AP Seminar Performance Task 2: Individual Research-Based Essay and Presentation

Directions and Stimulus Materials

January 2018

Contents

Introduction

This performance task, highlighted in bold below, is one of three parts of the overall assessment for AP Seminar, and one of two performance tasks. The assessment for this course is comprised of:

Performance Task 1: Team Project and Presentation

- Component 1: Individual Research Report
- Component 2: Team Multimedia Presentation and Oral Defense

Performance Task 2: Individual Research-Based Essay and Presentation

- **Component 1: Individual Written Argument**
- **Component 2: Individual Multimedia Presentation**
- **Component 3: Oral Defense**

End-of-Course Exam

- Part A: Three Short-Answer Questions (based on one source)
- Part B: One Essay Question (based on four sources)

The attached pages include the directions for Performance Task 2, information about the weighting of the task within the overall assessment, and detailed information as to the expected quantity and quality of work that you should submit.

Also included are the stimulus materials for the task. These materials are theme-based and broadly span the academic curriculum. After analyzing the materials, develop a research question that suits your individual interest based on a thematic connection between at least two of the stimulus materials. Your research question must be rich enough to allow you to engage in meaningful exploration and write and present a substantive, defensible argument.

AP Seminar Performance Task 2: Individual Research-Based Essay and Presentation

Student Version

Weight: 35% of the AP Seminar score

Task Overview

This packet includes a set of stimulus materials for the AP Seminar Performance Task 2: Individual Research-Based Essay and Presentation.

You must identify a research question prompted by analysis of the provided stimulus materials, gather information from a range of additional sources, develop and refine an argument, write and revise your argument, and create a presentation that you will be expected to defend. Your teacher will give you a deadline for when you need to submit your written argument and presentation media. Your teacher will also give you a date on which you will give your presentation.

Task Components	Length	Date Due (fill in)
Individual Written Argument	2000 words	
Individual Multimedia Presentation	6–8 minutes	
Oral Defense	Respond to 2 questions	

In all written work, you must:

- Acknowledge, attribute, and/or cite sources using in-text citations, endnotes or footnotes, and/or through bibliographic entry. You must avoid plagiarizing (see the attached AP Capstone Policy on Plagiarism and Falsification or Fabrication of Information).
- Adhere to established conventions of grammar, usage, style, and mechanics.

Task Directions

1. **Individual Written Argument** (2000 words)
    - Read and analyze the provided stimulus materials to identify thematic connections among the sources and possible areas for inquiry.
    - Compose a research question of your own prompted by analysis of the stimulus materials.
    - Gather information from a range of additional sources representing a variety of perspectives, including scholarly work.
    - Analyze, evaluate, and select evidence. Interpret the evidence to develop a well-reasoned argument that answers the research question and conveys your perspective.

- Throughout your research, continually revisit and refine your original research question to ensure that the evidence you gather addresses your purpose and focus.
- Identify opposing or alternate views and consider their implications and/or limitations as you develop resolutions, conclusions, or solutions to your research question.
- Compose a coherent, convincing and well-written argument in which you:
  - Identify and explain the relationship of your inquiry to a theme or connection among at least two of the stimulus materials prompted by your reading.
  - Incorporate at least one of the stimulus materials.
  - Place your research question in context.
  - Include a variety of perspectives.
  - Include evidence from a range of sources.
  - Establish an argument that links claims and evidence.
  - Provide specific resolutions, conclusions and/or solutions.
  - Evaluate objections, limitations or competing perspectives and arguments.
  - Cite all sources that you have used, including the stimulus materials, and include a list of works cited or a bibliography.
  - Use correct grammar and style.
- Do a word count and keep under the 2000-word limit (excluding footnotes, bibliography, and text in figures or tables).
- Remove references to your name, school, or teacher.
- Upload your document to the AP Digital Portfolio.

2. **Individual Multimedia Presentation** (6–8 minutes)
   - Develop and prepare a multimedia presentation that will convey your argument to an audience of your peers.
   - Be selective about the information you choose for your presentation by focusing on key points you want your audience to understand.
   - Design your oral presentation with supporting visual media, and consider audience, context, and purpose.
   - Prepare to engage your audience using appropriate strategies (e.g., eye contact, vocal variety, expressive gestures, movement).
   - Prepare notecards or an outline that you can quickly reference as you are speaking so that you can interact with supporting visuals and the audience.
   - Rehearse your presentation in order to refine your design and practice your delivery.
   - Check that you can do the presentation within the 6- to 8-minute time limit.

- Deliver a 6–8 minute multimedia presentation in which you:
  - Contextualize and identify the importance of your research question.
  - Explain the connection between your research and your analysis of the stimulus materials.
  - Deliver an argument that connects claims and evidence.
  - Incorporate, synthesize and interpret evidence from various perspectives.
  - Offer resolutions, conclusions, and/or solutions based on evidence and consider the implications of any suggested solutions.
  - Engage the audience with an effective and clearly organized presentation design.
  - Engage the audience with effective techniques of delivery and performance.

3. **Individual Oral Defense** (two questions)

   Defend your research process, use of evidence, and conclusion(s), solution(s), or recommendation(s) through oral responses to two questions asked by your teacher. Be prepared to describe and reflect on your process as well as defend and extend your written work and oral presentation.

Sample Oral Defense Questions

Here are some examples of the types of questions your teacher might ask you during your oral defense. These are *examples only*; your teacher may ask you different questions, but there will still be one question that relates to each of the following two categories.

1. **Reflection on Research Process**
   - What information did you need before you began your research, and how did that information shape your research?
   - What evidence did you gather that you didn't use? Why did you choose not to use it?
   - How valid and reliable are the sources you used? How do you know? Which sources didn't work?
   - How did you select the strategies you used to gather information or conduct research? Were they effective?
   - How did your research question evolve as you moved through the research process? Did your research go in a different direction than you originally planned/hypothesized?
   - What information did you need that you weren't able to find or locate? How did you go about trying to find that information?
   - How did you handle the differing perspectives in order to reach a conclusion?

2. **Extending argumentation through effective questioning and inquiry**
   - What additional questions emerged from your research? Why are these questions important?
   - What advice would you have for other researchers who consider this topic?
   - What might be the real-world implications or consequences (influence on others' behaviors or decision-making processes) of your findings? What are the implications to your community?
   - If you had more time, what additional research would you conduct related to this issue?
   - Explain the level of certainty you have about your conclusion, solution, or recommendation.
   - How does your conclusion respond to any of the other research or sources you examined?
   - How did you use the conclusions and questions of others to advance your own research?

AP Capstone™ Policy on Plagiarism and Falsification or Fabrication of Information

A student who fails to acknowledge the source or author of any and all information or evidence taken from the work of someone else through citation, attribution or reference in the body of the work, or through a bibliographic entry, will receive a score of 0 on that particular component of the AP Seminar and/or AP Research Performance Task. In AP Seminar, a team of students that fails to properly acknowledge sources or authors on the Team Multimedia Presentation will receive a group score of 0 for that component of the Team Project and Presentation.

A student who incorporates falsified or fabricated information (e.g. evidence, data, sources, and/or authors) will receive a score of 0 on that particular component of the AP Seminar and/or AP Research Performance Task. In AP Seminar, a team of students that incorporates falsified or fabricated information in the Team Multimedia Presentation will receive a group score of 0 for that component of the Team Project and Presentation.

Looking-Glass House

By Lewis Carroll

From *Through the Looking-Glass*, Chapter 1

One thing was certain, that the *white* kitten had had nothing to do with it:—it was the black kitten's fault entirely. For the white kitten had been having its face washed by the old cat for the last quarter of an hour (and bearing it pretty well, considering); so you see that it *couldn't* have had any hand in the mischief.

The way Dinah washed her children's faces was this: first she held the poor thing down by its ear with one paw, and then with the other paw she rubbed its face all over, the wrong way, beginning at the nose: and just now, as I said, she was hard at work on the white kitten, which was lying quite still and trying to purr—no doubt feeling that it was all meant for its good.

But the black kitten had been finished with earlier in the afternoon, and so, while Alice was sitting curled up in a corner of the great arm-chair, half talking to herself and half asleep, the kitten had been having a grand game of romps with the ball of worsted Alice had been trying to wind up, and had been rolling it up and down till it had all come undone again; and there it was, spread over the hearth-rug, all knots and tangles, with the kitten running after its own tail in the middle.

'Oh, you wicked little thing!' cried Alice, catching up the kitten, and giving it a little kiss to make it understand that it was in disgrace. 'Really, Dinah ought to have taught you better manners! You *ought*, Dinah, you know you ought!' she added, looking reproachfully at the old cat, and speaking in as cross a voice as she could manage—and then she scrambled back into the arm-chair, taking the kitten and the worsted with her, and began winding up the ball again. But she didn't get on very fast, as she was talking all the time, sometimes to the kitten, and sometimes to herself. Kitty sat very demurely on her knee, pretending to watch the progress of the winding, and now and then putting out one paw and gently touching the ball, as if it would be glad to help, if it might.

'Do you know what to-morrow is, Kitty?' Alice began. 'You'd have guessed if you'd been up in the window with me—only Dinah was making you tidy, so you couldn't. I was watching the boys getting in sticks for the bonfire—and it wants plenty of sticks, Kitty! Only it got so cold, and it snowed so, they had to leave off. Never mind, Kitty, we'll go and see the bonfire to-morrow.' Here Alice wound two or three turns of the worsted round the kitten's neck, just to see how it would look: this led to a scramble, in which the ball rolled down upon the floor, and yards and yards of it got unwound again.

'Do you know, I was so angry, Kitty,' Alice went on as soon as they were comfortably settled again, 'when I saw all the mischief you had been doing, I was very nearly opening the window, and putting you out into the snow! And you'd have deserved it, you little mischievous darling! What have you got to say for yourself? Now don't interrupt me!' she went on, holding up one finger. 'I'm going to tell you all your faults. Number one: you squeaked twice while Dinah was washing your face this morning. Now you can't deny it, Kitty: I heard you! What's that you say?' (pretending that the kitten was speaking.) 'Her paw went into your eye? Well, that's *your* fault, for keeping your eyes open—if you'd shut them tight up, it wouldn't have happened. Now don't make any more excuses, but listen! Number two: you pulled Snowdrop away by the tail just as I had put down the saucer of milk before her! What, you were thirsty, were you? How do you know she wasn't thirsty too? Now for number three: you unwound every bit of the worsted while I wasn't looking!

'That's three faults, Kitty, and you've not been punished for any of them yet. You know I'm saving up all your punishments for Wednesday week—Suppose they had saved up all *my* punishments!' she went on, talking more to herself than the kitten. 'What *would* they do at the end of a year? I should be sent to prison, I suppose, when the day came. Or—let me see—suppose each punishment was to be going without a dinner: then, when the miserable day came, I should have to go without fifty dinners at once! Well, I shouldn't mind *that* much! I'd far rather go without them than eat them!

'Do you hear the snow against the window-panes, Kitty? How nice and soft it sounds! Just as if some one was kissing the window all over outside. I wonder if the snow *loves* the trees and fields, that it kisses them so gently? And then it covers them up snug, you know, with a white quilt; and perhaps it says, "Go to sleep, darlings, till the summer comes again." And when they wake up in the summer, Kitty, they dress themselves all in green, and dance about—whenever the wind blows—oh, that's very pretty!' cried Alice, dropping the ball of worsted to clap her hands. 'And I do so *wish* it was true! I'm sure the woods look sleepy in the autumn, when the leaves are getting brown.

'Kitty, can you play chess? Now, don't smile, my dear, I'm asking it seriously. Because, when we were playing just now, you watched just as if you understood it: and when I said "Check!" you purred! Well, it *was* a nice check, Kitty, and really I might have won, if it hadn't been for that nasty Knight, that came wiggling down among my pieces. Kitty, dear, let's pretend—' And here I wish I could tell you half the things Alice used to say, beginning with her favourite phrase 'Let's pretend.' She had had quite a long argument with her sister only the day before—all because Alice had begun with 'Let's pretend we're kings and queens;' and her sister, who liked being very exact, had argued that they couldn't, because there were only two of them, and Alice had been reduced at last to say, 'Well, *you* can be one of them then, and *I'll* be all the rest." And once she had really frightened her old nurse by shouting suddenly in her ear, 'Nurse! Do let's pretend that I'm a hungry hyaena, and you're a bone.'

But this is taking us away from Alice's speech to the kitten. 'Let's pretend that you're the Red Queen, Kitty! Do you know, I think if you sat up and folded your arms, you'd look exactly like her. Now do try, there's a dear!' And Alice got the Red Queen off the table, and set it up before the kitten as a model for it to imitate: however, the thing didn't succeed, principally, Alice said, because the kitten wouldn't fold its arms properly. So, to punish it, she held it up to the Looking-glass, that it might see how sulky it was—'and if you're not good directly,' she added, 'I'll put you through into Looking-glass House. How would you like *that*?'

'Now, if you'll only attend, Kitty, and not talk so much, I'll tell you all my ideas about Looking-glass House. First, there's the room you can see through the glass—that's just the same as our drawing room, only the things go the other way. I can see all of it when I get upon a chair—all but the bit behind the fireplace. Oh! I do so wish I could see *that* bit! I want so much to know whether they've a fire in the winter: you never *can* tell, you know, unless our fire smokes, and then smoke comes up in that room too—but that may be only pretence, just to make it look as if they had a fire. Well then, the books are something like our books, only the words go the wrong way; I know that, because I've held up one of our books to the glass, and then they hold up one in the other room.

'How would you like to live in Looking-glass House, Kitty? I wonder if they'd give you milk in there? Perhaps Looking-glass milk isn't good to drink—But oh, Kitty! now we come to the passage. You can just see a little *peep* of the passage in Looking-glass House, if you leave the door of our drawing-room wide open: and it's very like our passage as far as you can see, only you know it may be quite different on beyond. Oh, Kitty! how nice it would be if we could only get through into Looking-glass House! I'm sure it's got, oh! such beautiful things in it! Let's pretend there's a way of getting through into it, somehow, Kitty. Let's pretend the glass has got all soft like gauze, so that we can get through. Why, it's turning into a sort of mist now, I declare! It'll be easy enough to get through—' She was up on the chimney-piece while she said this, though she hardly knew how she had got there. And certainly the glass *was* beginning to melt away, just like a bright silvery mist.

In another moment Alice was through the glass, and had jumped lightly down into the Looking-glass room. The very first thing she did was to look whether there was a fire in the fireplace, and she was quite pleased to find that there was a real one, blazing away as brightly as the one she had left behind. 'So I shall be as warm here as I was in the old room,' thought Alice: 'warmer, in fact, because there'll be no one here to scold me away from the fire. Oh, what fun it'll be, when they see me through the glass in here, and can't get at me!'

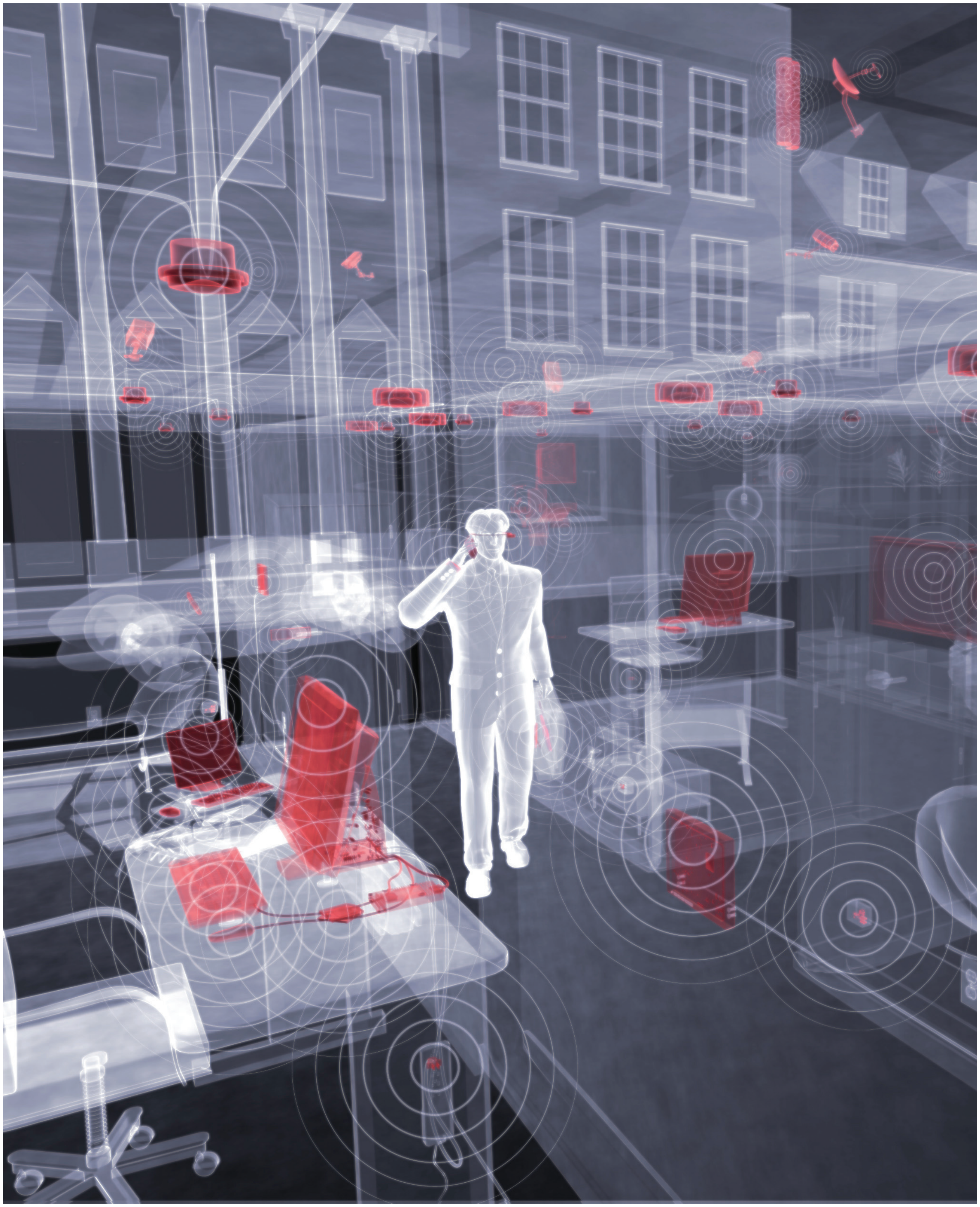
Then she began looking about, and noticed that what could be seen from the old room was quite common and uninteresting, but that all the rest was as different as possible. For instance, the pictures on the wall next the fire seemed to be all alive, and the very clock on the chimney-piece (you know you can only see the back of it in the Looking-glass) had got the face of a little old man, and grinned at her.

'They don't keep this room so tidy as the other,' Alice thought to herself, as she noticed several of the chessmen down in the hearth among the cinders: but in another moment, with a little 'Oh!' of surprise, she was down on her hands and knees watching them. The chessmen were walking about, two and two!

Extra Sensory Perception

By Gershon Dublon and Joseph A. Paradiso

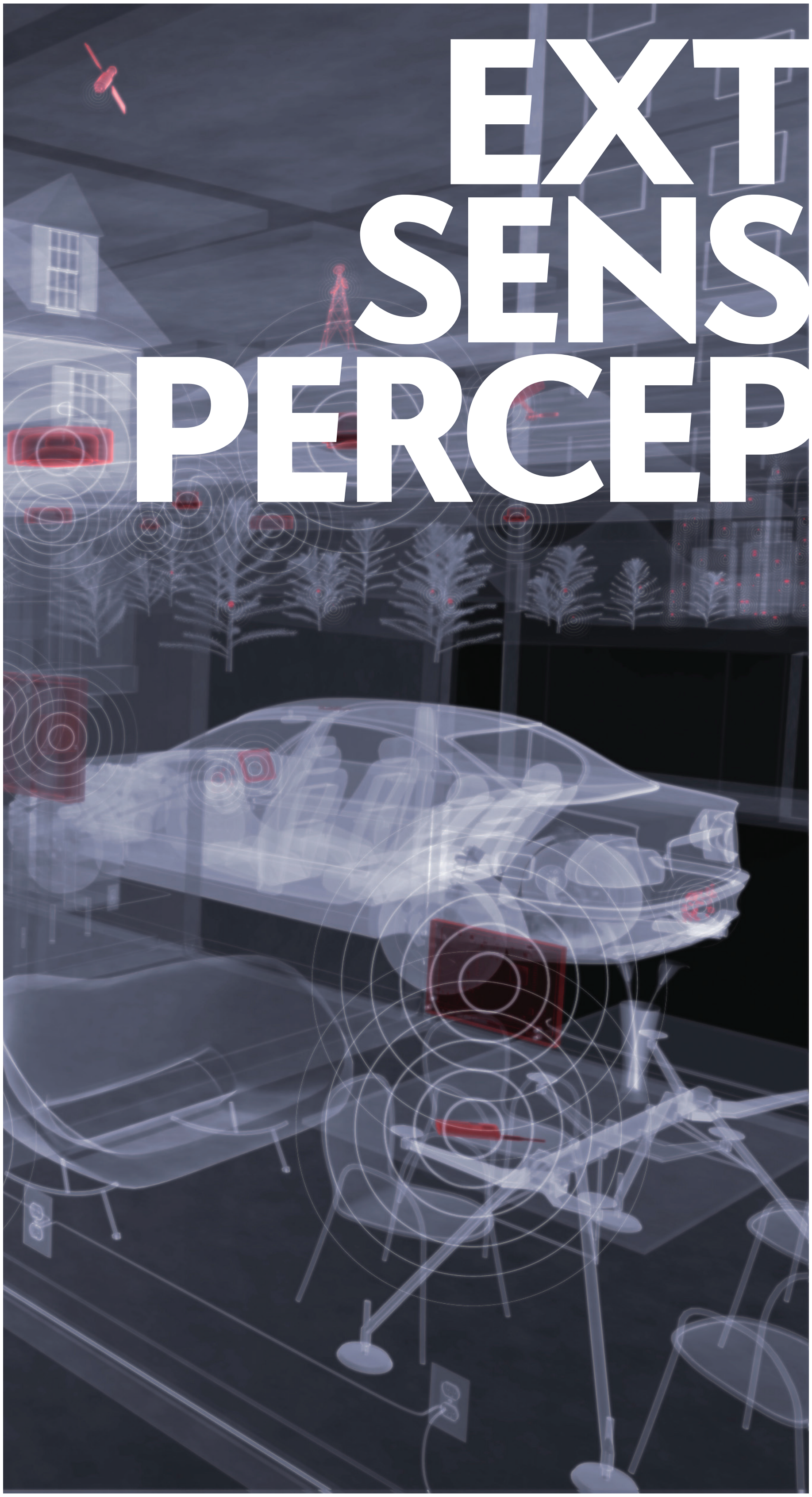
From *Scientific American*, July 2014



36 Scientific American, July 2014

COMPUTER SCIENCE

EXTRA SENSORY PERCEPTION



How a world filled with sensors will change the way we see, hear, think and live

By Gershon Dublon and Joseph A. Paradiso

IN BRIEF

The modern world is filled with network-connected electronic sensors, but most of the data they produce are invisible to us, "siloed" for use by specific applications. If we eliminate those silos and enable sensor data to be used by any network-connected device, the era of ubiquitous computing will truly arrive.

Although it is impossible to know precisely how ubiquitous computing will change our life, a likely possibility is that electronic sensors embedded in the environment will function as extensions of the human nervous system. Wearable computing devices could become, in effect, sensory prosthetics.

Sensors and computers could make it possible to virtually travel to distant environments and "be" there in real time, which would have profound implications for our concepts of privacy and physical presence.

Illustration by Mirko Ilić

Gershon Dublon is a Ph.D. student at the M.I.T. Media Lab, where he develops new tools for exploring and understanding sensor data.

Joseph A. Paradiso is an associate professor of media arts and sciences at the Media Lab. He directs the Media Lab's Responsive Environments Group, which explores how sensor networks augment and mediate human experience, interaction and perception.

HERE'S A FUN EXPERIMENT: TRY COUNTING THE ELECTRONIC SENSORS surrounding you right now. There are cameras and microphones in your computer. GPS sensors and gyroscopes in your smartphone. Accelerometers in your fitness tracker. If you work in a modern office building or live in a newly renovated house, you are constantly in the presence of sensors that measure motion, temperature and humidity.

Sensors have become abundant because they have, for the most part, followed Moore's law: they just keep getting smaller, cheaper and more powerful. A few decades ago the gyroscopes and accelerometers that are now in every smartphone were bulky and expensive, limited to applications such as spacecraft and missile guidance. Meanwhile, as you might have heard, network connectivity has exploded. Thanks to progress in microelectronics design as well as management of energy and the electromagnetic spectrum, a microchip that costs less than a dollar can now link an array of sensors to a low-power wireless communications network.

The amount of information this vast network of sensors generates is staggering—almost incomprehensible. Yet most of these data are invisible to us. Today sensor data tend to be "siloed," accessible by only one device for use in one specific application, such as controlling your thermostat or tracking the number of steps you take in a day.

Eliminate these silos, and computing and communications will change in profound ways. Once we have protocols that enable devices and applications to exchange data (several contenders exist already), sensors in anything can be made available to any application. When that happens, we will enter the long-predicted era of ubiquitous computing, which Mark Weiser envisioned in this magazine a quarter of a century ago [see "The Computer for the 21st Century"; September 1991].

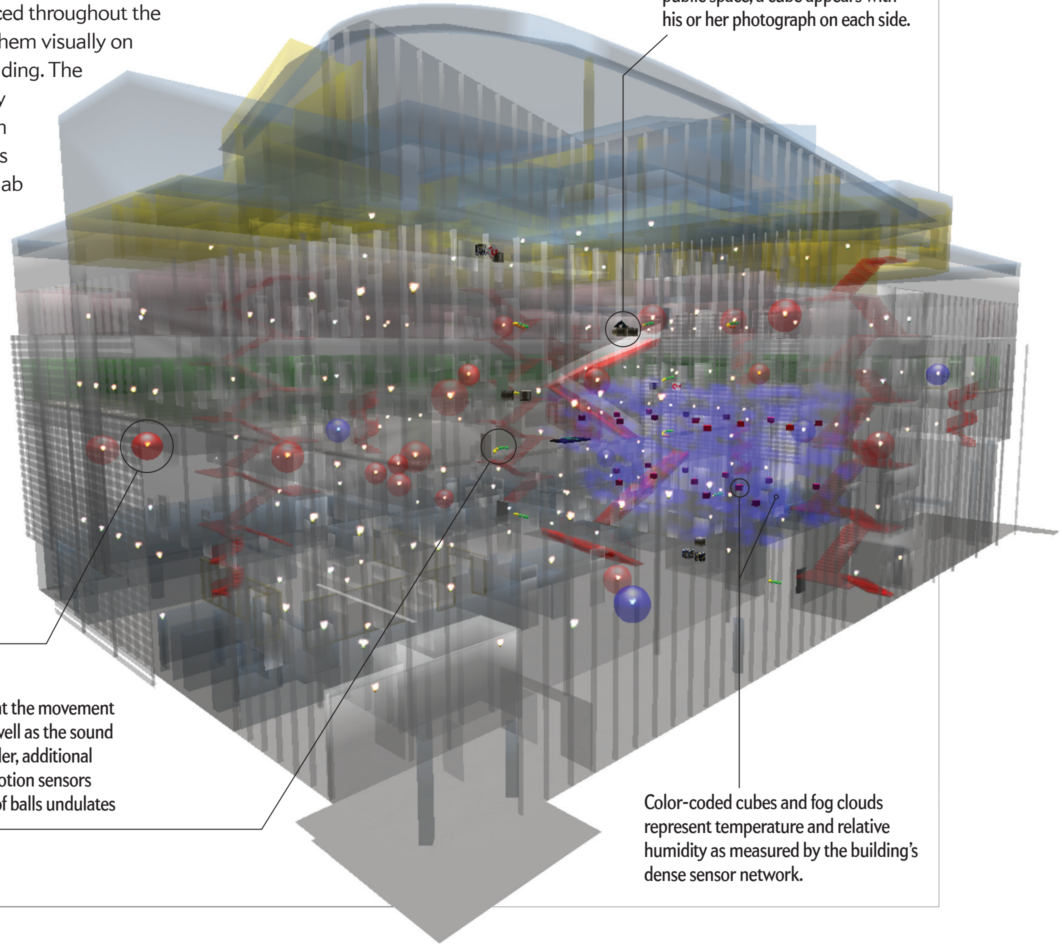
We doubt the transition to ubiquitous computing will be incremental. Instead we suspect it will be a revolutionary phase shift much like the arrival of the World Wide Web. We see the beginnings of this change with smartphone applications such as Google Maps and Twitter and the huge enterprises that have emerged around them. But innovation will explode once ubiquitous sensor data become freely available across devices. The next wave of billion-dollar tech companies will be context aggregators, who will assemble the sensor information around us into a new generation of applications.

Predicting what ubiquitous computing and sensor data will mean for daily life is as difficult as predicting 30 years ago how the Internet would change the world. Fortunately, media theory can serve as a guide. In the 1960s communications theorist Marshall McLuhan spoke of electronic media, mainly television, becoming an extension of the human nervous system. If only McLuhan were around today. When sensors are everywhere—and when the information they gather can be grafted onto human perception in new ways—where do our senses stop? What will "presence" mean when we can funnel our perception freely across time, space and scale?

HOW IT WORKS

The Reality Browser

The authors' sensor-browsing software, called DoppelLab, gathers data from sensors placed throughout the M.I.T. Media Lab and depicts them visually on a translucent model of the building. The browser updates automatically in real time, so users can log on from anywhere and see what is happening in any room in the lab at any moment. Temperature, motion, sound and other properties are depicted with icons.



COURTESY OF GERSHON DUBLON AND DOPPELLAB DEVELOPMENT TEAM

VISUALIZING SENSOR DATA

We perceive the world using all our senses, but we digest most digital data through tiny two-dimensional screens on mobile devices. It is no surprise, then, that we are stuck in an information bottleneck. As the amount of information about the world explodes, we find ourselves less able to remain present in that world. Yet there is a silver lining to this abundance of data, as long as we can learn to use it properly. That is why our group at the M.I.T. Media Lab has been working for years on ways to translate information gathered by networks of sensors into the language of human perception.

Just as browsers like Netscape gave us access to the mass of data contained on the Internet, so will software browsers enable us to make sense of the flood of sensor data that is on the way. So far the best tool for developing such a browser is the video game engine—the same software that lets millions of players interact with one another in vivid, ever changing three-dimensional environments. Working with the game engine Unity 3D, we have developed an application called DoppelLab that takes streams of data collected by sensors placed throughout an environment and renders the information in graphic form, overlaying it on an architectural computer-aided design (CAD) model of the building. At the Media Lab, for example, DoppelLab collects data from sensors throughout the building and displays the results on a computer screen in real time. A user looking at the screen can see the temperature in every room, or the foot traffic in any given area, or even the location of the ball on our smart Ping-Pong table.

DoppelLab can do much more than visualize data. It also gathers sounds collected by microphones scattered about the building and uses them to create a virtual sonic environment. To guarantee privacy, audio streams are obfuscated at the originating sensor device, before they are transmitted. This renders speech unintelligible while maintaining the ambience of the space and the vocal character of its occupants. DoppelLab also makes it possible to experience data recorded in the past. One can observe a moment in time from various perspectives or fast-forward to examine the data at different timescales, uncovering hidden cycles in the life of a building.

Sensor browsers such as DoppelLab have immediate commercial applications—for example, as virtual-control panels for large, sensor-equipped buildings. In the past a building manager who wanted to track down a problem in the heating system might have sorted through spreadsheets and graphs, cataloguing anomalous temperature measurements and searching for patterns that would point to the source. Using DoppelLab, that person can see the current and desired temperature in every room at once and quickly spot issues that span multiple rooms or floors. More than that, planners, designers and building occupants alike can see how the infrastructure is being used. Where do people gather and when? What effects do changes in the building have on how people interact and work within it?

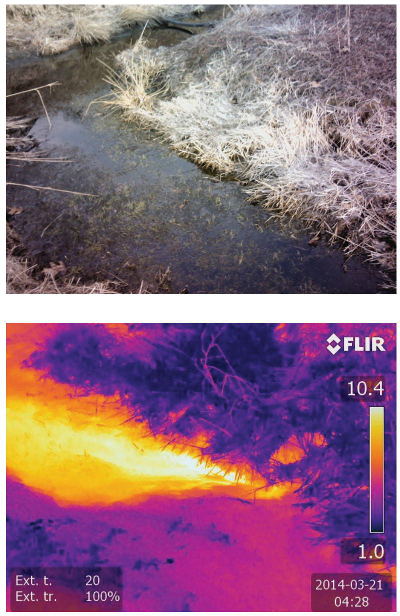
But we did not make DoppelLab with commercial potential in mind. We built it to explore a bigger and more intriguing matter: the impact of ubiquitous computing on the basic meaning of presence.

REDEFINING PRESENCE

WHEN SENSORS AND COMPUTERS make it possible to virtually travel to distant environments and "be" there in real time, "here" and "now" may begin to take on new meanings. We plan to explore this shifting concept of presence with DoppelLab and with a project called the Living Observatory at Tidmarsh Farms, which aims to immerse both physical and virtual visitors in a changing natural environment.

Since 2010 a combination of public and private environmental organizations have been transforming 250 acres of cranberry bogs in southern Massachusetts into a protected coastal wetland system. The bogs, collectively called Tidmarsh Farms, are co-owned by one of our colleagues, Glorianna Davenport. Having built her career at the Media Lab on the future of documentary, Davenport is fascinated by the idea of a sensor-rich environment producing its own "documentary." With her help, we are developing sensor networks that document ecological processes and enable people to experience the data those sensors produce. We have begun populating Tidmarsh with hundreds of wireless sensors that measure temperature, humidity, moisture, light, motion, wind, sound, tree sap flow and, in some cases, levels of various chemicals.

Efficient power management schemes will enable these sensors to live off their batteries for years. Some of the sensors will be equipped with solar cells, which will provide enough of a power boost to enable them to stream audio—the sound of the breeze, of nearby birds chirping, of raindrops falling on the surrounding leaves. Our geosciences colleagues at the University of Massachusetts Amherst are outfitting Tidmarsh with sophisticated ecological sensors, including submersible fiber-optic temperature gauges and instruments that measure dissolved oxygen levels in the water. All these data will flow to a database on our servers, which users can query and explore with a variety of applications.



INFRARED CAMERAS in a sensor-laden bog spot groundwater (*seen here in yellow*) flowing into colder surface water. While surface water tracks closely to the air temperature, groundwater maintains a steady temperature year-round.

COURTESY OF TIDMARSH FARMS, INC.

Some of these applications will help ecologists view environmental data collected at the marsh. Others will be designed for the general public. For example, we are developing a DoppelLab-like browser that can be used to virtually visit Tidmarsh from any computer with an Internet connection. In this case, the backdrop is a digital rendering of the topography of the bog, filled with virtual trees and vegetation. The game engine adds noises and data collected by the sensors in the marsh. Sound from the microphone array is blended and cross-faded according to a user's virtual position; you will be able to soar above the bog and hear everything happening at once, listen closely to a small region, or swim underwater and hear sound collected by hydrophones. Virtual wind driven by real-time data collected from the site will blow through the digital trees.

The Living Observatory is more of a demonstration project than a practical prototype, but real-world applications are easy to imagine. Farmers could use a similar system to monitor sensor-laden plots, tracking the flow of moisture, pesticides, fertilizers or animals in and around their cropland. City agencies could use it to monitor the progression of storms and floods across a city while finding people in danger and getting them help. It is not a stretch to imagine using this technology in our everyday life. Many of us already look up restaurants on Yelp before going out. One day we will be able to check out a restaurant's atmosphere (is it crowded and noisy right now?) before heading across town.

Eventually this kind of remote presence could provide the next best thing to teleportation. We sometimes use DoppelLab to connect to the Media Lab while away on travel because hearing the buzz and seeing the activity brings us a little bit closer to home. In the same way, travelers could project themselves into their homes to spend time with their families while on the road.

AUGMENTING OUR SENSES

IT IS A SAFE BET that wearable devices will dominate the next wave of computing. We view this as an opportunity to create much more natural ways to interact with sensor data. Wearable computers could, in effect, become sensory prostheses.

Researchers have long experimented with wearable sensors and actuators on the body as assistive devices, mapping electrical signals from sensors to a person's existing senses in a process known as sensory substitution. Recent work suggests that neuroplasticity—the ability of our brain to physically adapt to new stimuli—may enable perceptual-level cognition of "extra senso-

SCIENTIFIC AMERICAN ONLINE See a sensor browser demo at ScientificAmerican.com/jul2014/sensors

ry" stimuli delivered through our existing sensory channels. Yet there is still a huge gap between sensor network data and human sensory experience.

We believe one key to unlocking the potential of sensory prostheses will be gaining a better handle on the wearer's state of attention. Today's highest-tech wearables, such as Google Glass, tend to act as third-party agents on our shoulders, suggesting contextually relevant information to their wearer (recommending a particular movie as a wearer passes a movie theater, for example). But these suggestions come out of the blue. They are often disruptive, even annoying, in a way that our sensory systems would never be. Our sensory systems allow us to tune in and out dynamically, attending to stimuli if they demand it but otherwise focusing on the task at hand. We are conducting experiments to see if wearable computers can tap into the brain's inherent ability to focus on tasks while maintaining a preattentive connection to the environment.

When sensors and computers make it possible to virtually travel to distant environments, "here" and "now" may begin to take on new meanings.

Our first experiment will determine whether a wearable device in the field can pick out which of a set of audio sources a user is listening to. We would like to use this information to enable the wearer of a device to tune into the live microphones and hydrophones at Tidmarsh in much the same way that they would tune into different natural sources of sounds. Imagine concentrating on a distant island in a pond and slowly beginning to hear the faraway sounds, as if your ears were sensitive enough to extend the distance. Imagine walking along a stream and hearing sound from under the water or looking up at the trees and hearing the birdsong at the top of the canopy. This approach to delivering digital information could mark the beginning of a fluid connection between our sensory systems and networked sensor data. There will probably come a time when sensory or neural implants provide that connection; we hope these devices, and the information they provide, will fold into our existing systems of sensory processing rather than further displacing them.

DREAM OR NIGHTMARE?

FOR MANY PEOPLE, ourselves included, the world we have just described has the potential to be frightening. Redefining presence means changing our relationship with our surroundings and with one another. Even more concerning, ubiquitous computing has tremendous privacy implications. Yet we believe there are many ways to build safeguards into technology.

A decade ago, in one of our group's projects, Mat Laibowitz deployed 40 cameras and sensors in the Media Lab. He designed a huge lamp switch into each device so it could be easily and obviously deactivated. In today's world, there are too many cameras, microphones and other sensors scattered for any one person to deactivate—even if they do have an off switch. We will have to come up with other solutions.

One approach is to make sensors respond to context and a person's preferences. Nan-Wei Gong explored an idea of this kind when she was with our research group several years ago. She built a special key fob that emitted a wireless beacon informing nearby sensor devices of its user's personal privacy preferences. Each badge had a large button labeled "No"; on pressing the button, a user was guaranteed an interval of total privacy wherein all sensors in range were blocked from transmitting his or her data.

Any solution will have to guarantee that all the sensor nodes around a person both receive and honor such requests. Designing such a protocol presents technical and legal challenges. Yet research groups around the world are already studying various approaches to this conundrum. For example, the law could give a person ownership or control of data generated in his or her vicinity; a person could then choose to encrypt or restrict those data from entering the network. One goal of both DoppelLab and the Living Observatory is to see how these privacy implications play out in the safe space of an open research laboratory. As pitfalls and sinister implications reveal themselves, we can find solutions. And as the recent revelations from former NSA contractor Edward Snowden have shown us, transparency is critical, and threats to privacy need to be dealt with legislatively, in an open forum. Barring that, we believe that grassroots, open-source hardware and software development is the best defense against systemic invasions of privacy.

Meanwhile we will be able to start seeing what kinds of new experiences await us in a sensor-driven world. We are excited about the prospects. We think it is entirely possible to develop technologies that will fold into our surroundings and our bodies. These tools will get our noses off the smartphone screen and back into our environments. They will make us more, rather than less, present in the world around us. SA

MORE TO EXPLORE

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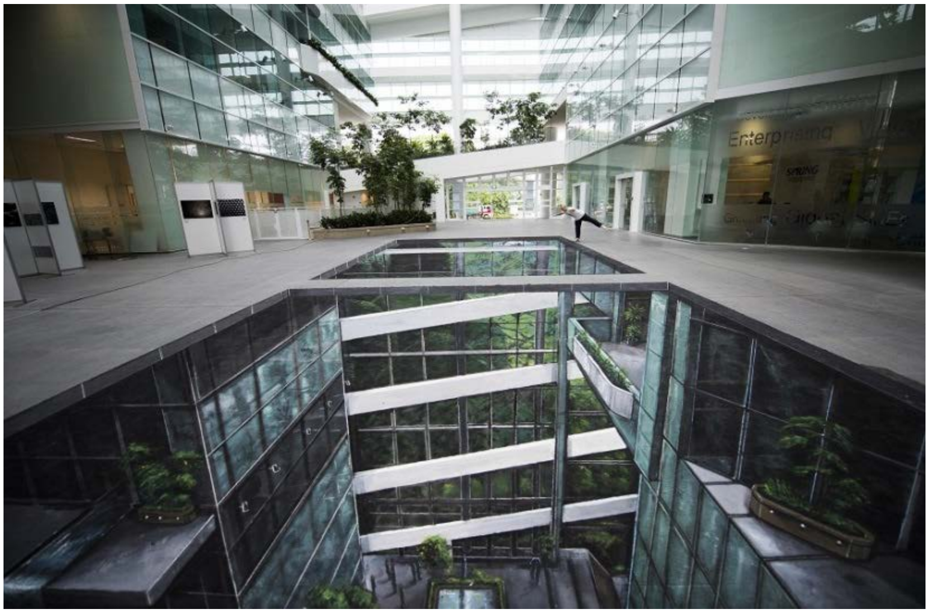
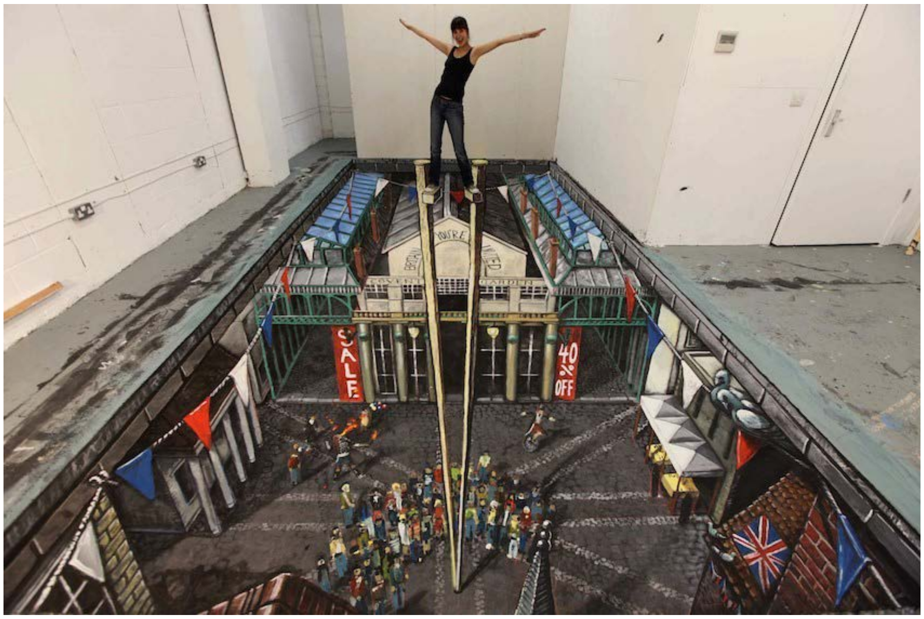
3D Pavement Art

By Joe Hill

http://joehill-art.com/page4.htm

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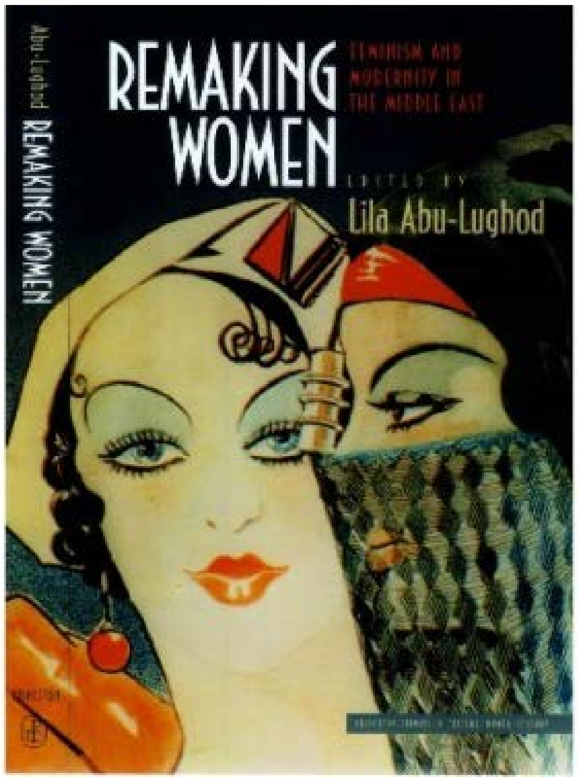
Attitudes Toward Muslim Women in the West

From an interview with Lila Abu-Lughod by the Asia Society
(http://asiasociety.org/lila-abu-lughod-attitudes-toward-muslim-women-west)



Publisher: Princeton University Press, Princeton (1998)

Lila Abu-Lughod has worked on women's issues in the Middle East for over twenty years. She has authored and edited several books on the topic, including *Writing Women's Worlds: Bedouin Stories* (Berkeley: University of California Press, 1993), *Remaking Women: Feminism and Modernity in the Middle East* (Princeton: Princeton University Press, 1998), *and Veiled Sentiments: Honor and Poetry in a Bedouin Society* (Berkeley: University of California Press, 1986). She is Professor of Anthropology and Women's and Gender Studies at Columbia University in New York.

In this interview, Professor Abu-Lughod discusses women and Islam in the wake of the American war in Afghanistan.

Following the events of September 11th, the American public sphere has been saturated with discussions of what is unique about "Muslim" societies. To what extent is the character of Muslim societies determined by Islam? How can we begin to think about these societies, and what distinguishes them from our own?

Many aspects of societies around the world cannot be understood without reference to the history and influences of the major religions in terms of which people live their lives. This is just as true for people living in the Middle East, Africa, Southeast Asia and other Muslim regions as it is for those living in Europe and the United States, where Christianity has historically dominated. The point to stress is that despite this, it is just as unhelpful to reduce the complex politics, social dynamics, and diversity of lives in the U.S. to Christianity as it is to reduce these things to Islam in other regions. We should ask not how Muslim societies are distinguished from "our own" but how intertwined they are, historically and in the present, economically, politically, and culturally.

Muslim women have of course figured prominently in this public discussion. You have suggested recently that "understanding Muslim women" will not serve to explain anything. Could you elaborate on this claim?

Many of us have noticed that suddenly, after 9/11 and the American response of war in Afghanistan, the hunger for information about Muslim women seems insatiable. My own experience of this was in the form of an avalanche of invitations to appear on news programs and at universities and colleges. On the one hand I was pleased that my expertise was appreciated and that so many people wanted to know more about a subject I had spent twenty years studying. On the other hand, I was suspicious because it seemed that this desire to know about "women and Islam" was leading people away from the very issues one needed to examine in order to understand what had happened.

Those issues include the history of Afghanistan-with Soviet, U.S., Pakistani, and Saudi involvements; the dynamics of Islamist movements in the Middle East; the politics and economics of American support for repressive governments. Plastering neat cultural icons like "the Muslim woman" over messier historical and political narratives doesn't get you anywhere. What does this substitution accomplish? Why, one has to ask, didn't people rush to ask about Guatemalan women, Vietnamese women (or Buddhist women), Palestinian women, or Bosnian women when trying to understand those conflicts? The problem gets framed as one about another culture or religion, and the blame for the problems in the world placed on Muslim men, now neatly branded as patriarchal.

The British in India and the French in Algeria both enlisted the support of women for their colonial projects (i.e., part of the colonial enterprise was ostensibly to "save" native women). Do you think the current rhetoric about women in Afghanistan suffers from the same problem? Is there something about the colonial/neo-colonial context that lends itself to this kind of representation (which would explain why such rhetoric cannot be employed for, say, African American women in this country)?

Yes, I ask myself about the very strong appeal of this notion of "saving" Afghan women, a notion that justifies American intervention (according to First Lady Laura Bush's November radio address) and that dampens criticism of intervention by American and European feminists. It is easy to see through the hypocritical "feminism" of a Republican administration. More troubling for me are the attitudes of those who do genuinely care about women's status. The problem, of course, with ideas of "saving" other women is that they depend on and reinforce a sense of superiority by westerners.

When you save someone, you are saving them from something. You are also saving them to something. What violences are entailed in this transformation? And what presumptions are being made about the superiority of what you are saving them to? This is the arrogance that feminists need to question. The reason I brought up African American women, or working class women in the U.S., was that the smug and patronizing assumptions of this missionary rhetoric would be obvious if used at home, because we've become more politicized about problems of race and class. What would happen if white middle class women today said they needed to save those poor African American women from the oppression of their men?

You mentioned that the veil or burqa has been spoken of and defended by Muslim women as "portable seclusion" and that veiling should not be associated with lack of agency. Can you explain why this is the case?

It was the anthropologist Hanna Papanek, working in Pakistan, who twenty years ago coined this term of "portable seclusion." I like the phrase because it makes me see burqas as symbolic "mobile homes" that free women to move about in public and among strange men in societies where women's respectability, and protection, depend on their association with families and the homes which are the center of family lives.

The point about women's veiling is of course too complicated to lay out here. But there were three reasons why I said it could not so simply be associated with lack of agency. First, "veiling" is not one thing across different parts of the Muslim world, or even among different social groups within particular regions. The variety is extraordinary, going from headscarves unselfconsciously worn by young women in rural areas to the fuller forms of the very modern "Islamic dress" now being adopted by university women in the most elite of fields including medicine and engineering. Second, many of the women around the Muslim world who wear these different forms of cover describe this as a choice. We need to take their views seriously, even if not at face value. Beyond that, however, we need to ask some hard questions about what we actually mean when we use words like "agency" and "choice" when talking about human beings, always social beings always living in particular societies with culturally variable meanings of personhood. Do we not all work within social codes? What does the expression we often use here "the tyranny of fashion" suggest about agency in dress codes?

ARTHUR SCHLESINGER, JR.

The Historian as Participant

Source: Daedalus, Vol. 100, No. 2, The Historian and the World of the Twentieth Century (Spring, 1971), pp. 339-358

After a marked recession in the nineteenth century, "eyewitness history"—history written by persons who themselves took part in the events they record—has undergone a revival in the later twentieth century. This revival has met with a certain skepticism and resistance from professional historians. Yet it may well be related to deeper tendencies within modern society; and, since these tendencies will only intensify in the foreseeable future, we may expect eyewitness history to continue to spread among us for some time to come. For this reason the phenomenon deserves examination.

Let us begin with some distinctions. The term eyewitness history, I have suggested, covers historical accounts written by those who directly observed at least some of the events described. Such observation may take place at a high or a low level. Plainly the historian who participates in decisions at the summit will have one kind of knowledge; but it is an error, I think, to suppose that the historian who served, say, as an infantryman in the Second World War was not affected by that experience and would not write, as a historian, about the war with insight he might not otherwise have had. Eyewitness history is obviously a branch of that larger field, contemporary history, by which one means historical accounts written by persons alive in the time in which the events take place.

Eyewitness history must be distinguished from memoirs, which are eyewitness accounts *not* written from the historical viewpoint. There is something distinctive, one assumes, about the historical temperament and the historical approach; the historian surely brings to the observation and analysis of events a perspective different from that brought by the nonhistorian. Bernal Diaz, Saint-Simon, Boswell, Caulaincourt, U. S. Grant, for example, were all formidable participant-observers or memoirists, but they cannot be said to have perceived events as historians would have perceived them. Memoirs are part of the raw material of history, but they are written for their own purposes—to set down one man's experience or to chronicle notable events or to discharge vanities or rancors—rather than to discern causation in the flow of events over time. Thus memoirs were produced in steady volume through the nineteenth and early twentieth centuries, while eyewitness history, on the other hand, rose and fell, and now has risen again.[1]

For there is nothing new, of course, in the idea that historians should write from their own direct experience. "Of the events of the [Peloponnesian] war," observed Thucydides, "I have described nothing but what I either saw myself, or learned from others of whom I made the most careful and particular enquiry." Confident that the war "would be great and memorable above any previous war," Thucydides, he tells us, began work on his history when the Athenians and the Peloponnesians first took up arms against one another. As an Athenian, he was soon swept up in the conflict himself; and it seems unlikely that he would have carried his history as far as he did had it not been for his failure as a commander in the field. The twenty year exile imposed by his native city after the disaster of Amphipolis liberated him to visit battlefields, interview veterans, verify or disprove second-hand tales, and reconcile conflicting testimony; "the task was a laborious one, because eye-witnesses of the same occurrences gave different accounts of them, as they remembered or were interested in the actions of one side or the other."[2]

It would be wrong to conclude that only failed soldiers could become effective eyewitness historians; Xenophon and Caesar are contrary examples. It would also be wrong to suppose that most classical history was contemporary history. The eyewitness historian Flavius Josephus of Jerusalem (another failed soldier, who collected the materials for his history of the Judaeo-Roman war during his years as a Roman captive) complained that the later Hellenic historians had ignored the events of their own country and age, turning instead to the remote history of Assyria and Media. Josephus much preferred their predecessors who had "devoted themselves to writing the history of their own times, in which their personal participation in events gave clarity to their presentment and every falsehood was certain of exposure by a public that knew the facts."[3]

When the Renaissance revived traditions of secular history, historians felt free to write about the present as well as the past. Nor was there prejudice against participants. Guiccardini and Machiavelli were eyewitness historians of sixteenth-century Florence, as was Clarendon of seventeenth-century England. When historians could not take part in the events they were writing about, they often took part in such events as were available to them and believed that such participation benefited them as historians. "The discipline and evolution of a modern battalion," wrote Gibbon, "gave me a clearer notion of the phalanx and the legions, and the captain of the Hampshire grenadiers (the reader may smile) has not been useless to the historian of the Roman empire."[4] Until the later nineteenth century, most of the great historians were, in one way or another, captains of the Hampshire grenadiers—from Bacon and Raleigh to Macaulay, Tocqueville, Guizot, Carlyle, Bagehot, Bancroft, Parkman, Henry Adams. They were all involved in the public world; they were not men just of the study and the lamp.

In the later nineteenth century, however, a new question arose, I think for the first time—the question whether participation in public events might not disqualify the participant from writing about these events as a historian; whether, indeed, experience in the public world might not be incompatible with the ideal of historical objectivity. Such questions were a direct consequence of the professionalization of history. Historians were now increasingly segregated in universities, enshrined in academic chairs, surrounded by apprentices; and the crystallization of this distinct and specific status brought with it a tendency to reject, first, historians who participated in the events they described and, soon, historians who participated in anything beyond the profession of history. Indeed, it may have been unconsciously felt that eyewitness history, by involving the historical profession in ongoing conflicts, might raise threats to the hard-won new status. As Sir Walter Raleigh, one of the few historians to suffer the ultimate criticism of the executioner's ax, had warned two and a half centuries before, "Whosoever, in writing a modern history, shall follow truth too near the heels, it may haply strike out his teeth."[5]

Professionalization conceived historical research and writing as a self-sufficient, full-time, life-long vocation. Felix Gilbert has recalled to us Meinecke's heartfelt statement:

> We must be aware of the inner difficulties with which a rising historian has to struggle today. At first, he will have to concentrate on studies in

a very narrow and isolated area. He is confronted by tasks and problems of a professional character and he must tackle them in a prescribed manner. Editions and specialized documentary studies—usually not chosen by himself but assigned to him or recommended to him—will usually absorb the first decade of his scholarly life. Today scholarship, having become an organized large-scale enterprise, presses most heavily on the individual scholar in the most susceptible years of his development.[6]

Professionalization meant rigorous training in the techniques of the craft; it meant specialization; it meant bureaucratization; it meant a stern insistence on critical methods as the guarantee of objectivity; it meant a deep pride in the independence and autonomy of the historical guild and an ardent conviction that the new professional techniques were winning history unprecedented new successes. "The historians of former times," wrote Acton, "unapproachable for us in knowledge and in talent, cannot be our limit. We have the power to be more rigidly impersonal, disinterested and just than they."[7]

Such severe standards created the image of the historian as a monastic scholar, austerely removed from the passing emotions and conflicts of his own day. From this viewpoint, participation in the public world meant the giving of hostages—to parties, to institutions, to ideologies. In retrospect, it seemed that Macaulay was too deeply a Whig, Bancroft too deeply a Jacksonian, Henry Adams too deeply an Adams. The view arose that not only participant-historians but even historians who wrote about contemporaneous events were too deeply compromised to fulfill the pure historical vocation.

As late as the days before the Second World War, a professional historian who carried his lectures up to his own time was deemed rash and unhistorical; a professional historian who wrote on contemporary events was considered to have lapsed into journalism; a professional historian who took part in events and wrote about them later was a rarity. Most scholars still felt that a generation or so was required before current affairs underwent the sea change into history. Today, however, few American universities would hesitate to offer courses which start with the Second World War and end with yesterday's newspaper. Only the most ascetic scholars now object to attempts to write serious accounts of the very recent past. And contemporary history has inevitably brought along with it eyewitness history as a vital component.

How to account for this unexpected emergence of contemporary history into academic respectability? The fundamental explanation lies, I think, in the acceleration of the rate of social change—an acceleration produced by the cumulative momentum of science and technology. Each decade generates both more innovations and more effective ways of introducing innovations into the social process. This acceleration, which Henry Adams was first among historians to understand, has meant, among other things, that the "present" becomes the "past" more swiftly than ever before in the history of man. If Rip Van Winkle had made a habit of coming back from the Catskills every twenty years, he would find each new visit more perplexing and more incredible. This steady increase in the velocity of history inevitably affects the psychology of the historian. What historians perceive as the "past" is today chronologically much closer than it was when historical change was the function, not of days, but of decades. In the twelfth century, the historian's "past" was centuries back; in the nineteenth century it was a generation or two back. Now it is yesterday.

At the same time, the emergence of a more extensive educated public than the world has ever known has increased the popular demand for knowledge about the problems that torment modern man—especially when, with the invention of nuclear weapons, these problems, if not brought under control, might rush civilization on to the final catastrophe. History becomes an indispensable means of organizing public experiences in categories conducive to understanding. And the popular appetite for knowledge is further whetted by the development of television, bringing with it new experiences and new stimuli as well as creating the unprecedented situation in which history-in-the-making is now made, or at least observed, in every living room. Moreover, the fear of dehumanization so pervasive in the high-technology society, the felt threats to individual identity, also doubtless invite the effort to rehumanize the historical process produced by eyewitness history.

Along with these developments, there have been novel happenings within the historical field itself. Great manuscript collections, in the United States, at least, now tend to be open to scholars sooner than ever before. Franklin D. Roosevelt, in leaving his papers to the National Archives of the United States and providing for their early accessibility to students, set a salutary example which all subsequent Presidents have followed. Where the Adams papers, for example, were closed for decades, where the papers of even so recent a President as Herbert Hoover were impounded for a generation, the Roosevelt precedent will make it difficult for public men of the future—again, at least in the United States—to lock up their manuscripts indefinitely. Hereafter the presumption will surely be in favor of making papers available to scholars as speedily as prudent standards of security and discretion permit. The alternative presumption will be that the deponent has something to hide.

Yet the very accessibility of contemporary manuscript collections has had another and somewhat paradoxical effect: it has demonstrated to scholars the inadequacy of documents by themselves as sources for twentieth-century history. In the early nineteenth century, if a public figure had a message to send, paper was the only means, save face-to-face conversation, of communication. Moreover, quill pen in hand, he could write only a limited number of letters. Historians studying these good old days can relax fairly comfortably in the archives, confident that the documents will not only be competent sources but will not be too numerous to be read by a single student.

Those days, alas, are gone forever. The revolution in the technology of communications—especially the invention of the typewriter and the telephone—has depreciated the value of the document. While the typewriter has increased the volume of paper, the telephone has reduced its importance. Far more documents are produced, and there is far less in them. If a contemporary statesman has something of significance to communicate, if speed and secrecy are of the essence, he will confide his message, not to a letter, but to the telephone. Until the Federal Bureau of Investigation opens up its library of wire taps, we must assume that these vital historical moments will elude the documentary record.

Ironically the rise of contemporary history has itself doubtless contributed to the condition of documentary impoverishment. The growing insistence that papers should, as a matter of right, be immediately opened to scholars may lead to a dilution and distortion of the written record. Public officials, fearing next decade's graduate students, become reluctant to put in writing the real reasons behind some of their actions. Theodore Roosevelt was not the last politician to take the precaution of writing memoranda for the files or letters to friends in order to present his own version of public events or decisions. Yet this very condition of documentary impoverishment serves as a further stimulus to contemporary history; for, if the eyewitness is part of the cause, he can also be part of the cure. As Flavius Josephus pointed out nearly two thousand years ago, a primary justification of the eyewitness historian is the evidence he preserves. "To place on record events never previously related and to make contemporary history accessible to later generations," Josephus wrote, "is an activity deserving of notice and commendation. Genuine research consists not in the mere rearrangement of material that is the property of others, but in the establishment of an original body of historical knowledge."[8]

This variety of factors helps explain the comeback this century of the historian who writes out of his own direct experience. The revival began outside the guild when participants who lacked the professional badge but possessed the historical temperament began to write the history of events they themselves had witnessed. Winston Churchill's *The World Crisis* (1923-1929) was an early and influential example, followed, of course, by *The Second World War* (1948-1954). In the meantime the two world wars brought professional historians themselves into the public arena, whether as soldiers, diplomats, intelligence analysts, political advisers, or official historians; and many were tempted to apply their craft to the dramatic events unfolding before their eyes. Some even may have had the illusion they could influence affairs; Johannes von Müller was not the last historian in search of a hero.

Yet the traditional case of the professional historian against contemporary history remained. That case derived essentially from the ancient proposition *veritas temporis filia.* Truth was seen as the daughter of time: written history became better the farther away the historian was from the events he was describing. So Sir Herbert Butterfield analyzed the stages of historiographical growth:

> If we consider the history of the historical writing that has been issued, generation after generation, on a given body of events, we shall generally find that in the early stages of this process the narrative which is produced has a primitive and simple shape. As one generation of students succeeds another, however, each developing the historiography of this particular subject, the narrative passes through certain typical stages until it is brought to a high and subtle form of organisation.[9]

History, in this view, regularly passed from the "heroic" phase, in which contemporary writers portrayed personal goodness and badness as dominant motives and employed melodrama as the dominant tone, into the "technical" phase, when later historians could at last see men as trapped in a structural predicament with right and wrong on both sides and the dominant tone one of tragedy.

The technical historian, recollecting in tranquility, was presumed to have solider knowledge, clearer perspective, and surer freedom from emotion and prejudice. "That history which is most liable to large-scale structural revision," Professor Butterfield argued, "is contemporary history—the first version of events as they appear from the special platform of particular actors in the drama, often indeed a version used for militant purposes in the conflicts of the time." When historians studied the conflicts of the past, they should therefore give little credence to "the contemporary ways of formulating that conflict."[10] And, of all forms of contemporary history, eyewitness history logically contained more pitfalls than any other, was more vulnerable to interest, bias, illusion, and wishful thinking.

There is plainly great force in this argument. It seems plausible that historians coming along later should have access to a wider range of materials than eyewitness historians could have had. It seems plausible that they should be more free of passion and prepossession. It seems plausible that, with their knowledge of the way things have come out, they could more accurately identify the critical factors in the process. One can see the evolution described by Professor Butterfield at work today, for example, in the movement from "heroic" to "technical"—from melodramatic to tragic—renditions of the origins of the Cold War.

The traditional argument for the inferiority of contemporary history, and especially of eyewitness history, thus rests on alleged deficiencies in both the collection and the interpretation of historical facts. But is this all there is to be said? Certainly if eyewitnesses are going to write an increasing amount of modern history, it is perhaps appropriate to reexamine this traditional case.

One may start by inquiring whether the superiority supposedly possessed by the technical historian in the collection of historical facts is all that self-evident. Guiccardini's caution—"Documents are rarely falsified at the start. It is usually done later, as occasion or necessity dictates"[11]—suggests one advantage enjoyed by the eyewitness historian: he has the chance of seeing evidence before it is cooked. Probably Guiccardini's warning has less application in the xerox age, where the ease of immediate duplication complicates the task of subsequent falsification. But one can never be sure, as when one hears President Johnson read Walter Cronkite a memorandum claiming to direct the Defense Department in February 1968 to prepare alternatives to further escalation in Vietnam—a document directly contrary in sense to the one that the Secretary of Defense says he then received from the White House.

Moreover, personal participation in a historical episode may well make the historian more critical of his materials. In writing about the past, the technical historian often is tempted to use letters, diaries, memoranda, newspapers as if they were reliable forms of evidence. When such evidence is construed under the pressure of direct experience, however, it may become more apparent that *A*'s letters are his own self-serving versions of events, that *B's* diaries are designed, consciously or not, to dignify the diarist and discredit his opponents, that *C*'s memoranda are written to improve the record and that the newspapermen recording the transactions had only the dimmest idea what was really going on.

The technical historian is inevitably the prisoner of the testimony that happens to survive. He cannot, like Thucydides, cross-examine witnesses; nor, like Flavius Josephus, does he expose himself to a public that knows the facts. Mr. Dooley well summed up the truth of the matter: "Th' further ye get away fr'm anny peeryod th' betther ye can write about it. Ye are not subjict to interruptions be people that were there."[12] Hence one vital importance of eyewitness history for the future technical historian: it can, as Josephus suggested, help meet the need to supplement documents if we are to recover the full historical transaction.

Tocqueville, in the notes for his unwritten second volume on the French Revolution, discriminates between facts available to technical historians and facts reported by eyewitness historians:

> We are still too close to these events to know many details (this seems curious, but it is true); details often appear only in posthumous revelations and are frequently ignored by contemporaries. But what these writers know better than does posterity are the movements of opinion, the popular inclinations of their times, the vibrations of which they can still sense in their minds and hearts. The true traits of the principal persons and of their relationships, of the movements of the masses are often better described by witnesses than recorded by posterity. These are the necessary details. Those close to them are better placed to trace the general history, the general causes, the grand movements of events, the spiritual currents which men who are further removed may no longer find.[13]

Tocqueville's point about the grand movements applies equally to people. "It is not true," said Santayana, "that contemporaries misjudge a man. Competent contemporaries judge him . . . much better than posterity, which is composed of critics no less egotistical, and obliged to rely exclusively on documents easily misinterpreted."[14] Charles Francis Adams made a related point in this introduction to his grandparents' letters. "Our history," he wrote, "is for the most part wrapped up in the forms of office . . . Statesmen and Generals rarely say all they think." They are seen for the most part "when conscious that they are upon a theatre," and in their papers "they are made to assume a uniform of grave hue."

> The solitary meditation, the confidential whisper to a friend, never meant to reach the ear of the multitude, the secret wishes, not blazoned forth to catch applause, the fluctuations between fear and hope that most betray the springs of action,—these are the guides to character, which most frequently vanish with the moment that called them forth, and leave nothing to posterity but those coarser elements for judgment, that are found in elaborated results.[15]

Moreover, the controversy produced by exercises in what has been acrimoniously called "instant history"—the claims and counterclaims made by participants while they are still around—indispensably enrich the historical record.

It may further be the case that eyewitness historians often have a more realistic judgment about the operative facts. Practical experience may yield qualities of insight hard to achieve in the library; historians who *know* how laws are passed, decisions made, battles fought are perhaps in a better position to grasp the actuality of historical transactions. Thus Woodrow Wilson, praising Tocqueville and Bagehot, remarked that they were great analysts because they "were not merely students, but also *men of the world,* for whom the only acceptable philosophy of politics was a generalization from actual daily observation of men and things."[16]

Participation may not only sharpen the historian's judgment; it may also stimulate and amplify what might be called the historian's reconstructive imagination. To take part in public controversy, to smell the dust and sweat of conflict, to experience the precariousness of decision under pressure may help toward a better understanding of the historical process. When I was a very young historian, a so-called revisionist school used to write about the coming of the American Civil War on the assumption that the burning emotions of the day, especially those seizing the abolitionists, were somehow artificial and invalid. But personal immersion in a historical experience leaves the historian no doubt that mass emotions are realities with which he no less than statesmen must deal. Far from being gratuitous and needless, as the revisionist historians once tried to tell us, the way people think and feel is an organic part of history.

This is something that the technical historian misses, as Professor Butterfield has noted: "The reader of technical history learns too little from it of the hopes and fears of the majority of men, too little of their joy in nature and art, their falling in love, their family affection, their spiritual questings, and their ultimate vision of things." Since this is so, Professor Butterfield himself has wondered "whether technical history can claim to give us the mirror of life any more than modern physics provides us with an actual picture of the universe."[17] If technical history cannot claim to give us the mirror of life, can one be so certain about the advantages allegedly provided by the stages of historiographical growth? If I may cite a personal example, I have no question that, by writing *A Thousand Days* the year after President Kennedy's death, I was able to suggest something about the mood and relationships of the Kennedy years which no future historian could ever get on the basis of the documents—indeed, which I myself could not have reproduced, with the fading of memory, the knowledge of consequences, and the introduction of new preoccupations and perspectives, had I tried to write the book ten or twenty years later. Page Smith (in *The Historian and History*) argues persuasively that, for historians writing years after the fact, "the difficulty of re-creating faithfully the events and their causes will be greater and demand a more powerful effort of the will and the creative imagination than that demanded of the participant-historian."[18]

The case against the eyewitness historian in the domain of facts thus seems on examination less compelling than the arguments of the technical historian at first suggest. Against the doctrine that truth is the daughter of time one may perhaps place Emerson's dictum: "Time dissipates to shining ether the solid angularity of facts."[19]

Are the traditional arguments against eyewitness history in the domain of interpretation any more satisfactory? The theory of the stages of historiographical growth assumes the purifying effects of the passage of time, with distance steadily removing distortions of interest and emotion until a final version can be attained, or at least approached. Professor Butterfield has well stated the ideal: "I should not regard a thing as 'historically' established unless the proof were valid for the Catholic as well as the Protestant, for the Liberal as well as the Marxist."[20]

But little appears more wistful in retrospect than the confidence of technical historians that the deepening of research and the lengthening of perspective will ineluctably produce scholarly consensus on the large historical questions. It is not obvious in practice that time has been, in fact, the father of truth, if by truth we mean the agreement of historians. We know now that time cannot be counted to winnow out prejudice and commitment and leave the scholar, all passion spent, in tranquil command of the historical reality.

The passage of time does not, for example, liberate the historian from his deepest values and prepossessions. Posterity, in Santayana's phrase, is "composed of critics no less egotistical." "Historians of every period," David Butler has well said, "seem able to acquire equally deep emotions about their subject matter," and he recalls that his grandfather, A. F. Pollard, the noted scholar, "expressed far more vehement views about Martin Luther than I have ever ventured about any contemporary politician."[21] The major difference on the question of bias is that the bias of the eyewitness historian is infinitely easier to detect and thus to discount. Wherever vital issues are involved, whether the events are as close to us as the war in Vietnam or as remote as the fall of the Roman Empire, distance will not insure convergence. All interesting historical problems may be said to be in permanent contention; that is why they are interesting. One comes to feel that historians agree only when the problems as well as the people are dead.

As long as the problems are still alive, the passage of time only offers new possibilities for distortion. The present, as historians well know, re-creates the past. This is partly because, once we know how things have come out, we tend to rewrite the past in terms of historical inevitability. And it is partly because each new generation in any case projects its own obsessions on the screen of the past. But, despite E. H. Carr, hindsight may not be the safest principle on which to base the writing of history. What Hamilton in the 70th *Federalist* called "the dim light of historical research"[22] is not always an x-ray beam, penetrating to the underlying structure of reality; it is more often a flickering candle, revealing only those surfaces of things a time-bound historian is able to see.

"Every true history," said Croce, summing up the epistemological issue, "is contemporary history."[23] So a religious age interprets political conflicts in religious terms and an economic age interprets religious conflicts in economic terms, and so on until one must conclude that, if truth is the daughter of time, it takes a wise father to know his own children. In the words of Dewey, "We are committed to the conclusion that all history is necessarily written from the standpoint of the present, and is, in an inescapable sense, the history not only of the present but of that which is contemporaneously judged to be important in the present."[24] One must ask forgiveness for summoning high authority to labor so elementary a point, except that the point is all too rarely applied to the validity of eyewitness history. If eyewitness history lacks perspective, so does technical history and in much the same sense.

If history thus provides an infinite regression of historical interpretations, how then are we to say that one interpretation is "truer" than another?—if truth is to mean more than felt relevance to a climate of opinion. And, if there is no obvious answer to this question, can it be that eyewitness history not only offers an essential supplement to technical history but may—at least in some ways and certain circumstances—supply a more satisfying and enduring version of events?

Far from historical truth being unattainable in contemporary history, it may almost be argued that in a sense truth is *only* attainable in contemporary history. For contemporary history means the writing of history under the eye of the only people who can offer contradiction, that is, the witnesses. Every historian of the past knows at the bottom of his heart how much artifice and extrapolation go into his reconstructions; how much of his evidence is partial, ambiguous, or hypothetical; and how safe he is in his speculations because, barring recourse to spirit mediums, no one can easily say him nay, except other historians, and all they have to put up is other theories.

Once men are dead, the historian can never really know whether his reconstruction bears much relation to what actually happened. As Lionel Trilling observed in an essay on Tacitus, "To minds of a certain sensitivity 'the long view' is the falsest historical view of all, and indeed the insistence on the length of perspective is intended precisely to overcome sensitivity—seen from sufficient distance, it says, the corpse and the hacked limbs are not so very terrible, and eventually they even begin to compose themselves into a 'meaningful pattern.' "[25] "*Restored* history," wrote Ruskin in *The Stones of Venice*, "is of little more value than restored painting or architecture . . . The only history worth reading is that written at the time of which it treats, the history of what was done and seen, heard out of the mouths of the men who did and saw."[26]

To reject the testimony of men and women as to the significance of their own actions and lives, to say that, while they *thought* they were acting on such-and-such motives, we, so much wiser, *know* they were acting on quite other motives, is to commit the sin of historical reductionism. It is, as Page Smith well says, to "deprive these lives of their meaning by judgments imposed long after the event," and this is "to deny our forebears their essential humanity." In doing this, we not only diminish them; we diminish ourselves. We tie ourselves to reductionist theories which subsequent generations have every right to turn against us. We surrender, Page Smith warns, "our belief in ourselves, in the integrity of our own lives."[27]

Professor Butterfield himself has made much this same point in his brilliant critique of Sir Lewis Namier for draining "the intellectual content out of the things that politicians do" and for refusing to realize the operative force of ideas" and thereby divesting history of "the ideas and intentions which give [policies] so much of their meaning."[28] The denial that people in the past understood why they were doing things can lead only to the conclusion that we don't know why we are doing things either; and the difficulty of sustaining this position may well be an important reason for the failure of a great deal of historical revisionism. After much theorizing through the years, American historians today (like Bernard Bailyn) have come to a position about the causes of the American Revolution not too far from that taken in 1789 by David Ramsay in his *History of the American Revolution*; so historians today, instead of dismissing the rhetoric of Jacksonian democracy as "campaign claptrap" (the phrase is Lee Benson's),[29] are returning to the view that the Jacksonians may have meant what they said; so historians today, after a long pursuit of other causes, generally agree with those who personally fought the American Civil War that it was more "about" slavery than about anything else. Of course these current historical judgments are time-bound too and undoubtedly will be revised; but one feels that historians will return more often to contemporaneous interpretations than to subsequent reinterpretations. If the actors themselves gave lucid and urgent testimony as to why they lived, struggled, died, is it not a form of intellectual arrogance for historians to come along later and pretend to know better?*

This argument assumes, of course, the reality of a certain measure of human choice and self-determination. It rejects philosophies of historical determinism. This does not imply extravagant claims about the extent of human freedom. One may accept Tocqueville's formulation of the problem: "It is true that around every man a fatal circle is traced beyond which he cannot pass; but within the wide verge of that circle he is powerful and free."[30]

In short, the insight generated by participation is not confined to perceptions and interpretations of specific episodes. It goes, I would argue, to very general conceptions of history. For historians

* This argument is, of course, incomplete. There are some things the future historian *can* know better; and the problem of the conflict between contemporaneous consciousness of reality and the facts as determined later is too much a digression to go into at length here. A couple of examples, however, may suggest the issue. Thus Bernard Bailyn has argued that a major cause of the American Revolution was the theory held by leading colonists that George III was carrying out a conspiracy against the English constitution—a theory which Sir Lewis Namier has shown to be an illusion. Or consider the question of the profitability of slavery in the United States. The new economic historians, especially Alfred Conrad and John Meyer, employing refined tools of economic analysis, have demonstrated persuasively that—contrary to the contemporaneous impression—the slavery system was profitable. The contemporaneous impression had important historical consequences, but it was apparently wrong.

In other words, contemporaneous perceptions may well be misperceptions, which is doubtless why Professor Butterfield warns against yielding to "the contemporary ways of formulating . . . conflict." Still the misconceptions of the American colonists in the 1770's or of the slaveholders in the 1850's are a vital segment of the historian's story; and, while it is part of the historian's job to test the validity of contemporaneous perceptions, he must always take care not to replace the categories of the actors by his own latter-day categories when he discusses the motives of action. Full historical reconstruction requires attention to Sorel's reminder in *Reflections on Violence:* "We are perfectly aware that the historians of the future are bound to discover that we laboured under many illusions, because they will see behind them a finished world. We, on the other hand, must act, and nobody can tell us today what these historians will know; nobody can furnish us with the means of modifying our motor images in such a way as to avoid their criticisms." Georges Sorel, *Reflections on Violence* (New York: Collier Books, 1961), p. 149.

are frequently the victims, if more often in a small than a grand way, of what James has called "our indomitable desire to cast the world into a more rational shape in our minds than the shape into which it is thrown there by the crude order of experience." The historian's compulsion is the passion for pattern. Reconstructing events in the quiet of his study, he likes to tidy things up, to find interconnections and unities. "The form of inner consistency," to borrow James's language, "is pursued far beyond the line at which collateral profits stop."[31]

If, however, the historian has taken part in great events, he has learned that things rarely happen in a tidy, patterned, rational way. General George Marshall used to say that battlefield decisions were taken under conditions of "chronic obscurity"—that is, under excessive pressure on the basis of incomplete and defective information. This is probably the character of most critical decisions in the field of public policy. The eyewitness historian tends to preserve the felt texture of events and to recognize the role of such elements as confusion, ignorance, chance, and sheer stupidity. The technical historian, coming along later, revolts against the idea of "chronic obscurity" and tries to straighten things out. In this way, he often imputes pattern and design to a process which, in its nature, is organic and not mechanical. Historians reject the conspiratorial interpretation of history; but, in a benign way, they sometimes become its unconscious proponents, ascribing to premeditation what belongs to fortuity and to purpose what belongs to accident.

Participation may, of course, breed its own deformations. Again we may look to Tocqueville to suggest the appropriate distinctions:

> I have come across men of letters, who have written history without taking part in public affairs, and politicians, who have only concerned themselves with producing events without thinking of describing them. I have observed that the first are always inclined to find general causes, whereas the others, living in the midst of disconnected daily facts, are prone to imagine that everything is attributable to particular incidents, and that the wires they pull are the same that move the world. It is to be presumed that both are equally deceived.

For himself, Tocqueville added, he detested those "absolute systems" which represented all events as depending on first causes and linked by the chain of fatality—systems which, as it were, "suppress men from the history of the human race." Many important facts, he continued, can only be explained by accidental circumstances; many others remain totally inexplicable. "Chance, or rather that tangle of secondary causes which we call chance, for want of the knowledge how to unravel it, plays a great part in all that happens on the world's stage; although I firmly believe that chance does nothing that has not been prepared beforehand."[32]

This is an accurate account of the play of events as eyewitness historians tend to see it; and it is why such historians would probably agree with a couple of Emerson's aphorisms (and urge that they be framed above every historian's desk):

> In analysing history, do not be too profound, for often the causes are quite superficial.

And:

> I have no expectation that any man will read history aright who thinks that what was done in a remote age, by men whose names have resounded far, has any deeper sense than what he is doing today.[33]

History infused by this spirit has its own distinctive character. Without prolonged philosophical digression, one can refer to James's insistence in "The Dilemma of Determinism" on the reality of the idea of chance and the argument against historical inevitability developed so brilliantly in our own day by Isaiah Berlin. My impression is that the experience of participation tends to inoculate historians against what James called "a temper of intellectual absolutism, a demand that the world shall be a solid block, subject to one control."[34] The inoculation does not always take; Marx—a contemporary historian and a participant in events if never an eyewitness historian—remains a monumental exception. But, in the main, historians who have been immersed in the confusion of events seem less inclined to impose an exaggeratedly rational order on the contingency and obscurity of reality.

I am not contending that eyewitness history, or contemporary history in general, are "better" than technical history, whatever such a judgment might mean. Obviously we need both, and the dialectic between them is a major part of the historical exercise. I would only suggest that the conventional reasons for professional disdain may not be so impressive as historians once thought—that eyewitness history has its own and distinctive strengths and advantages.

In any case, eyewitness history appears to meet significant intellectual and social needs and therefore will be with us for some time to come. If this is so, then let eyewitness historians abide by the highest standards of their peculiar trade and write always in the spirit of Clarendon:

And as I may not be thought altogether an incompetent person for this communication, having been present as a member of Parliament in those councils before and till the breaking out of the Rebellion, and having since had the honour to be near two great kings in some trust, so I shall perform the same with all faithfulness and ingenuity, with an equal observation of the faults and infirmities of both sides, with their defects and oversights in pursuing their own ends; and shall no otherwise mention small and light occurrences than as they have been introductions to matters of the greatest moment; nor speak of persons otherwise than as the mention of their virtues or vices is essential to the work in hand: in which as I shall have the fate to be suspected rather for malice to many than of flattery to any, so I shall, in truth, preserve myself from the least sharpness that may proceed from private provocation or a more public indignation; in the whole observing the rules that a man should, who deserves to be believed.[35]

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SCENTS AND SENSIBILITY: A MOLECULAR LOGIC OF OLFACTORY PERCEPTION

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by

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INTRODUCTION

The image in the painting *La Bonne Aventure* is not a nose (Fig. 1). It is a portrayal by the surrealist René Magritte of his own brain's representation of the external world. It is a vignette that reveals a tension between image and reality, a tension that is a persistent source of creativity in art, brought to its culmination by the surrealists. The problem of how the brain represents the external world is not only a central theme in art but is at the very core of philosophy, psychology, and neuroscience. We are interested in how the chemosensory world is represented in the brain.

All organisms have evolved a mechanism to recognize sensory information in the environment and transmit this information to the brain where it then must be processed to create an internal representation of the external world. There are many ways for organisms to probe the external world. Some smell it, others listen to it, many see it. Each species therefore lives in its own unique sensory world of which other species may be partially or totally unaware. A whole series of specific devices alien to human perception have evolved: biosonar in bats, infrared detectors in snakes, electrosensitive organs in fish, and a sensitivity to magnetic fields in birds. What an organism detects in its environment is only part of what is around it and that part differs in different organisms. The brain functions, then, not by recording an exact image of the world, but by creating its own selective picture; a picture largely determined by what is important for the survival and reproduction of the species.

Sensory impressions, therefore, are apprehended through the lens of the particular perceiving brain and the brain must therefore be endowed with an *a priori* potential to recognize the sensory world (1). Our perceptions are not direct recordings of the world around us, rather they are constructed internally according to innate rules. Colors, tones, tastes, smells are active constructs created by our brains out of sensory experience. They do not exist as such outside of sensory experience (2). Biological reality, I argue, therefore

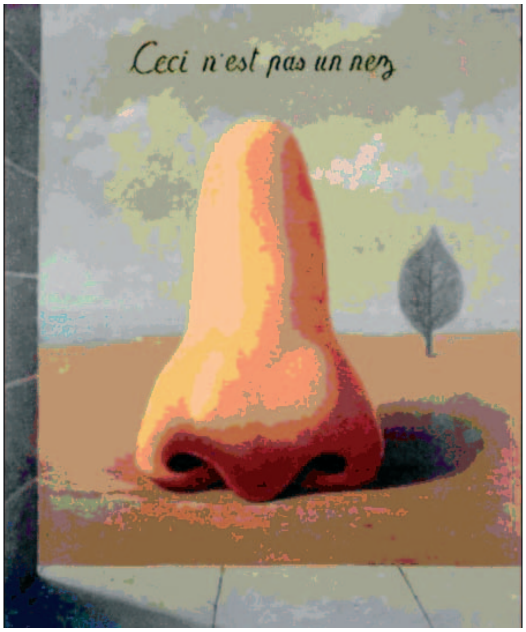

Figure 1. La Bonne Aventure. The painting *La Bonne Aventure* (Fortune Telling), by René Magritte (1937) portrays a monumental nose. I have added the inscription "Ceci n'est pas un nez" (This is not a nose) in Magritte's script to emphasize the tension between image and reality, a conflict inherent in much of his art as well as in the science of perception.

reflects the particular representation of the external world that a brain is able to build and a brain builds with genes.

If our genes are indeed the arbiters of what we perceive from the outside world, then it follows that an understanding of the function of these genes could provide insight into how the external world is represented in our brain. But what can molecular biology really tell us about so elusive a brain function as perception? Molecular biology was invented to solve fundamental problems in genetics at a molecular level. With the demystification of the brain, with the realization that the mind emerges from the brain and that the cells of the brain often use the very same principles of organization and function as a humble bacterium or a liver cell, molecular biology and genetics could now interface with neuroscience to approach the previously tenuous relationship between genes and behavior, cognition, memory, emotion, and perception.

Why would a molecular neuroscientist interested in perception choose to focus on the elusive sense of smell? In humans, smell is often viewed as an aesthetic sense, as a sense capable of eliciting enduring thoughts and memories. Smell however is the primal sense. It is the sense that affords most organisms the ability to detect food, predators, and mates. Smell is the central sensory modality by which most organisms communicate with their environment. Second, humans are capable of recognizing hundreds of thousands of different odors. For molecular neuroscientists studying the brain, the mechanism by which an organism can interact with the vast universe of molecular structures defined as odors provides a fascinating problem in molecular recognition and perceptual discrimination. Finally, the problem of perception necessarily involves an understanding of how sensory input is ultimately translated into meaningful neural output: thoughts and behavior. In olfaction, the sensory input is extremely well defined and consists of chemicals of precise molecular structure. The character of the input in olfaction is far simpler than that of a visual image, for example, which consists of contour, texture, color, movement and form of confounding complexity. Representation of an olfactory image is simpler and reduces to the problem of how precisely defined chemical structures are transformed in brain space.

As molecular neurobiologists, Linda Buck and I approached olfactory sensory perception by dividing it into two problems: First, what mechanisms have evolved to allow for the recognition of the vast array of molecular structures we define as odorants? Clearly, there must be receptors in the sensory neurons of the nose capable of associating with odor molecules. Do we have a relatively small number of "promiscuous" receptors, each capable of interacting with a large number of odorous molecules? Alternatively, olfactory recognition may involve a very large number of "chaste" receptors each capable of interacting with a limited set of odor molecules. The second problem is conceptually more difficult: how does the olfactory sensory system discriminate among the vast array of odorous molecules that are recognized by the nose? Put simply, how does the brain know what the nose is smelling? This question will ultimately require knowledge of how the different odors are represented and encoded in the brain.

A LARGE FAMILY OF ODORANT RECEPTOR GENES

We approached the problem of odor recognition directly by isolating the genes encoding the odorant receptors (3). The experimental design we employed to isolate these genes was based on three assumptions: First, the odorant receptors were likely to belong to the superfamily of receptors, the G-protein coupled receptors (GPCRs), that transduce intracellular signals by coupling to GTP binding proteins (4,5,6,7). Second, the large repertoire of structurally distinct, odorous molecules suggests that the odorant receptors themselves must exhibit significant diversity and are therefore likely to be encoded by a multigene family. Third, the expression of the odorant receptors should be restricted to the olfactory epithelium. Experimentally, we used the polymerase chain reaction (PCR) to amplify members of the GPCR gene superfamily expressed in olfactory sensory neurons. We then asked whether any of the PCR products were indeed members of a large multigene family. We observed that restriction enzyme cleavage of a single PCR band generated a set of DNA fragments whose molecular weight summed to a value significantly greater than that of the original PCR product (3). In this manner, we identified a multigene family that encodes a large number of GPCRs whose expression is restricted to the olfactory sensory neurons. The receptors were subsequently shown to interact with odors translating the energy of odor binding into alterations in membrane potential (8,9,10,11).

The completed sequence of both the murine and human genome ultimately identified 1300 odorant receptors in the mouse (12,13) and 500 in humans (14,15,16). If mice possess 20,000 genes, then as much as 5% of the genome, one in 20 genes encodes the odorant receptors. A large family of odorant receptors is observed not only in vertebrates but in the far simpler sensory systems of invertebrates. A somewhat smaller but highly diverse family of about 80 odorant receptor genes has been identified in the *Drosophila* genome (17,18,19,50,67). The invertebrate, *C. elegans*, with only 302 neurons and 16 olfactory sensory neurons expresses about 1000 odorant receptor genes (20,21). These experiments provide a solution to the first question; we recognize the vast array of molecular structures defined as odorants by maintaining in our genome a large number of genes encoding odorant receptors.

The observation that over 1000 receptors are required to accommodate the detection of odors suggests a conceptual distinction between olfaction and other sensory systems. Color vision in humans, for example, allows the discrimination of several hundred hues with only three different photoreceptors (22,23). These photoreceptors each have distinct but overlapping absorption spectra. Discrimination of color is thought to result from comparative processing of the information from these three classes of photoreceptors. Whereas three photoreceptors can absorb light across the entire visible spectrum, our data suggest that a small number of odorant receptors cannot recognize the full spectrum of distinct molecular structures perceived by the mammalian nose. Rather, olfactory perception requires a large number of receptors each capable of recognizing a small number of odorous ligands.

The large number of odorant receptor genes when compared with receptor numbers in other sensory systems, perhaps reflects the fact that in vision and hearing the character of the sensory stimulus is continuously variable. Color is distinguished by quantitative differences in a single parameter, the wavelength of light. Similarly, one important parameter of hearing, the frequency of sound, is continuously variable. The diversity of chemical structures of odors do not exhibit continuous variation of a single parameter and therefore cannot be accommodated by a small number of receptors. Rather, the full spectrum of distinct molecular structures perceived by the olfactory system requires a large number of receptors, each capable of interacting with a small number of specific odorous ligands.

A TOPOGRAPHIC MAP IN THE OLFACTORY BULB

We next turned to the question of olfactory discrimination: how does the brain know what the nose is smelling? The identification of a large family of receptor genes allowed us to pose this question in molecular terms. We could now ask how the brain knows which of the numerous receptors have been activated by a given odor. The elucidation of a mechanism by which the brain

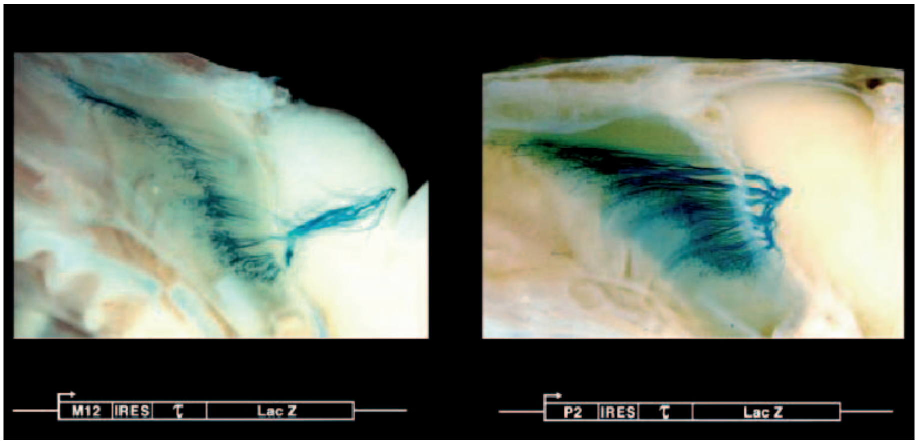

Figure 2. Convergence of Axons from Neurons Expressing a Given Receptor. Odorant receptor loci were modified by homologous recombination in ES cells to generate strains of mice in which cells expressing a given receptor also express a fusion of the microtubule associated protein, tau, with β-galactosidase. These whole mount photographs reveal neurons expressing either the M12 (left) or P2 (right) receptors along with their axons as they course through the cribriform plate to a single locus in the olfactory bulb. Neurons expressing different receptors converge on different glomeruli. The genetic modifications that assure the coordinate expression of receptor and tau-lacZ are shown beneath the whole mount view. Reprinted from *Cell*, Vol 87, 1996, pp 675-686, Mombaerts *et al.,* with permission from Elsevier.

distinguishes the different combinations of receptors activated by different odors would provide a logic of odor discrimination. This problem was further simplified by the demonstration that an individual sensory neuron expresses only one of the 1000 receptor genes (10,24). This observation emerged from single neuron cDNA cloning experiments, and allowed us to translate the problem of how the brain determines which receptor has been activated to a far simpler problem: how does the brain know which neuron has been activated by a given odor. As in other sensory systems, an invariant spatial pattern of olfactory sensory projections could provide a topographic map of receptor activation that defines the quality of a sensory stimulus.

In other sensory systems, spatially segregated afferent input from peripheral sensory neurons generates a topographic map that defines the location of a sensory stimulus within the environment as well as the quality of the stimulus itself. Olfactory sensory processing does not extract spatial features of the odorant stimulus. Relieved of the requirement to map the position of an olfactory stimulus in space, we asked whether the olfactory system might employ spatial segregation of sensory input to encode a quality of an odorant. Robert Vassar in my lab and Kerry Ressler in Linda Buck's lab therefore analyzed the spatial patterns of receptor expression in the olfactory epithelium by *in situ* hybridization and observed that cells expressing a given receptor are restricted to one of four broad but circumscribed zones (25,26).

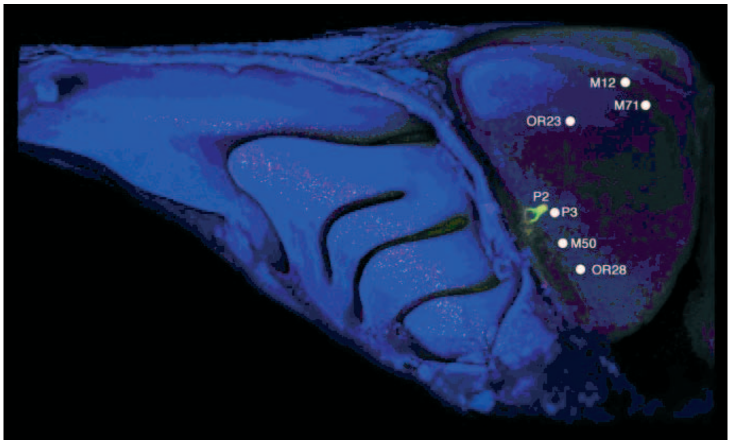

Figure 3. A Topographic Map of Olfactory Sensory Axons in the Bulb. A whole mount reveals neurons expressing two modified P2 alleles: P2-IRES-tau-lacZ (red) or P2-IRES-GFP (green). These neurons send axons that co-converge on the same glomerulus in the olfactory bulb. Neurons expressing other receptors converge on different glomerular loci that are shown schematically. All nuclei are stained blue with TOTO-3. The relative positions of the different glomeruli are maintained in different mice revealing an invariant topographic map in the olfactory bulb.

The overriding feature of this organization, however, is that within a zone neurons expressing a given receptor are not topographically segregated, rather they appear randomly dispersed. When they performed *in situ* hybridization experiments to the bulb, the first relay station for olfactory sensory neurons in the brain, they observed that topographic order was restored (27,28). Neurons expressing a given receptor, although randomly distributed in the epithelium, project to spatially invariant glomeruli in the olfactory bulb generating a topographic map.

Peter Mombaerts, then a fellow in the lab, developed a genetic approach to visualize axons from olfactory sensory neurons expressing a given odorant receptor as they project to the brain (29). We modified receptor genes by targeted mutagenesis in the germ line of mice. These genetically altered receptor genes now encode a bicistronic mRNA that allows the translation of receptor along with tau-lacZ, a fusion of the microtubule-associated protein tau with β-galactosidase. In these mice, olfactory neurons that transcribe a given receptor also express tau-lacZ in their axons, permitting the direct visualization of the pattern of projections in the brain (Fig. 2).

We observe that neurons expressing a receptor project to only two topographically-fixed loci, or glomeruli, in the bulb creating mirror image maps in each bulb. Neurons expressing different receptors project to different glomeruli. The position of the individual glomeruli is topographically defined and is similar for all individuals in a species (Fig. 3). Individual odors could activate a subset of receptors that would generate specific topographic patterns of activity within the olfactory bulb such that the quality of an olfactory stimulus could be encoded by spatial patterns of glomerular activity.

The identification of an anatomic olfactory sensory map poses four questions. The first, addresses the singularity of receptor gene choice. What mechanism assures that a sensory neuron expresses only a single receptor and then projects with precision to one of 1000 topographically fixed glomerular loci? Second, does the anatomic map translate into a functional map such that different odors elicit different patterns of activity? Third, can we relate specific spatial patterns of glomerular activity to specific behaviors? Finally how is the map read? How does the brain look down upon a spatial pattern of activity and associate this pattern with a particular odor?

RECEPTOR CHOICE AND THE TOPOGRAPHIC MAP

The topographic map in the olfactory system differs in character from the orderly representation inherent in the retinotopic, tonotopic, or somatotopic sensory maps. In these sensory systems, the peripheral receptor sheet is represented in the central nervous system (CNS), such that neighbor relations in the periphery are preserved in the CNS (reviewed in 30,31). In this manner, peripheral receptor cells may acquire a distinct identity that is determined by their spatial position in the receptor sheet. Spatial patterning in the periphery can therefore endow individual neurons with positional information that directs their orderly representation in the brain.

The olfactory system, however, does not exhibit an orderly representation of receptor cells in the periphery. Neurons expressing a given receptor are randomly dispersed within a given zone and order is restored in the bulb where neurons expressing a given receptor converge on discrete loci to create a topographic map. Olfactory neurons differ from one another not by virtue of their position in a receptor sheet, but rather by the nature of the receptor they express. The tight linkage between the choice of an odorant receptor and the site of axon convergence suggests a model in which the odorant receptor is expressed on dendrites, where it recognizes odorants in the periphery, and also on axons, where it governs target selection in the bulb. In this manner, an olfactory neuron would be afforded a distinct identity that dictates the nature of the odorant to which it responds as well as the glomerular target to which its axon projects. If the odorant receptor also serves as a guidance molecule, this leads to two experimental predictions. First, the receptor should be expressed on axons as well as on dendrites and second, genetic modifications in the receptor sequence might alter the topographic map.

The first prediction was tested by Gilad Barnea who generated specific antibodies against two odorant receptors and examined the sites of receptor expression on sensory neurons (32). Antibodies were raised against extracellular and cytoplasmic epitopes of the mouse odorant receptors, MOR28 and MOR11-4. In the sensory epithelium, we observe intense staining in the den-

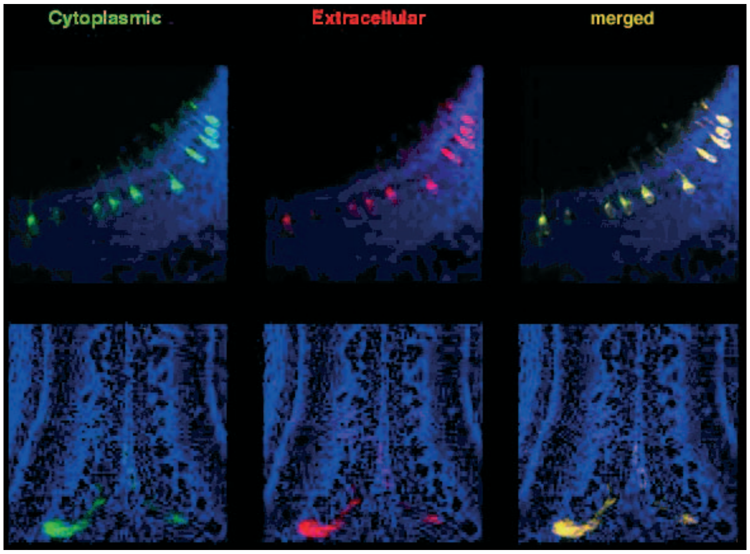

Figure 4. Odorant Receptor is Expressed on both Dendrites and Axons of Olfactory Sensory Neurons. The mouse sensory epithelium (upper panel) or olfactory bulb (lower panel) was stained with antibody to either an extracellular or cytoplasmic epitope of the MOR28 receptor. These experiments reveal the expression of odorant receptor in the cell body and dendrites in the epithelium as well as on axon termini within a defined glomerulus in the bulb. Antibody staining in the olfactory bulb coincides with the site of convergence of MOR28 axons. Adapted with permission from 32. Reprinted from *Science* 304,1468, 2004, with permission from *Science*.

dritic knobs, the site of odor binding. In the olfactory bulb, antibody stains axon termini whose arbors are restricted to two glomeruli (Fig. 4). Antibody staining of the bulb from mice bearing the MOR28-IRES-tau-lacZ allele reveals that the glomeruli stained by antibody to MOR28 also receives the tau-lacZ fibers. Thus the receptor is expressed on both dendrites and the axons of sensory neurons.

In a second series of experiments performed by a student Fan Wang, we provided genetic evidence suggesting that the receptor on axons is indeed a guidance molecule. We modified our gene targeting approach to ask whether substitutions of the P2 receptor coding sequence alter the projections of neurons that express this modified allele (33). We replaced the coding region of the P2 gene with the coding regions of several other receptors, and examined the consequences on the formation of the topographic map. Substitution of the P2 coding region with that of the P3 gene, a linked receptor gene homologous to P2 and expressed in the same epithelial zone, results in the projection of axons to a glomerulus distinct from P2 that resides immediately adjacent to the wild type P3 glomerulus. Other substitutions that replace the P2 coding sequences with receptor sequences expressed either in different zones or from different chromosomal loci also result in the convergence of fibers to glomeruli distinct from P2. These observations, along with recent experiments involving more extensive genetic modifications (34,35) provide support for the suggestion that the olfactory receptor plays an instructive role in axon targeting as one component of the guidance process.

How may the odorant receptors participate in the guidance process? In one model, the odorant receptor is expressed on the axon termini along with other guidance receptors where it recognizes positional cues elaborated by the bulb. Each of the 1000 distinct types of sensory neuron will therefore bear a unique combination of guidance receptors that define a code dictating the selection of a unique glomerular target. Such a model does not necessarily imply that there are 1000 distinct cues, each spatially localized within the bulb. Rather, a small number of graded cues may cause the differential activation of the different odorant receptors on axon termini. In this manner, the different affinities of individual receptors for one or a small number of cues, and perhaps different levels of receptor, might govern target selection. Such a model is formally equivalent to models of retinotopy in which a gradient of guidance receptor on retinal axons is matched by a positional gradient of guidance cues in the tectum (reviewed in 31).

THE SINGULAR AND STABLE CHOICE OF RECEPTOR

If the odorant receptor defines the functional identity of a sensory neuron and also determines the site of projection in the brain, then the expression of a single receptor gene in a neuron is an essential feature in models of olfactory perception. This immediately poses the question as to what mechanism has evolved to assure the expression of a single receptor gene from the family of 1000 genes in the chromosome. One model for the control of olfactory receptor (OR) expression invokes the existence of 1000 different sensory neurons, each expressing a unique combination of regulatory factors that governs the choice of a different OR gene. This deterministic model predicts that all OR genes will contain different *cis*-regulatory sequences that are recognized by unique sets of transcription factors. An alternative, stochastic model of receptor gene selection suggests that all odorant receptor genes within a zone contain the same *cis*-regulatory information and are controlled by the same set of transcription factors. In this model a special mechanism must exist to assure that only one receptor gene is chosen. Moreover, once a specific receptor is chosen for expression, this transcriptional choice must be stable for the life of the cell because receptor switching after stable synapse formation would seriously perturb odor discrimination.

A series of transgene experiments performed by Ben Shykind in my own laboratory, as well as in other labs, provide evidence for a mechanism of receptor choice that is stochastic (36,37). We have generated mice in which the endogenous P2 allele has been replaced with the P2-IRES-tau-lacZ allele. We have also introduced a randomly integrated P2-IRES-GFP transgene into the chromosome of this strain. In a deterministic model, we predict that a unique combination of transcription factors would activate both the endoge-

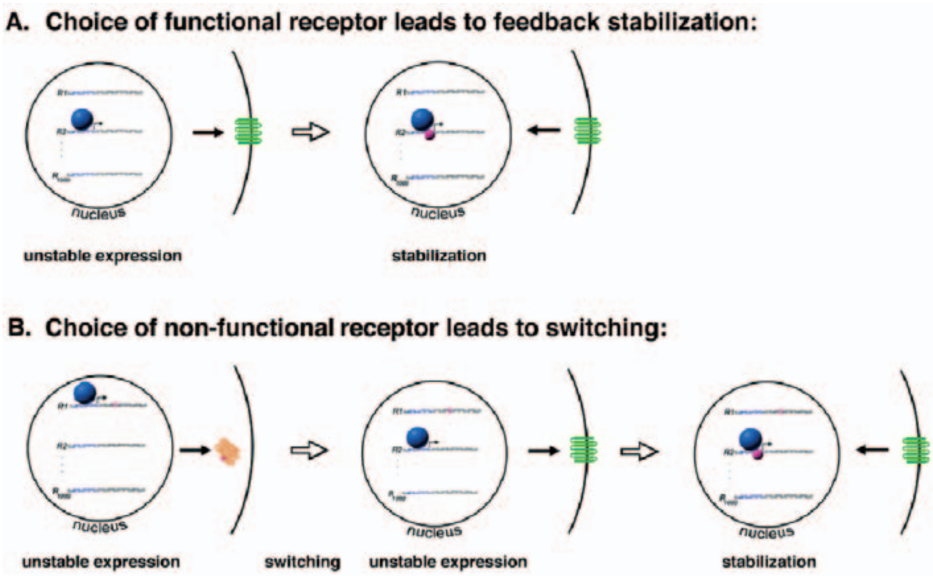

Figure 5. A Feedback Model Assuring the Stable Expression of a Functional Receptor. (A) The transcriptional machinery represented by a blue sphere expresses only one of 1000 odorant receptor genes (in this instance, R2). R2 encodes a functional receptor that elicits a feedback signal that leads to the stabilization of receptor choice (symbolized by a red sphere). (B) If the transcriptional machinery chooses the non-functional receptor, R1, which is not competent to mediate feedback stabilization, switching occurs. The transcriptional machine is then free to select a second receptor for expression that will ultimately mediate feedback stabilization. This model provides a mechanism to assure that a neuron expresses a functional odorant receptor.

nous and transgenic P2 alleles such that cells that express lacZ from the endogenous P2-IRES-tau-lacZ allele should also express GFP from the P2 transgene. Examination of the sensory epithelium in these mice, however, reveals a singularity of P2 expression. Cells that express the endogenous P2 allele never express the transgene. In a conceptually similar experiment, we generated transgenic mice that harbor an integrated array of multiple P2 transgenes that include P2-IRES-tau-lacZ and P2-IRES-GFP linked at the same chromosomal locus. In these strains, we also observe a singularity of transgene expression. Neurons that express the P2-IRES-tau-lacZ transgene do not express the linked P2-IRES-GFP gene. Taken together, these experiments provide support for a model in which receptor choice is not deterministic, rather it is stochastic.

Once a single receptor gene is chosen for expression, this transcriptional choice must be stable for the life of the cell because receptor switching after stable synapse formation would seriously perturb odor discrimination. In recent experiments, Ben Shykind in my lab along with the Reed and Sakano labs devised genetic strategies that permit the analysis of the stability of receptor choice (38,39,40). We have employed a lineage tracer to map the fate of sensory neurons that express either an intact or a nonfunctional deletion of the MOR28 gene. Mature neurons that express an intact MOR28 receptor, but have not yet formed stable synapses in the brain, can switch receptor expression, albeit at low frequency. Thus, we observe that switching is an inherent property of wild type receptor gene choice. Neurons that choose to express a mutant MOR28 receptor subsequently extinguish its expression and switch at high frequencies to express alternate receptors such that a given neuron stably transcribes only a single receptor gene. These observations suggest a mechanism of OR gene choice in which a cell selects only one receptor allele but can switch at low frequency. Expression of a functional receptor would then elicit a signal that suppresses switching and stabilizes odorant receptor expression. Neurons that initially express a mutant receptor fail to receive this signal and switch genes until a functional receptor is chosen (Fig. 5).

The mouse genome contains 340 OR pseudogenes, whereas the human genome contains 550 pseudogenes, several of which continue to be transcribed (12,16). Expression of a pseudogene would result in the generation of sensory neurons incapable of odor recognition. A mechanism that allows switching provides a solution to the pseudogene problem such that if pseudogenes are chosen, another transcriptional opportunity is provided assuring that each neuron expresses a functional receptor. This model of serial monogamy assures that neurons will express a single receptor throughout their life. This feedback model in which expression of a functional odorant receptor suppresses switching to other OR genes is reminiscent of one mechanism of allelic exclusion in T and B lymphocytes.

CLONING A MOUSE FROM AN OLFACTORY SENSORY NEURON

What mechanism assures that a single receptor gene is chosen stochastically in a sensory neuron? One model invokes DNA recombination of odorant receptor genes at a single active expression site in the chromosome. DNA recombination provides *Saccharomyces cerevisiae* (41), trypanosomes (42) and lymphocytes (43) with a mechanism to stochastically express one member of a set of genes that mediate cellular interactions with the environment. One attractive feature shared by gene rearrangements in trypanosomes and lymphocytes is that gene choice is a random event, a feature of receptor gene selection in olfactory sensory neurons. However, efforts to demonstrate a recombination event involving OR genes have been seriously hampered by the inability to obtain populations of neurons or clonal cell lines that express the same receptor. Kristin Baldwin in my laboratory, in a collaboration with Rudy Jaenisch, Kevin Eggan and Andy Chess at MIT, addressed this problem by generating ES cell lines and cloned mice derived from the nuclei of olfactory sensory neurons expressing the P2 receptor (Fig. 6) (44). The generation of cloned mice from cells of the nose derives from an initial insight of Woody Allen in his 1978 futuristic comedy, *Sleeper*. In this film, efforts are made to resurrect a totalitarian leader by cloning from his only surviving body part, his nose. Twenty-five years later, science successfully imitated art with the

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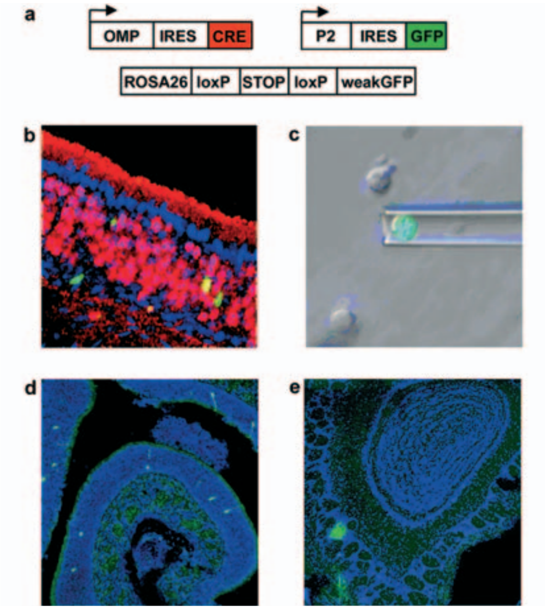

Figure 6. Cloning a Mouse from Olfactory Sensory Neurons Expressing the P2 Odorant Receptor. (a) A genetic strategy to label P2-expressing sensory neurons with GFP as well as to mark olfactory sensory neurons by virtue of a unique deletion in DNA. (b) The olfactory epithelium of a mouse with the genetic modifications described above. A single nucleus expressing the P2 odorant receptor gene was picked and introduced into an enucleated oocyte. The epithelium was stained with antibody to Cre recombinase (red) to mark sensory neurons and GFP (green) to identify P2-expressing cells. (c) A green neuron expressing P2-IRES-GFP was picked from dissociated olfactory epithelium of donor animals. (d) The olfactory epithelium from a mouse cloned from a nucleus expressing the P2 receptor shows the normal distribution of P2-expressing cells. Axons from these neurons converge on a single glomerulus in the olfactory bulb. (e) All nuclei are stained with TOTO-3 blue. The observation that mice cloned from a nucleus expressing the P2 receptor gene do not preferentially express this gene in the sensory epithelium suggests that DNA recombination events do not accompany receptor gene choice. Adapted with permission from 44. Reprinted from *Nature* 428, 44-49, 2004, Eggan *et al.,* with permission from *Nature*.

generation of mice cloned from a single sensory neuron from the nose.

We would predict that if DNA recombination accompanies receptor gene choice then the olfactory epithelium from cloned mice derived from a sensory neuron expressing the P2 gene should be clonal with respect to receptor expression, such that all cells transcribe the rearranged P2 allele. Analysis of the sequence and organization of the DNA surrounding the P2 allele expressed in cloned mice revealed no evidence for either gene conversion or local transposition at the P2 locus. In addition, the pattern of receptor gene expression in the sensory epithelium of cloned mice was normal. Multiple odorant receptor genes are expressed without preference for the P2 allele transcribed in the donor nucleus (Fig. 6). These data, along with similar experiments by Peter Mombaerts (45), demonstrate that the mechanism responsible for the choice of a single odorant receptor gene does not involve

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irreversible changes in DNA. In a broader context, the generation of fertile cloned mice that are anatomically and behaviorally indistinguishable from wild type indicates that the genome of a postmitotic, terminally differentiated olfactory neuron can re-enter the cell cycle and be reprogrammed to a state of totipotency after nuclear transfer. The stochastic choice of a single OR gene is therefore not accomplished by DNA recombination but rather by a rate limiting transcriptional process, perhaps involving a single transcriptional machine capable of stably accommodating only one OR gene.

OLFACTION IN THE FLY: A FUNCTIONAL MAP IN THE ANTENNAL LOBE

The identification of an anatomic map in the olfactory bulb immediately poses the question as to whether this map provides a meaningful representation of odor quality that is translated into appropriate behavioral output. Recently, we have become interested in how the olfactory world is represented in the brain of the fruit fly. *Drosophila* provides an attractive system to understand the logic of olfactory perception. Fruit flies exhibit complex behaviors controlled by an olfactory system that is anatomically and genetically simpler than that of vertebrates. Genetic analysis of olfaction in *Drosophila* may therefore provide a facile system to understand the mechanistic link between behavior and the perception of odors. The recognition of odors in *Drosophila* is accomplished by sensory hairs distributed over the surface of the third antennal segment and the maxillary palp. Olfactory neurons within sensory hairs send projections to one of the multiple glomeruli within the antennal lobe of the brain (46,47). Leslie Vosshall and Allan Wong showed that most sensory neurons express only one of about 80 odorant receptor genes. Neurons expressing the same receptor project with precision to one or rarely two spatially invariant glomeruli in the antennal lobe, the anatomic equivalent of the olfactory bulb of mammals (48,49,50) (Fig. 7).

The anatomic organization in *Drosophila* is therefore remarkably similar to that of the olfactory system of mammals, suggesting that the mechanism of odor discrimination has been shared despite the 600 million years of evolution separating insects from mammals. This conservation may reflect the maintenance of an efficient solution to the complex problem of recognition and discrimination of a vast repertoire of odors in the environment. In both flies and mice, the convergence of like axons into discrete glomerular structures provides a map of receptor activation in the first relay station for olfactory information in the brain, such that the quality of an odorant may be reflected by spatial patterns of activity, first in the antennal lobe or olfactory bulb and ultimately in higher olfactory centers.

An understanding of the logic of odor perception requires functional analysis to identify odor-evoked patterns of activity in neural assemblies and ultimately the relevance of these patterns to odor discrimination. We have performed two-photon calcium imaging to examine the relationship between the anatomic map and the functional map in the antennal lobe (51). Jing Wang and Allan Wong in my lab developed an isolated *Drosophila* brain preparation that is

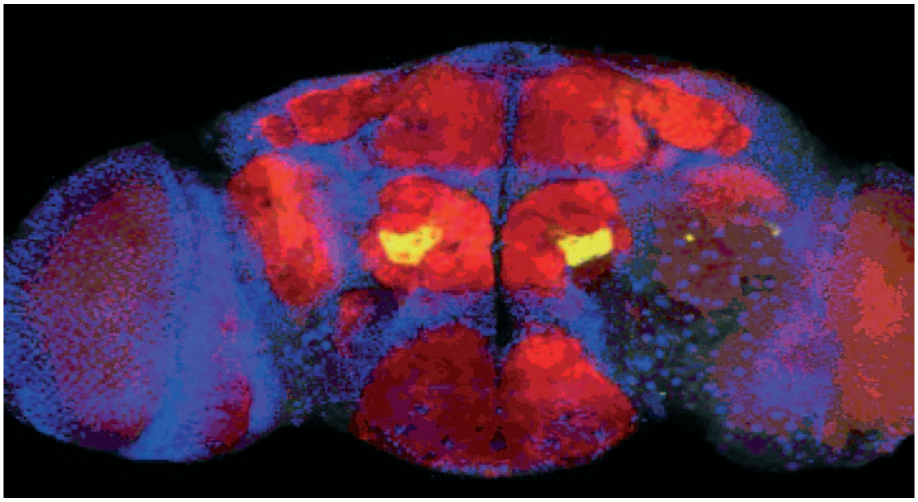

Figure 7. An Olfactory Sensory Map in the Fly Antennal Lobe. Neurons expressing the odorant receptor, OR47b, also express the transgene, synaptobrevin GFP, revealing convergence on a single spatially invariant glomerulus that is bilaterally symmetric in the antennal lobe.

amenable to two-photon imaging and is responsive to odor stimulation for up to five hours. We expressed the calcium-sensitive fluorescent protein G-CaMP in primary olfactory sensory neurons and projection neurons. G-CaMP consists of a circularly permuted EGFP flanked at the N-terminus by the calcium-binding site of calmodulin and at the C-terminus by the M13 fragment of myosin light chain kinase (52). In the presence of calcium, calmodulin interacts with the M13 fragment eliciting a conformation change in EGFP. The resulting elevations in fluorescent intensity reflect changes in the intracellular calcium concentration, a presumed mirror of electrical activity. Moreover, the ability to express G-CaMP in genetically defined populations of neurons allowed us to determine with certainty the locus of neural activity. Odor-evoked changes in fluorescence intensity within the antennal lobe are monitored by a laser-scanning two-photon microscope (53).

This imaging technique has allowed us to measure the responsivity of 23 glomeruli to 16 different odors (51). A number of interesting features of the glomerular response to odors are revealed by these experiments. First, different odors elicit different patterns of glomerular activation and these patterns are conserved among different animals (Fig. 8). At odor concentrations likely to be encountered in nature, the map is sparse and glomeruli are narrowly tuned.

Second, the patterns of activity are insular, such that neighboring glomeruli do not necessarily respond together to a given odor. Each glomerulus visualized anatomically appears to be a functional unit. Third, the patterns of glomerular activity are qualitatively similar upon imaging either sensory or projection neurons. These observations suggest the faithful transmission of sensory input to higher brain centers. Fourth, we have coupled genetic experiments with

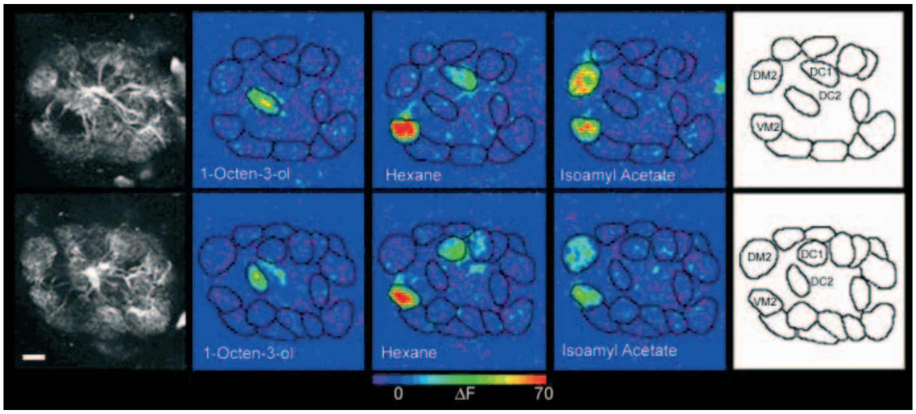

Figure 8. Different Odors Elicit Different Patterns of Glomerular Activation that are Conserved Among Different Organisms. Two different flies (upper and lower panels) bearing the GH146-Gal4 and UAS-G-CaMP transgenes were exposed to three odors. Glomerular responses reveal different patterns of activity for the different odors that are conserved in different animals. The panels to the left show the pre-stimulation images that reveal glomerular structure and the panels to the right identify the specific glomeruli schematically. Reprinted from *Cell*, Vol 112, 2003, pp 271-282, Wang *et al.,* with permission from Elsevier.

imaging to demonstrate that the odor-evoked profile for a given glomerulus directly reflects the responsivity of an individual odorant receptor. This finding is consistent with prior molecular and anatomic studies that reveal that neurons that express only a single receptor in like axons converge on a single glomerulus. Thus these studies, along with other imaging approaches in insects (54,55), demonstrate that the anatomic map is indeed functional and suggests that each odor elicits a sparse pattern of glomerular activation that may confer a signature for different odors in the brain. Imaging experiments in vertebrates similarly reveal a functional representation of the anatomic map (56,57,58).

SPATIAL REPRESENTATIONS AND INNATE BEHAVIOR

All animals exhibit innate behaviors in response to specific sensory stimuli that are likely to result from the activation of developmentally programmed circuits. Allan Wong and Jing Wang in my lab, in collaboration with Greg Suh, David Anderson and Seymour Benzer at Caltech, asked whether we can relate patterns of glomerular activity elicited by an odor to a specific behavior (59). Some time ago Benzer observed that *Drosophila* exhibits robust avoidance to odors released by stressed flies. Gas chromatography and mass spectrometry identified one component of this "*Drosophila* stress odorant (DSO)" as CO_2. Exposure of flies to CO_2 alone also elicits an avoidance behavior at levels of CO_2 as low as 0.1% (Fig. 9).

We therefore performed imaging experiments with the calcium-sensitive fluorescent indicator G-CaMP and two-photon microscopy to ask whether we

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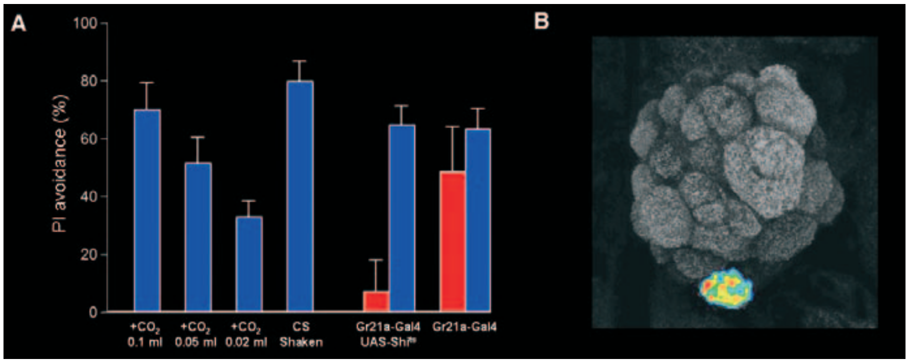

Figure 9. CO_2 Activates a Single Glomerulus and Elicits Avoidance Behavior. (A) Avoidance of air from stressed flies (CS) as well as of increasing concentrations of CO_2. Inhibition of synaptic transmission in GR21A neurons that project to the V glomerulus using shibire^{ts} blocks CO_2 avoidance. Red and blue bars indicate avoidance behavior at the nonpermissive (28°C) and permissive (21°C) temperatures, respectively. (B) Two-photon imaging in a strain harboring GR21A-Gal4 and UAS G-cAMP reveals robust activation of the V glomerulus.

could discern a pattern of glomerular activity in response to DSO and CO_2. We first examined flies in which the G-CaMP indicator is driven in all neurons by the pan-neural activator, Elav-Gal4. DSO activates only two glomeruli, DM2 and the V glomerulus, whereas CO_2 activates only the V glomerulus. Activation of the V glomerulus was detected at CO_2 levels as low as 0.05% and this glomerulus was not activated by any of 26 other odorants tested (Fig. 9).

We demonstrated that axonal projections to V originate from sensory neurons expressing the receptor, GR21A (50). We therefore performed calcium imaging with flies in which the UAS G-CaMP reporter was driven by a GR21A promoter Gal4 activator. CO_2, as well as DSO activated GR21A sensory termini in the V glomeruli. We next asked whether the GR21A sensory neurons are necessary for the avoidance response to CO_2. Inhibition of synaptic transmission in the GR21A sensory neurons that innervate the V glomerulus, using a temperature-sensitive *shibire* gene, shi^{ts} (60), blocks the avoidance response to CO_2 (Fig. 9). Inhibition of synaptic release in the vast majority of other olfactory sensory neurons or in projection neurons other than those that innervate the V glomerulus, had no effect on this behavior.

The identification of a population of olfactory sensory neurons innervating a single glomerulus that mediates robust avoidance to a naturally occurring odorant provides insight in the neural circuitry that underlies this innate behavior. These observations suggest that a dedicated circuit that involves a single population of olfactory sensory neurons mediates detection of CO_2 in *Drosophila*. The simplicity of this initial olfactory processing offers the possibility of tracing the circuits that translate odor detection into an avoidance response.

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HOW IS THE MAP READ?

Our experiments indicate that different odors elicit different patterns of glomerular activity within the antennal lobe and moreover that defined patterns of activity can be associated with specific behaviors. We can look at the pattern of activity in the fly antennal lobe with a two-photon microscope and discern, with a reasonable degree of accuracy what odorant the fly has encountered in nature. Thus we can with our eyes and our brain determine what odors the fly has encountered, but how does the fly brain read the sensory map?

A topographic map in which different odors elicit different patterns of activity in the antennal lobe suggests that these spatial patterns reflect a code defining odor quality. However, the mere existence of a map, whether anatomic or functional, does not prove that spatial information is the underlying parameter of an odor code. It has been suggested, for example, that the quality of an odor is reflected in temporal dynamics of a distributed ensemble of projection neurons (61,62). In this model, a given odor might activate a small number of glomeruli and a large ensemble of projection neurons (PNs) such that different odors elicit different temporal patterns of activity in the same PN. This temporal hypothesis in its simplest form postulates that the brain exploits circuit dynamics to create spatiotemporal patterns of neuronal activation to achieve a larger coding space. Whatever the code, patterns of activity in the antennal lobe must be translated by higher sensory centers to allow the discrimination of complex olfactory information. If odor quality is encoded by spatial patterns, we might expect that a representation of the glomerular map is retained in the protocerebrum.

We have begun to address the question of how the map in the antennal lobe is represented in higher olfactory centers by examining the pattern of projections of the neurons that connect the glomeruli to the protocerebrum. Allan Wong and Jing Wang randomly labeled individual projection neurons to visualize their processes that connect defined glomeruli with their targets in the mushroom body and protocerebrum. We have used an enhancer trap line in which Gal4 is expressed in a subpopulation of projection neurons along with the FLP-out technique, to label single projection neurons with a CD8-GFP reporter (63). A similar experimental approach has been used to determine the lineage relationship of individual PNs and to examine their pattern of axonal projections (64,65). We observe that most PNs send dendrites to a single glomerulus. Projection neurons that receive input from a given glomerulus extend axons that form a spatially invariant pattern in the protocerebrum (Fig. 10). PNs from different glomeruli exhibit patterns of axonal projections that are distinct, but often interdigitated (Fig. 11). Our data reveal a striking invariance in the spatial patterns of axon arbors of PNs that innervate a given glomerulus, a precision of connectivity that assures the specificity of information transfer.

The precision of projections of PNs reveals a spatial representation of glomerular activity in higher brain centers but the character of the map differs from that observed in the antennal lobe. Axon arbors in the protocerebrum are

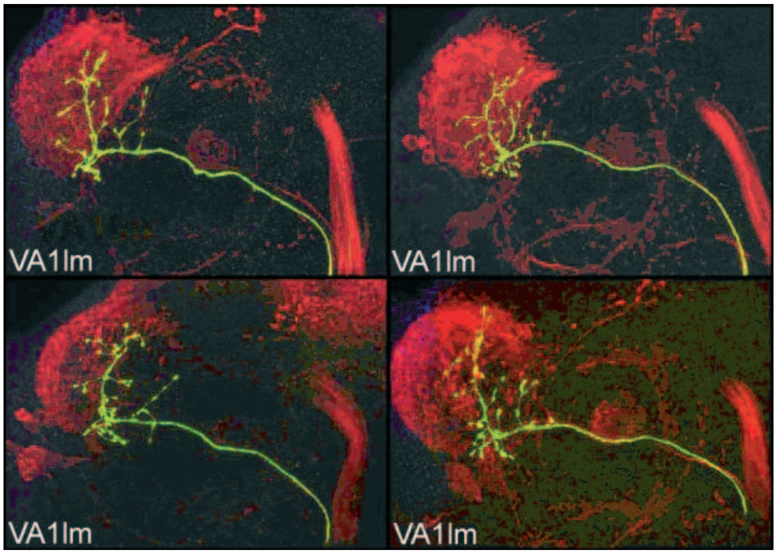

Figure 10. Projection Neurons that Innervate to the Same Glomerulus have Similar Axonal Projection Patterns. Individual projection neurons that connect to the VA1 LM glomeruli are visualized in the protocerebrum in different flies. These images reveal a striking constancy in the projection pattern among PNs that project to a given glomerulus. These observations reveal an invariant topographic map in the protocerebrum that differs in character from the map in the antennal lobe (with permission from 63). Reprinted from *Cell*, Vol 109, 2002, pp 229-241, Wong *et al.,* with permission from Elsevier.

diffuse and extensive, often extending the entire dimension of the brain hemisphere (Fig. 10,11). This is in sharp contrast to the tight convergence of primary sensory axons, whose arbors are restricted to a small 5–10 μm spherical glomerulus. As a consequence, the projections from different glomeruli, although spatially distinct, often interdigitate. Thus, the point-to-point segregation observed in the antennal lobe is degraded in the second order projections to the protocerebrum. This affords an opportunity for the convergence of inputs from multiple different glomeruli essential for higher order processing. Third order neurons in the protocerebrum might synapse on PNs from multiple distinct glomeruli, a necessary step in decoding spatial patterns to allow the discrimination of odor and behavioral responses.

CONCLUDING REMARKS

These data suggest a model in which the convergence of information from deconstructed patterns in the antennal lobe are reconstructed by “cardinal cell assemblies” that sit higher up in a hierarchical perceptual system in the protocerebrum. Olfactory processing will initially require that the structural

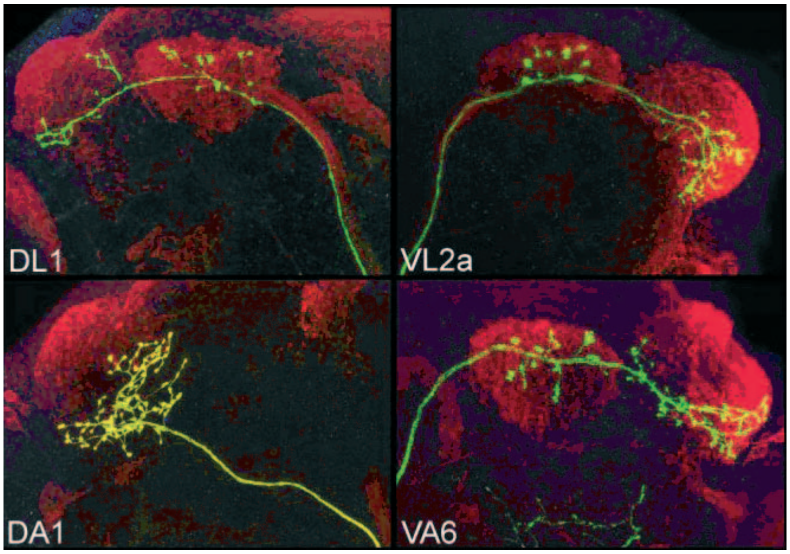

Figure 11. Axonal Patterns from Projection Neurons that Innervate to Different Glomeruli are Distinct. Axonal projections from single PNs can be visualized as they branch in the mushroom body and ultimately arborize in the protocerebrum. Projections neurons that connect to different glomeruli exhibit different patterns of axonal projections. The axon arbors in the protocerebrum are dispersed unlike the insular segregated arbors in the glomerulus, affording the possibility for integration in higher olfactory centers (with permission from 63). Reprinted from *Cell*, Vol 109, 2002, pp 229-241, Wong *et al.*, with permission from Elsevier.

elements of an odor activate an unique set of receptors that in turn result in the activation of a unique set of glomeruli. The odorous stimuli must then be reconstructed in higher sensory centers that determine which of the numerous glomeruli have been activated. The identification of a spatially invariant sensory map in the protocerebrum that is dispersive affords an opportunity for integration of multiple glomerular inputs by higher odor neurons.

The elucidation of an olfactory map in both the olfactory bulb or antennal lobe and in higher olfactory centers leaves us with a different order of problems. Though we may look at these odor-evoked images with our brains and recognize a spatial pattern as unique and can readily associate the pattern with a particular stimulus, the brain does not have eyes. Who in the brain is looking at the olfactory image? Who reads the map? How are spatially defined bits of electrical information in the brain decoded to allow the perception of an olfactory image? We are left with an old problem, the problem of the ghost in the machine.

Finally, how do we explain the individuality of olfactory perception? The innately configured representation of the sensory world, the olfactory sensory maps that I have described, must be plastic. Our genes create only a substrate upon which experience can shape how we perceive the external world. Surely the smell of a madeleine does not elicit in all of us that "vast structure of recollection" it evoked for Marcel Proust. For Proust, smell is the evocative sense, the sense that brings forth memory and associations with a richness not elicited by other sensory stimuli. Nowhere is this more apparent than in the eloquent words recalling the madeleine incident from *"Remembrance of Things Past"* (66).

"But when from a long distant past nothing subsists, after the people are dead, after the things are broken and scattered, still alone, more fragile but with more vitality, more unsubstantial, more persistent, more faithful, the smell and taste of things remain, poised a long time, like souls ready to remind us, waiting and hoping for their moment, amid the ruins of all the rest; and bear unfaltering in the tiny and impalpable drop of their essence, the vast structure of recollection."

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