hermaphrodites (morphs between males and females), and the non-adapted set consisted of Eurasian males and females (morphs between Asian and Caucasian), or vice versa.

We also carried out three traditional face area localizer conditions: 1) faces vs. houses, 2) faces vs. cars, and 3) faces vs. phase-scrambled faces, using a standard even block design (16 seconds on, 16 seconds off).

We used two predicted time-courses to fit BOLD responses over time. The slow time-course assumes that adaptation occurs on a relatively long time scale (several seconds or longer), and consequently in the case of adaptation scans, the neural response is dominated by the effects of the 4-minute pre-adaptation period and the uneven duty cycle. The slow time-course, therefore, predicts larger BOLD responses to non-adapted as compared to adapted stimuli. BOLD responses to localizer conditions were fit using a standard time course that assumes that larger BOLD responses will be found for one of the two sets of stimuli (e.g. faces or houses).

The transient time-course assumes that the majority of adaptation occurs on a much more rapid time scale (a few seconds or less), and therefore predicts a transient increase in BOLD response whenever the stimulus type changes, for both adaptation and

localizer conditions. Figure 3.1 shows example BOLD responses that are better described by either a slow or transient time-course.

Over all, fitting responses with a slow time-course produced significantly more activation (number of voxels active at $p < 0.05$) than fitting with a transient time course ($p < 0.001$; 3 factor ANOVA, subject x condition x time-course). This suggests that a significant proportion of the adaptation in our study occurred on a time scale of several seconds or longer. Further analyses were therefore based on slow time-course predictors.

Figure 3.2 shows parameter maps of coherence values based on the slow time-course. Activity was distributed across inferior occipital (iOcc) and fusiform areas (FuG), as well as the cingulate gyrus (CG). Coherence maps based on the transient time-course showed significantly less activity. However, where activation was found with the transient time course, the location of activity was qualitatively similar to the adaptation found using the slow time course (Figure 3.2).

Across all four subjects we tend to see robust activity in phase with the non-adapted face images (red/magenta) for all three adaptation conditions. As might be expected, we see little or no out-of-phase activity (green) in any of the adaptation experiments. The other two localizers (not shown) had similar patterns of activity as the face vs. house localizer condition.

In all our adaptation sessions, we used a finite stimulus set. Consequently, in a single scanning session, subjects were exposed to a given face as many as 29 times when it was from the adapting set and as few as 2 times when it was a face from the non-adapt

set. Therefore, our contingent and configural conditions presumably include significant adaptation to individual faces, as well as adaptation to gender and ethnicity cues.

Averaged across subjects, the contingent and configural condition had 2.8 and 2.7 times as many active voxels, respectively, as the individual condition. However, a single factor ANOVA comparing the number of voxels active at a coherence threshold of $p < 0.05$ (unblurred) across the three adaptation conditions fell below significance ($p = 0.07$). A 1-tailed paired t-test ($p < 0.05$, Bonferroni adjusted) did find fewer voxels active in the individual adaptation condition than in the contingent adaptation condition. There was no significant difference in the number of active voxels between configural and individual adaptation conditions. Nor was there a significant difference in the number of active voxels between contingent and configural conditions, suggesting that neurons do not have a strong bias towards being tuned along male-female and Asian-Caucasian “cardinal axes” (Engel, Zhang, & Wandell, 1997).

Activated areas were defined using a combination of Talaraich coordinates (Talairach, & Tournoux, 1988) and anatomical landmarks (Table 3.1). As would be expected, we found areas within iOcc and FuG that responded selectively to face vs. non-face stimuli in the localizer scans (Haxby, Hoffman, & Gobbini, 2000).

In adaptation conditions, we see activity close to the regions that showed activation in response to faces in localizer conditions. However, we also see activity in the CG in adaptation scans. In the contingent condition, all subjects showed significant activity within the CG; in the individual and configural conditions, three of the four subjects showed significant activity within the CG. Very little activity was found within

the CG for localizer conditions. Our finding of face-selective responses with CF may have implications for the difficulties in face processing found in autism spectrum disorders (Schultz, & Robins, 2005).

The blurring carried out for Figures 3.2 and 3.3 require that voxels over a 6 mm region or greater show a mean activity of at least $p=.05$. Such clustering criteria helps to reduce false positives due to multiple comparisons (Friston, Rotshtein, Geng, Sterzer, & Henson, 2006). However, one consequence of such clustering is that the activity is represented on a relatively coarse spatial scale.

It has recently been shown that individual voxels can show orientation selective responses that are driven by differences in selectivity across cortical distances of less than a millimeter (Haynes & Rees, 2005; Kamitani & Tong, 2005). However, these classification algorithms rely on analyzing responses within a predetermined ROI. Moreover, these algorithms are susceptible to small differences in mean response between conditions, and to differences in the time course between the uneven and even block designs. Therefore, to quantify spatial overlap on a finer scale between conditions, we calculated the pair-wise cross-correlation for each voxel between coherence values (unblurred) in each possible pair of conditions. This was done using an ROI for each subject that included all voxels that showed significant activity, either in or out of phase, with the presentation of faces (blurred, $p<0.05$) in all adaptation and localizer conditions.

Figure 3.4a shows the mean correlation coefficient between each condition across all voxels averaged across subjects. A positive correlation coefficient (shown in red) indicates overlap between voxels of high coherence values between two conditions, i.e.

both conditions produce similar spatial patterns of responses; negative correlations are shown in green. Figures 4b and c show the same cross-correlation analysis for activity within ventral and dorsal areas, respectively (Puce, Allison, Gore, & McCarthy, 1995).

All three localizer conditions show strong mutual correlations that are presumably being driven by co-localized responses to faces across the three localizers. This correlation may be particularly strong because all three localizers were carried out within the same session, thereby minimizing differences in field distortions and misalignment across localizer scans. Responses to the contingent, configural and identity conditions were also mutually correlated, despite being run in separate sessions. This suggests that similar areas were activated in the three adaptation conditions.

Importantly, responses in adaptation conditions are not particularly well correlated with responses in phase with faces in the localizer scans. Regions showing selective adaptation effects show surprisingly little spatial overlap with traditionally defined face areas. Indeed, correlations in activity between adaptation and localizer conditions were as likely to be negatively as they were likely to be positively correlated. Thus, regions showing adaptation to individuals or to gender and ethnicity show surprisingly little spatial overlap with traditionally defined face areas. This pattern of results was found in ventral as well as dorsal areas, suggesting that differences in spatial distribution exist on a relatively fine scale; and is consistent with recent findings of heterogeneity of selectivity within ventral regions using high-resolution imaging (Grill-Spector, Sayres, & Ress, 2006).

DISCUSSION

Face processing involves many stages: first, we recognize that a face is present; then we further classify the face or identify it as an individual that we know. It has previously been shown that within areas isolated by traditional face area localizers, there are subdivisions that differentiate between different types of face processing. For example, within the areas that respond to face localizer scans, the inferior Occipital cortex (iOcc) tends to be sensitive to the physical information present in a face, whereas the right fusiform gyrus (FuG) tends to be more sensitive to identity information (Rotshtein, Henson, Treves, Driver, & Dolan, 2005). Another recent study has shown that the FuG and posterior superior temporal sulcus tend to be more sensitive to identity information, whereas information about emotion tends to be processed in a more anterior portion of the superior temporal sulcus (Winston, Henson, Fine-Goulden, & Dolan, 2004). Previous studies have also found evidence for distributed networks for face processing that can fall outside traditionally defined areas (Winston, Henson, Fine-Goulden, & Dolan, 2004; Haxby et al., 2001).

Here, we examined sensitivity to the configural cues that underlie face processing. It has previously been shown psychophysically that subjects adapt to gender, and ethnicity cues (Chapter 2; Webster, Kaping, Mizokami, & Duhamel, 2004), as well as to individual identity (Leopold, O'Toole, Vetter, & Blanz, 2001). Here, using a slow adaptation technique, we measured adaptation to conjunctions of configural cues using both psychophysical and fMRI adaptation.

The slow adaptation paradigm used in our fMRI experiment differs significantly from those used in previous rapid event-related studies, which measure responses to a rapid change of identity (or a change along some other configural dimension) as compared to the immediate repetition of a single face (Loffler, Yourganov, Wilkinson, & Wilson, 2005; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Winston, Henson, Fine-Goulden, & Dolan, 2004). Worryingly, it has been shown that fMRI measurements of selectivity can differ depending on whether fast or slow adaptation paradigms are used (Fang, Murray, & He, 2007), presumably because adaptation depends not only on the selectivity of underlying neurons, but also on their susceptibility to adaptation. For example, in V1 orientation-selective release from adaptation is only observed using a slow adaptation technique (Fang, Murray, Kersten, & He, 2005). In our study, we examined both fast and slow adaptation effects by fitting data with both transient and slow predicted time courses. We found that slow adaptation effects (over several seconds) were significantly more powerful than transient adaptation effects (occurring over a few seconds). However, where activation was found with the transient time course, the location of activity was qualitatively similar to the adaptation found on a slow time scale (Figures 3.2 and 3.3).

We find here, that the regions of cortex showing selectivity for the configural cues that identify gender, ethnicity and identity fall within iOcc, FuG, and the cingulate gyrus (CG). There was no significant difference in the extent of activation between the configural and the contingent condition, suggesting a lack of strong biases in tuning towards “cardinal” axes of male-female and Asian-Caucasian. This suggests that adaptation is driven by configural similarities along any orientation, rather than clustering

along ‘cardinal’ dimensions of gender and ethnicity. Activation was stronger in configural and contingent adaptation conditions than in the individual adaptation condition, but this effect was below significance.

We expected to find adaptation effects in the FuG, since activity in response to faces is regularly observed in this area. However, the robust adaptation effects in the CG were less expected. This area has been associated much more consistently with a variety of other tasks, including error processing, selective and competitive attention, expectancy and reward (Shidara & Richmond, 2002; Carter et al., 1998; Petit, Courtney, Ungerleider, & Haxby, 1998). One possibility is that responses within the CG were driven by the greater ‘novelty’ of the non-adapted faces (or some other state-change such as expectancy that might differ across even and un-even block designs). However, if this were the case we might have expected to find responses within the CG to the transient time course for both adaptation and localizer conditions (assuming that the CG was sensitive to novelty changes on a relatively short time scale of a few seconds). There was no evidence of this in our data, as shown in Figure 3.3.

One previous study has found the CG to be associated with the encoding of a variety of faces (Haxby et al., 1996), and a second found CG activity during a reverse learning paradigm that involved learning and responding to contingencies between face identity and emotional expression (Kringelbach & Rolls, 2003). Our data suggest that highly selective face sensitive neurons do exist within the CG. It is not entirely surprising that this area has seemed unresponsive in many previous studies - the traditional localizer approach is not well suited for identifying areas in which neurons are face-sensitive and

highly selective in their face tuning. In areas containing neurons with highly selective tuning, any given neuron would rarely (if ever) be activated when presented with a series of random faces, resulting in a weak collective fMRI response to traditional localizer scans.

Our cross-correlation technique enables examination of the spatial distribution of activity patterns on a fine-scale. Such patterns would be masked by blurring, clustering, or averaging of the fMRI response across different observers' brains (Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Winston, Henson, Fine-Goulden, & Dolan, 2004). We found that adaptation responses across contingent, configural and identity conditions were correlated with each other, suggesting similar spatial distributions of activity. Overall, these results are consistent with the notion that the dimensions of gender, ethnicity and identity are simply different dimensions along which facial similarity can be varied, without necessarily involving separate processing regions.

Regions showing adaptation effects were relatively uncorrelated with regions responding to faces in the localizer scans, within both dorsal and ventral regions of cortex. The lack of spatial correlation between traditionally defined face regions and adaptation-sensitive regions is likely to be due to the insensitivity of traditional localizer scans to produce responses within areas containing highly selective neurons. Because traditional localizers present a random assortment of faces (Kanwisher, McDermott, & Chun, 1997), strong responses to localizer scans will be found within areas containing very broadly tuned face-sensitive neurons. However, neurons that are very broadly tuned will respond to all faces regardless of their ethnicity or gender, and will therefore show weak or non-existent selective adaptation effects. In contrast, as described above, very

selectively tuned neurons will only show a weak collective response to a series of random faces. For many studies examining face processing (e.g. prosopagnosia, recognition, configural vs. featural processing), regions showing selective face tuning are likely to be at least as important as those less selective regions that tend to be identified using traditional localizer scans.

Table 3.1. Brain areas showing significant BOLD responses for each subject by condition.

	S1	S2	S3	S4
<i>Contingent</i>	FuG CG	iOcc FuG CG	iOcc FuG CG	iOcc FuG CG
<i>Configural</i>	iOcc FuG CG	CG	iOcc FuG CG	iOcc FuG CG
<i>Individual</i>	FuG CG	CG	iOcc FuG	iOcc FuG CG
<i>Faces vs. houses</i>	iOcc FuG	FuG	iOcc FuG	iOcc FuG

FuG: Fusiform gyrus; CG: Cingulate gyrus; iOcc: Inferior occipital cortex

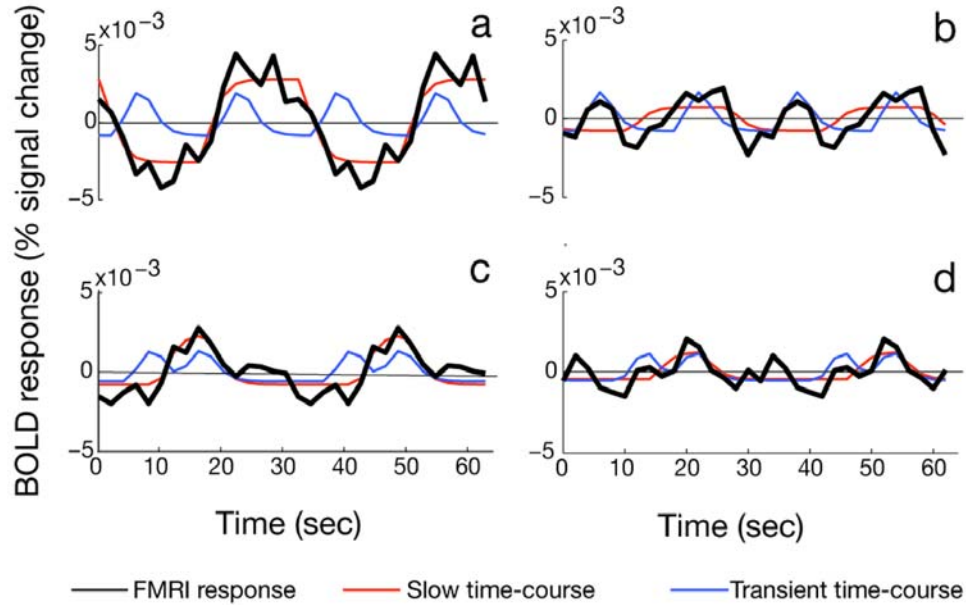


Figure 3.1. Example BOLD responses described by slow or transient time-courses. BOLD responses were fit by either a slow (a,c) or transient (b,d) time-course. The top two panels are responses to the even-duty faces vs. houses condition; the response is better fit by: **a**) the slow time-course (in FuG), and **b**) the transient time-course (in CG). The bottom two panels are responses to the uneven-duty contingent condition; here, the response is better fit by: **c**) the slow time-course (in FuG), and **d**) transient time-course (in CG). We defined ROIs as regions localized to either FuG (which includes lingual areas) or the CG that were active in either the contingent or faces vs. houses condition using the slow time course (regions shown as active in rows 1 and 4 of Figures 2 and 3).

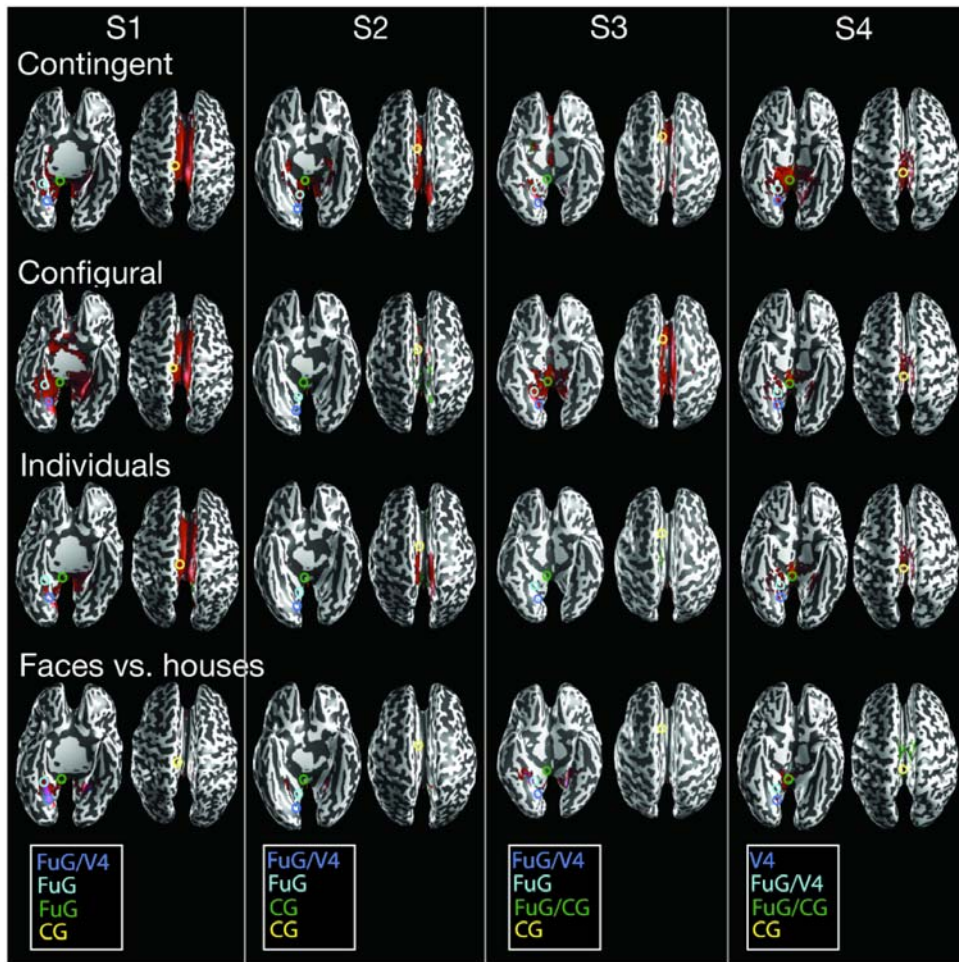


Figure 3.2. Coherence maps based on the slow time-course. Data were spatially blurred in the 3d representation using a Gaussian filter with a half-width at half height of 6.7 mm. Responses in phase (using the slow time-course) with the non-adapted face set (adaptation conditions) or face images (localizer) are in red ($p=.05$), and magenta ($p=.01$); activity in phase with the adapted face set or house images are in green ($p=.05$). P-values of .05 and .01 correspond to coherence values .169 and .236, respectively. Areas V4, FuG, and CG are circled.

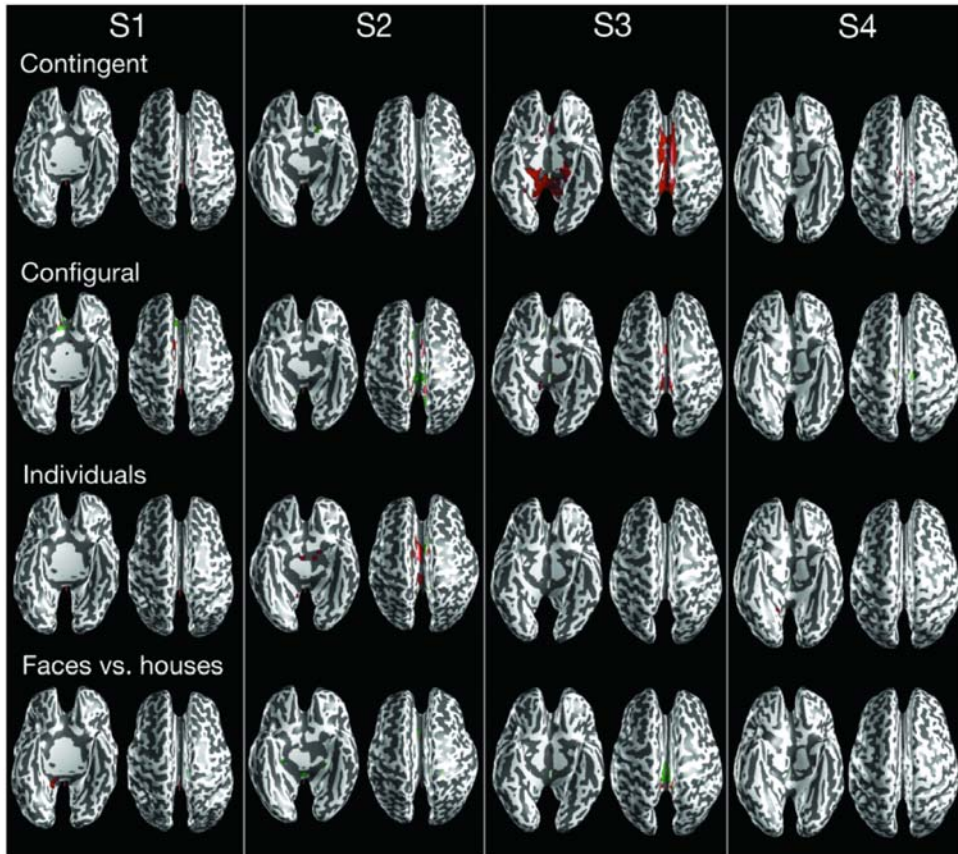


Figure 3.3. Coherence maps based on the transient time-course. on inflated brains. Data were spatially blurred in the 3d representation using a Gaussian filter with a half-width at half height of 6.7 mm. Responses in phase (using the slow time-course) with the non-adapted face set (adaptation conditions) or face images (localizer) are in red ($p=.05$), and magenta ($p=.01$); activity in phase with the adapted face set or house images are in green ($p=.05$). P-values of .05 and .01 correspond to coherence values .169 and .236, respectively. Areas V4, FuG, and CG are labeled.

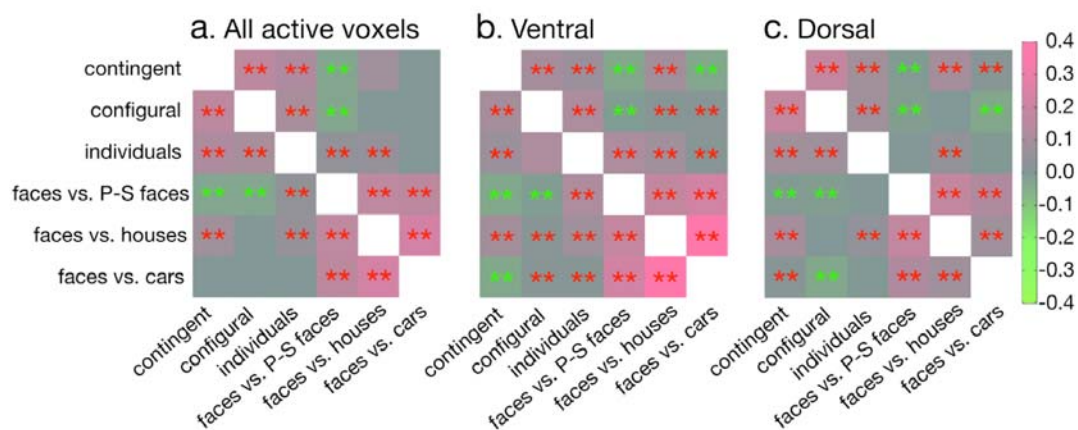


Figure 3.4. Correlation coefficients between conditions, averaged across: a) all voxels, b) ventral regions only (includes iOcc and FuG), c) dorsal regions only (includes CG). Significance values of $p < 0.05$ (*) and $p < 0.01$ (**) were determined using a Monte-Carlo simulation procedure in which we scrambled the location of voxels. Because of the large number of voxels included in the analysis, even very low correlation values can be significant. Significantly positively and negatively correlated activity is indicated by red and green asterisks, respectively.

ACKNOWLEDGMENTS

Many thanks to Michael A. Webster for help and advice. This work was supported by NSF IGERT fellowship DGE-0333451 (MN) and NEI-014645 (IF).

Chapter 3 of this dissertation, “Function Imaging Study of Selective Mechanisms for Face Properties”, contains work that has been published in:

Ng, M., Ciaramitaro, V.M., Anstis, S.A., Boynton, G.M., Fine, I. (2006). Selectivity for the configural cues that identify the gender, ethnicity, and identity of faces in human cortex. *Proc Nat Ac Sci*. 103(51):19552-57.

Permission to include work from these manuscripts was granted by the co-authors.

REFERENCES

- Boynton, G. M., Engel, S. A., Glover, G. H., & Heeger, D. J. (1996). Linear systems analysis of functional magnetic resonance imaging in human V1. *J Neurosci*, *16*(13), 4207-4221.
- Engel, S. A., Glover, G. H., & Wandell, B. A. (1997). Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cereb Cortex*, *7*(2), 181-192.
- Engel, S., Zhang, X., & Wandell, B. (1997). Colour tuning in human visual cortex measured with functional magnetic resonance imaging. *Nature*, *388*(6637), 68-71.
- Fang, F., Murray, S. O., Kersten, D., & He, S. (2005). Orientation-tuned fMRI adaptation in human visual cortex. *J Neurophysiol*, *94*(6), 4188-4195.
- Fang, F., Murray, S. O., & He, S. (2007). Duration-dependent fMRI adaptation and distributed viewer-centered face representation in human visual cortex. *Cereb Cortex*, *17*(6), 1402-1411.
- Friston, K. J., Rotshtein, P., Geng, J. J., Sterzer, P., & Henson, R. N. (2006). A critique of functional localisers. *Neuroimage*, *30*(4), 1077-1087.
- Grill-Spector, K., Sayres, R., & Ress, D. (2006). High-resolution imaging reveals highly selective nonface clusters in the fusiform face area. *Nat Neurosci*, *9*(9), 1177-1185.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends Cogn Sci*, *4*(6), 223-233.
- Haxby, J. V., Ungerleider, L. G., Horwitz, B., Maisog, J. M., Rapoport, S. I., & Grady, C. L. (1996). Face encoding and recognition in the human brain. *Proc Natl Acad Sci U S A*, *93*(2), 922-927.
- Haynes, J. D. & Rees, G. (2005). Predicting the orientation of invisible stimuli from activity in human primary visual cortex. *Nat Neurosci*, *8*(5), 686-691.
- Kamitani, Y. & Tong, F. (2005). Decoding the visual and subjective contents of the human brain. *Nat Neurosci*, *8*(5), 679-685.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J Neurosci*, *17*(11), 4302-4311.
- Krauskopf, J., Williams, D. R., & Heeley, D. W. (1982). Cardinal directions of color space. *Vision Res*, *22*(9), 1123-1131.
- Kringelbach, M. L. & Rolls, E. T. (2003). Neural correlates of rapid reversal learning in a simple model of human social interaction. *Neuroimage*, *20*(2), 1371-1383.
- Leopold, D. A., O'Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nat Neurosci*, *4*(1), 89-94.

- Loffler, G., Yourganov, G., Wilkinson, F., & Wilson, H. R. (2005). fMRI evidence for the neural representation of faces. *Nat Neurosci*, 8(10), 1386-1390.
- Petit, L., Courtney, S. M., Ungerleider, L. G., & Haxby, J. V. (1998). Sustained activity in the medial wall during working memory delays. *J Neurosci*, 18(22), 9429-9437.
- Puce, A., Allison, T., Gore, J. C., & McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *J Neurophysiol*, 74(3), 1192-1199.
- Rotshtein, P., Henson, R. N., Treves, A., Driver, J., & Dolan, R. J. (2005). Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nat Neurosci*, 8(1), 107-113.
- Schultz, R. & Robins, D. (2005). Functional neuroimaging studies of autism spectrum disorders. In F. R. Volkmar, R. Paul, A. Klin, & D. J. Cohen (Eds.), *Handbook of Autism and Pervasive Developmental Disorders, Two Volume Set*. Hoboken: Wiley.
- Sereno, M. I., McDonald, C. T., & Allman, J. M. (1994). Analysis of retinotopic maps in extrastriate cortex. *Cereb Cortex*, 4(6), 601-620.
- Shidara, M. & Richmond, B. J. (2002). Anterior cingulate: single neuronal signals related to degree of reward expectancy. *Science*, 296(5573), 1709-1711.
- Talairach, J. & Tournoux, P. (1988). *Co-Planar Stereotaxic Atlas of the Human Brain: 3-Dimensional Proportional System : An Approach to Cerebral Imaging*. Thieme Medical Publishers.
- Teo, P. C., Sapiro, G., & Wandell, B. A. (1997a). Creating connected representations of cortical gray matter for functional MRI visualization. *IEEE Trans Med Imaging*, 16(6), 852-863.
- Teo, P. C., Sapiro, G., & Wandell, B. A. (1997b). Creating connected representations of cortical gray matter for functional MRI visualization. *IEEE Trans Med Imaging*, 16(6), 852-863.
- Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, 428(6982), 557-561.
- Winston, J. S., Henson, R. N., Fine-Goulden, M. R., & Dolan, R. J. (2004). fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. *J Neurophysiol*, 92(3), 1830-1839.

Chapter 4

A Psychophysical Study of the Effect of Face Adaptation on Search, Detection and Discrimination

ABSTRACT

In Chapters 2 and 3 of this dissertation, we demonstrated that adaptation to gender, ethnicity and a combination of both features induces selective shifts in category appearance; and results in BOLD activation within a cluster of brain regions, including occipital cortex, the fusiform gyrus and the cingulate gyrus. Here, we investigated whether this adaptation has any perceptual consequences beyond a shift in the perceived category boundary. We measured the effects of adaptation on a RVSP, spatial search and discrimination task, and found that adaptation had no discernable effect on performance for any of these three tasks.

INTRODUCTION

In Chapter 2, we demonstrated that robust face adaptation effects are found using our face stimuli and adaptation paradigm. We measured (for example) the shift in the probability that Asian morphed faces that varied in their maleness would be reported as appearing male, before and after adaptation to male Asian faces. A simplistic explanation for such category shifts and the reductions in fMRI response shown in Chapter 3 is that adaptation either reduces the responsivity of mechanisms tuned for the adapting category, or shifts their selectivity away from the category boundary (Grill-Spector & Malach, 2001). Changes such as these should have perceptual consequences beyond a category shift. In this study, we then tested the effects of adaptation on three tasks: rapid serial visual search (RSVP), spatial search, and discrimination.

Many of us have noticed the phenomenon that among a crowd of Asian faces, a Caucasian face is immediately noticeable. Similarly, in a women's clothing store, a man is easily spotted. The distinctive feature of maleness "pops out" from the uniform feature of femaleness surrounding it. This phenomenon is consistent with the notion that adaptation to a particular face category may result in a reduction of the response to the adapted face category, and thereby make a face belonging to a novel face category more detectable.

In our first experiment, we used an RSVP task where subjects were asked to detect which of two intervals containing a rapidly presented set of face images contained (for example) a male-Asian face. Distractor faces belonged to other face categories, and subjects had to report which of the two RSVP intervals contained a face belonging to the

target category. We tested whether adaptation to either the test face category or the distractor face categories had any effect on performance, and found no effects of adaptation in either case.

One possibility is our failure to find adaptation effects was due to the rapid presentation of the RSVP task being relatively unnatural. Normally, faces appear in different spatial locations, and one has the ability to control the amount of time that each face is viewed. The rapid presentation of the RSVP task may have resulted in subjects using different strategies or mechanisms (possibly more low-level) for detecting the target faces than would be used in a more naturalistic task.

We therefore tested for adaptation effects using a search task that might mimic a more natural circumstance. Studies examining search using low level features such as orientation, shape and color, have shown that stimuli do tend to “pop-out” when they are of higher luminance (Dawson & Thibodeau, 1998; Theeuwes, 1995), contrast (Nothdurft, 1993) or chromatic saturation than distractors (D'Zmura & Mangalick, 1994; Treisman & Gelade, 1980).

Additionally, as described above (Introduction) it has been shown that adaptation can affect search. McDermott et al. (McDermott, Mulligan, Bebis, & Webster, 2006; Webster, Raker, & Malkoc, 1998) found that subjects' ability to detect a target ellipse of variable color was affected by whether they had adapted to backgrounds drawn from the same or different color axes. Targets were located more quickly on the background axis that observers were pre-exposed to. In the second experiment of this chapter, we asked subjects to detect a face belonging to a particular category, as quickly as possible, which was present among distractors. In contrast to previous results on the effects of adaptation

on color search, we found no effects of adaptation on searches for a particular face category.

As described above, the simplistic explanation for the category shifts and reductions in fMRI response found as a consequence of adaptation is that adaptation either reduces the responsivity of mechanisms tuned for the adapting category, or shifts their selectivity away from the category boundary. One possible explanation for our failure to find significant adaptation effects in the RSVP (Experiment 1) and spatial search (Experiment 2) tasks might be that the mechanisms involved have a saturated response for faces that are near the extreme of each category dimension (i.e. are fully male, female, Asian, Caucasian); and as a result, a shift in selectivity may not have a significant effect on the response to faces that are nowhere near the category boundary.

In Experiment 4, we tested whether adaptation to a particular face category improved the ability of subjects to make fine discriminations near category boundaries that included the adapting category. For example, we examined whether adaptation to male Asians could improve the ability of subjects to discriminate which of two Eurasian male faces was slightly more Asian. Again, we found that adaptation had no effect on discrimination performance.

METHODS

1. Subjects

A total of 70 subjects gave informed consent to participate in these experiments, which were approved by the internal review boards either at The Salk Institute for Biological Studies, or University of California, San Diego. All subjects, ages 18-30 years

of age, had normal or corrected-to-normal vision. Subjects received either money or course credit for their participation. Five subjects were not included in data analysis because they failed to complete the experiments. A separate cohort of subjects participated in each of the four experiments.

2. Stimuli

Frontal-view gray-scale face images of Asian (A), Caucasian (C), male (M), and female (F) faces of neutral-expression were taken from the Ekman 1976 face set and the Cohn-Kanade AU-Coded Facial Expression Database; others were photographs of students and staff of UCSD and The Salk Institute. The un-morphed face image set contained 88 exemplars, 22 faces for each category.

Morph images were created by morphing a pair of face images (MorphMan, version 4.0; STOIK Imaging, Moscow, Russia) varying (for example) from male to female. Each morph continuum contained 50 images ranging from fully male to fully female. 10 morph continuums were created for each morphing dimension (e.g. 10 sets of Asian male-female morphs, 10 sets of Caucasian male-female morphs, and so on).

Subjects maintained a viewing distance of 57 cm and images were presented on a Sony computer monitor using MATLAB and the COGENT toolbox on a Dell desktop computer. Stimuli therefore subtended 6.8 degrees of visual angle in Experiments 1, 2 & 4, and 4.1 degrees of visual angle in Experiment 3.

Experiment 1: RSVP

The experimental paradigm is shown in Figure 4.1. Each subject participated in two testing sessions, separated by 1 or 2 days. The first session was designed to establish a baseline rate of RSVP presentation for each subject, without adaptation. In the first testing session each trial consisted of two intervals in which a series of face images were presented in rapid succession (RSVP). Before each block of 70 trials subjects were told that their task was to identify which of the two intervals contained a face image belonging to the target category, for example, female-Caucasian. Each interval contained 5 face images; in one interval all 5 of the face images were distractors, and in the other interval one of the five face images belonged to the target face category. Each interval was followed by a 500 ms phase-scrambled face image.

An auditory tone at the end of the second interval alerted the observer to make a forced-choice: “1” or “2”, to indicate whether the target appeared in the first or second interval. A correct answer was followed by a decrease in the fixation spot size plus a high tone; an incorrect answer was followed by an increase in the fixation spot size plus a low tone.

After each pair of RSVP intervals subjects were given as long as needed to make a response. During this first testing session the presentation rate during the two RSVP test intervals varied across 7 speeds using a method of constant stimuli. We then fit the responses as a function of presentation rate with a cumulative normal psychometric function and interpolated to find the speed at which the observer achieved 65% correct performance. A total of 280 baseline trials (4 blocks of 70 trials) were carried out for each subject.

In the second session, each block of trials began by pre-adapting subjects using an initial 3-min adaptation period. The only difference from the pre-adaptation procedure in Experiment 1 was that in Experiment 2 subjects were adapted to three (rather than one or two) face categories. A typical subject might begin by being adapted to FA, MC and MA faces, presented in pseudo-random alternation. For each individual subject, the same 3 categories were used as adaptors throughout the entire session.

After this three-minute adaptation period, subjects then moved to the testing phase where they again had to identify in which of two RSVP intervals a face belonging to the target category appeared. In this second session, the rate of presentation was held constant at a rate for which the subject had performed at 65% correct during the first, non-adapted testing session.

The target face either belonged to the least adapted or the most adapted category. In the case of our example experiment shown in Figure 4.1, subjects were pre-adapted to FA, MC and MA faces. In that case the target category would either be the least adapted category, FC or the most adapted category, MA. The identities of distractor and target faces were always different from the identities of the faces used as adaptors. The remaining distractor faces belonged to the three categories that were not the target category; for example, on a trial where the target type was MA, the distractor faces would be FA, FC, and MC. In this second session, each trial was preceded by a 12-sec top-up adaptation period. For a test period of 2 seconds, subjects were exposed to adaptors for approximately 83% of the testing period (excluding the pre-adapt period).

The target category alternated between each block of 35 trials, with half the subjects being tested on the least adapted category for blocks 1 and 3, and the other half of subjects being tested on the most adapted category for blocks 1 and 3. Across subjects, all possible combinations of adaptors and test faces were used in a counterbalanced design. A total of 140 adaptation trials (4 blocks of 35 trials) were carried out for each subject.

Experiment 2A: Four-face display spatial search

The experimental paradigm is shown in Figure 4.2. Subjects pre-adapted for 3-min to three of the four adaptation categories, as in Experiment 2. On each trial, an auditory tone indicated the onset of the trial and four faces (one from each of the four categories) appeared in the corners of the computer screen, equidistant from the center. Subjects were instructed to report the location of the target face category as quickly as possible, which could belong to any of the four possible categories (MA, MC, FA, FC). The target type randomly changed every 4 trials. The spatial location of each face category was selected randomly. Both response times and accuracy were recorded.

A 15-sec top-up adaptation period (1 image/sec) was interposed between each set of four trials. During this adaptation period subjects were instructed to fixate on a central fixation spot. At the end of this top-up adaptation period we displayed “Search for Male Asian” (for example) centrally on the screen for 500 msec to inform the subjects of the target category for the next four trials. For a test period of 1.5 seconds (average across subjects), subjects were exposed to adaptors for approximately 90% of the testing period (excluding the pre-adapt period).

Subjects were told to fixate during the pre-adaptation and top-up periods, and to freely view the screen and locate the target as quickly and accurately as possible when the test stimuli were presented. Each of the four spatial locations was identified with a unique key: top left = “A”, bottom left = “Z”, top right = “K”, bottom right = “M”. Positive and negative feedback were given after every trial via a change in the color and size of the fixation spot.

Each subject participated in two testing sessions, separated by 1 or 2 days. The only difference between the two testing sessions was in the choice of the categories that were used for adaptation. In Session 1 observers might be adapted to FA, FC and MA faces, resulting in the most adapted category being FA, and the least adapted category being MC. FC and MA categories were adapted to an intermediate level. In this case, in Session 2, the adapting set would be MC, FC, MA; the most adapted category would be MC, the least adapted category would be FA and FC and MA would again be adapted to an intermediate level. Across subjects, all possible combinations of adaptor conditions were tested in a counterbalanced design. Each subject carried out a total of 800 trials across both sessions.

Experiment 2B: two-face display spatial search

One concern was that our failure to find a result in Experiment 2A was due to having three adapting face categories, rather than adapting along a single facial dimension or using two adapting face categories, as was done in Experiment 1. The results from Experiment 1 suggest that the strongest category shifts are found when

adaptation occurs along a single dimension. We therefore repeated Experiment 2A, using a procedure that allowed us to adapt along a single dimension.

The procedure was identical to that in Experiment 2A, except that all faces were Caucasian. Subjects were adapted to either male or female faces, and were asked to identify the location of either the male or the female face. In this case, only two face images were presented, one male and one female, on either side of the fixation spot. The location of each face type was random. The left and right spatial locations were identified using keys “Q” and “P”, respectively.

Each subject participated in two testing sessions, separated by 1 to 3 days. Subjects adapted to (for example) female face images in session 1 and male face images in session 2, or vice versa. For a test period of 500 msec, subjects would be exposed to adaptors for approximately 95% of the testing period (excluding the pre-adapt period). Each subject carried out 800 trials across both sessions. We counterbalanced whether the female or male faces were the adaptors across subjects in Session 1.

Experiment 3: discrimination

The experimental paradigm is shown in Figure 4.3. Each subject participated in two testing sessions, separated by 1 to 3 days.

In the first stage of the first session, we obtained each subjects’ individual perceptual categorical boundary between male and female for the 10 morph continuums used in the experiment. Subjects were presented with a pseudo-random series of morphed images and reported whether they appeared female or male by pressing “F” or “M”, respectively for each image. A subset of the morphed images from each of the ten gender

morph continuums was shown; 0, 12, 24, 37, 49, 61, 73, 86 and 98% male. The morph appearing male 50% of the time, averaged across all ten morph continuums, was defined to be the categorical boundary for each observer. Subjects were then randomly assigned in a counterbalanced manner, to either an adapted-category or nonadapted-category condition. In the adapted-category condition, the test images belonged to the same category as the adapting images. For example, subjects adapted to male face images might be asked to discriminate which of two morphed images appeared more male, where one image was the at the male-female category boundary and the second image was slightly more male. In the nonadapted-category condition, subjects were tested on faces that belonged to the opposite category to the adapting faces. For example, subjects that adapted to males might be asked to discriminate which of two morphed images appeared more male, where one image was at the male-female category boundary and the second image was slightly more female.

Figure 4.3a schematizes the discrimination points that were tested. Four positions along each half of the gender continuum were tested, each separated by 10% of the distance along the entire male-female continuum. The zero point, “ P_0 ”, is the subject’s category boundary. The remaining points are denoted as “ $P_{10\%}$ ”, “ $P_{20\%}$ ”, and “ $P_{30\%}$ ”, sampling the space between the category boundary and faces that are 30% of the way towards the adapting category (note that this morph x-axis is not linear). This resulted in six possible discrimination comparisons for each condition. Adapted-category subjects were tested on P_0 vs. $P_{10\%}$ / $P_{20\%}$ / $P_{30\%}$, and $P_{10\%}$ vs. $P_{20\%}$ / $P_{30\%}$, and $P_{20\%}$ vs. $P_{30\%}$. Nonadapted-category subjects were tested on P_0 vs. $P_{-10\%}$ / $P_{-20\%}$ / $P_{-30\%}$, and $P_{-10\%}$ vs. $P_{-20\%}$ / $P_{-30\%}$, and $P_{-20\%}$ vs. $P_{-30\%}$.

The first (baseline) session did not have an initial adaptation period (Figure 8b). Each block began with a message on the screen that instructed subjects to advance to a trial by pressing the spacebar. Two test images then appeared in rapid succession, at a rate of 500 ms per image. Each image was followed by a 250 ms phase-scrambled image. All faces were Caucasian, and the pair of test images presented in the two intervals within a single trial always belonged to the same morph continuum. The order in which the test images appeared within a trial was random. Five of the ten available morph continuums were tested in each of the two sessions. On each trial subjects reported whether the face image in the first or the second interval had appeared more male by pressing "1" or "2", respectively. Each trial was followed by a pseudo-adaptation top-up period consisting of 4 sec of phase-scrambled images presented at a rate of 1 image/sec. (These phase-scrambled images were created using the appropriate face category images that would be used as adaptors during the second test session). Positive and negative feedback were given via a change in the size and color of the fixation spot. Every 4 blocks, subjects were shown their percent correct and wrote this value down. This provided them with additional feedback and introduced a mandatory break. Each block contained 90 trials and subjects carried out 360 trials in each of the two sessions.

In the second session subjects were pre-adapted for 3-minutes to either male or female faces before each block of trials, using the same procedure as in Experiment 2B. After the pre-adaptation period, a message on the screen instructed subjects to advance to a trial by pressing the spacebar. Subjects then were asked to perform the same discrimination task (which image is more male) as carried out during the previous baseline session (Figure 4.3). Between each trial, there was an 8-sec top-up adaptation

period. For a test period of 1 sec, subjects were exposed to adaptors for approximately 87.5% of the testing period (excluding the pre-adapt period). Each subject carried out a total of 720 test trials across both sessions. All possible combinations of discrimination comparisons were tested in a counterbalanced design.

RESULTS

Experiment 1: RSVP

Of the seventeen subjects that participated, four subjects' data were discarded. For three of these subjects, fits to the baseline psychometric functions were too poor to obtain a speed threshold for 65% correct performance. A fourth subject performed at ceiling on the baseline experiment (our fastest possible presentation rate was 67 msec/image), leaving no room for improvement in the adaptation portion of the experiment.

We were interested in determining whether subjects would be better at identifying which interval contained target face images when the target faces belonged to the least adapted category, as compared to the most adapted face category. In the adaptation phase of the experiment, the average percent correct for the most adapted face category (collapsed across all face image categories) was 66.68% (SEM +/-2.27). The average percent correct for the least adapted category was 64.67% (SEM +/-2.85). Performance was not significantly different between the most and the least adapted face category ($t(12)=.6953$, $p=.5001$, 2-tailed dependent t-test). In fact, adaptation seemed to have no effect on performance on the RSVP task. Performance for the most and least adapted categories were not significantly different from 65% correct, the performance level

predicted by the baseline experiment. (Most adapted category: $t(12)=.7399$, $p=.2368$, 1-tailed dependent t-test; least adapted category $t(12)=.1157$, $p=.5451$).

Experiment 2A: four-face display spatial search

2A.1. Response times

Figure 4.4a shows the effect of adaptation on the average amount of time it took each subject to search for the least, intermediate and most adapted face image categories, for both the first and the second session (data from the two face categories that were adapted to an intermediate level were collapsed for each subject).

A comparison of search times between sessions (collapsing across adaptation levels) showed significant learning; subjects required significantly less search time in the second session ($F(1,70)=11.12$, $p<.0014$), presumably due to practice effects. However, we did not find that the amount of adaptation affected the time required to search for a target face category, for either session (session 1: $F(2,33)=.1952$, $p=.8236$; session 2: $F(2,33)=.1280$, $p=.8803$). There was no interaction between practice effects and the adaptation condition ($F(,2,2)=1.2969$, $p=.2800$).

2A.2. Accuracy

Percent correct for each adaptation condition for each session are shown in Figure 4.4b. The percent correct averaged across subjects for searching the least, intermediate and most adapted face categories in session 1 was 95.74% (SEM ± 1.05), 96.06% (SEM ± 1.06), 97.03% (SEM $\pm .52$), respectively; and in session 2, 95.83% (SEM ± 1.13),

95.92% (SEM \pm .84), 97.25% (SEM \pm .83), respectively. Accuracy was not significantly different between the different adaptation levels for either session (session 1: $F(2,33)=.5446$, $p=.5852$; session 2: $F(2,33)=.7113$, $p=.4984$), or across sessions ($F(5,66)=.5059$, $p=.7708$).

2A.3. Normalized data

To directly compare the adaptation level on search time, we normalized the search times observed for intermediate and high levels of adaptation based on the search time required for the least adapted condition, as shown in Figure 4.4c. Values greater than 1 indicate that search was faster than for the least adapted condition; values less than 1 indicate that search was slower than for the least adapted condition. This manipulation of the data reduced data variance due to inter-subject variance in search times. Normalized search times were not significantly different from 1, suggesting that the adaptation condition had no effect on search time (session 1: normalized intermediate, $t(11)=1.4451$, $p=.1763$; normalized most, $t(11)=2.0436$, $p=.0657$; $p=.0532$; session 2: normalized intermediate, $t(11)=.0555$, $p=.9568$; normalized most, $t(11)=1.5318$, $p=.1538$).

Experiment 2B: two-face display spatial search

2B.1. Response times

The effect of adaptation on the average amount of time it took each subject to search for the non-adapted as compared to the adapted face category is shown in Figure 4.5a. Response times were not significantly lower for non-adapted than for adapted face

categories in either session (session 1: $t(9)=1.4108$, $p=.9040$; session 2: $t(9)=1.2392$, $p=.1233$). We again found a significant decrease in response times from Session 1 to 2, which can be attributed to practice effects ($t(19)$, $p<.0001$).

2B.2. Accuracy

The effect of adaptation on accuracy is shown in Figure 4.5b. In session 1, the average percent correct across subjects for the adapted face category was 97.85% (SEM $\pm.68$), and the percent correct for the non-adapted face category was 98.40% (SEM $\pm.45$), respectively. In session 2, the average percent correct for the adapted category was 98.20% (SEM $\pm.62$), and 98.10% (SEM $\pm.50$) for the non-adapted category. There was no significant difference in accuracy across conditions, for either session ($F(3,36)=.1803$, $p=.9091$).

Experiment 3: discrimination

Figure 4.6 compares performance before and after adaptation for each discrimination comparison. The red symbols represent adapted-category performance (if adaptation was to male face images, then discriminations were carried out between morph images that were slightly male); the blue symbols represent nonadapted-category performance (if adaptation was to male face images, then discriminations were carried out between morph images that were slightly female).

Interestingly, performance was not significantly different between P_0 vs. $P_{\pm 10\%}$, $P_{\pm 10\%}$ vs. $P_{\pm 20\%}$, and $P_{\pm 20\%}$ vs. $P_{\pm 30\%}$ (all comparison, $p>0.1$). Given that the x-axis was

determined by the MorphMan software, there was no reason to assume that discrimination performance would be always be the same for morph pairs separated by 10% along the x-axis.

As expected, subjects found it easier to discriminate which of two images was more male when the morph images to be discriminated were further separated along the morph continuum, e.g. performance for P_0 vs. $P_{\pm 30\%}$ and P_0 vs. $P_{\pm 20\%}$ was better than for P_0 vs. $P_{\pm 10\%}$, and performance for $P_{\pm 10\%}$ vs. $P_{\pm 30\%}$ was better than for $P_{\pm 10\%}$ vs. $P_{\pm 20\%}$ for all conditions.

As would be expected, during the first baseline session in which no adaptation occurred, there was no significant difference in performance between adapted-category (open red squares) and nonadapted-category (open blue circles) performance, across any of the discrimination comparisons (P_0 vs. $P_{\pm 10\%}$: $t(18)=1.110$, $p=.2817$; P_0 vs. $P_{\pm 20\%}$: $t(18)=.028$, $p=.9780$; P_0 vs. $P_{\pm 30\%}$: $t(18)=.444$, $p=.6623$; $P_{\pm 10\%}$ vs. $P_{\pm 20\%}$: $t(18)=1.035$, $p=.3142$; $P_{\pm 10\%}$ vs. $P_{\pm 30\%}$: $t(18)=.031$, $p=.9754$; $P_{\pm 20\%}$ vs. $P_{\pm 30\%}$: $t(18)=.361$, $p=.7226$).

For the adapted-category condition, there was no difference in performance between the baseline no-adapt condition (open red squares) and performance during the second session that included adaptation (closed red squares), across any of the discrimination comparisons (P_0 vs. $P_{10\%}$: $t(9)=.0396$, $p=.9692$; , P_0 vs. $P_{20\%}$: $t(9)=.8327$, $p=.4266$; P_0 vs. $P_{30\%}$: $t(9)=.1.170$, $p=.2771$; $P_{10\%}$ vs. $P_{20\%}$: $t(9)=.6680$, $p=.5209$; $P_{10\%}$ vs. $P_{30\%}$: $t(9)=.0441$, $p=.9658$; $P_{20\%}$ vs. $P_{30\%}$: $t(9)=1.119$, $p=.2950$).

Similarly, for the nonadapted-category condition, there was no difference in performance between the baseline no-adapt condition (open blue circles) and performance during the second adaptation session (filled blue circles), across any of the

discrimination comparisons (P_0 vs. $P_{-10\%}$: $t(9)=1.1507$, $p=.2795$; P_0 vs. $P_{-20\%}$: $t(9)=.0826$, $p=.9360$; P_0 vs. $P_{-30\%}$: $t(9)=1.1765$, $p=.2696$; $P_{-10\%}$ vs. $P_{-20\%}$: $t(9)=.2696$; $P_{-10\%}$ vs. $P_{-30\%}$: $t(9)=.6585$, $p=.5267$; $P_{-20\%}$ vs. $P_{-30\%}$: $t(9)=.1651$, $p=.8725$).

Finally, during the second adaptation session there was no difference in performance between the adapted-category (filled red squares) and the nonadapted-category (filled blue circles), across any of the discrimination comparisons (P_0 vs. $P_{\pm 10\%}$: $t(18)=.1080$, $p=.9150$; P_0 vs. $P_{\pm 20\%}$: $t(18)=.8710$, $p=.3953$; P_0 vs. $P_{\pm 30\%}$: $t(18)=.556$, $p=.5848$; $P_{\pm 10\%}$ vs. $P_{\pm 20\%}$: $t(18)=.2560$, $p=.8009$; $P_{\pm 10\%}$ vs. $P_{\pm 30\%}$: $t(18)=.6930$, $p=.4973$; $P_{\pm 20\%}$ vs. $P_{\pm 30\%}$: $t(18)=.715$, $p=.4840$).

Adapted-category accuracy

The average percent correct before and after adaptation was as follows for the adapted-category: P_0 vs. $P_{10\%}$: 70.42% (SEM +/-2.61) and 70.29% (SEM +/-2.92), $t(9)=.0396$, $p=.4846$; P_0 vs. $P_{20\%}$: 81.96 (SEM +/-2.62) and 84.61% (SEM +/-2.45), $t(9)=.8327$, $p=.7867$; P_0 vs. $P_{30\%}$: 89.41% (SEM +/-2.49) and 84.67% (SEM +/-2.48), $t(9)=1.1570$, $p=.1385$; $P_{10\%}$ vs. $P_{20\%}$: 71.10% (SEM +/-2.34), 73.24% (SEM +/-2.90), $t(9)=.6680$, $p=.7395$; $P_{10\%}$ vs. $P_{30\%}$: 82.35% (SEM +/-2.11) and 82.48% (SEM +/-2.07), $p=.5171$; $P_{20\%}$ vs. $P_{30\%}$: 70.21% (SEM +/-3.04), and 73.84% (SEM +/-1.92), $t(9)=.8525$.

Nonadapted-category accuracy

The average percent correct before and after adaptation was as follows for the nonadapted-category: P_0 vs. $P_{-10\%}$: 65.95% (SEM +/-3.06) and 70.67% (SEM +/- 1.91), $t(9)=1.1507$, $p=.1397$; P_0 vs. $P_{-20\%}$: 81.85% (SEM +/-3.35) and 81.67% (SEM +/-2.32), $t(9)=.0826$, $p=.5320$; P_0 vs. $P_{-30\%}$: 87.85% (SEM +/-2.47) and 86.67% (SEM +/-2.59),

$t(9)=.4501$, $p=.6683$; $P_{-10\%}$ vs. $P_{-20\%}$: 75.40% (SEM +/-3.44) and 72.17% (SEM +/-3.03),
 $t(9)=1.1765$, $p=.8652$; $P_{-10\%}$ vs. P_{-30} : 82.21% (SEM +/-3.61) and 84.50% (SEM +/-2.06),
 $t(9)=.6585$, $p=.2634$; $P_{-20\%}$ vs. P_{-30} : 71.88% (SEM +/-3.48) and 71.33 (SEM +/-2.94),
 $t(9)=.1651$, $p=.5637$.

DISCUSSION

Like other groups (Webster & MacLin, 1999; Webster, Kaping, Mizokami, & Duhamel, 2004; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003), we find that the face adaptation technique results in dramatic shifts in the categorical appearance of faces (Ng, Ciaramitaro, Anstis, Boynton, & Fine, 2006). However we failed to find any evidence that similar adaptation protocols resulted in any change in temporal search (RSVP), spatial search, or discrimination performance.

The robust shifts in category appearance found in Chapter 2 suggest that our failure to find an effect of adaptation on RSVP, search or discrimination performance was not due to a failure to produce adequate adaptation effects. Nor is it likely that adaptation effects were masked by variability in our data. Measurements in all three experiments of Chapter 4 were remarkably reliable, and there was no indication in any of the experiments of a trend that simply failed to reach significance.

One potential explanation is that shifts in category boundaries are not due to changes in either the neutral point or the slopes of response curves, but rather to a shift in the criterion for where the boundary is. It has been argued that the role of adaptation for higher level stimuli may not be to increase sensitivity for perceptual judgments, but rather

to adjust the boundaries of our perceptual categories to match the distribution of the environment around us (Webster, Werner, & Field, 2005). However, explaining adaptation effects as a criterion shift rather than as a change in response does not explain why such strong fMRI adaptation is found for face stimuli by both our group (Chapter 3) and others. Strong adaptation effects have been found across relatively large regions of cortex for both individual faces (Loffler, Yourganov, Wilkinson, & Wilson, 2005; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Winston, Henson, Fine-Goulden, & Dolan, 2004; Gauthier et al., 2000) and categories of faces (Ng, Ciaramitaro, Anstis, Boynton, & Fine, 2006), after relatively short periods of adaptation, with adapted faces producing less BOLD response than non-adapted faces.

As described above, one way to think about adaptation is in terms of visual coding – neurons have limited representational capacity, and firing carries an energy cost. According to visual coding models, the role of adaptation is to represent the visual world as efficiently as possible. A good model for how visual coding models have been applied is in the domain of color processing, where these models have been used to explain three aspects of neural tuning and adaptation.

In the natural environment, the mean chromatic stimulus is gray. Consequently, an efficient coding scheme predicts opponent mechanisms showing low responses near the white-point to minimize overall firing rates. Visual coding models also predict basic chromatic adaptation effects - a change in the mean chromaticity of the environment should shift the mid-point of the opponent mechanisms so as to minimize overall firing rates (Boynton, 1956).

In the natural environment, stimuli also tend to be clustered around mean gray, and are rarely highly saturated. Efficient coding therefore predicts that mechanisms should respond logarithmically or sigmoidally as a function of chromatic saturation, in order to maximize discrimination abilities near the white-point (the majority of stimuli), at the expense of discrimination abilities for very saturated stimuli (which are rare in natural environments). A change in the distribution of chromaticities therefore predicts a change in the shape of response slopes (Macleod, & von der Twer, 2003).

Differences in the effect of adaptation on luminance as compared to contrast discrimination support the notion that the strongest adaptation effects on discrimination will be found within mechanisms that saturate as a function of stimulus intensity. Responses as a function of luminance saturate at high luminance levels, and particularly strong effects of adaptation are found within luminance regimes where responses to non-adapted stimuli are saturated, whereas responses to adapted stimuli are below the saturation level (Whittle, 1992; Ohzawa, Sclar, & Freeman, 1985). Responses to contrast show far less saturation than for luminance, and effects of adaptation on contrast discrimination tend to be comparatively weak (e.g. Greenlee & Heitger, 1988; Regan & Beverly, 1985; see also (Webster, Werner, & Field, 2005).

A third way of maximizing efficiency is to de-correlate the responses of mechanisms, so that each mechanism contains as much independent information as possible. In the case of chromatic stimuli this determines the direction of the chromatic axes, where “luminance”, “red-green”, “blue-yellow” axes show relatively independent responses to natural scene stimuli (Buchsbaum & Gottschalk, 1983; Dominy & Lucas, 2001; Regan et al., 1998; Gegenfurtner & Rieger, 2000; Wurm, Legge, Isenberg, &

Luebker, 1993; Nagy & Sanchez, 1992). A change in the correlative statistics of the natural environment (as occurs in the McCullough adaptation (McCullough, 1965)) therefore, predicts a change the direction of the chromatic axes so as to minimize the correlation between axes.

What do would visual coding models predict for the effects of face adaptation on search or discrimination? The quality of “femaleness” does not consist of a single feature. Rather, femaleness is represented by a variety of cues that are fairly unreliable individually, but tend to be highly correlated with each other within female faces (rounder cheeks, larger eyes, etc.). According to visual coding theories, adaptation does not adapt individual mechanisms tuned for each of the individual underlying cues, but rather results in adaptation to the conjunction of these features along axes whose orientations best de-correlate these features. This may provide an explanation for why we seem to see opponent coding for dimensions such as gender and ethnicity, even though these qualities are clearly delineated by a complex multiplicity of cues (Barlow, 1991; Barlow, & Földiák, 1989).

However, unlike chromatic stimuli, faces tend not to cluster near the mid-point of category boundaries - gender-neutral and Eurasian faces are relatively rare. As a result, visual coding models should not predict sigmoidal or logarithmic responses resulting in maximum sensitivity near the category boundary, and should not predict saturation of responses for fully male or female stimuli. It would not be optimal to sacrifice discriminability for stimuli at the ends of our morph continuum given that, with the stimuli that we used, these endpoints were typical of normal faces. This may partially explain why we did not find adaptation effects in either the search or discrimination

tasks. However, a visual coding explanation, which assumes that mechanisms are not saturated for fully male and female faces, still predicts at least weak changes in discrimination performance as a consequence of adaptation. Perhaps we might have obtained adaptation effects if we had used hyper-male or hyper-female faces as the endpoints of our morph continuum. Another interesting prediction is that adaptation effects might occur for expression, since faces expressing extreme happiness or anger are less common in the natural environment than faces expressing gentle contentment and a mild peevishness. However, while visual coding models might predict that adaptation effects for faces would be relatively weak, it is still difficult to generate a plausible visual coding model for adaptation that includes large shifts on both category boundaries and fMRI responses, yet no discernable effect on performance in search or discrimination tasks.

The most likely explanation may be that discrimination and search performance is in fact determined by our subjects' ability to discriminate low level features (such as orientation and contrast), rather than their ability to represent faces. Given that faces are highly over-learned, there may be a super-abundance of representational capacity devoted to face processing. Indeed, a surprising amount of visual cortex is devoted to face processing – similar or greater than to the amount of cortex in V1 (Kanwisher, McDermott, & Chun, 1997; Dougherty et al., 2003). Given that face stimuli are so heavily over-represented, it seems plausible that limits in discrimination and search performance might be mainly due to signal-to-noise and/or limits in representational capacity at lower levels of processing. In that case, our adaptation protocols would be expected to have little or no effect on either discrimination or search performance.

Low level adaptation may possibly explain why Watson et al. (Watson, Rhodes, & Clifford, 2006) has found that adaptation to an “average Asian face” does improve the ability to identify learned Asian individuals, and adapting to an “average Caucasian face” improves the ability to identify learned Caucasian individuals. Their task required identifying learned individual compared to a single baseline “average face” to which subjects had adapted. Consequently, adaptation to low level properties may have enhanced differences between the “average face” and the learned individual faces. In our experiment, the adaptor and test faces always had different identities, thus reducing (though not entirely excluding) the potential for low level adaptation.

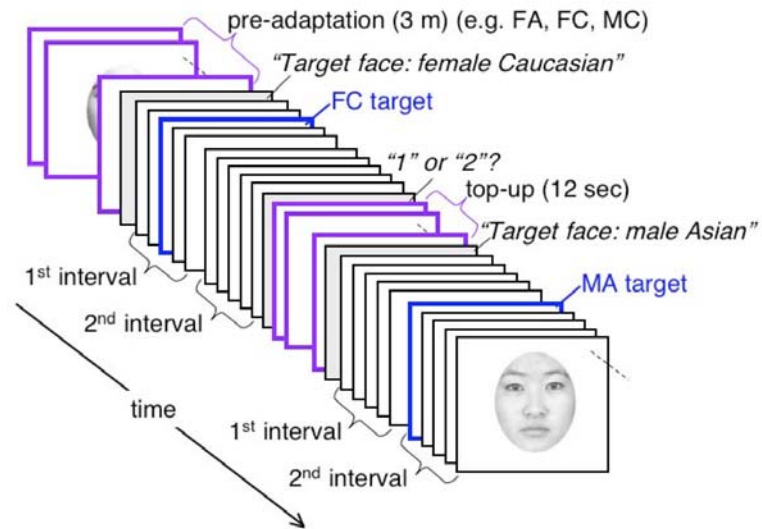


Figure 4.1. Experiment 1 design: RSVP. Subjects were pre-adapted to faces from 3 categories and topped-up between each trial. The target face category was cued before the onset of a trial. One of the two intervals contained the target face image. In the baseline session, there was no pre-adaptation and phase-scrambled face images replaced adapting face images during the top-up period. Each trial was preceded by a pseudo-adaptation top-up period that lasted 4 sec and contained phase-scrambled images of faces (these phase-scrambled images were created using the appropriate face category images that would be used as adaptors during the second test session). An auditory tone indicated the onset of each of the two RSVP intervals.

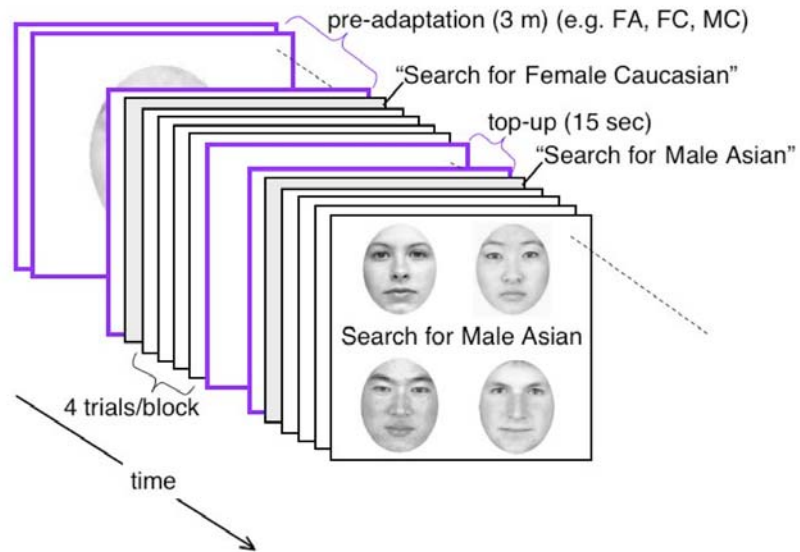


Figure 4.2. Experiment 2 design: spatial search. Subjects were pre-adapted to faces from 3 categories and topped-up between each block of 4 trials. The target face category was cued before each block. A face from each of the 4 categories appeared on each trial.

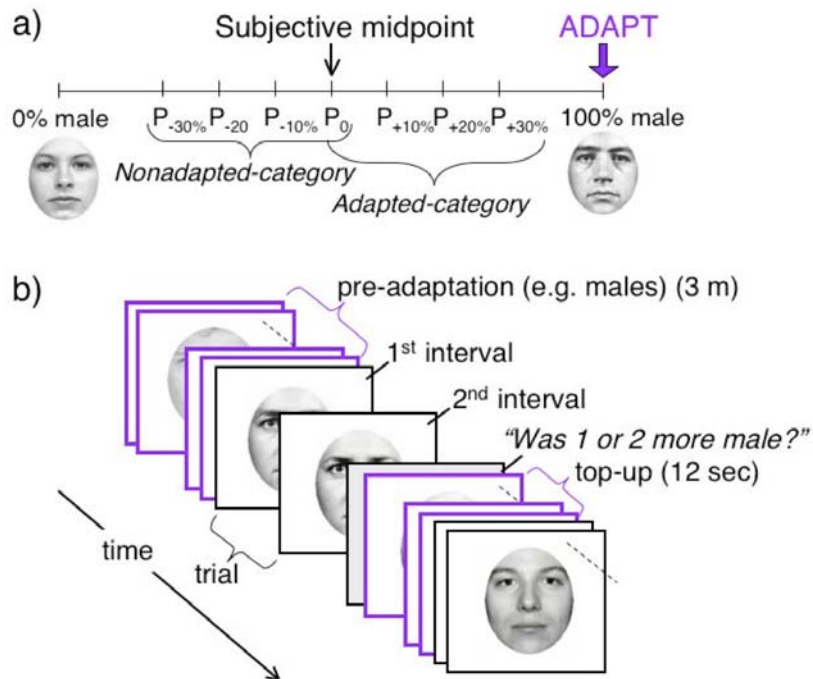


Figure 4.3. Experiment 3 design: discrimination. a) Gender morph continuum. Subjects adapted to male faces, for example, discriminate faces on either side of their subjective midpoint: the non-adapted or adapted-category. b) Subjects were pre-adapted and topped-up between each trial (baseline testing excluded the pre-adaptation period and substituted the top-up period with shorter duration of phase-scrambled face images). Each test face image is followed with a mask.

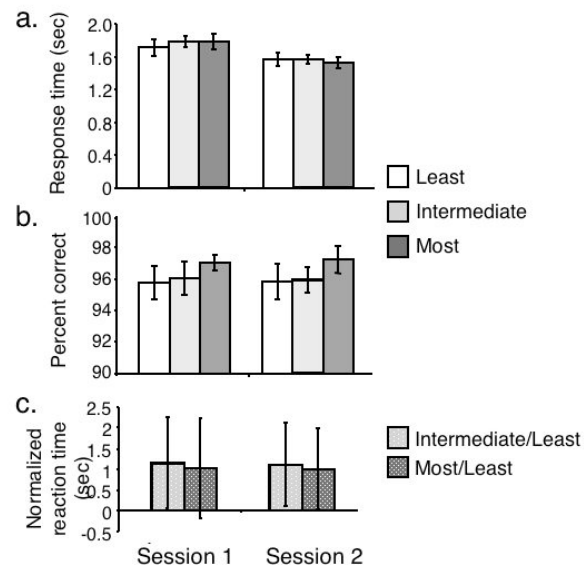


Figure 4.4. Results for experiment 2A: four-face display spatial search. a) Average response times for search of the least (white), intermediate (gray), most (black) adapted target face categories. A significant decrease in response times from session 1 to 2 were attributed to practice effects ($p < .0014$). b) There was no significant difference in percent correct across adaptation levels and sessions. c) Normalized reaction times show no significant difference from 1, indicating no advantage or disadvantage to adaptation beyond the least level of adaptation.

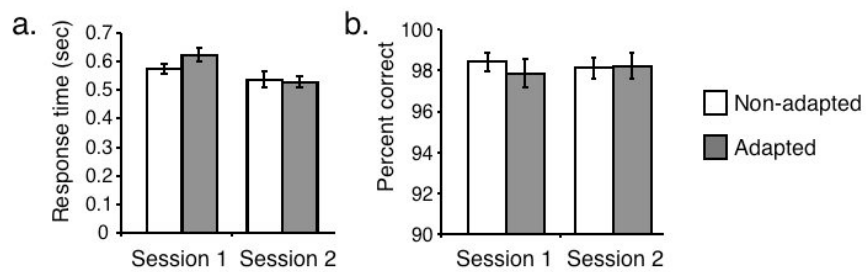


Figure 4.5. Results for experiment 2b: two-face display spatial search. a) Average response times for search of the non-adapted (white) and adapted (dark) face categories by session. b) The average percent correct.

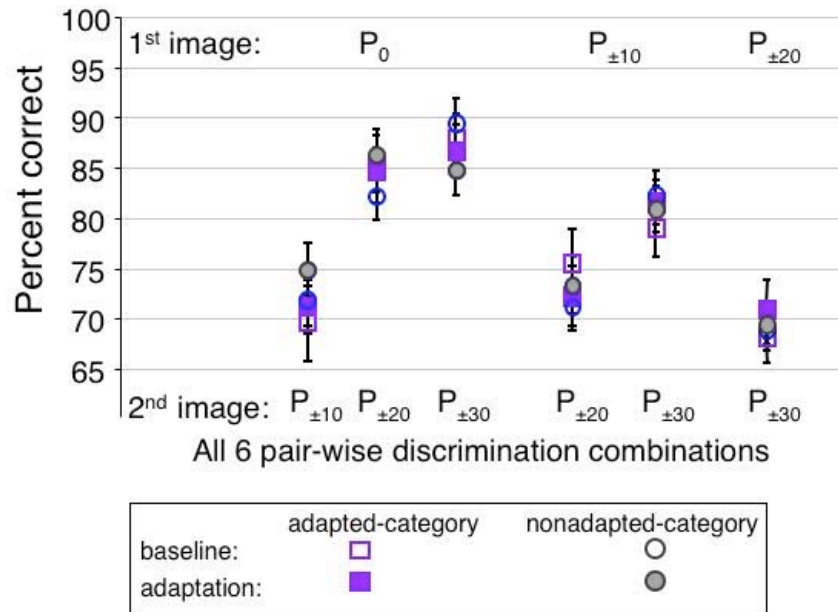


Figure 4.6. Results for experiment 3: discrimination. Performance before and after adaptation for each discrimination comparison across all subjects. Percent correct for adapted-category (square) and nonadapted-category (circle) discrimination. There was no significant difference in performance between adaptation conditions (filled symbols), nor was there any difference between baseline and adaptation.

ACKNOWLEDGMENTS

Many thanks to Donald I. A. MacLeod, Horace B. Barlow and Michael A. Webster for helping us interpret our lack of positive results. This research was supported by National Institutes of Health Grants EY-12925 (GMB), EY-014645 (IF).

A manuscript, “Face adaptation does not improve performance on search and discrimination tasks”, which includes both Chapter 2, “Psychophysical Study of Selective Mechanisms for Face Properties” and Chapter 4, “Psychophysical Study of Face Adaptation Perceptual Consequences”, of this dissertation has been submitted to *Journal of Vision* for review. Permission to reprint work in this dissertation has been granted by all the co-authors.

REFERENCES

- Barlow, H. B. (1991). A theory about the functional role and synaptic mechanism of after-effects. In C. Blakemore (Ed.), *Vision: Coding and Efficiency* (pp. 363-75). Cambridge: Cambridge University Press.
- Barlow, H. B., & Földiák, P. (1989). Adaptation and decorrelation in the cortex. In *The computing neuron* (pp. 54-72). Boston: Addison-Wesley Longman Publishing Co., Inc.
- Boynton, R. M. (1956). Rapid chromatic adaptation and the sensitivity functions of human color vision. *J Opt Soc Am*, 46(3), 172-79.
- Buchsbaum, G., & Gottschalk, A. (1983). Trichromacy, opponent colours coding and optimum colour information transmission in the retina. *Proc R Soc Lond B Biol Sci*, 220(1218), 89-113.
- D'Zmura, M., & Mangalick, A. (1994). Detection of contrary chromatic change. *J Opt Soc Am A Opt Image Sci Vis*, 11(2), 543-46.
- Dawson, M. R., & Thibodeau, M. H. (1998). The effect of adapting luminance on the latency of visual search. *Acta Psychol (Amst)*, 99(2), 115-39.
- Dominy, N. J., & Lucas, P. W. (2001). Ecological importance of trichromatic vision to primates. *Nature*, 410(6826), 363-66.
- Dougherty, R. F., Koch, V. M., Brewer, A. A., Fischer, B., Modersitzki, J., & Wandell, B. A. (2003). Visual field representations and locations of visual areas V1/2/3 in human visual cortex. *J Vis*, 3(10), 586-98.
- Gegenfurtner, K. R., & Rieger, J. (2000). Sensory and cognitive contributions of color to the recognition of natural scenes. *Curr Biol*, 10(13), 805-08.
- Greenlee, M. W., & Heitger, F. (1988). The functional role of contrast adaptation. *Vision Res*, 28(7), 791-97.
- Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol (Amst)*, 107(1-3), 293-321.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J Neurosci*, 17(11), 4302-11.
- Leopold, D. A., O'Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nat Neurosci*, 4(1), 89-94.
- MacLeod, D. I., & von der Twer, T. (2003). The Pleistochrome: optimal opponent codes for natural colours. In R. Mausfeld, & D. Heyer (Eds.), *Colour Perception: Mind and the Physical World* Oxford University Press, USA.
- McCollough, C. (1965). Color adaptation of edge-detectors in the human visual system. *Science*, 149(3688), 1115-16.

- McDermott, K., Mulligan, J. B., Bebis, G., & Webster, M. A. (2006). Visual search and eye movements in novel and familiar contexts. *Proc SPIE*, 6057.
- Nagy, A. L., & Sanchez, R. R. (1992). Chromaticity and luminance as coding dimensions in visual search. *Hum Factors*, 34(5), 601-14.
- Ng, M., Ciaramitaro, V. M., Anstis, S., Boynton, G. M., & Fine, I. (2006). Selectivity for the configural cues that identify the gender, ethnicity, and identity of faces in human cortex. *Proc Natl Acad Sci U S A*, 103(51), 19552-57.
- Nothdurft, H. C. (1993). The conspicuousness of orientation and motion contrast. *Spat Vis*, 7(4), 341-63.
- Ohzawa, I., Sclar, G., & Freeman, R. D. (1985). Contrast gain control in the cat's visual system. *J Neurophysiol*, 54(3), 651-67.
- Regan, D., & Beverly, K. I. Postadaptation orientation discrimination. (1985). *Journal of the Optical Society of America A*, 2(2), 147-55.
- Regan, B. C., Julliot, C., Simmen, B., Vienot, F., Charles-Dominique, T., & Mollon, J. D. (1998). Frugivory and colour vision in *Alouatta seniculus*, a trichromatic platyrrhine monkey. *Vision Res*, 38, 3321-27.
- Rhodes, G., Jeffery, L., Watson, T. L., Clifford, C. W., & Nakayama, K. (2003). Fitting the mind to the world: face adaptation and attractiveness aftereffects. *Psychol Sci*, 14(6), 558-66.
- Theeuwes, J. (1995). Abrupt luminance change pops out; abrupt color change does not. *Percept Psychophys*, 57(5), 637-44.
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognit Psychol*, 12(1), 97-136.
- Watson, T., Rhodes, G., & Clifford, C. W. G. (2006). *Improved facial identity recognition following adaptation*. Paper presented at the Vision Sciences Society Sarasota, FL.
- Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, 428(6982), 557-561.
- Webster, M. A., & MacLin, O. H. (1999). Figural aftereffects in the perception of faces. *Psychon Bull Rev*, 6(4), 647-53.
- Webster, M. A., Raker, V. E., & Malkoc, G. (1998). Visual search and natural color distributions. *Human Vision and Electronic Imaging III*, 3299, 198-509.
- Webster, M. A., Werner, J. S., & Field, D. J. (2005). Adaptation and the Phenomenology of Perception. In C. W. Clifford, & G. Rhodes (Eds.), *Fitting the Mind to the World: Adaptation and After-Effects in High-Level Vision (Advances in Visual Cognition)*, Volume 2 (pp. 241-80). Oxford University Press, USA.
- Whittle, P. (1992). Brightness, discriminability and the "crispning effect". *Vision Res*, 32(8), 1493-507.

Wurm, L. H., Legge, G. E., Isenberg, L. M., & Luebker, A. (1993). Color improves object recognition in normal and low vision. *J Exp Psychol Hum Percept Perform*, 19(4), 899-911.

Chapter 5

Conclusions

SUMMARY OF RESULTS

Face perception is the specialized ability that enables processing of facial properties, including gender, ethnicity, expression and identity. This ability lends itself to performing important automated tasks that we perform on a daily basis, such as recognition, discrimination, and searching for a particular face among a crowd of faces. When face perception is impaired, social interactions and any number of activities in our common repertoire can be severely challenged. Not surprisingly, this highly developed skill is supported by a significant portion of cortex, which is devoted to the processing of various facial properties.

The studies described in this dissertation used adaptation paradigms to investigate face-selective mechanisms in a series of psychophysical and brain imaging experiments.

There exist singly and jointly tuned mechanisms selective for the gender and ethnicity of faces

In Chapter 2, we examined the tuning of face-selective mechanisms using a psychophysical adaptation paradigm and found that there exist both *singly* (selective for either gender or ethnicity) and *jointly* (selective for both gender and ethnicity) tuned mechanisms.

It has previously been shown that adapting along a single dimension, i.e. female, that a gender-neutral face would appear male (Webster, Kaping, Mizokami, & Duhamel, 2004). This provides evidence for a mechanism selective for gender. By adapting and testing along a combination of two dimensions, we found that there existed jointly tuned

mechanisms, which are selective for a combination of both gender and ethnicity of faces in Chapter 2. Why a mechanism that encodes more than one property should exist may reflect efficient coding schemas. Gender and ethnicity are two of the most common properties by which faces are categorized. Mechanisms selective for both of these properties may, for example, aid quicker recognition. It would be interesting to see if other types of facial property (for example, attractiveness, expression, and age) show similar tuning.

Brain regions in occipital and temporal cortices are selective for a continuum of face selectivity

In Chapter 3, we isolated the brain regions involved in processing gender, ethnicity and identity using an fMRI adaptation paradigm (analogous to the psychophysical paradigm used in Chapter 2).

Looking for a particular face in a crowd utilizes a continuum of selectivity. First, faces are immediately distinguished apart from all the non-face elements in a scene. The neural regions responsible for this initial step are likely to be those identified by a traditional face area localizer, which isolates areas that respond more to faces than to non-face stimuli (Kanwisher, McDermott, & Chun, 1997). Second, if one is trying to locate Madeleine Albright, one would select all the female Caucasian faces. Using an fMRI adaptation paradigm, we found brain regions selective for gender and ethnicity that are nearby, but do not overlap with the face sensitive areas isolated by traditional localizer scans (Chapter 3). And finally, Madeleine Albright's face would be individuated from all the female Caucasian faces. Again, using an fMRI adaptation paradigm, we

identified unique brain areas selective for individual identity (Chapter 3; Ng, Ciaramitaro, Anstis, Boynton, & Fine, 2006).

Adaptation does not improve performance on perceptual tasks in face-experts

As adults, we are all face processing experts. Without much effort, we can discriminate a male face from a female face, and detect a friend's face from a group of unfamiliar faces. Can adaptation improve these expert skills?

In Chapter 4, we sought to find perceptual advantages as a result of face adaptation in several psychophysical tasks, but found no discernible improvement in performance. This may be because faces are highly over-learned and there is superabundance of representational capacity devoted to face processing. Given that face stimuli are so heavily over-represented, it seems plausible that limits in discrimination and search performance might be mainly due to signal-to-noise and/or limits in representational capacity at lower levels of processing. In the case of face processing performance on search and discrimination tasks may be mediated by lower level mechanisms than those affected by adaptation.

REFERENCES

- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J Neurosci*, 17(11), 4302-11.
- Ng, M., Ciaramitaro, V. M., Anstis, S., Boynton, G. M., & Fine, I. (2006). Selectivity for the configural cues that identify the gender, ethnicity, and identity of faces in human cortex. *Proc Natl Acad Sci U S A*, 103(51), 19552-57.
- Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, 428(6982), 557-561.