

PI: VON DER HEYDT, RUDIGER	Title: Neural Visual Coding: Image to Object Representation	
Received: 11/05/2007	FOA: PA07-070	Council: 05/2008
Competition ID: VERSION-2A-FORMS	FOA Title: RESEARCH PROJECT GRANT (PARENT R01)	
2 R01 EY002966-29A1	Dual:	Accession Number: 3039812
IPF: 4134401	Organization: JOHNS HOPKINS UNIVERSITY	
Former Number:	Department: Arts & Sciences	
IRG/SRG: CVP	AIDS: N	Expedited: N
Subtotal Direct Costs (excludes consortium F&A) Year 29: 292,159 Year 30: 299,745 Year 31: 307,575 Year 32: 306,656 Year 33: 314,648	Animals: Y Humans: N Clinical Trial: N Exemption: 10 HESC: N	New Investigator: N
<i>Senior/Key Personnel:</i>		
<i>Organization:</i>		
<i>Role Category:</i>		
Joachim von der Heydt PhD	The Johns Hopkins University	PD/PI

SF 424 (R&R)

1. * TYPE OF SUBMISSION	2. DATE SUBMITTED	Applicant Identifier
	3. DATE RECEIVED BY STATE	State Application Identifier
<input type="radio"/> Pre-application <input type="radio"/> Application <input checked="" type="radio"/> Changed/Corrected Application	4. Federal Identifier EY002966	

5. APPLICANT INFORMATION

* Organizational DUNS:001910777

* Legal Name: The Johns Hopkins University

Department: Arts & Sciences

* Street1: _____

* City: Baltimore

Province:

Division: Mind/Brain Institute

Street2: 3400 N. Charles St

County:

* Country: USA: UNITED STATES

* State: MD: Maryland

* ZIP / Postal Code: 21218

Person to be contacted on matters involving this application			
Prefix:	* First Name:	Middle Name:	* Last Name:
Ms.	Nancy		Kerner
* Phone Number: 410-516-7111		Fax Number: 410-516-5063	Email: nkerner1@jhu.edu
Suffix:			

6. * EMPLOYER IDENTIFICATION NUMBER (EIN) or (TIN): 1-_____	7. * TYPE OF APPLICANT O: Private Institution of Higher Education
8. * TYPE OF APPLICATION: <input type="radio"/> New <input type="radio"/> Resubmission <input checked="" type="radio"/> Renewal <input type="radio"/> Continuation <input type="radio"/> Revision	Other (Specify): Small Business Organization Type <input type="radio"/> Women Owned <input type="radio"/> Socially and Economically Disadvantaged
If Revision, mark appropriate box(es). <input type="radio"/> A. Increase Award <input type="radio"/> B. Decrease Award <input type="radio"/> C. Increase Duration <input type="radio"/> D. Decrease Duration <input type="radio"/> E. Other (specify):	9. * NAME OF FEDERAL AGENCY: National Institutes of Health
* Is this application being submitted to other agencies? <input type="radio"/> Yes <input checked="" type="radio"/> No What other Agencies?	10. CATALOG OF FEDERAL DOMESTIC ASSISTANCE NUMBER: TITLE:

11. * DESCRIPTIVE TITLE OF APPLICANT'S PROJECT: Neural Visual Coding: Image to Object Representation
--

12. * AREAS AFFECTED BY PROJECT (cities, counties, states, etc.) N/A
--

13. PROPOSED PROJECT:	14. CONGRESSIONAL DISTRICTS OF:
* Start Date * Ending Date	a. * Applicant b. * Project
07/01/2008 06/30/2013	MD-007 N/A

15. PROJECT DIRECTOR/PRINCIPAL INVESTIGATOR CONTACT INFORMATION			
Prefix:	* First Name:	Middle Name:	* Last Name:
Dr.	Joachim	Rudiger	von der Heydt
Position/Title: Professor		* Organization Name: The Johns Hopkins University	
Department: Arts & Sciences		Division: Mind/Brain Institute	
* Street1: _____		Street2: 3400 N. Charles St	
* City: Baltimore		County:	
Province:		* Country: USA: UNITED STATES	
* Phone Number: 410-516-6416		Fax Number: 410-516-8648	
		* State: MD: Maryland	
		* ZIP / Postal Code: 21218	
		* Email: von.der.heydt@jhu.edu	

16. ESTIMATED PROJECT FUNDING	17. * IS APPLICATION SUBJECT TO REVIEW BY STATE EXECUTIVE ORDER 12372 PROCESS?
a. * Total Estimated Project Funding \$2,431,520.00 b. * Total Federal & Non-Federal Funds \$2,431,520.00 c. * Estimated Program Income \$0.00	a. YES <input type="radio"/> THIS PREAPPLICATION/APPLICATION WAS MADE AVAILABLE TO THE STATE EXECUTIVE ORDER 12372 PROCESS FOR REVIEW ON: DATE: b. NO <input checked="" type="radio"/> PROGRAM IS NOT COVERED BY E.O. 12372; OR <input type="radio"/> PROGRAM HAS NOT BEEN SELECTED BY STATE FOR REVIEW

18. By signing this application, I certify (1) to the statements contained in the list of certifications* and (2) that the statements herein are true, complete and accurate to the best of my knowledge. I also provide the required assurances * and agree to comply with any resulting terms if I accept an award. I am aware that any false, fictitious, or fraudulent statements or claims may subject me to criminal, civil, or administrative penalties. (U.S. Code, Title 18, Section 1001)

* I agree

* The list of certifications and assurances, or an Internet site where you may obtain this list, is contained in the announcement or agency specific instructions.

19. Authorized Representative

Prefix:	* First Name:	Middle Name:	* Last Name:	Suffix:
Ms.	Nancy		Kerner	
* Position/Title: Sponsored Projects Coordinator		* Organization Name: The Johns Hopkins University		
Department: Business & Research Administr		Division: Arts & Sciences		
* Street1: Mergenthaler Hall, Rm 225		Street2: 3400 N. Charles St		
* City: Baltimore		County:	* State: MD: Maryland	
Province:	* Country: USA: UNITED STATES		* ZIP / Postal Code: 21218	
* Phone Number: 410-516-7111	Fax Number: 410-516-5063		* Email: nkerner1@jhu.edu	

* Signature of Authorized Representative	* Date Signed
Nancy Kerner	11/05/2007

20. Pre-application File Name: Mime Type:

21. Attach an additional list of Project Congressional Districts if needed.

File Name: Mime Type:

424 R&R and PHS-398 Specific Table Of Contents

Page Numbers

SF 424 R&R Face Page -----	1
Table of Contents -----	3
Performance Sites -----	4
Research & Related Other Project Information -----	5
Project Summary/Abstract (Description) -----	6
Public Health Relevance Statement (Narrative attachment) -----	7
Facilities & Other Resources -----	8
Equipment -----	9
Research & Related Senior/Key Person -----	10
Biographical Sketches for each listed Senior/Key Person -----	12
Current and Pending Support for each listed Senior/Key Person -----	14
Research & Related Budget - Year 1 -----	15
Research & Related Budget - Year 2 -----	18
Research & Related Budget - Year 3 -----	21
Research & Related Budget - Year 4 -----	24
Research & Related Budget - Year 5 -----	27
Budget Justification -----	30
Research & Related Budget - Cumulative Budget -----	32
PHS 398 Specific Cover Page Supplement -----	33
PHS 398 Specific Research Plan -----	35
Specific Aims -----	38
Significance and Related R&D -----	39
Preliminary Studies/Phase I Final Report -----	43
Experimental/Research Design and Methods -----	54
Progress Report Publication List -----	61
Vertebrate Animals -----	62
Bibliography & References Cited -----	65
PHS 398 Checklist -----	68

RESEARCH & RELATED Project/Performance Site Location(s)

Project/Performance Site Primary Location

Organization Name: The Johns Hopkins University

* Street1:

Street2: 3400 N. Charles St.

* City: Baltimore

County:

* State: MD: Maryland

Province:

* Country: USA: UNITED STATES

* Zip / Postal Code: 21218

File Name

Mime Type

Additional Location(s)

RESEARCH & RELATED Other Project Information

1. * Are Human Subjects Involved? <input type="radio"/> Yes <input checked="" type="radio"/> No		
1.a. If YES to Human Subjects		
Is the IRB review Pending? <input type="radio"/> Yes <input type="radio"/> No		
IRB Approval Date:		
Exemption Number: _ 1 _ 2 _ 3 _ 4 _ 5 _ 6		
Human Subject Assurance Number		
2. * Are Vertebrate Animals Used? <input checked="" type="radio"/> Yes <input type="radio"/> No		
2.a. If YES to Vertebrate Animals		
Is the IACUC review Pending? <input type="radio"/> Yes <input checked="" type="radio"/> No		
IACUC Approval Date: 07-12-2007		
Animal Welfare Assurance Number A3272-01		
3. * Is proprietary/privileged information <input type="radio"/> Yes <input checked="" type="radio"/> No included in the application?		
4.a. * Does this project have an actual or potential impact on <input type="radio"/> Yes <input checked="" type="radio"/> No the environment?		
4.b. If yes, please explain:		
4.c. If this project has an actual or potential impact on the environment, has an exemption been authorized or an environmental assessment (EA) or environmental impact statement (EIS) been performed? <input type="radio"/> Yes <input type="radio"/> No		
4.d. If yes, please explain:		
5.a. * Does this project involve activities outside the U.S. or <input type="radio"/> Yes <input checked="" type="radio"/> No partnership with International Collaborators?		
5.b. If yes, identify countries:		
5.c. Optional Explanation:		
6. * Project Summary/Abstract	7173-Project_Summary_11_02_07.pdf	Mime Type: application/pdf
7. * Project Narrative	1878-Narrative_10_29_07.pdf	Mime Type: application/pdf
8. Bibliography & References Cited	8591-Bibliography_11_02_07.pdf	Mime Type: application/pdf
9. Facilities & Other Resources	7358-Facilities_10_29_07.pdf	Mime Type: application/pdf
10. Equipment	6080-Equipment_10_29_07.pdf	Mime Type: application/pdf

Project Summary

Research is proposed to advance our understanding of the neural mechanisms of visual perceptual organization and their relation to selective attention. The long-term objective is to understand the interface between sensory representations and cognitive processes at the neural signal level. The proposed research focuses on the mechanisms of figure-ground organization as evident from the neural representation of border ownership, i.e., the assignment of contours to objects. The general method is single-cell recording from the visual cortex of awake behaving macaques. Three broad aims have been identified for the next five years.

The first aim is to provide quantitative descriptions of the spatial integration mechanisms of border ownership selective V2 neurons. Previous studies have shown that these mechanisms extend far beyond the classical receptive field of the neurons. Two methods with factorial design will be applied. These methods allow to measure nonlinear interactions of the extra-classical regions with the classical receptive field as well as interactions between extra-classical regions. The two methods are complementary. One uses fragmentation of figures, the other uses occlusion of critical features.

The second aim is to study persistence of figure-ground organization in the visual cortex. Experiments are proposed to (1) determine the influence of the type of figure-ground cue and its duration on the subsequent persistence of border ownership signals, (2) determine whether the persistence depends on attention being directed to the figure, and (3) whether border ownership signals persist across eye movements and stimulus movements.

The third aim is to study the role of the neural organization mechanisms in object-based selective attention. Building on previous results showing that V2 neurons combine border ownership coding with the influence of volitional selective attention, new experiments will test visual conditions in which an object is partially occluded, so that only two unconnected portions of it remain visible. The results will show whether the border ownership mechanisms can link features across the gap, and whether object-based attention can do so.

The proposed research will help to clarify the basis of selective attention which is important for understanding both normal and impaired vision. Although the proposal is focused on vision, the research will help to identify the sensory-cognitive interface also in other modalities. The insight gained from this project will contribute to the understanding of the basis of cognitive disorders such as dyslexia.

Narrative

Selective attention is perhaps the most important function in vision. We can choose to process the words in one line of text and ignore all others, which enables us to read. But sometimes we do not see things that are right in front of our eyes—the cause of many traffic accidents.

Dyslexic children cannot detect the difference between strings of letters that others can easily see. The goal of the proposed research is to understand a process in the brain that dissects images into objects before objects are recognized, providing an internal representation from which attention can select.

Facilities

Laboratory:

Two experimental setups in shielded rooms for single-cell recording, each equipped with pentium computers for visual stimulus generation, experimental control and data collection, eye movement monitoring, and spike sorting; 20" color monitors for visual stimulation. Custom software for running neurophysiological and psychophysical experiments.

Workshops:

Electronics and machinist staff and workshops are shared with other labs in the Mind/Brain Institute.

Equipment

- Pentium PCs with 20" color monitors, used for data analysis, figure generation and work processing.
- ISCAN video eye tracker systems equipped with beam splitters (2) used to monitor eye position during visual neurophysiology experiments.
- Free-view lens stereoscope installed in one setup.
- Surgical microscopes (2) used for maintaining craniotomies and positioning micro-electrodes during daily recording experiments.
- Custom behavioral/neurophysiological rigs (2) consisting of commercial and custom electronic and mechanical equipment used to control behavior, advance electrodes and record and amplify eye movements and neurophysiological signals.
- Spectra Pritchard photometer.

RESEARCH & RELATED Senior/Key Person Profile (Expanded)

PROFILE - Project Director/Principal Investigator

Prefix Dr.	* First Name Joachim	Middle Name Rudiger	* Last Name von der Heydt	Suffix PhD
Position/Title: Professor		Department: Arts & Sciences		
Organization Name: The Johns Hopkins University		Division: Mind/Brain Institute		
* Street1: <input type="text"/>		Street2: 3400 N. Charles St		
* City: Baltimore	County:	* State: MD: Maryland Province:		
* Country: USA: UNITED STATES	* Zip / Postal Code: 21218			

*Phone Number 410-516-6416	Fax Number 410-516-8648	* E-Mail von.der.heydt@jhu.edu
-------------------------------	----------------------------	-----------------------------------

Credential, e.g., agency login: vonderheydt2

* Project Role: PD/PI

Other Project Role Category:

	File Name	Mime Type
*Attach Biographical Sketch	7121-Bio_11_02_07.pdf	application/pdf
Attach Current & Pending Support	2143-Research_Support_11_02_07.pdf	application/pdf

RESEARCH & RELATED Senior/Key Person Profile (Expanded)

Additional Senior/Key Person Form Attachments

When submitting senior/key persons in excess of 8 individuals, please attach additional senior/key person forms here. Each additional form attached here, will provide you with the ability to identify another 8 individuals, up to a maximum of 4 attachments (32 people).

The means to obtain a supplementary form is provided here on this form, by the button below. In order to extract, fill, and attach each additional form, simply follow these steps:

- Select the "Select to Extract the R&R Additional Senior/Key Person Form" button, which appears below.
- Save the file using a descriptive name, that will help you remember the content of the supplemental form that you are creating. When assigning a name to the file, please remember to give it the extension ".xfd" (for example, "My_Senior_Key.xfd"). If you do not name your file with the ".xfd" extension you will be unable to open it later, using your PureEdge viewer software.
- Using the "Open Form" tool on your PureEdge viewer, open the new form that you have just saved.
- Enter your additional Senior/Key Person information in this supplemental form. It is essentially the same as the Senior/Key person form that you see in the main body of your application.
- When you have completed entering information in the supplemental form, save it and close it.
- Return to this "Additional Senior/Key Person Form Attachments" page.
- Attach the saved supplemental form, that you just filled in, to one of the blocks provided on this "attachments" form.

Important: Please attach additional Senior/Key Person forms, using the blocks below. Please remember that the files you attach must be Senior/Key Person Pure Edge forms, which were previously extracted using the process outlined above. Attaching any other type of file may result in the inability to submit your application to Grants.gov.

- 1) Please attach Attachment 1
- 2) Please attach Attachment 2
- 3) Please attach Attachment 3
- 4) Please attach Attachment 4

ADDITIONAL SENIOR/KEY PERSON PROFILE(S)	Filename
	MimeType

Additional Biographical Sketch(es) (Senior/Key Person)	Filename
	MimeType

Additional Current and Pending Support(s)	Filename
	MimeType

3 pages redacted--biosketch omitted as requested

RESEARCH & RELATED BUDGET - SECTION A & B, BUDGET PERIOD 1

* ORGANIZATIONAL DUNS: 0019107770000

* Budget Type: Project Subaward/Consortium

Enter name of Organization: The Johns Hopkins University

* Start Date: 07-01-2008

* End Date: 06-30-2009

Budget Period: 1

A. Senior/Key Person

Prefix	* First Name	Middle Name	* Last Name	Suffix	* Project Role	Base Salary (\$)	Cal. Months	Acad. Months	Sum. Months	* Requested Salary (\$)	* Fringe Benefits (\$)	* Funds Requested (\$)
--------	--------------	-------------	-------------	--------	----------------	------------------	-------------	--------------	-------------	-------------------------	------------------------	------------------------

Total Funds Requested for all Senior Key Persons in the attached file

Additional Senior Key Persons: File Name: Mime Type: Total Senior/Key Person **97,422.00**

B. Other Personnel

* Number of Personnel	* Project Role	Cal. Months	Acad. Months	Sum. Months	* Requested Salary (\$)	* Fringe Benefits	* Funds Requested (\$)
1	Post Doctoral Associates	2.40			12,600.00	1,008.00	13,608.00
2	Graduate Students		9.00	3.00	47,000.00	899.00	47,899.00
	Undergraduate Students						
	Secretarial/Clerical						
1	Electronics Technician	1.20			1,655.00	563.00	2,218.00
1	Animal Research Specialist	7.80			30,252.00	10,285.00	40,537.00
1	Electrical Engineer	1.20			7,787.00	2,647.00	10,434.00
1	Machinist	1.20			6,106.00	2,075.00	8,181.00
1	Machinist	0.60			3,152.00	1,072.00	4,224.00
8	Total Number Other Personnel					Total Other Personnel	127,101.00
Total Salary, Wages and Fringe Benefits (A+B)							224,523.00

RESEARCH & RELATED Budget {A-B} (Funds Requested)

RESEARCH & RELATED BUDGET - SECTION C, D, & E, BUDGET PERIOD 1

* ORGANIZATIONAL DUNS: 0019107770000

* **Budget Type:** Project Subaward/Consortium**Enter name of Organization:** The Johns Hopkins University* **Start Date:** 07-01-2008* **End Date:** 06-30-2009**Budget Period:** 1**C. Equipment Description**

List items and dollar amount for each item exceeding \$5,000

Equipment Item

* Funds Requested (\$)

Total funds requested for all equipment listed in the attached file

Total Equipment

Additional Equipment:

File Name:

Mime Type:

D. Travel**Funds Requested (\$)**

1. Domestic Travel Costs (Incl. Canada, Mexico, and U.S. Possessions)

5,000.00

2. Foreign Travel Costs

Total Travel Cost**5,000.00****E. Participant/Trainee Support Costs****Funds Requested (\$)**

1. Tuition/Fees/Health Insurance

2. Stipends

3. Travel

4. Subsistence

5. Other:

Number of Participants/Trainees**Total Participant/Trainee Support Costs**

RESEARCH & RELATED Budget (C-E) (Funds Requested)

RESEARCH & RELATED BUDGET - SECTIONS F-K, BUDGET PERIOD 1

* ORGANIZATIONAL DUNS: 0019107770000

* **Budget Type:** Project Subaward/Consortium**Enter name of Organization:** The Johns Hopkins University* **Start Date:** 07-01-2008* **End Date:** 06-30-2009**Budget Period:** 1

F. Other Direct Costs	Funds Requested (\$)
1. Materials and Supplies	25,000.00
2. Publication Costs	1,200.00
3. Consultant Services	
4. ADP/Computer Services	1,500.00
5. Subawards/Consortium/Contractual Costs	
6. Equipment or Facility Rental/User Fees	
7. Alterations and Renovations	
8. Animal Procurement & Care	17,100.00
9. Grad Student Tuition Remission	15,078.00
10. Student Health Insurance	2,758.00
Total Other Direct Costs	62,636.00

G. Direct Costs	Funds Requested (\$)
Total Direct Costs (A thru F)	292,159.00

H. Indirect Costs				
	Indirect Cost Type	Indirect Cost Rate (%)	Indirect Cost Base (\$)	* Funds Requested (\$)
1. MTDC		64	274,323.00	175,567.00
Total Indirect Costs				175,567.00
Cognizant Federal Agency		DHHS, Stephen Virbitsky, 215-861-4470		
(Agency Name, POC Name, and POC Phone Number)				

I. Total Direct and Indirect Costs	Funds Requested (\$)
Total Direct and Indirect Institutional Costs (G + H)	467,726.00

J. Fee	Funds Requested (\$)
---------------	-----------------------------

K. * Budget Justification	File Name:	Mime Type: application/pdf
	8567-Budget_Justification_10_29_07.pdf	
(Only attach one file.)		

RESEARCH & RELATED Budget (F-K) (Funds Requested)

RESEARCH & RELATED BUDGET - SECTION A & B, BUDGET PERIOD 2

* ORGANIZATIONAL DUNS: 0019107770000

* Budget Type: Project Subaward/Consortium

Enter name of Organization: The Johns Hopkins University

* Start Date: 07-01-2009

* End Date: 06-30-2010

Budget Period: 2

A. Senior/Key Person

Prefix	* First Name	Middle Name	* Last Name	Suffix	* Project Role	Base Salary (\$)	Cal. Months	Acad. Months	Sum. Months	* Requested Salary (\$)	* Fringe Benefits (\$)	* Funds Requested (\$)
--------	--------------	-------------	-------------	--------	----------------	---------------------	----------------	-----------------	----------------	----------------------------	---------------------------	------------------------

Total Funds Requested for all Senior Key Persons in the attached file

Additional Senior Key Persons:

File Name:

Mime Type:

Total Senior/Key Person

100,344.00

B. Other Personnel

* Number of Personnel	* Project Role	Cal. Months	Acad. Months	Sum. Months	* Requested Salary (\$)	* Fringe Benefits	* Funds Requested (\$)
1	Post Doctoral Associates	2.40			12,978.00	1,038.00	14,016.00
2	Graduate Students		9.00	3.00	48,410.00	926.00	49,336.00
	Undergraduate Students						
	Secretarial/Clerical						
1	Electronics Technician	1.20			1,705.00	579.00	2,284.00
1	Animal Research Specialist	7.80			31,160.00	10,595.00	41,755.00
1	Electrical Engineer	1.20			8,020.00	2,727.00	10,747.00
1	Machinist	1.20			6,289.00	2,138.00	8,427.00
1	Machinist	0.60			3,246.00	1,104.00	4,350.00
8	Total Number Other Personnel						130,915.00
Total Salary, Wages and Fringe Benefits (A+B)							231,259.00

RESEARCH & RELATED Budget {A-B} (Funds Requested)

RESEARCH & RELATED BUDGET - SECTION C, D, & E, BUDGET PERIOD 2

* ORGANIZATIONAL DUNS: 0019107770000

* **Budget Type:** Project Subaward/Consortium

Enter name of Organization: The Johns Hopkins University

* **Start Date:** 07-01-2009* **End Date:** 06-30-2010**Budget Period:** 2**C. Equipment Description**

List items and dollar amount for each item exceeding \$5,000

Equipment Item

* Funds Requested (\$)

Total funds requested for all equipment listed in the attached file

Total Equipment

Additional Equipment:

File Name:

Mime Type:

D. Travel

Funds Requested (\$)

1. Domestic Travel Costs (Incl. Canada, Mexico, and U.S. Possessions)

5,000.00

2. Foreign Travel Costs

Total Travel Cost

5,000.00

E. Participant/Trainee Support Costs

Funds Requested (\$)

1. Tuition/Fees/Health Insurance

2. Stipends

3. Travel

4. Subsistence

5. Other:

Number of Participants/Trainees

Total Participant/Trainee Support Costs

RESEARCH & RELATED Budget (C-E) (Funds Requested)

RESEARCH & RELATED BUDGET - SECTIONS F-K, BUDGET PERIOD 2

* ORGANIZATIONAL DUNS: 0019107770000

* **Budget Type:** Project Subaward/Consortium**Enter name of Organization:** The Johns Hopkins University* **Start Date:** 07-01-2009* **End Date:** 06-30-2010**Budget Period:** 2

F. Other Direct Costs	Funds Requested (\$)
1. Materials and Supplies	25,000.00
2. Publication Costs	1,200.00
3. Consultant Services	
4. ADP/Computer Services	1,500.00
5. Subawards/Consortium/Contractual Costs	
6. Equipment or Facility Rental/User Fees	
7. Alterations and Renovations	
8. Animal Procurement & Care	17,100.00
9. Grad Student Tuition Remission	15,831.00
10. Student Health Insurance	2,855.00
Total Other Direct Costs	63,486.00

G. Direct Costs	Funds Requested (\$)
Total Direct Costs (A thru F)	299,745.00

H. Indirect Costs				
	Indirect Cost Type	Indirect Cost Rate (%)	Indirect Cost Base (\$)	* Funds Requested (\$)
1.	MTDC	64	281,059.00	179,878.00
			Total Indirect Costs	179,878.00
Cognizant Federal Agency		DHHS, Stephen Virbitsky, 215-861-4470		
(Agency Name, POC Name, and POC Phone Number)				

I. Total Direct and Indirect Costs	Funds Requested (\$)
Total Direct and Indirect Institutional Costs (G + H)	479,623.00

J. Fee	Funds Requested (\$)
---------------	-----------------------------

K. * Budget Justification	File Name:	Mime Type: application/pdf
	8567-Budget_Justification_10_29_07.pdf	
(Only attach one file.)		

RESEARCH & RELATED Budget (F-K) (Funds Requested)

RESEARCH & RELATED BUDGET - SECTION A & B, BUDGET PERIOD 3

* ORGANIZATIONAL DUNS: 0019107770000

* Budget Type: Project Subaward/Consortium

Enter name of Organization: The Johns Hopkins University

* Start Date: 07-01-2010

* End Date: 06-30-2011

Budget Period: 3

A. Senior/Key Person

Prefix	* First Name	Middle Name	* Last Name	Suffix	* Project Role	Base Salary (\$)	Cal. Months	Acad. Months	Sum. Months	* Requested Salary (\$)	* Fringe Benefits (\$)	* Funds Requested (\$)
---	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----

Total Funds Requested for all Senior Key Persons in the attached file

Additional Senior Key Persons:

File Name:

Mime Type:

Total Senior/Key Person

103,354.00

B. Other Personnel

* Number of Personnel	* Project Role	Cal. Months	Acad. Months	Sum. Months	* Requested Salary (\$)	* Fringe Benefits	* Funds Requested (\$)
1	Post Doctoral Associates	2.40			13,367.00	1,069.00	14,436.00
2	Graduate Students		9.00	3.00	49,862.00	954.00	50,816.00
	Undergraduate Students						
	Secretarial/Clerical						
1	Electronics Technician	1.20			1,756.00	597.00	2,353.00
1	Animal Research Specialist	7.80			32,095.00	10,913.00	43,008.00
1	Electrical Engineer	1.20			8,261.00	2,809.00	11,070.00
1	Machinist	1.20			6,477.00	2,202.00	8,679.00
1	Machinist	0.60			3,344.00	1,137.00	4,481.00
8	Total Number Other Personnel						134,843.00
Total Salary, Wages and Fringe Benefits (A+B)							238,197.00

RESEARCH & RELATED Budget {A-B} (Funds Requested)

RESEARCH & RELATED BUDGET - SECTION C, D, & E, BUDGET PERIOD 3

* ORGANIZATIONAL DUNS: 0019107770000

* **Budget Type:** Project Subaward/Consortium

Enter name of Organization: The Johns Hopkins University

* **Start Date:** 07-01-2010* **End Date:** 06-30-2011**Budget Period:** 3

C. Equipment Description		
List items and dollar amount for each item exceeding \$5,000		
Equipment Item		* Funds Requested (\$)
Total funds requested for all equipment listed in the attached file		
		Total Equipment
Additional Equipment:	File Name:	Mime Type:

D. Travel	Funds Requested (\$)
1. Domestic Travel Costs (Incl. Canada, Mexico, and U.S. Possessions)	5,000.00
2. Foreign Travel Costs	
Total Travel Cost	5,000.00

E. Participant/Trainee Support Costs	Funds Requested (\$)
1. Tuition/Fees/Health Insurance	
2. Stipends	
3. Travel	
4. Subsistence	
5. Other:	
Number of Participants/Trainees	Total Participant/Trainee Support Costs

RESEARCH & RELATED Budget (C-E) (Funds Requested)

RESEARCH & RELATED BUDGET - SECTIONS F-K, BUDGET PERIOD 3

* ORGANIZATIONAL DUNS: 0019107770000

* **Budget Type:** Project Subaward/Consortium**Enter name of Organization:** The Johns Hopkins University* **Start Date:** 07-01-2010* **End Date:** 06-30-2011**Budget Period:** 3

F. Other Direct Costs	Funds Requested (\$)
1. Materials and Supplies	25,000.00
2. Publication Costs	1,200.00
3. Consultant Services	
4. ADP/Computer Services	1,500.00
5. Subawards/Consortium/Contractual Costs	
6. Equipment or Facility Rental/User Fees	
7. Alterations and Renovations	
8. Animal Procurement & Care	17,100.00
9. Grad Student Tuition Remission	16,624.00
10. Student Health Insurance	2,954.00
Total Other Direct Costs	64,378.00

G. Direct Costs	Funds Requested (\$)
Total Direct Costs (A thru F)	307,575.00

H. Indirect Costs				
	Indirect Cost Type	Indirect Cost Rate (%)	Indirect Cost Base (\$)	* Funds Requested (\$)
1. MTDC		64	287,997.00	184,318.00
			Total Indirect Costs	184,318.00
Cognizant Federal Agency		DHHS, Stephen Virbitsky, 215-861-4470		
(Agency Name, POC Name, and POC Phone Number)				

I. Total Direct and Indirect Costs	Funds Requested (\$)
Total Direct and Indirect Institutional Costs (G + H)	491,893.00

J. Fee	Funds Requested (\$)
---------------	-----------------------------

K. * Budget Justification	File Name:	Mime Type: application/pdf
	8567-Budget_Justification_10_29_07.pdf	
(Only attach one file.)		

RESEARCH & RELATED Budget (F-K) (Funds Requested)

RESEARCH & RELATED BUDGET - SECTION A & B, BUDGET PERIOD 4

* ORGANIZATIONAL DUNS: 0019107770000

* Budget Type: Project Subaward/Consortium

Enter name of Organization: The Johns Hopkins University

* Start Date: 07-01-2011

* End Date: 06-30-2012

Budget Period: 4

A. Senior/Key Person

Prefix	* First Name	Middle Name	* Last Name	Suffix	* Project Role	Base Salary (\$)	Cal. Months	Acad. Months	Sum. Months	* Requested Salary (\$)	* Fringe Benefits (\$)	* Funds Requested (\$)
--------	--------------	-------------	-------------	--------	----------------	---------------------	----------------	-----------------	----------------	----------------------------	---------------------------	------------------------

Total Funds Requested for all Senior Key Persons in the attached file

Additional Senior Key Persons:

File Name:

Mime Type:

Total Senior/Key Person

106,455.00

B. Other Personnel

* Number of Personnel	* Project Role	Cal. Months	Acad. Months	Sum. Months	* Requested Salary (\$)	* Fringe Benefits	* Funds Requested (\$)
1	Post Doctoral Associates	2.40			13,768.00	1,101.00	14,869.00
2	Graduate Students		9.00	3.00	51,358.00	982.00	52,340.00
	Undergraduate Students						
	Secretarial/Clerical						
1	Electronics Technician	1.20			1,808.00	615.00	2,423.00
1	Animal Research Specialist	7.80			33,058.00	11,240.00	44,298.00
1	Electrical Engineer	1.20			8,509.00	2,893.00	11,402.00
1	Machinist	1.20			6,672.00	2,269.00	8,941.00
1	Machinist	0.60			3,444.00	1,171.00	4,615.00
8	Total Number Other Personnel						138,888.00
Total Salary, Wages and Fringe Benefits (A+B)							245,343.00

RESEARCH & RELATED Budget {A-B} (Funds Requested)

RESEARCH & RELATED BUDGET - SECTION C, D, & E, BUDGET PERIOD 4

* ORGANIZATIONAL DUNS: 0019107770000

* **Budget Type:** Project Subaward/Consortium**Enter name of Organization:** The Johns Hopkins University* **Start Date:** 07-01-2011* **End Date:** 06-30-2012**Budget Period:** 4**C. Equipment Description**

List items and dollar amount for each item exceeding \$5,000

Equipment Item

* Funds Requested (\$)

Total funds requested for all equipment listed in the attached file

Total Equipment

Additional Equipment:

File Name:

Mime Type:

D. Travel**Funds Requested (\$)**

1. Domestic Travel Costs (Incl. Canada, Mexico, and U.S. Possessions)

5,000.00

2. Foreign Travel Costs

Total Travel Cost**5,000.00****E. Participant/Trainee Support Costs****Funds Requested (\$)**

1. Tuition/Fees/Health Insurance

2. Stipends

3. Travel

4. Subsistence

5. Other:

Number of Participants/Trainees**Total Participant/Trainee Support Costs**

RESEARCH & RELATED Budget (C-E) (Funds Requested)

RESEARCH & RELATED BUDGET - SECTIONS F-K, BUDGET PERIOD 4

* ORGANIZATIONAL DUNS: 0019107770000

* **Budget Type:** Project Subaward/Consortium**Enter name of Organization:** The Johns Hopkins University* **Start Date:** 07-01-2011* **End Date:** 06-30-2012**Budget Period:** 4

F. Other Direct Costs	Funds Requested (\$)
1. Materials and Supplies	25,000.00
2. Publication Costs	1,200.00
3. Consultant Services	
4. ADP/Computer Services	1,500.00
5. Subawards/Consortium/Contractual Costs	
6. Equipment or Facility Rental/User Fees	
7. Alterations and Renovations	
8. Animal Procurement & Care	8,100.00
9. Grad Student Tuition Remission	17,455.00
10. Student Health Insurance	3,058.00
Total Other Direct Costs	56,313.00

G. Direct Costs	Funds Requested (\$)
Total Direct Costs (A thru F)	306,656.00

H. Indirect Costs				
	Indirect Cost Type	Indirect Cost Rate (%)	Indirect Cost Base (\$)	* Funds Requested (\$)
1. MTDC		64	286,143.00	183,132.00
Total Indirect Costs				183,132.00
Cognizant Federal Agency		DHHS, Stephen Virbitsky, 215-861-4470		
(Agency Name, POC Name, and POC Phone Number)				

I. Total Direct and Indirect Costs	Funds Requested (\$)
Total Direct and Indirect Institutional Costs (G + H)	489,788.00

J. Fee	Funds Requested (\$)
---------------	-----------------------------

K. * Budget Justification	File Name:	Mime Type: application/pdf
	8567-Budget_Justification_10_29_07.pdf	
(Only attach one file.)		

RESEARCH & RELATED Budget (F-K) (Funds Requested)

RESEARCH & RELATED BUDGET - SECTION A & B, BUDGET PERIOD 5

* ORGANIZATIONAL DUNS: 0019107770000

* Budget Type: Project Subaward/Consortium

Enter name of Organization: The Johns Hopkins University

* Start Date: 07-01-2012

* End Date: 06-30-2013

Budget Period: 5

A. Senior/Key Person

Prefix	* First Name	Middle Name	* Last Name	Suffix	* Project Role	Base Salary (\$)	Cal. Months	Acad. Months	Sum. Months	* Requested Salary (\$)	* Fringe Benefits (\$)	* Funds Requested (\$)
---	-----	-----	-----	-----	-----	-----				-----	-----	-----

Total Funds Requested for all Senior Key Persons in the attached file

Additional Senior Key Persons:

File Name:

Mime Type:

Total Senior/Key Person

109,648.00

B. Other Personnel

* Number of Personnel	* Project Role	Cal. Months	Acad. Months	Sum. Months	* Requested Salary (\$)	* Fringe Benefits	* Funds Requested (\$)
1	Post Doctoral Associates	2.40			14,181.00	1,135.00	15,316.00
2	Graduate Students		9.00	3.00	52,899.00	1,012.00	53,911.00
	Undergraduate Students						
	Secretarial/Clerical						
1	Electronics Technician	1.20			1,863.00	633.00	2,496.00
1	Animal Research Specialist	7.80			34,049.00	11,577.00	45,626.00
1	Electrical Engineer	1.20			8,764.00	2,980.00	11,744.00
1	Machinist	1.20			6,872.00	2,337.00	9,209.00
1	Machinist	0.60			3,547.00	1,206.00	4,753.00
8	Total Number Other Personnel						143,055.00
							Total Salary, Wages and Fringe Benefits (A+B)
							252,703.00

RESEARCH & RELATED Budget {A-B} (Funds Requested)

RESEARCH & RELATED BUDGET - SECTION C, D, & E, BUDGET PERIOD 5

* ORGANIZATIONAL DUNS: 0019107770000

* **Budget Type:** Project Subaward/Consortium**Enter name of Organization:** The Johns Hopkins University* **Start Date:** 07-01-2012* **End Date:** 06-30-2013**Budget Period:** 5

C. Equipment Description		
List items and dollar amount for each item exceeding \$5,000		
Equipment Item		* Funds Requested (\$)
Total funds requested for all equipment listed in the attached file		
	Total Equipment	
Additional Equipment:	File Name:	Mime Type:

D. Travel	Funds Requested (\$)
1. Domestic Travel Costs (Incl. Canada, Mexico, and U.S. Possessions)	5,000.00
2. Foreign Travel Costs	
Total Travel Cost	5,000.00

E. Participant/Trainee Support Costs	Funds Requested (\$)
1. Tuition/Fees/Health Insurance	
2. Stipends	
3. Travel	
4. Subsistence	
5. Other:	
Number of Participants/Trainees	Total Participant/Trainee Support Costs

RESEARCH & RELATED Budget {C-E} (Funds Requested)

RESEARCH & RELATED BUDGET - SECTIONS F-K, BUDGET PERIOD 5

* ORGANIZATIONAL DUNS: 0019107770000

* **Budget Type:** Project Subaward/Consortium**Enter name of Organization:** The Johns Hopkins University* **Start Date:** 07-01-2012* **End Date:** 06-30-2013**Budget Period:** 5

F. Other Direct Costs	Funds Requested (\$)
1. Materials and Supplies	25,000.00
2. Publication Costs	1,200.00
3. Consultant Services	
4. ADP/Computer Services	1,500.00
5. Subawards/Consortium/Contractual Costs	
6. Equipment or Facility Rental/User Fees	
7. Alterations and Renovations	
8. Animal Procurement & Care	8,100.00
9. Grad Student Tuition Remission	17,980.00
10. Student Health Insurance	3,165.00
Total Other Direct Costs	56,945.00

G. Direct Costs	Funds Requested (\$)
Total Direct Costs (A thru F)	314,648.00

H. Indirect Costs				
	Indirect Cost Type	Indirect Cost Rate (%)	Indirect Cost Base (\$)	* Funds Requested (\$)
1. MTDC		64	293,503.00	187,842.00
			Total Indirect Costs	187,842.00
Cognizant Federal Agency		DHHS, Stephen Virbitsky, 215-861-4470		
(Agency Name, POC Name, and POC Phone Number)				

I. Total Direct and Indirect Costs	Funds Requested (\$)
Total Direct and Indirect Institutional Costs (G + H)	502,490.00

J. Fee	Funds Requested (\$)
---------------	-----------------------------

K. * Budget Justification	File Name:	Mime Type: application/pdf
	8567-Budget_Justification_10_29_07.pdf	
(Only attach one file.)		

RESEARCH & RELATED Budget (F-K) (Funds Requested)

Budget Justification

A. Personnel:

J. Rudiger von der Heydt, Ph.D., Principal Investigator (6.0 cal. months), with a salary of \$72,703 and fringe benefits of \$24,719 in Year One, with a 3% increase every year for five years. Dr. von der Heydt will design experiments, and supervises collaborators in experimental design, animal procedures, data recording and analysis. Analysis and interpretation of results and writing is also done.

██████████ PostDoc (2.4 cal. months), with a salary of \$12,600 and fringe benefits of \$1,008 in Year One, with a 3% increase every year for five years. ██████████ has two main functions: one is to analyze data from previous and ongoing experiments. The other is to maintain and develop the software for the experiments and data analysis. This task is crucial to the productivity of the laboratory as the experiments are run with sophisticated custom-made software. Both functions include instruction and assistance to graduate students in their thesis research.

██████████ Animal Research Specialist (7.8 cal. months), is essential in keeping all the other activities in the lab running. Besides the normal lab keeping, her main tasks are the handling and behavioral training of monkeys, daily animal procedures in preparation for recording and finishing up. This includes monitoring behavioral performance and modifying training schedules accordingly, as well as instructing and assisting doctoral students. ██████████ performs surgical procedures and assists the PI and students in these procedures, performs post-operative care, keeps surgical and training logs, and monitors compliance with animal welfare regulations. She is also responsible for purchasing microelectrodes and fabricates special types of electrodes herself, an essential tool in our experiments.

Two Grad Students (9 acad. months, 3 sum. months), with a stipend of \$23,500 each and fringe benefits (Student FICA) of \$450 each in Year One with a 3% increase every year for five years. The students are necessary to carry out a major part of the proposed experiments, including design and implementation (programming) of the tests, recording and analysis of the data, and of course preparing publications. The research in this proposal requires about 10 student years of skillful work.

██████████ Machinist (1.2 cal. months), ██████████ Machinist (0.6 cal. months), ██████████ Electrical Engineer (1.2 cal. months), and ██████████ Electronics Technician (1.2 cal. months), are necessary for construction and maintenance of the equipment. In particular, we need new improved micro drives and recording amplifiers for efficient recording in awake animals. Our workshops build these efficiently in custom designs for all laboratories in our Institute. We need to construct a second optical stereoscopic system.

- B. Domestic travel costs will total \$25,000 for a five year period of \$5,000 per year.
- C. Supplies for the project will total \$125,000 for a five year period of \$25,000 per year.
- D. Publications costs will total \$6,000 for a five year period of \$1,200 per year.
- E. Animal Procurement & Care will total \$67,500 for a five year period. The cost per year is as follows: Year One through Year Three at \$17,100 per year, Year Four through Year Five at \$8,100 per year.
- F. Computer Services will total \$7,500 for a five year period of \$1,500 per year.
- G. Annual Tuition is \$37,695 of which Grad Students receive 20% remission. Student health insurance is \$1,379 per student per year. For two Grad Students, the cost of tuition plus health insurance for a five year grant period is as follows: Year One for \$17,836, Year Two for \$18,687, Year Three for \$19,578, Year Four for \$20,514, and Year Five for \$21,145.

RESEARCH & RELATED BUDGET - Cumulative Budget

	Totals (\$)	
Section A, Senior/Key Person		517,223.00
Section B, Other Personnel		674,802.00
Total Number Other Personnel	40	
Total Salary, Wages and Fringe Benefits (A+B)		1,192,025.00
Section C, Equipment		
Section D, Travel		25,000.00
1. Domestic	25,000.00	
2. Foreign		
Section E, Participant/Trainee Support Costs		
1. Tuition/Fees/Health Insurance		
2. Stipends		
3. Travel		
4. Subsistence		
5. Other		
6. Number of Participants/Trainees		
Section F, Other Direct Costs		303,758.00
1. Materials and Supplies	125,000.00	
2. Publication Costs	6,000.00	
3. Consultant Services		
4. ADP/Computer Services	7,500.00	
5. Subawards/Consortium/Contractual Costs		
6. Equipment or Facility Rental/User Fees		
7. Alterations and Renovations		
8. Other 1	67,500.00	
9. Other 2	82,968.00	
10. Other 3	14,790.00	
Section G, Direct Costs (A thru F)		1,520,783.00
Section H, Indirect Costs		910,737.00
Section I, Total Direct and Indirect Costs (G + H)		2,431,520.00
Section J, Fee		

PHS 398 Cover Page Supplement

OMB Number: 0925-0001
Expiration Date: 9/30/2007

1. Project Director / Principal Investigator (PD/PI)

Prefix: * First Name:
 Middle Name:
 * Last Name:
 Suffix:

* New Investigator? No Yes

Degrees:

2. Human Subjects

Clinical Trial? No Yes

* Agency-Defined Phase III Clinical Trial? No Yes

3. Applicant Organization Contact

Person to be contacted on matters involving this application

Prefix: * First Name:
 Middle Name:
 * Last Name:
 Suffix:

* Phone Number: Fax Number:

Email:

* Title:

* Street1:

Street2:

* City:

County:

* State:

Province:

* Country: * Zip / Postal Code:

PHS 398 Research Plan**1. Application Type:**

From SF 424 (R&R) Cover Page and PHS398 Checklist. The responses provided on these pages, regarding the type of application being submitted, are repeated for your reference, as you attach the appropriate sections of the research plan.

*Type of Application:

New Resubmission Renewal Continuation Revision

2. Research Plan Attachments:

Please attach applicable sections of the research plan, below.

- | | |
|---|---|
| 1. Introduction to Application
(for RESUBMISSION or REVISION only) | <input type="text"/> |
| 2. Specific Aims | <input type="text" value="4331-Specific_Aims_11_02_07.pdf"/> |
| 3. Background and Significance | <input type="text" value="7837-Background_and_Significance_11_02_07.pdf"/> |
| 4. Preliminary Studies / Progress Report | <input type="text" value="4005-Progress_Report_11_02_07.pdf"/> |
| 5. Research Design and Methods | <input type="text" value="4763-Research_Design_and_Methods_11_02_07.pdf"/> |
| 6. Inclusion Enrollment Report | <input type="text"/> |
| 7. Progress Report Publication List | <input type="text" value="1565-Progress_Report_Publication_List_11_02_07.pdf"/> |

Human Subjects Sections

Attachments 8-11 apply only when you have answered "yes" to the question "are human subjects involved" on the R&R Other Project Information Form. In this case, attachments 8-11 may be required, and you are encouraged to consult the Application guide instructions and/or the specific Funding Opportunity Announcement to determine which sections must be submitted with this application.

- | | |
|---------------------------------------|----------------------|
| 8. Protection of Human Subjects | <input type="text"/> |
| 9. Inclusion of Women and Minorities | <input type="text"/> |
| 10. Targeted/Planned Enrollment Table | <input type="text"/> |
| 11. Inclusion of Children | <input type="text"/> |

Other Research Plan Sections

- | | |
|---|---|
| 12. Vertebrate Animals | <input type="text" value="7899-Vertebrate_Animals_11_02_07.pdf"/> |
| 13. Select Agent Research | <input type="text"/> |
| 14. Multiple PI Leadership | <input type="text"/> |
| 15. Consortium/Contractual Arrangements | <input type="text"/> |
| 16. Letters of Support | <input type="text"/> |
| 17. Resource Sharing Plan(s) | <input type="text"/> |

18. Appendix

Attachments

IntroductionToApplication_attDataGroup0

File Name**Mime Type**

SpecificAims_attDataGroup0

File Name

4331-Specific_Aims_11_02_07.pdf

Mime Type

application/pdf

BackgroundSignificance_attDataGroup0

File Name

7837-Background_and_Significance_11_02_07.pdf

Mime Type

application/pdf

ProgressReport_attDataGroup0

File Name

4005-Progress_Report_11_02_07.pdf

Mime Type

application/pdf

ResearchDesignMethods_attDataGroup0

File Name

4763-Research_Design_and_Methods_11_02_07.pdf

Mime Type

application/pdf

InclusionEnrollmentReport_attDataGroup0

File Name**Mime Type**

ProgressReportPublicationList_attDataGroup0

File Name

1565-Progress_Report_Publication_List_11_02_07.pdf

Mime Type

application/pdf

ProtectionOfHumanSubjects_attDataGroup0

File Name**Mime Type**

InclusionOfWomenAndMinorities_attDataGroup0

File Name**Mime Type**

TargetedPlannedEnrollmentTable_attDataGroup0

File Name**Mime Type**

InclusionOfChildren_attDataGroup0

File Name**Mime Type**

VertebrateAnimals_attDataGroup0

File Name

7899-Vertebrate_Animals_11_02_07.pdf

Mime Type

application/pdf

SelectAgentResearch_attDataGroup0

File Name**Mime Type**

MultiplePILeadershipPlan_attDataGroup0

File Name**Mime Type**

ConsortiumContractualArrangements_attDataGroup0

File Name**Mime Type**

LettersOfSupport_attDataGroup0

File Name**Mime Type**

ResourceSharingPlans_attDataGroup0

File Name**Mime Type**

Appendix

File Name

Mime Type

Specific Aims

Research is proposed to advance our understanding of the neural mechanisms of visual perceptual organization and their relation to selective attention. The long-term objective is to understand the interface between sensory representations and cognitive processes at the neural signal level. The proposed research focuses on the mechanisms of figure-ground organization as evident from the neural representation of border ownership, i.e., the assignment of contours to objects. The general method is single-cell recording from the visual cortex of awake behaving macaques. Three broad aims have been identified for the next five years.

The first aim is to provide quantitative descriptions of the spatial integration mechanisms of border ownership selective V2 neurons. Previous studies have shown that these mechanisms extend far beyond the classical receptive field of the neurons. Two methods with factorial design, developed in the previous grant period, will be applied. These methods allow to measure nonlinear interactions of the surround regions with the classical receptive field as well as interactions between surround regions. The two methods are complementary. One uses fragmentation of figures, the other uses occlusion of critical features.

The second aim is to study persistence of figure-ground organization in the visual cortex. Based on results from the previous grant period we hypothesize the existence of a short-term memory for figure-ground organization that is (i) automatic (stimulus driven), (ii) works in parallel for multiple figures in the visual field, (iii) can hold information for durations in the order of a second, and (iv) can be set and reset within a tenth of a second. Experiments are proposed to (1) determine the influence of the type of figure-ground cue and its duration on the rise and subsequent persistence of border ownership signals, (2) determine whether the persistence depends on attention being directed to the figure, and (3) whether border ownership signals transfer across eye movements and stimulus movements.

The third aim is to study the role of the neural organization mechanisms in object-based selective attention. Building on previous results showing that V2 neurons combine border ownership coding with the influence of volitional selective attention, new experiments will test visual conditions in which an object is partially occluded so that only unconnected portions of it remain visible. The results will show whether the border ownership mechanisms can link features across gaps, and whether object-based attention mechanisms can do so.

Background and Significance

Note on resubmission. The proposal has been thoroughly revised according to the critique by the referees in the first round. It has been changed mainly in three ways: (1) Previous Aim 3 with the deactivation experiment was dropped, as suggested, and so were the perception studies; instead, new neurophysiological experiments were added, expanding the studied on the role of attention, as suggested by critique 3; (2) To improve clarity, the material has been rearranged, the text rewritten and figures explaining the logic were added; (3) Important results on the interaction of attention with figure-ground organization and the model have been published. The other major result, on the persistence of BOS signals, is close to being submitted for publication. New preliminary results on the spatial integration mechanisms and on persistence under eye movements were included.

c.1. Introduction

To understand a process we need to know the goal of processing (Marr, 1982)[1]. A difficulty in studying a sensory system is that its output is an internal representation and not easily observable. We can only infer the goal of processing. Considerable knowledge about the visual process comes from experiments in which human subjects respond to visual stimuli. This knowledge is indispensable for interpreting the results of neurophysiological experiments. Observations relating to the perception of figure and ground and the perceptual interpretation of images in terms of objects laid out in space, led to the studies reviewed below.

In this section we will first introduce the concept of border ownership coding, briefly summarize the main results of our earlier studies and relate them to other studies of neural figure-ground coding. We will then explain the motivations for the proposed new studies and put the anticipated results in perspective.

Abbreviations: BOS – border ownership; RF – receptive field; cRF – classical receptive field

c.1.1. Figure-ground organization

Figure-ground organization is the general term for the tendency observed in human vision to interpret certain 2D configurations in terms of foreground and background, or as cascades of objects arranged in different depths, with nearer objects occluding farther objects. Figure-ground organization can be described in two different ways. One can specify the depth relationship between adjacent image regions, or one can specify the assignment of contours, that is, which side of a contour is foreground. Both descriptions have been used in theoretical and psychophysical studies, and often the choice is just a matter of convenience. But the two descriptions also correspond to different theories of how figure-ground relationships are coded in the brain. Accordingly, neurophysiological experiments have either examined the representation of surfaces, or the representation of contours. We will first explain the latter type of experiments and comment on the other in Section c.3.

c.2. Explicit representation of border ownership in the visual cortex

c.2.1. Standard test with squares

An important observation was that neurons respond to the same contrast edge differently, depending on how the edge is 'owned' by a figure, as illustrated in *Fig. 1a-b* [2]. Note that the edge in the receptive field (RF, red ellipse) is identical in top and bottom displays, but the figure is on opposite sides of the RF. The local edge contrast is reversed between *a* and *b*. For either contrast the neuron responds more strongly when the square is on the left. We say, the neurons is selective for 'border ownership' (BOS) and call the response difference related to side-of-figure the border ownership signal.

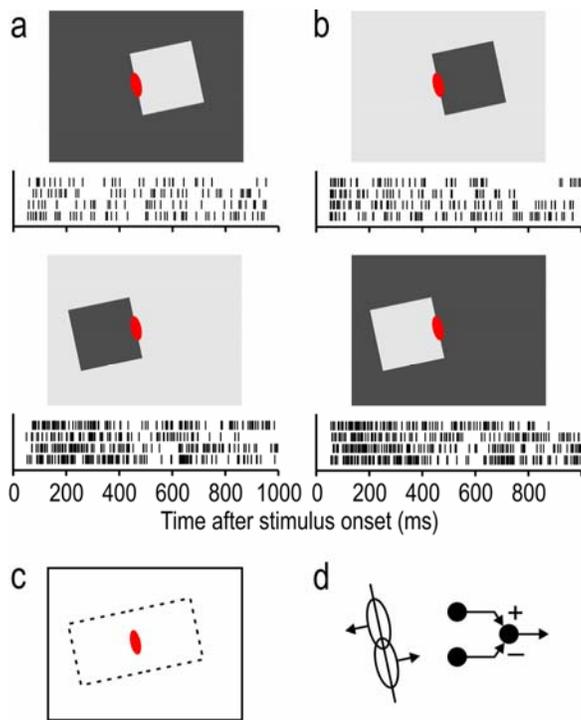


Fig. 1. Standard border ownership test. Raster plots show responses of a V2 neuron.

Because BOS selective neurons are found for any orientation, one can think of each piece of contour as being represented by two groups of neurons with opposite BOS preference, with the strength of BOS assignment being encoded in the activity difference between the two groups (*Fig. 1d*).

c.2.2. The range of image context integration

Comparing the top and bottom displays in *Fig. 1a*, it can be seen that they are identical within the region occupied by the two squares (*Fig. 1c, dashed line*). Thus, any difference between the responses indicates that the neuron is influenced by features outside this region (image context integration). By varying the size of the squares we can vary this region of identical stimulation and thereby explore the range of context integration. Most BOS selective neurons showed differential responses over a large range, often beyond the limits of our display (20 deg visual angle), but the difference tends to decrease with figure size. For comparison, the typical size of the classical RF size was 1-2 deg.

The BOS signal can be measured similarly for edges in other configurations by placing the edge to be tested in the RF and comparing the response to a display x with the response to display x' , where x' is created from x by mirror reflecting the image at the test edge and reversing the colors so as to keep the local stimulus identical. The proposed experiments are based on this principle.

c.2.3. Evidence for figure-ground coding or simply a random asymmetry of the 'non-classical' RF?

Figure-ground organization interprets 2D images in terms of a 3D world. We have shown in several studies that 'BOS selectivity' (as measured by our standard test) correlates with a number of depth cues, that is, cues that produce perception of depth ordering in humans. For each of the following we found (1) depth-order selective neurons and (2) correlation of preferred depth order with BOS preference: binocular disparity [3], motion/dynamic occlusion [4], and overlay cues (e.g. T-junctions) [2]. For example, a fraction of V2 neurons responded to stereoscopic 'cyclopean' edges and were selective for the direction of the depth change at the edge [5]. If such a neuron prefers, say, 'left-side-near' over 'right-side-near', then the neuron will generally have a preference for 'figure left' in the standard test (which uses figures without disparity) [3]. This combination of side-of-figure selectivity with selectivity for depth cues is unequivocal evidence for figure-ground mechanisms.

Thus, similar as in perception of BOS, the neural assignment of a contour segment can be determined by global shape (Gestalt cues) as well as local depth cues, such as stereo, motion/dynamic occlusion and static overlay cues.

Another proof of the close relationship between the neural signals and BOS perception is the neural coding of transparent overlay described in the Progress Report (Section d.4).

c.2.4. The question of the mechanisms underlying border ownership selectivity

After discussing the functional interpretation of BOS signals we will now turn to the question of the underlying mechanisms. Measurements of the time course of the instantaneous firing rates showed that BOS signals emerged as early as 50 ms after stimulus onset and reached their half-maximal level around 70-90ms [2,6]. This short latency argues for mechanisms in lower-level cortical areas and against the involvement of object recognition mechanisms of the inferotemporal cortex. We further found little, if any, increase in the latency of BOS signals with the size of the figure in the standard test [7]. Enlarging the figure increases the distance in cortex that needs to be bridged by signals to provide side-of-figure information. We have argued that this finding is a problem for models explaining BOS coding by propagation of signals via horizontal fibers in V2 (horizontal propagation hypothesis) and proposed a different model with a two-level hierarchical network [8]. Other studies have used the latency argument for clarifying the surround mechanisms of V1 receptive fields

[9]. However, we are not aware of published measurements of the length and conduction velocity of horizontal fibers in V2. In the absence of such data the argument from the latencies may not be convincing. The challenge for a physiological model is to reconcile the extent of context integration with short latency of BOS signals.

In Research Design Section e.1 we propose experiments that will examine the spatial characteristics of the context integration mechanisms by testing fragmented figures. These experiments will test a critical prediction of the horizontal propagation hypothesis: the connectedness of the integration zones. The experiments proposed in Section e.3 examine the horizontal propagation hypothesis in the light of our new results on the role of BOS mechanisms in selective attention. Here, the horizontal propagation scheme predicts a limitation in the representation of disconnected parts of an object, in contrast to an alternative mechanism [8].

c.2.5. Psychophysical evidence for the existence of BOS neurons in the human visual cortex

Based the finding of BOS coding, we demonstrated the existence of BOS selective neurons in the human visual cortex [10]: The tilt after effect depends on BOS. By adapting the neurons with opposite BOS preference differentially, we could simultaneously produce tilt aftereffects of opposite direction at the same visual field location.

c.2.6. Comparison between V1 and V2

We have compared areas V1 *and* V2 in several studies [2,3,5,11] and found substantial differences. Border ownership selectivity was less frequent in V1 than in V2, but BOS selective cells with extensive context integration were found also in V1. Cells that combine gestalt-based BOS selectivity and stereo edge selectivity are common in V2, but virtually absent in V1.

c.3. ***Relationship between border ownership and region coding***

Neural figure-ground representation was first demonstrated by Lamme and colleagues [12-14] in area V1 in form of enhancement of activity representing the figure region compared to the surrounding region. Figure and surround were textured and the activity of neurons with receptive fields in the figure region was compared with their activity evoked by displays in which the same texture filled the entire display.

It is not clear how this finding relates to BOS coding. Lamme's figure enhancement of V1 neurons starts later than the BOS signals in V2 (or V1). Lamme et al. [12,13] interpret the delay between response onset and figure enhancement as evidence for feedback from higher cortical levels. However, considering the conduction delays in horizontal fibers, the delay could also be interpreted as evidence for intra-areal mechanisms. BOS coding has been studied in V1 and V2, but we are not aware of studies of V2 with Lamme's paradigm.

There is a principle difference between the two paradigms. In Lamme's paradigm, figure enhancement is found in neurons responding to local texture elements. Orientation selective neurons, for example code for the orientation of texture bars, but not for the shape of the figure. Thus, figureness information needs to be separated from texture information and combined with shape information, at a later stage. In our paradigm, the BOS assignment is represented by the very neurons that also code for the shape of the figure. This makes the interpretation simpler, and, in our view, more interesting.

c.4. ***Studying the role of border ownership mechanisms cognitive processing***

The goal of the research proposed here is to test the hypothesis of an intermediate stage of processing between the stage of local-feature representation and central object recognition mechanisms. We hypothesize that the intermediate stage creates a visual data structure and at the same time provides an interface for top-down cognitive processes.

The visual cortex is traditionally viewed as a stage at the bottom of a hierarchy leading to higher level processes for object recognition, localization, control of attention etc. Consequently, most neurophysiological studies of cognitive processes in vision have investigated higher cortical areas such as V4, IT, parietal and prefrontal cortices. Relatively few have explicitly focused on the intermediate stage, the hypothetical interface between cognitive processes and the visual feature representation. These include studies of attention effects in V1 [15,16] and MT [17] and the demonstration of a correlate of working memory in V1 [18].

Two discoveries described in the Progress Report indicate that understanding BOS coding as a process that merely adds the figure-ground aspect to the local feature map, resulting in an improved image representation,

would be too narrow an interpretation. One is the observation of persistence in BOS signals, showing that the new representation is more durable than the local-feature representation. The other is the finding of a linkage between BOS coding and top-down attention mechanisms, suggesting that the BOS mechanisms not only serve to identify potential visual objects ('figures') in the feature map, but play a role also in the selection of the corresponding feature signals for purposeful processing.

To understand the finding of persistence we need to know if BOS signals transfer across eye movements, and object movements, if the persistence is related to attention, and to carry out experiments that might clarify the underlying mechanism.

Persistence of neural signals has been reported in studies of working memory, as demonstrated with delayed match-to-sample tasks [18,19]. These tasks require the subject to actively remember cue information and thus involve attention. Animals have to be specifically trained on such a task. Working memory-related activity has been observed at cortical levels as low as area V1. But we found persistence of BOS signals in monkeys performing a fixation task, which does not require extensive training and induces the animal to ignore visual stimuli other than the fixation target. It appears to be automatic and pre-attentive. Thus, the persistence of BOS signals might reflect a general short-term storage mechanism rather than a task specific working memory.

Our attention study suggests that the mechanisms that create BOS signals also provide a structure for top-down attention. In a model study we proposed that this structure might enable top-down mechanisms to selectively enhance the signals for features that should go together (or suppressing the other feature signals). We need to follow up on this finding and test displays in which objects are partially occluded so that only two disconnected parts are visible. These experiments will test the limits of V2 context integration mechanisms. The results will also be crucial in deciding between different physiological hypotheses of context integration, the horizontal propagation scheme versus the grouping-by-feedback mechanism as proposed in our model.

It is important to point out that mechanisms involving feedback, or back-projection from higher to lower cortical levels, are not necessarily instantiations of top-down processing. We reserve the term 'top-down' for centrally generated processes such as volitional attention, centrally programmed visual search, and memory-based scene interpretation. 'Feedback' refers to computational circuits, and 'back-projection' refers to anatomical structures. Both can be features of stimulus-driven, 'bottom-up' mechanisms. It is often thought that extensive image context integration must involve top-down processes. In this proposal we argue that it might be largely the result of bottom-up mechanisms (i.e., mechanisms that do not depend on attention, intention, or object memory), but might involve feedback from other prestriate areas beyond V2.

c.5. Significance of the proposed research

The proposed research will advance our understanding of the interface between sensory representation and cognitive processes. It will illuminate the fine structure of the selective attention mechanism and the internal visual representation it acts on. Although the proposal is focused on vision, the results will have implications also for other sensory systems because a sensory-cognitive interface is a building block of fundamental importance for conscious perception in any modality.

In a world that confronts us with visual information generated by machines it is important that we understand the brain mechanisms that organize the visual input and let us see what we want to see. Computers can generate artificial images and change displays faster than natural vision, but our visual brain has evolved for processing natural images. Now it has to deal with visual inputs that are quite different from those for which it has been optimized. We need to understand how the brain generates the internal representations, what draws attention and what is ignored, and why this is so. We hope that this research will also contribute to the understanding of visual disorders, such as dyslexia, in which the efficient interplay between perceptual organization and selective attention seems to be impaired.

Progress Report/Preliminary Studies

Abbreviations: BOS – border ownership; RF – receptive field; cRF – classical receptive field

d.1. Previous Aims.

There were three specific aims. (1) Analyze the spatial mechanisms of neural BOS assignment, specifically, the mechanism of image context integration beyond the classical receptive field. (2) Study the dynamics of BOS signals, specifically, examine if BOS signals show hysteresis. (3) Study the role of the figure-ground organization stage as an interface for top-down processes in visual cognition.

d.2. Overview.

(1) We developed and applied new methods to reveal the features of a figure-ground stimulus that contribute to BOS signal of the individual neuron [20,21].

(2) We have completed and published a study of the neural representation of contours in transparent overlay [22]. The analysis of the BOS signals showed that displays that are physically composed of five squares of different gray levels are coded as two crossed bars, in parallel to perception which interprets part of the luminance variations as an overlaying transparent object or a shadow, and groups the remaining edges into a second, underlying object.

(3) We studied the dynamics of BOS signals in situations in which a figure display is followed by a neutral (ambiguous) edge display. We found persistence of BOS signals that exceeds those of ordinary feature responses by an order of magnitude. The experiments proposed in Section e.2 are designed to follow up on this surprising discovery.

(4) We have completed and published a study of the role of figure-ground organization in selective attention. We found that BOS assignment occurs independently of attention and that top-down attention influences the individual neuron in a way that is asymmetric about the receptive field. The attention asymmetry correlates with the neurons BOS preference: the side of attentional enhancement tends to be the same as the preferred side of BOS. This indicates that the attention influence is mediated by the same circuits that produce BOS selectivity [6]. As we will discuss in Research Design Section e.3.4, this result is critical for discriminating between the hypothesis that BOS assignment is brought about by dedicated 'grouping' circuits [8,23] and the hypothesis of self-organization of a network of edge detectors [24]. A logical extension of the grouping model [8] qualitatively explains the new findings on top-down attentional modulation [6]. The experiments proposed in Section e.3 are designed to follow up on these results.

List of published and unpublished results during the report period (peer-reviewed papers in boldface; for other results a published abstract or the title of a paper in preparation are listed).

a. Figure-ground mechanisms provide structure for selective attention. *Nature Neuroscience* 2007. [6]

b. Neural Representation of Transparent Overlay. *Nature Neuroscience* 2007. [22]

c. Figure and ground in the visual cortex: V2 combines stereoscopic cues with Gestalt rules. *Neuron* 2005. [3]

d. Single-cell recordings reveal short-term memory for figure-ground organization (in preparation).

e. Onset, persistence and reset of border ownership signals. *Soc Neurosci Abstr* 2006. [25] (Abstract)

f. Dissociation of color and figure-ground effects in the watercolor illusion. *Spatial Vision* 2006. [26]

g. Border-ownership dependent tilt aftereffect. *J Opt Soc Am (A)* 2005. [10]

h. A reverse correlation method for studying the neural mechanisms of visual context integration in border ownership assignment. *Soc Neurosci Abstr* 2006. [20] (Abstract)

i. The contribution of T-junctions and L-junctions to neural border ownership signals. *Soc Neurosci Abstr* 2007. [21] (Abstract)

j. Border-ownership coding in monkey area V2: dynamics of image context integration. *Soc Neurosci Abstr* 2003. [27] (Abstract)

k. The latencies of V2 neurons in signaling border contrast, depth polarity, and border ownership (paper in preparation).

l. Neural selectivity for three-dimensional shape of edges (in revision).

m. Stereoscopic mechanisms for structural depth in macaque visual cortex (in revision).

In collaboration with Dr. Ernst Niebur, under separate funding:

n. A neural model of figure-ground organization. *J Neurophysiol.* 2007. [8]

o. Synchrony and the binding problem in macaque visual cortex. *Soc Neurosci Abstr* 2006. [28] (Abstract), and paper submitted to *J Vision*.

p. A spiking neuronal model for border ownership assignment. *Soc Neurosci Abstr* 2007. [29] (Abstract)

d.3. Visual context integration in border ownership selective neurons

d.3.1. Reverse correlation method

We tried three different versions of our reverse correlation method to reveal the spatial integration in BOS selectivity. As in the standard BOS test [2], one edge of a rectangular figure was placed in the receptive field under study and the border ownership signal was measured by taking the difference between the responses to figures on the two sides of the RF (the edge in the RF being identical). The same displays were then presented with additively superimposed dynamic binary noise (e.g., 16 by 15 pixels, figure occupying 5 by 5) and the spike-triggered average (STA) of the noise was computed for either location of figure (only the noise entered the analysis). The noise enhanced or reduced the local contrast along the borders of the figure and we expected that this should modulate the BOS signal according to the sensitivity of the BOS mechanism at that location. Thus, the difference between the STA for the two figure locations should reveal the hypothetical filters in the extra-classical RF whose outputs modulate the response evoked in the cRF. Because we are estimating nonlinear aspects of the RF, the test requires long recording times to obtain results. We studied about 100 cells in two monkeys. However, the method revealed the hypothetical filters only in a small fraction of the cells (significance was assessed by randomization statistics) [20]. We considered various possible reasons for the negative results, such as the low cut-off frequency of BOS modulation (about 4Hz, O'Herron & von der Heydt, unpublished results), and the bistable behavior of the BOS signal that will be described below, and optimized the timing of figure and noise presentations accordingly. However, the improvements were small and the yield was still low with this method. It is possible that figure and noise do not interact as with expected, or that the tessellation of the noise interferes with the figure-ground organization process. We have therefore developed two other, more efficient methods and these will be described next.

d.3.2. Factorial methods

Two methods were designed to measure the influence of specific features of the stimulus, such as edges, corners, and T-junctions. One uses variable occlusion of features, the other employs fragmented figures.

Occluder method

A variable number of 'occluders' is added to the test figure displays. We applied this to displays of 2 overlapping rectangles, measuring the BOS signal for the border between the figures (test edge). These displays have a few locations that provide the critical information about the direction of overlay. We used spheres with simulated illumination and shading to create the appearance of 3D objects that occlude the T- and L-junctions of the figures. The 'occluders' were clearly visible as distinct objects, but their average luminance was close to that of the background. A total 5 or 6 occluders were applied in all factorial combinations. The design involved 7-8 binary factors (direction of overlay, contrast polarity of the test edge, and presence/absence of the 5-6 occluders). ANOVA was performed on the square-root-transformed spike counts.

While the occluders by themselves evoked small if any responses, their presence on the figures effectively modulated the test edge response. The 5-occluder test (60 tests in 47 BOS selective cells) revealed significant modulating influences in 26% of the critical features on average. Features in the preferred BOS configuration had mostly enhancing effects, whereas features in the non-preferred BOS configuration had mostly suppressive effects (that is, consistent with the cell's BOS preference). On average, 68% of the effects were consistent. Interestingly 76% of the T-junction effects, but only 59% of the L-junction effects were in the consistent direction. Thus, the mechanisms seem to weigh T-junction as more reliable evidence for BOS assignment than L junctions. In several neurons, the BOS signal was influenced by junctions at 3 different locations.

Fragmentation method

A limitation of the method just described is that the occluders not only occlude, but also add features to the display. Therefore, we cannot argue with certainty that an enhancement of responses is due to the facilitatory

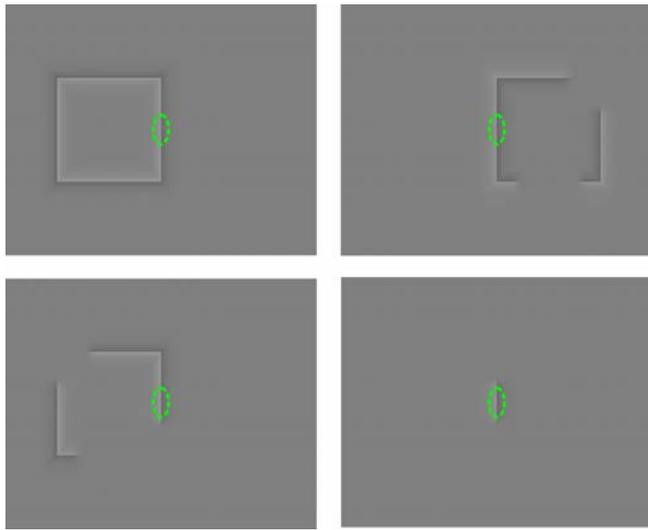


Fig. 2. Examples of fragmented figure displays.

influence of a T-junction, for example, and not to an inhibitory influence of the occluder at that location. To avoid this ambiguity, we devised displays with 'invisible occluders'. We generated test figures with 'Cornsweet edges' (Fig. 2). These were derived from the ordinary contrast-defined figures that we used before by high-pass filtering in the spatial frequency domain. In effect, these figures consist of sharp edges with luminance (or color) tapering off exponentially to the background value on both sides. At low contrast, such figures look like solid figures. At higher contrast, the luminance gradients become visible, but the inner of a figure still looks brighter (or darker) than the background although it actually has the same luminance. We then applied occluder patches of background gray to turn on and off parts of the figures. The occluder patches had an opaque interior with a cosine gradient of transparency at their borders, so that, when placed on a figure edge, they produced a gradual transition of the edge from full contrast to zero contrast. Thus, we could occlude a

peace of edge without creating sharp terminations. This method enables us to fragment any configuration of test figures deliberately. It turned out that figures with Cornsweet edges are as efficient as solid figures in producing BOS modulation. Because the edges are symmetrical (with gradients on both sides) they do not provide figure-ground information by themselves. As in previous experiments, we always tested both polarities of contrast and compared situations that were identical in and around the classical RF. For control, the fragments were also tested without an edge in the cRF.

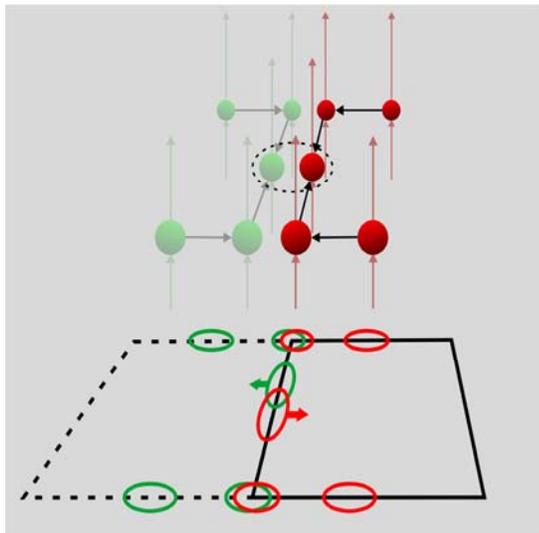


Fig. 3. Generation of border ownership selectivity by horizontal signal propagation (Model A).

To discuss the results, we consider two models of context integration: The horizontal propagation model [24] which assumes that the BOS selectivity of neurons is determined by their connectivity pattern within V2 (Fig. 3). Of the two encircled cells, one (red) is facilitated in the presence of a convex shape on the right, while the other (green) is facilitated by contours of convex shapes on the left. (In the model [24] The connectivity pattern was modeled in analogy to the functional connectivity of V1 [30].)

The 'grouping cell model' [8] achieves context integration by a different mechanism. It assumes specific grouping circuits that are separate from the cortical feature representation (Fig. 4). 'Grouping cells' integrate contour signals of neurons with co-circular receptive fields and, by feedback, adjust the gain of the same neurons. In this scheme, each V2 neuron is connected to grouping circuits integrating contours on one side of its RF, so that its gain is increased if a convex shape is present on that side. For example, a

V2 neuron with right BOS preference (red) would be connected to a grouping cell for that side, and its partner neuron with BOS preference left (green) would be connected to a different grouping cell for the other side.

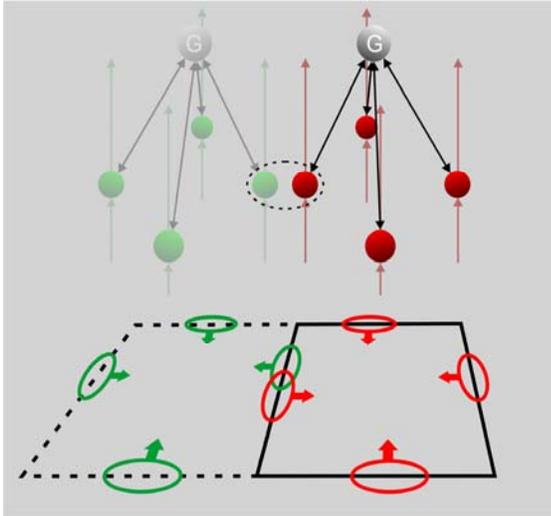


Fig. 4. Generation of border ownership selectivity by a grouping mechanism (Model B).

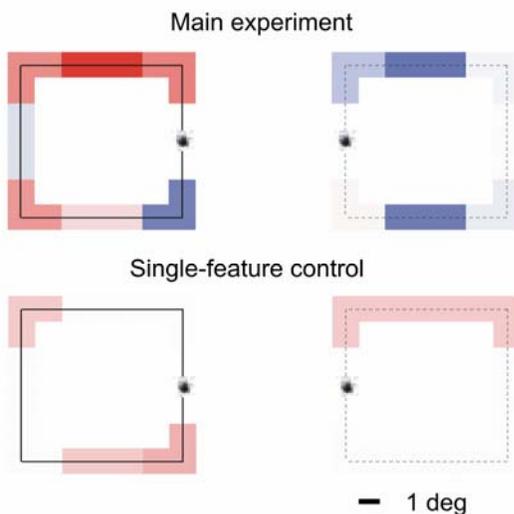


Fig. 5. Modulation of responses by contour segments outside the cRF. V2 neuron with 'left' preference. Red indicates enhancement, blue, suppression of responses. Gray spot, map of cRF.

The two models make different predictions. In the horizontal propagation model the length of intracortical horizontal fibers is a limitation. A maximal length of about 3 mm (as found in V1 [31]), corresponds to less than a degree of visual angle in the foveal representation. For larger figures, signals must propagate over chains of neurons, and this can occur only if all neurons along the chain are directly activated by the stimulus, that is, along the contours (propagation over chains of 2 links are illustrated in Fig. 3). This is because the horizontal signals are modulatory, but cannot create activation. Thus, the prediction is that locations far from the cRF can only contribute to the BOS signal if closer locations on the contour also contribute. In other words, the contours must be continuous except for gaps smaller than the visual angle that can be bridged by monosynaptic connections[30]. In the grouping cell model connectedness is not required, because the grouping cells simply integrate co-circular features. Thus, close and far features can contribute independently.

The Cornsweet figure test revealed modulating influences in 26% of the features on average (51 different tests in 35 BOS selective cells). In this test, suppression on the non-preferred side was more frequent than enhancement on the preferred side: features on the preferred side had enhancing effects in 72% of cases, whereas features in the non-preferred side had suppressive effects in 91% of cases. Results from an example cell are illustrated in Fig. 5. Note that the single features produced weak responses that were not correlated with the modulating effects in the main experiment. Effects of the features closest to the cRF (the near corners) were found more often than effects of the more remote features (42% vs. 20%), which would be consistent with the horizontal propagation model. However, analyzing a subset of test displays in which the near corners were missing showed significant BOS modulation in 64% of the cells, and a subset in which the near corners and the adjacent horizontal edges were missing still showed modulation in 34% of the cells. This indicates that the horizontal propagation model is not sufficient to explain BOS coding in V2.

d.4. Border ownership signals in transparent overlay

Besides figure-ground organization, border ownership assignment occurs also in situations of transparent overlay. These situations do not require a 3D interpretation. For example, in the transparent cross of Fig. 6b, either the dark or the light bar can be interpreted as transparent and overlaying. Studying this configuration is important because perception indicates that it is represented as two overlaying objects (bars), whereas the stimulus actually consists of just two bright and two dark squares on a gray background.

The BOS selectivity of neurons gives us a handle for studying this representation. We compared displays of a single square (Fig. 6a) with the transparent display (Fig. 6b) and a display of 4 squares with rounded corners that does not produce perception of transparency (Fig. 6c). Note that the edge marked by a red ellipse is owned left in a and c, but right in b. The curves at the bottom show the time course of the averaged BOS

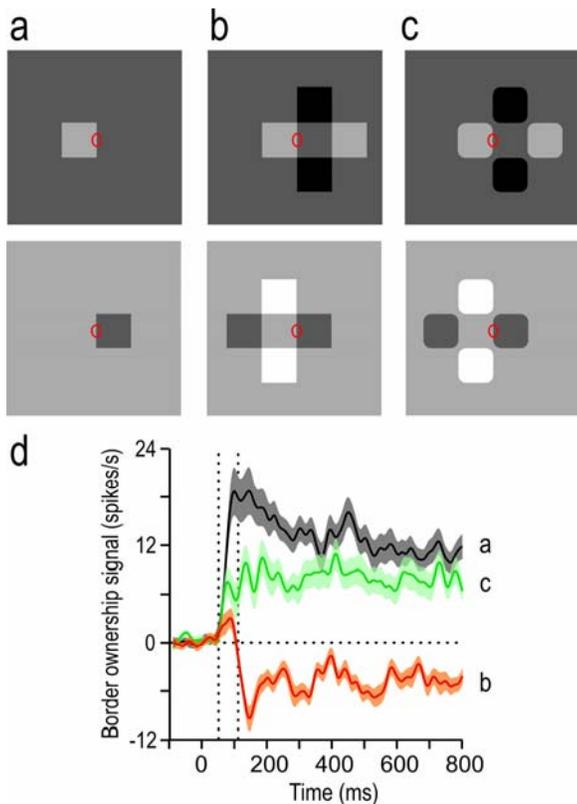


Fig. 6. Border ownership signals in transparent overlay. The edge in the RF is identical in all displays, but BOS is reversed in *b* compared to *a* and *c*. The BOS signal is defined as the difference between responses to top and bottom displays.

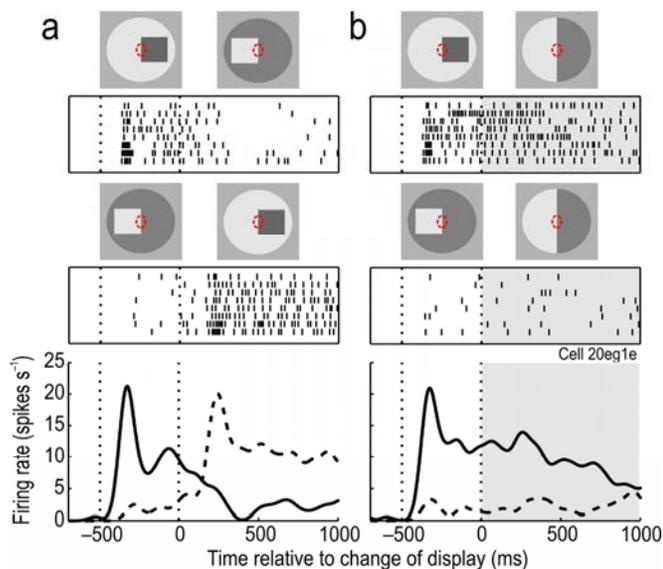


Fig. 7. Responses of a V2 neuron in our standard persistence test.

trials, both sequences end with the same bipartite field (Fig. 7b top and below). In this case the displays are completely identical after the switch (time 0-1000).

signals of V2 neurons. It can be seen that the signal for *b* (red curve) was reversed compared to *a* and *c*. This shows that the neurons assign BOS according to the transparent interpretation. Particularly striking is the difference between the responses to *b* (red) and *c* (green) which differ only in the presence/absence of 'X-junctions'. Note also that the reversal in *b* occurred with a delay (dashed vertical lines). These results show that V2 codes configuration *b* as two crossed bars rather than representing the four squares that make up the display. It organizes information in terms of plausible objects (or shadows).

d.5. Persistence of border ownership signals

Phenomena of figure-ground perception, particularly the slow spontaneous reversals observed in ambiguous displays like Rubin's vase/face figure, suggest that the internal representation of visual objects that has some persistence. We studied the dynamics of the BOS signal with the goal to explore this persistence.

In a first series of experiments we measured BOS signals for a border between two abutting figures while the luminance/color of the background was varied periodically so as to modulate the perceived ownership of this border. We were looking for hysteresis of the signal, expecting that it would be of short duration, as suggested by perceptual studies of iconic memory. However, it proved difficult to separate hysteresis effects from phase shifts produced by signal integration and adaptation that occur at many levels in the system.

We then discovered that persistence of BOS signals can be demonstrated directly in a simple paradigm. This persistence was of much longer duration than expected. The robustness of this effect allowed us to explore it in a variety of situations.

d.5.1. The persistence paradigm

The paradigm is illustrated with the responses of an example neuron in Fig. 7. The left side (a) shows display sequences in which BOS switches from right to left (top) or from left to right (below). We used this to measure how fast BOS signals respond to a change. Fig. 7b shows the display sequences for measuring persistence. Each trial starts with the presentation of a fixation point. A short time after the beginning of fixation a figure is displayed (time -500 to 0) on one side of the RF. The figure appears within a circular aperture centered on the RF. At time 0 the display switches (leaving the edge in the receptive field unchanged). In trials of type (a) the figure flips to the opposite side, in trials of type (b) the display switches to a bipartite field. The side where the figure appears in the initial display is varied randomly between trials. Note that in type (b) (Fig. 7b top and below). In this case the displays are

d.5.2. Responses of an example V2 neuron.

The raster plot in *Fig. 7a*, top, shows that the neuron responds strongly when the figure appears on the preferred side (right) and changes to a low firing rate after the figure flipped to the opposite side. *Fig. 7a*, bottom, shows the responses to presentations in reversed order. The responses reverse fast. Plots of the mean firing rate (bottom) show that the responses cross over about 150ms after the figure reversal. In contrast, when the initial figure display is switched to an edge with ambiguous assignment, the neuron continues to fire at a high rate, or low rate, depending on the preceding figure presentation (*Fig. 7b*). (Note that the identical edge was displayed in the classical RF throughout in all conditions).

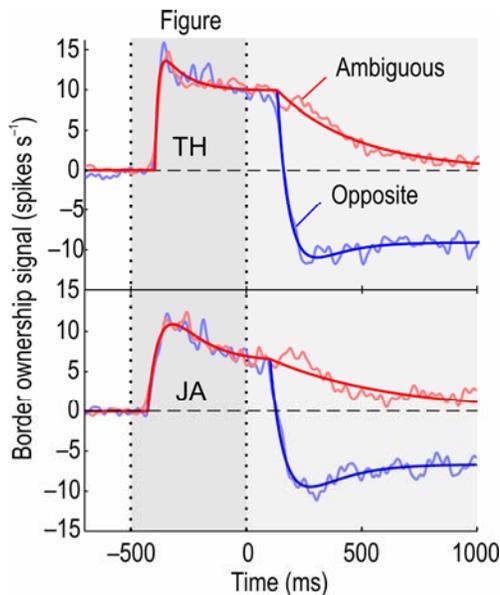


Fig. 8. Time course of the population border ownership signals in two monkeys.

d.5.3. Population signal

As in previous experiments, we define the BOS signal as the firing rate difference between figure on preferred side and figure on opposite side. The averaged signals of the BOS selective neurons from two monkeys (65 and 48 neurons, respectively) are shown in *Fig. 8*, for switching to ambiguous edge (red trace), and for switching sides (blue trace). The smooth curves are chains of exponentials fitted to the averaged BOS signals (a sum of two exponentials with constant for the figure phases and a single exponential without constant for the ambiguous phase; the transition points were determined by the fit). It can be seen that the BOS signal rose steeply after figure onset (at time -500) and subsequently declined slightly during the figure phase. When, at time 0, the figure was replaced by an ambiguous edge, the signal remained positive and then decayed slowly over the next second (red). By contrast, when the initial figure was replaced by a figure on the opposite side, the BOS signal changed rapidly to negative (blue). The time constant of the decay in the ambiguous phase (406 ms, confidence limits 368, 445) was much longer than the time constants for the initial rise (18 ms) and the reversal (61 ms) (both monkeys pooled).

d.5.4. Control for afterimage

Finding persistence of responses on a 500 ms time scale is so unusual in the visual cortex that we first suspected it might be due to an afterimage. The 0.5s presentation of a bright or dark square might leave an afterimage on one side of the ambiguous edge which might act like a real figure, producing a border-ownership signal. To control for this possibility, we included a test condition with a flickering figure in which the gray values (or colors) of the square and its surround were rapidly alternated, eliminating the afterimage (as shown by a psychophysical test in human). The flickering figure caused fluctuations of the border ownership signal in the figure phase, but during the ambiguous edge phase we found the same slow decay as for stationary figures. The time constant of the decay was not significantly different between flicker condition (581 ms, confidence limits 440, 721) and static condition (494, confidence limits 439, 548; 34 neurons). We concluded that persistence of the border ownership signal is not due to an afterimage.

d.5.5. Clarifying the mechanism of persistence

We used several variations of this paradigm to clarify the nature of persistence.

c.5.5.1. The duration of the initial figure presentation was not critical the persistence of the BOS signal. With a figure duration as short as 50 ms we found nearly the same amplitude of the signal and its decay was only slightly faster.

c.5.5.2. Do border ownership signals decay passively, like the voltage across a capacitor that is charged and discharged through a resistor? Then the effects of successive stimulations should accumulate, like the charge on the capacitor. We investigated this by presenting figures twice within a fixation period, each time followed by a 1-second ambiguous edge presentation. The second figure could appear either on the same side as the first figure, or on the opposite side. We then determined whether the side of the first figure presentation influenced the border ownership signal during and after the second presentation (*Fig. 9*, blue and red traces). Despite a clear difference at the onset of the second figure (time 0) the signals converged in the response to the second

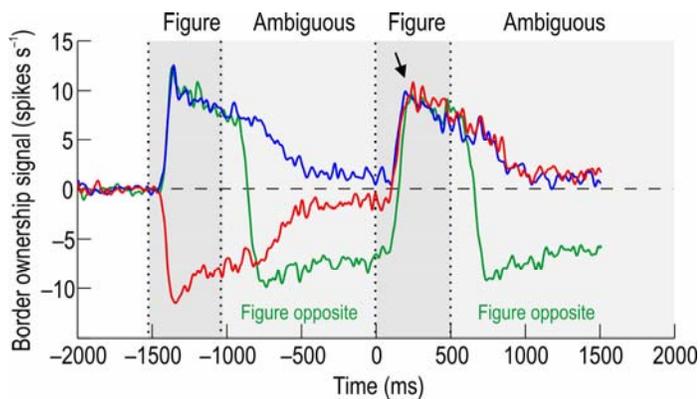


Fig. 9. Reset of the BOS signal by a new figure presentation.

c.5.5.3. Is the bistable behavior a property of a network of V2 neurons? We found that neuronal signals in V2 depend on the stimulus history (compare, for example, red and blue curves in *Fig. 9*). The identical edge stimulus is represented by different activity, depending on the previous activation. The simplest circuit that would achieve this is a pair of neurons that mutually inhibit each other, while both are continuously excited (e.g., by recurrent self-activation, or by input neurons that are activated by the edge stimulus). This is analogous to a flip-flop circuit in electronics which can be set by an external signal to one state or the other, and then hold this state in the absence of an input signal. This hypothesis seems plausible because it does not require the assumption of a cellular process with long time constant. The mutual inhibitory connections constitute a positive feedback loop which can maintain a firing rate difference over a long time, provided that at least one of the partner neurons keeps firing. However, if the activity of both partners is interrupted, the stored information is lost.

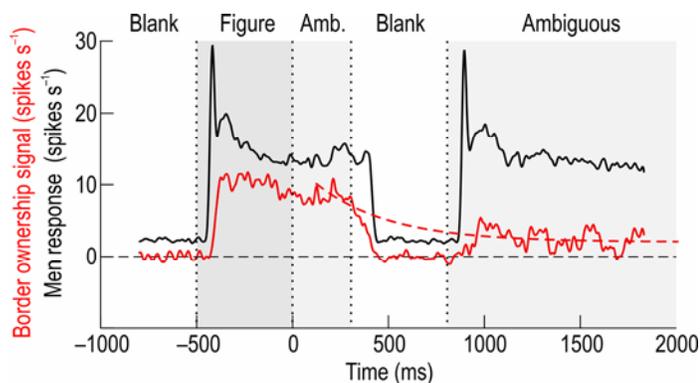


Fig. 10. The BOS signal survives interruption of activity

figure (arrow) and were virtually identical during the subsequent decay phase. In a third condition we flipped the figure back and forth twice (green trace). In this case, the signal was strongly negative at the beginning of the second cycle (time 0), but during the subsequent figure presentation it reached the same amplitude as in the other conditions (arrow). The capacitor-resistor circuit (or any linear low-pass filter in temporal frequency) would produce different signal levels during the second figure presentation because the charge accumulates. The border ownership signal did not accumulate over repeated figure presentations. Each new presentation seemed to reset the signal. The persistence of the signal is not like a passive afterglow, but more like a trace in a storage device that can be set and reset by the incoming signals.

This hypothesis can be tested by introducing a condition that effectively interrupts the activity of border ownership selective neurons in the cortex. We achieved this by inserting a blank field for 500 ms in the ambiguous edge phase (*Fig. 10*). When the display went blank the average firing rate returned to the resting level for several hundred milliseconds (black trace, compare the blank interval around 500 ms with the blank period at the beginning). Consequently, the border ownership signal (red trace) was zero during this interval. But when the ambiguous edge reappeared after the blank, the border ownership signal recovered. Indeed, it seemed to follow the same decay function as in *Fig. 8*, as if the edge stimulus had not been interrupted (dashed curve). This result rules out the hypothesis that information about the previous BOS assignment resides in the state of activity of V2 border-ownership neurons.

c.5.5.4. Alternative mechanisms

The information about the previous BOS assignment might be stored by molecular mechanisms, or in persisting activity of neurons outside V2. We have previously proposed a model of figure-ground organization based on grouping circuits and argued that these circuits must involve feedback from a higher-level area, most likely V4 [8]. In its present form, this model does not explain persistence and hysteresis. However, the general idea of the model, that figure-ground organization is brought about by dedicated circuits including 'grouping cells' at a higher level, is compatible with the present results. The hysteresis effect could be explained by assuming circuits of mutually inhibitory neurons as suggested above, not at the level of the BOS cells (V2), but at the level of the grouping cells. The above experiment shows that the hysteresis effect cannot be explained by figure-ground models based on self-organization within V2 [24].

d.5.6. Conclusion

Our experiments have shown that BOS signals in V2 persist for more than a second when a figure-ground display is followed by an ambiguous edge display; that the identical display is represented by different activity patterns in V2, depending on the preceding pattern of activity (hysteresis*); and that BOS signals can be reset within a fraction of a second by visual input that provides new figure-ground information. Persistence and hysteresis, and the ability to retain new information immediately, are characteristics of memory circuits.

* The differential representation of identical displays can be clearly seen in the activity marked by shading in Fig. 7. In Figs. 8-10, where BOS signals are plotted instead of responses, a positive signal in the ambiguous phase means hysteresis, because the BOS signal is the difference between responses to identical displays. Unlike hysteresis in ferromagnetism, which persists indefinitely, the BOS signals decay.

d.5.7. Open questions

The finding of persistence of BOS signals opens new avenues for studying the cortical processes underlying the formation of object representations and object-based attention. In this proposal, we focus on two general questions: (1) does the BOS signal survive translation of the retinal image, which can be caused either by an eye movement or by visual stimulus movement, and (2) does attention play a role in keeping the BOS signal alive? We have preliminary results speaking to the first question.

Trans-saccadic persistence

The question of position invariance is an important issue. It seems that a short-term memory for figure-ground structure would be of little use if it were tied to retinal location. If BOS information is represented in retinal coordinates with the precision given by the typical size of the classical RF of V2 neurons, and cannot be transferred to other neurons with different RF locations, the figure-ground structure is lost after each eye movement that displaces the contrast border by more than a degree or so, and has to be re-computed.

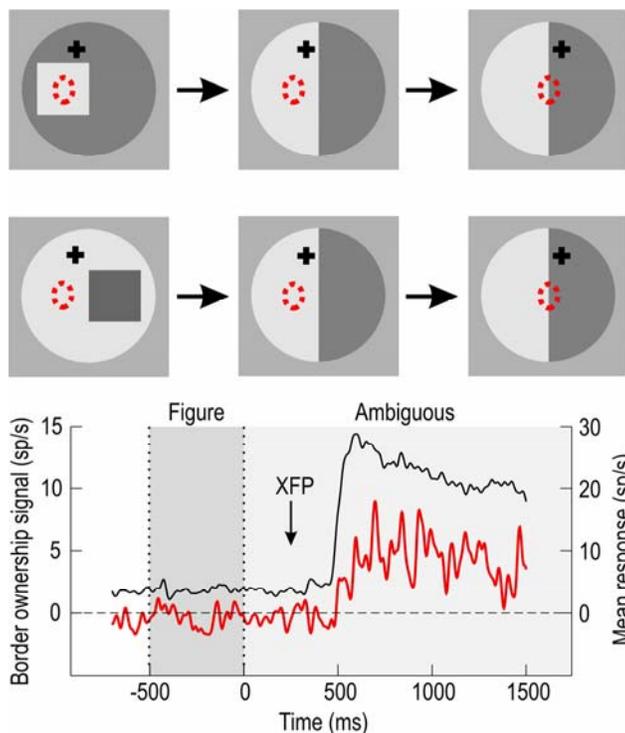


Fig. 11. *Trans-saccadic persistence of BOS signals. Cross indicates fixation point.*

before the saccade. At the time the neurons began to respond, the ambiguous edge had already been on the screen for about 500 ms. Still, simultaneously with the responses, a BOS signal emerged, reflecting the location of the figure in the initial presentation. Thus, BOS information was preserved not only over the 250 ms ambiguous presentation but also across the ensuing saccade.

Preliminary results from a first experiment indicate that the figure-ground representation in V2 does persist across saccades. The display sequence in this experiment was the same as in the basic persistence test (Fig. 7) except that the test edge of the figure was presented *beside* the RF under study, so that the neuron was not activated (Fig. 11, left stimulus displays). As in previous experiments, the figure was followed by an ambiguous edge at time 0 (Fig. 11, center displays). At time 250 ms, the fixation point was moved 2-3 deg (XFP), triggering a saccade that moved the RF onto the test edge (Fig. 11, right displays). (The experiment included also conditions in which the RF was initially located on the other side of the edge and the fixation point jumped in the opposite direction; thus, the initial location of the RF was equally often inside or outside the figure for each BOS condition). The plot at the bottom shows the average response (black) and BOS signal (red) of 14 neurons (the sign of the BOS signal of each neuron was assigned positive for the preferred side according to a separate test, our standard BOS test). The response curve (black) shows that the neurons were not activated by the presentation of the figure, as expected (there was no contrast in the classical RF), but responded only after the saccade, when their receptive fields landed on the test edge. Consequently, the BOS signal was zero

Studying the translation invariance of BOS signals is the aim of the experiments proposed in Research Design Sections e.2.2 and e.2.3.

The role of attention

As explained in Section d.6 below, we have found that BOS signals emerge without the influence of attention, and even ‘in the shadow of attention’. Thus, we can assume that in the persistence experiments just described also the BOS signal is generated pre-attentively. However, we do not know if attention plays a role in the persistence of the signal. Involvement of attention is a characteristic of *working memory*, as demonstrated with delayed match-to-sample tasks (see Background Section c.4). These tasks require the subject to actively remember cue information. Since the experiments described above were done with monkeys performing a simple fixation task, it seems that the persistence of BOS signals does not depend on the active participation of the subject. We hypothesize the existence of a *short term memory for visual organization* that is stimulus-driven, automatic, and ‘parallel’ (meaning that it can simultaneously store information for several objects in the display). The experiment in Research Design Section e.2.4 will address this question.

d.6. Figure-ground representation provides structure for selective attention

We have studied how attention interacts with figure-ground representation in area V2. Selective visual attention is often conceived as a spatial selection mechanism that acts on an image representation or local feature map (spatial filter hypothesis). The aim of this research was to test the hypothesis that top-down selective attention, rather than on an image representation, acts on an ‘intermediate stage’ in which borders are assigned to regions (interface hypothesis). In a first step, we wanted to determine if neural BOS coding emerges from a bottom-up process (in parallel for different objects in the display), or depends on the deployment of attention (Experiment 1). In Experiment 2 we tested configurations of overlapping figures. This test is prototypical for situations of partial occlusion which are ubiquitous in natural images. In these situations the stage of BOS assignment is critical. With a spatial selection mechanism alone it would be impossible to process the partially occluded objects correctly. Such a mechanism would extract shapes composed of a mixture of ‘intrinsic’ and ‘extrinsic’ contours (regions of occluded objects are bounded by two types of contour, those that are inherently related to the object—intrinsic contours—and those that are formed accidentally by interposition of another object—extrinsic contours [32]). Only the intrinsic contours should be processed together for shape recognition; extrinsic contours should be excluded. We summarize these results here only briefly because they have been published [6].

d.6.1. BOS signals emerge pre-attentively

The experiment with separated figures showed that BOS signals are largely independent of attention, emerging for attended as well as ignored objects. Although a large fraction (41%) of V2 neurons showed the influences of both, BOS and attention, the amplitude of the average BOS signal in these neurons was only slightly smaller for ignored objects than it was for attended objects, and the latency was exactly the same.

d.6.2. Extrinsic edge suppression

We then studied the neural representation of the contour that separates two overlapping figures. Here the spatial filter hypothesis and the interface hypothesis make opposite predictions. The spatial filter hypothesis predicts enhancement when attention is on the background figure, because the occluding contour is closer to the focus of attention than when attention is on the foreground figure. The interface hypothesis predicts suppression of the occluding contour. We found an effect of the side of attention in 48% of the cells tested, and 2/3 of these were also BOS selective. Nearly all of these cells showed suppression when the background figure was attended, in support of the interface hypothesis.

d.6.3. Attentional asymmetry of receptive fields

A surprising result of this experiment was that the attention effect was asymmetrical about the receptive fields of the individual neurons. Attention to the figure on one side of the receptive field enhanced the responses while attention on the figure on the other side reduced them, irrespective of which figure was in front. Thus, the neurons had a fixed ‘preferred side of attention’. Moreover, in the population, the preferred side of attention correlated with the preferred side of border ownership (*Fig. 12*).

The spatial asymmetry of the attention influence relative to the receptive fields was also apparent in the experiment with separated figures (in which only one figure was close to the RF): attention to a figure on the

preferred BO side produced a 3-times stronger enhancement on average than attention to a figure on the opposite side (compared to attention on a remote figure). Thus, even in the case of separated figures, when a spatial filter mechanism would be sufficient for object selection, neurons showed attentional asymmetry.

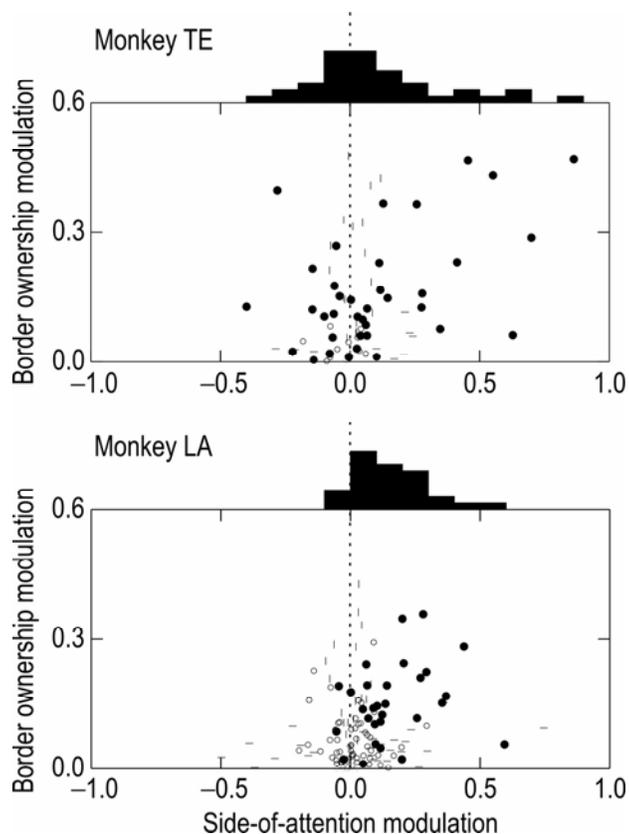


Fig. 12. Correlation of border-ownership and side-of-attention preferences in neurons of V2.

image context to generate border-ownership signals, it explains the spatial asymmetry of the attention influence, and it explains why the side of attention enhancement is generally the same as the preferred side of border ownership.

d.6.5. Conclusion

The significance of these results is twofold. First, they show that neural BOS assignment (figure-ground organization) is pre-attentive. Second, they demonstrate a linkage between top-down attention and BOS assignment, indicating the existence of a neuronal network that produces BOS assignment and also serves as a structure for attentive selection.

d.6.6. Open questions

The existence of grouping cells is hypothetical and their location is not known. The latency of BOS signals and their relative invariance with figure size suggest a location in a higher-level area such as V4, because such a feedback loop would involve fast myelinated fibers, and the length of this loop would not increase with figure size as would the length of horizontal fibers in V2. Area V4 appears as a likely site for grouping cells because it receives direct projections from the parietal area LIP which is an important stage in the generation of top-down visual attention [33]. The experiments proposed in Research Design Section e.3 will explore the limits of top-down attention modulation in V2 and will show if it is compatible with the horizontal propagation scheme.

d.7. Behavioral demonstration of BOS coding in monkeys

We are not aware of a behavioral study that has demonstrated figure-ground organization in monkeys. We carried out an experiment adapted from the classical demonstration of the effect of BOS on object recognition by Nakayama et al. [32]. The results from one monkey showed that BOS assignment affected object recognition just as strongly as it does in humans.

d.6.4. A model for object-based attention

Our previously proposed model of the BO mechanism [8,23] provides a plausible explanation for the attentional asymmetry and its correlation with BO preference: In a nutshell, the model proposes that BO selectivity is produced by specific neural circuits ('grouping cells') that integrate contour signals of neurons with co-circular receptive fields and, by feedback, adjust the gain of the same neurons. In this scheme, each V2 neuron is connected to grouping circuits integrating contour on one side of its RF, so that its gain is increased if a convex shape is present on that side.

The grouping cell network is the key to understanding the interplay between attention and figure-ground organization. Extending the model, we make the additional assumption that top-down attention excites the grouping cells at the focus of attention (or inhibits the grouping cells surrounding it). The spatial asymmetry of the attention effect and its correlation with border ownership are then obvious corollaries: because the border-ownership preference of a neuron is determined by the same connectivity, the side of attention enhancement and the preferred border-ownership side must be the same. The responses of a B cell are enhanced if the focus of attention is on the side of its grouping cell connection.

This simple model accounts for three aspects of the results described above. It explains how the system uses

d.8. Spike synchronization between neurons is specific to BOS selective pairs [28,34]

Using multi-electrode recordings, pairs of neurons with separate RFs were studied, comparing a condition in which both neurons are stimulated by edges of the same figure with a condition in which each neuron is stimulated by an edge of a different figure (with locally identical stimulation). Cross-correlation analysis of the spike trains of 32 pairs of neurons showed that cell pairs in which both members are BOS selective show significantly higher synchronization (mostly within 20ms) than other pairs. The difference related to BOS selectivity was stronger than the difference between 'feature binding' (edges belong to same figure) and 'non-binding' (edges belong to different figures). Our interpretation is that synchronization occurs between cells that participate in a network for context integration. Thus, synchronization reflects a specific connectivity, not a state of the system as proposed by the binding-by-synchrony hypothesis.

d.9. A computational model of figure-ground organization

A feedback model, as sketched above, was developed that reproduces the findings of neuronal BOS selectivity as well as perceptual observations of figure-ground organization. This model predicts firing rates and explains the mean values, as well as the time course of BOS signals [8]. Although we refer to this model many times in this proposal, the illustrations are simplifications and the discussion does not refer to the exact algorithm that was used. Specifically, we leave it open if opponent BOS cells interact by mutual inhibition. In the computational model, mutual inhibition between B cells was important because the G cell feedback acted by inhibiting the opponent B cell rather than by exciting the corresponding B cell. This was merely for computational simplicity, guaranteeing stability of the network. Some details of our results, for example the pattern of synchronization [34], suggest that a direct excitatory connection from G cell to B cell is more likely.

To be able to model also the spike synchronization between neurons (Section d.8), a spiking model was developed. This model is more realistic than the rate model. The algorithm models exact spike times and is also very efficient. It can simulate 10^5 neurons with more than 10^6 synapses approximately in real time. [29]

Research Design and Methods

Abbreviations: BOS – border ownership; RF – receptive field; cRF – classical receptive field

Three groups of experiments are proposed. They will use single-cell recording in awake behaving macaques to study (1) the mechanisms of visual context integration in border ownership coding, (2) the persistence of figure-ground organization in neuronal signals, and (3) the role of the figure-ground organization mechanisms in selective attention. We will concentrate on area V2, but study also area V1 in some experiments for comparison.

e.1. Study the mechanisms of visual context integration in border ownership selective neurons.

e.1.1. Purpose

BOS selectivity shows that neurons integrate the image context far beyond the classical receptive field. As a first step in understanding the underlying computations we need to know the spatial sensitivity distribution of the 'nonclassical' RF input in a representative population of single neurons. Knowing the spatial layout of the nonclassical input is crucial for distinguishing between two classes of models of figure-ground organization that are fundamentally different (see Progress Report Section d.3.2). As discussed below (Section e.3), the difference concerns not only the mechanism of organization proper, but also the possible mechanisms of selective attention.

e.1.2. Design

Two methods with factorial design, developed in the previous grant period, will be applied. These methods allow to measure nonlinear interactions of the extra-classical regions with the classical receptive field as well as interactions between extra-classical regions. The two methods are complementary. One uses fragmentation of figures, the other uses occlusion of critical features. The occluder method is suitable for displays in which localized features carry the figure-ground information, so that the occluders can be small.

We have designed a new method that is applicable to displays in which the global shape is the figural cue. It uses figures with edges with a localized luminance profile ('Cornsweet edges', *Fig. 2*). The interior of these 'Cornsweet figures' has the same luminance/color as the background, so that we can now use invisible occluders (patches of the background color) to switch contour segments on and off. With this method we can generate fragmented figures with arbitrary shapes and measure the influence of each fragment on the responses evoked by the central edge. The single features will also be tested in the absence of a central edge in the RF (cf. *Fig. 5*).

We will test single squares of different sizes (preliminary results), rectangles, and C-shaped figures (in which the BOS signal for the contour in the concave region will be studied). The idea of using these different shapes is that, because each figure can reveal sensitive regions only along its contour, the combined results of several tests will provide a more comprehensive picture. Each figure will be fragmented into 7-9 features (edges and corners) whose presentation will be varied in factorial manner. For the C-figure, which is composed of 15 edges and corners outside the cRF, pairs of symmetrical features will be bundled so as to reduce the number feature factors to 8. The features appear either on one side of the RF or the other (not on both at the same time). Thus, the feature factors are nested within side-of-figure. The sign of contrast of the edge in the classical RF is another factor (the sign of contrast of the variable features will always be consistent with that in the edge in the cRF). Thus, in total, we will vary 9-11 binary factors, resulting in 512-2048 stimulus conditions, each to be tested twice. We can test at least 6 conditions in a 3s fixation period. Thus, completion of a test will require a minimum of 171-683 behavioral trials.

e.1.3. Analysis

As in our previous studies, the responses will be analyzed with a linear regression model performed on square-root transformed spike counts. An important advantage of the design is that interactions can be measured not only between the remote features and the test edge in the cRF, but also between the remote features. Preliminary results showed that this analysis is feasible, at least to the level of 2nd order effects (corresponding to 3rd order if side of figure is counted), and produces interesting results.

e.2. Study persistence of visual organization.

e.2.1. Persistence in border ownership signals under static conditions

The following experiments are aimed at clarifying the mechanism of persistence. We will vary the priming stimulus and the conditions of the ambiguous phase.

Does the duration of the priming stimulus influence the time course of BOS signals in the persistence phase? In perception, the duration of visual aftereffects often depends on the duration of the adaptation period producing the aftereffect. Our preliminary data on persistence of BOS signals indicate that the duration of the figure presentation has little influence on persistence and decay during the following ambiguous edge presentation.

Design. We found that the decay is approximately exponential and thus can be described by a time constant. We will measure amplitude and time constant of decay of the BOS signal for various durations of figure presentation, from 14ms to 500ms.

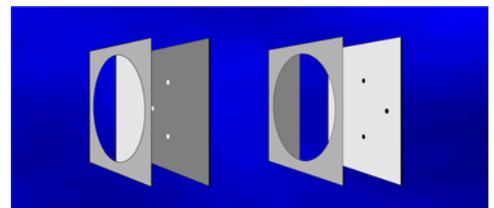
Does the persistence of the BOS signal depend on the type of priming?

We will measure and compare the decay of BOS signals produced by different cues: single figure (which was used in our experiments so far), overlap, stereoscopic disparity, and motion.

Perception of BOS seems to develop more slowly under some conditions than under others, and it is possible that the duration of persistence also varies with stimulus conditions. This would indicate that the persistence of BOS signals is not produced by a single mechanism. For example, it has been shown that the stereoscopic presentation of three dots (the minimum to define a plane) within an illusory figure can influence figure-ground perception dramatically. If the dots are presented with a ‘far’ disparity, the figure area turns into window through which a surface is seen in the background [35].

Similarly, when three dots with a ‘far’ disparity are presented on one side of our ambiguous edge display, that side becomes background and BOS is assigned to the opposite side (see *Fig. 13*). We will test such displays, presenting the stereoscopic dots outside the cRF, and measure BOS signals during and after the presentation of the dots. Preliminary results in a few cells show that the presentation of the dots does indeed produce a BOS signal at the central edge which rises more slowly than the signal in the case of a figure presentation. The signal also persists after the dots have disappeared. We need data from a larger population of cells for this and for other conditions of priming to measure and compare the time courses of the decay.

Fig. 13. The addition of just 3 dots with a ‘far’ disparity to a split-field display is sufficient to assign border ownership. Perspective illustration of how such displays are perceived. When the dots are on the left side, the central edge is assigned to the right, and when the dots are on the right side, the edge is assigned to the left.



Are there differences between neurons regarding persistence?

Our preliminary studies showed that of two neurons that are equally selective for BOS, one might show complete persistence, while the other might show no persistence at all. Thus, there seem to be substantial variations in the time constants of decay between cells. Once we have collected data with our basic persistence test from a larger population of neurons we will analyze the distribution of time constants and see if variations in amplitude and time constant of persistence can be related to the type of spiking (fast, regular, regular bursting) of the neurons. Finding such a correlation would be an important clue to identifying the neural substrate of the persistence. (A recent study shows that, in V4, the type of spiking is correlated with the degree of top-down attentional modulation [36]).

e.2.2. Transfer of border ownership signals across saccades

Perhaps the most important question regarding persistence is its invariance across eye movements. A short-term memory for figure-ground structure would be of little use if it were tied to retinal location. Our preliminary results indicated that the border ownership signal transferred across saccades. That is, a BOS signal appeared in neurons when the ambiguous edge was presented in their RF although the neurons had not been activated by the preceding figure display (Progress Report, *Fig. 11*). Thus, BOS information appeared in the cortical representation of a retinal location that had not represented BOS before.

We will explore the trans-saccadic persistence further. As explained in Progress Report Section d.5.7, the test sequence will begin with a square presented either beside the RF or centered on it, so that the RF is covered by a uniform stimulus region. The edge-selective cells that we will be studying will not be activated at this point. The square will then be replaced by the ambiguous edge display, the edge being aligned with an edge of the preceding square, for a brief interval. The fixation point is then moved so that a subsequent saccade brings the edge into the RF.

To explore the distance in visual space over which transfer occurs we will (1) vary the amplitude of the saccade; (2) measure transfer across several saccades.

Pilot experiments in two animals showed that the induced eye movements are reliable and accurate. The animals learn to anticipate the two possible displacements of the fixation point because they generally remain the same for a given neuron. As a result, the saccades are quite uniform.

e.2.3. Transfer of border ownership signals across object movements

Next, we ask whether the signal is translation invariant across object movement. From the engineering point of view it would be advantageous to keep BOS information if an object moves rather than compute it over and over again.

The experiment will be analogous the saccade experiment just described, but instead of moving the fixation point we will move the visual stimulus: a square is displayed with the test edge located beside the RF, the ambiguous edge is presented at the location of the test edge, and finally this edge is moved into the RF. We keep the fixation point still and move the stimulus. There are two variants of this experiment. In one, we will move only the edge; in the other, we will move the edge and the circular aperture. The latter is the exact analogue of the saccade test (e.2.2)

e.2.4. Is persistence of border ownership a product of attention?

Although the evidence shows that BOS signals emerge without the influence of attention [6], it is possible that attention plays a role in the persistence of the signal. The following experiment addresses this question.

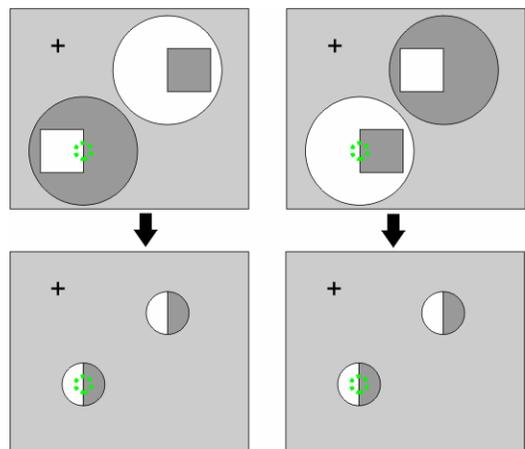


Fig. 14. Test for simultaneous persistence of BOS at two sites.

We will test persistence with 2 simultaneously presented figures that both switch to ambiguous edges (the figures initially appear in 2 large circular apertures which then contract, leaving only one edge of each figure exposed, *Fig. 14*). The monkey's task is to detect a small orientation change of one of two figures while maintaining gaze on a fixation point (electronic fixation window). The orientation change can occur at a random time during figure phase or ambiguous phase. The figure to be attended is specified at the beginning of each block of trials and varies between blocks. The results will show whether BOS persists at the attended as well as the unattended location. If it does, this would mean that persistence is a property of the organization stage; whatever is organized into a 'proto object' has persistence. If persistence is found only for the attended object, it would mean that it is the top-down process that keeps the activity alive; only the cells representing the attended object continue their activity into the ambiguous phase.

e.2.5. Persistence in contour signals for other attributes

To find persistence of activity in the visual cortex is new and surprising, especially under experimental conditions that do not involve a memory task, and for stimuli that the subject has been trained rather to ignore than to attend. We have not seen persistence of activity in other experiments in which visual stimuli were turned on and off. The difference is, of course, that in this case, the display goes blank (except for a fixation point) when stimulus is turned off. Under this condition, the responses of orientation selective neurons quickly return to the resting level (the black curve in *Fig. 10* shows the time course of the average response of a population of V2 neurons; note the abrupt drop of the firing rate in the blank period). In our persistence experiment, the neuron continues to be activated by a contrast edge in the RF. Thus, the question arises if the

ability to hold a level of activity is a property of certain neurons in V2 that might be observed not only for figure-ground organization but under other conditions as well.

Contrast and color

To address this question we will study the responses of V2 neurons to contrast changes of edge and bar stimuli. The display will begin with either a high or a low contrast, so as to produce different firing rates in the neuron under study, and then switch to an intermediate level of contrast which is the same in both cases. The question is if the activity in the latter phase is influenced by the level of activity in the foregoing phase, and if the effect is a positive aftereffect. A similar experiment will be performed in color selective neurons, changing the stimulus color from the preferred/anti-preferred color to neutral gray. We think it is unlikely that responses will persist under these conditions, but this needs to be shown.

Stereoscopic depth

We will perform a second experiment to test the question if persistence is specific to figure-ground organization. In this case we start the display with a split field made up of a stereoscopic edge in a circular window. The edge consists of a luminance step and a random-dot texture with different disparities on either side producing a step in depth [37]. After 0.5 s the texture will be made to fade gradually in one eye, leaving the depth ambiguous. The perceptual difference produced by the change is subtle, as the contrast edge remains, and there is still texture seen by one eye. For comparison, display sequences starting with a figure (as in the standard persistence test, but also with texture and disparity) will be included. V2 neurons with stereoscopic edge selectivity [5] will be tested. The question is again, will the level of activity in the initial, stereoscopic phase persist in the subsequent ambiguous phase.

The outcome of this experiment is open. (1) If persistence is specific to situations in which a figure is detected and represented as an object in front of a background, the prediction would be no persistence, because the split field shows only two surfaces at different depths behind a window, but no closed shape like a figure. (2) If persistence is a correlate of BOS coding in general, we would expect to see persistence, because the stereoscopic stimulus defines which surface is in front and which is in back (depth ordering), and the law is that the one in front owns the border. We have previously shown that about half of the cells that are selective for stereoscopic depth ordering are also BOS selective when tested with the side of a square; that is, they combine depth selectivity with sensitivity for global shape [3]. These cells, in a way, associate depth order at the edge with the presence of an occluding object on one side. Thus, a third possible result would be that these cells show persistence while the other stereo-edge selective cells do not show persistence. This would mean that persistence is specific to neurons involved in object representation.

e.3. Study the role of visual organization in selective attention.

e.3.1. Purpose

The aim of the third group of experiments is to further test our previous observation of a linkage between BOS and attention mechanisms. (We found that attentional modulation is often asymmetric about the RF and that the side of attentional enhancement tends to coincide with the preferred side of BOS of the neurons [6].) We will test a situation in which the task requires attention to an object whose center part is occluded by a second object. The question is whether the linkage holds up also in this more complicated situation or whether attentional selection can be dissociated from context integration for BOS.

Occlusion in the middle of an object is a particular challenge for a visual system as it has to identify separated features as belonging to the same object. This is certainly a problem that the brain has to be able to master if its owner lives in a cluttered environment, as for example the habitats of macaques. Studies on amodal completion and object-based attention have shown that the human visual system can deal with this kind of occlusion situation.

e.3.2. Predictions of two different models

The experiments to be described should also enable us to distinguish between the two fundamentally different neural mechanisms of context integration outlined in Progress Report Section d.3.2, the intra-cortical 'horizontal' propagation mechanism (A), and the grouping mechanism (B). We do not question the role of horizontal propagation mechanisms in context integration, which has been demonstrated in V1 [30]. Our goal is to clarify whether a grouping mechanism, as we have proposed, is necessary, or whether horizontal

propagation and spatial attention alone can account for the observed linkage between attentional modulation and BOS coding.

In principle, the two models of BOS selectivity sketched in *Fig. 3* and *Fig. 4* seem to be equivalent. In model A [24], the asymmetry of the attention influence can be explained by assuming that top-down attention enhances the effect of the lateral connections (cf. contour integration experiments in V1 [15,30]). The attention enhancement affects the region of the object to be attended. Because of the asymmetric connectivity, the influence of attention is asymmetric in the individual BOS neuron: the red neuron is facilitated only if an object to the right of its RF is attended, the green neuron only if an object to left is attended (*Fig. 3*). In model B [8], the asymmetry of the attention influence results because each BOS neuron is connected to a grouping cell on one side (*Fig. 4*).

e.3.3. Design

In each trial, two crossed bars are presented and, after a brief delay, a change occurs in one of them. The change can be either a small increase or decrease in length, or a small movement. The task of the monkey is to respond in different ways according to type of change, for example by saccading to the bar if its length changed, and somewhere else if the bar moved. Both types of change will involve the same movements of the two smaller sides of the bar, and either one will move in one direction or the other at random; for a bar movement, both move in phase, and for a length change, they move in antiphase. Thus, the task can only be performed correctly if the subject monitors both edges simultaneously. In a block of trials only one of the bars undergoes a change, and which of them changes will be specified by 'instruction trials' at the beginning of the block. Thus, the monkey knows which bar to attend.

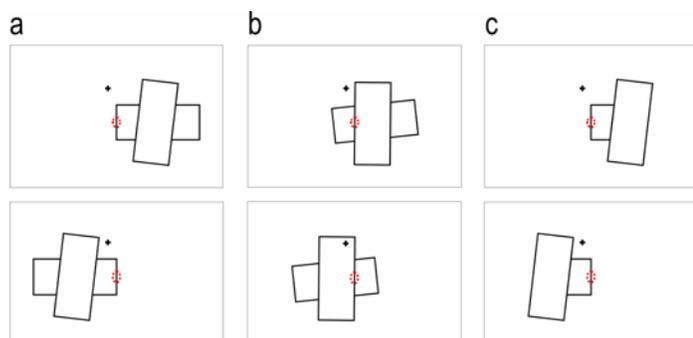


Fig. 15. Stimulus displays for testing grouping of fragmented objects

Fig. 15 shows schematically how the stimuli will be placed on the RF of the neuron under study. We will measure the BOS signal for the background bar (*Fig. 15a*) and for the foreground bar (*Fig. 15b*). The display of *Fig. 15c* will be used to measure if, in the case of the background bar, the BOS signal originates from the whole bar or only from the fragment at the RF (by comparing *a* and *c*). The orientation of the stimuli and their location relative to fixation will of course depend on the RF of the neuron.

There will be other control conditions not illustrated, such as testing the fragments of the occluded bar, and the contrast conditions (similar as in our transparency experiment [22], see *Fig. 6*). Also,

one monkey at least will also be trained for a similar experiment in which the task requires static shape discrimination [6] rather than discrimination of edge movements.

As in some of our previous attention experiments [6] animals will be trained to fixate a fixation spot (which will be controlled by eye movement recording) and to respond, as required by the task, by an eye movement. Thus, they have to make up their mind while fixating. The neural activity during the fixation period will be analyzed.

e.3.4. Interpretation of results

The experiment is similar to the overlapping figure experiment of our previous study [6] (Progress Report Section d.6) and thus we expect that the neuronal responses in V2 will be modulated by BOS and by attention.

The two models make different predictions for both, BOS and attentional modulation. In the horizontal propagation model, context enhancement cannot bridge the invisible portion of the background bar if the width of the occluding bar exceeds a limit (cf. Ref [30]). This width will be varied between 0.5--4 deg. The length of horizontal fibers is limited (in V1 the limit is about 3 mm [31], corresponding to less than a degree of visual angle in the foveal representation that we will study). Although signals can propagate over chains of neurons, this can occur only if all neurons along the chain are directly activated by the stimulus, that is, along the contours. This is because the horizontal signals are modulating the activity, but cannot create activation.

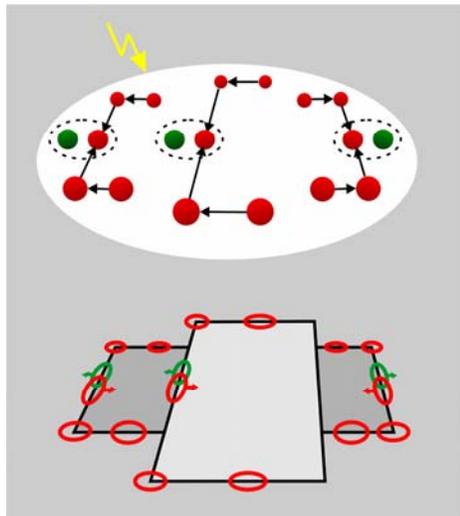


Fig. 16. Context integration and attentional modulation in the crossed-bar experiment, Model A

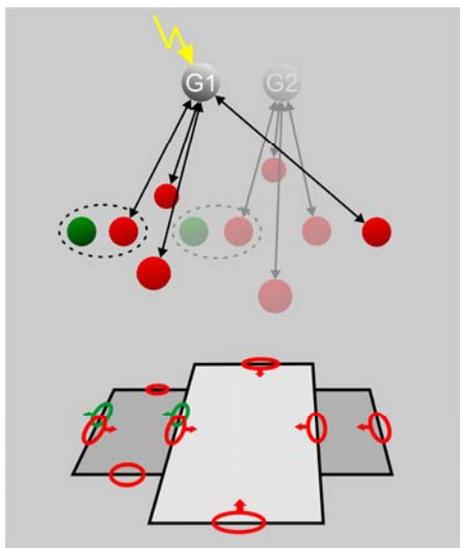


Fig. 17. Context integration and attentional modulation in the crossed-bar experiment, Model B.

The grouping cell model predicts context enhancement across the invisible portion because some grouping cells will sum edge signals from both ends of the bar. Connectedness is not required. Thus, model A predicts that the BOS signals should be equally strong in conditions *a* and *c* of Fig. 15, whereas model B predicts a reduction of the signal in *c* compared to *a*.

Also for the attention effect the predictions are different. In model A, attention enhances the entire region of the object to be attended, as indicated by the bright area in Fig. 16. This means that attentional enhancement should be observed irrespective of whether the foreground or the background bar is attended. Specifically, there can be no difference at the occluding edges (red and green cells in the center) because the model has no structure that would allow for a differential modulation. The only way to integrate the two fragments of the occluded bar would be to split the spotlight of attention and combine the selected information at a later stage.

In the grouping cell model, the features can be associated with two different pools of grouping cells, and each of these can be activated deliberately by top-down attention (Fig. 17). Thus, this model predicts attentional modulation in the representations of both foreground and background bars, with the sign of modulation depending on which bar is attended.

We will learn from this experiment if representations of fragmented objects can be formed at the level of V2, or if this occurs only at higher levels in the system. This will answer the question if the network of facilitatory horizontal connections and a spatial attention filter are sufficient to explain the interaction of figure-ground organization with attentional selection observed in V2.

e.4. Conclusion

The proposed experiments will further our understanding of the intermediate stage of visual processing, that, we hypothesize, serves as an interface between the local feature representation of V1 and top-down processes such as volitional selective attention. We specifically address the question if figure-ground organization and attention effects in V2 are based on the horizontal connectivity within V2, which would be analogous to contour integration mechanisms that have been demonstrated in V1, or have a principally different design that involves a dedicated grouping mechanism and cortical areas beyond V2. We have preliminary evidence arguing against the horizontal connectivity scheme, coming from latency measurements on the one hand, and from an experiment with fragmented figures on the other.

We propose three lines of approach, studies of the spatial input filters in BOS selectivity, studies of the persistence of BOS signals, and studies of the influence of top-down attention. These are conceptually quite different, but complementary. Specifically, evidence for short-term storage in the figure-ground representation would be strong support for our thesis that organization mechanisms in V2 provide a structure for cognitive processes. Without a storage mechanism it would be difficult to imagine how the visual structure created by the organization mechanisms could be accessed by attention (which also modulates the activity) without wiping out this structure. In this context, the preliminary results showing transfer of BOS signals across saccades are particularly exciting.

We are also planning to carry out modeling studies in parallel, under separate funding. The collaboration with the computational neuroscience lab of Dr. Ernst Niebur has been extremely helpful during the report period of

this grant in clarifying concepts and designing experiments. The proposed studies of the spatial layout of the extra-classical RF input will provide important basic information for the modeling. The other aspects of BOS coding, persistence and link to attention, impose important constraints on the model. It is very important to combine these different aspects in a comprehensive model. Putting all the diverse findings together and understanding the whole is challenge, but it does not seem impossible.

e.5. Procedures

Our *general methods* are standard in laboratories studying single neuron activity in behaving monkeys. The details have been described.[5,6,8] The animals are prepared by implanting, under general anesthesia, first three small posts for head fixation, and later two recording chambers (one over each hemisphere). Behavioral motivation is induced by controlling fluid intake and using small amounts of juice or water trial by trial to reward correct responses. Delays upon errors are used for negative reinforcement. Single-neuron activity is recorded extracellularly with epoxy-insulated tungsten or glass-insulated Pt-Ir microelectrodes inserted through the dura mater within small (3-5 mm) trephinations. The areas of recording are identified by their retinotopic organization and by histological reconstruction of the recording sites in brains slices stained for cytochrome oxidase.[5] Spike times are recorded at 10 kHz time resolution. Eye movements are recorded using an infra-red video based system (Iscan ETL-200) at 60Hz with a spatial resolution of 5120 (H) and 2560 (V). One eye is imaged through a hot mirror placing the camera on the axis of fixation. We found that this design reduced signal distortion and errors due to pupil contractions, compared to the usual off-axis camera method. The optical magnification in our system results in a resolution of the pupil position signal of 0.03 deg visual angle in the horizontal and 0.06 deg in the vertical. Noise and drifts of the signal of course reduce the accuracy. We have experience in experiments with stereoscopic stimuli.

Design and analysis. In the experiments involving several stimulus and behavioral parameters factorial design is used and responses are analyzed by general linear models on square-root transformed spike counts. The time intervals for spike counting are defined on the basis of peri-stimulus time histograms and averaged eye position signals.

e.6. Timetable

The experiments under Aim 1 are under way and would take about 2 more years of the new grant period. Those of Aims 2 and 3 will take about 4 years each. Although most of the experiments of Aim 2 only require the fixation task, there are many conditions and uncertainties about the outcome that might require modifications of the design. One experiment under Aim 2 and all experiments under Aim 3 involve a task that demands a perceptual judgment about a stimulus that is not directly viewed, and the monkey must decide before making an eye movement. Training this is difficult and it takes about a year for an animal before the recording can start. Thus, in my experience, it will take 5 years to complete these two aims.

Progress Report Publication List

Peer-reviewed papers:

Craft E, Schuetze H, Niebur E, von der Heydt R (2007) A neural model of figure-ground organization. *J Neurophysiol* 97: 4310-4326.

<http://jn.physiology.org/cgi/content/abstract/97/6/4310>

Qiu FT, Sugihara T, von der Heydt R (2007) Figure-ground mechanisms provide structure for selective attention. *Nat Neurosci* doi:10.1038/nn1989

<http://www.nature.com/neuro/journal/v10/n11/abs/nn1989.html>

Qiu FT, von der Heydt R (2007) Neural representation of transparent overlay. *Nat Neurosci* 10: 283-284.

<http://www.nature.com/neuro/journal/v10/n3/abs/nn1853.html>

von der Heydt R, Pierson R (2006) Dissociation of color and figure-ground effects in the watercolor illusion. *Spat Vis* 19: 323-340.

Qiu FT, von der Heydt R (2005) Figure and ground in the visual cortex: V2 combines stereoscopic cues with Gestalt rules. *Neuron* 47: 155-166.

<http://download.neuron.org/pdfs/0896-6273/PIIS0896627305004757.pdf>

von der Heydt R, Macuda TJ, Qiu FT (2005) Border-ownership dependent tilt aftereffect. *J Opt Soc Am (A)* 22: 2222-2229.

<http://josaa.osa.org/ViewMedia.cfm?id=85413&seq=0>

Peer-reviewed published abstracts:

Niebur E, Craft E, Schütze H, von der Heydt R (2006) A computational model of figure-ground organization. *Perception* 35 supplement: 122-123.

von der Heydt R, Pierson R (2005) Dissociation of color and figure-ground effects in the watercolor illusion. *J Vision* 5: 500a.

Craft E, Schuetze H, Niebur E, von der Heydt R (2004) A physiologically inspired model of border ownership assignment. *J Vision* 4/8: 728.

Sugihara T, Qiu FT, von der Heydt R (2004) Figure-ground organization and attention modulation in neurons of monkey area V2. *J Vision* 4/8: 197.

von der Heydt R, Sugihara T, Qiu FT (2004) Border ownership and attentional modulation in neurons of the visual cortex. *Perception* supplement 33: 46.

Vertebrate Animals

A. Description of the proposed use of animals.

1. Identification of species and number. *Macaca mulatta*, 2 per year. I plan experiments in 1-3 monkeys per year that have been trained in visual discrimination tasks. The training takes several months. I know from previous experience that this many animals are required to produce the data I need. A single study requires data from 2-300 neurons. Each animal yields useful recordings from 100 to 200 neurons, depending on a numbers of factors.

2i. Purpose of the study. The experiments are directed to an analysis of the neural mechanisms underlying the perception of form, color, and depth in the visual cortex. These studies will contribute to our knowledge of visual processing and cortical function in general, and will also lead to a better understanding of central visual disorders in humans.

2ii. Rationale for using the animals. The purpose of the study is to understand the mechanism of visual perception in the human at the level of the neural signals. Short of single cell recordings from the brains of humans while they perform a visual discrimination task, there is no way to study the brain mechanisms that are the object of this research without recording from the brains of alert animals.

2iii. Appropriateness of species. I need an animal with a visual system like that of humans, one that can be trained to perform a visual discrimination task, and one that has been studied extensively. Only the rhesus monkey fits those specifications.

2iv. Veterinary care. Veterinary care is provided by the Department of Comparative Medicine of the Johns Hopkins University.

3. Experimental protocol.

3i. Pretreatment. Each monkey is trained for about 3-4 months. Operant conditioning procedures are used and the animal is rewarded with water or fruit juice. The monkey learns to fixate his eyes on a small target for several seconds, repeatedly and effortlessly, and to respond to visual stimuli either by moving a lever, or by making an appropriate eye movement (eye movement responses are registered by means of video-based eye tracking). Training periods are gradually increased from « hr to about 4 hrs daily, with breaks during which the animal is fed dry fruit or nuts. During the training period, and the subsequent recording sessions, the animal's fluid intake is carefully controlled and monitored. Each animal works at a behavioral task for periods of 2-3 weeks, from Monday through Friday or Saturday, and gets at least 35ml fluid per kg body weight per day. If it gets less than the predetermined volume, it is given sufficient water and/or fruit to make up that amount. If it works for more, it is allowed to do so. In addition to this minimum daily intake of water we feed fruit. On Saturday, the animal is allowed as much water as it likes. On Sunday, the water intake is reduced again so that it will work on Monday. The animal is monitored daily for signs of dehydration such as weight loss and constipation. The daily records of body weight are kept in each animal's log book. Periods of training alternate with vacations of 1 week or more in which the

animal gets free water and the normal alimentation. I have many years of experience with this training scheme and found that the animals stay healthy and gain weight.

Surgery. After the initial training, surgery is performed to attach to the skull head-holding posts and recording chambers to which the microdrive carrying the electrode is secured at the time of recording (one chamber over each cerebral hemisphere). The head post are implanted several months before the recording chambers. This is necessary because part of the training and behavioral testing involves recording of eye movements which can only be done when the animal's head is restrained. The time for recording is limited because the chamber implants often cause bone resorption and get leaky over time. Therefore, the chambers are installed only when the animal is ready for recording.

They include aseptic preparation of the surgical site on the animal (shaving the area, scrubbing with Povidine Iodine scrub, then alcohol, then Povidine Iodine solution; scrubbing is done in circular motion, moving outwards from center), sterilization of instruments and linens, hand scrubbing, and wearing surgical gloves, caps, masks and gowns. The animal is first sedated with ketamine hydrochloride (20 mg/kg body weight) and, after injection of atropine sulfate (0.1 mg), deeply anesthetized with sodium pentobarbital (25 mg/ kg). The operation lasts 2-3 hours during which time additional pentobarbital is occasionally required. Head holding posts and recording chambers are attached to the skull by means of small anchoring screws inserted into bone and/or acrylic bone cement. The recording chambers are closed with a sealing lid. After the surgery the animal is allowed to recover under continuous observation by the responsible investigator. A topical anesthetic (Xylocaine 2%) is infiltrated into margins of the wound. Buprenorphine hydrochloride (Buprenex Injectable) is used for postoperative analgesia (0.03 mg/kg injected intramuscularly every 12 hours for two days; if the animal then shows any signs of discomfort the treatment is continued). When the animal is sufficiently alert and has gained muscular control it is returned to the cage. 1-2 weeks after surgery the first recording period is started, as described below. On the first day, the animal is brought to the laboratory and anesthetized with ketamine (11mg/kg) and atropine (0.1 mg), and a small hole (3-5 mm diameter) is drilled into the skull within the recording chamber. This surgery is also made under aseptic conditions with sterilized instruments and linens. It lasts about 15 minutes. The animal recovers in the primate chair before being returned to its cage.

3ii. Experimental manipulations. Microelectrode recording is done 4-6 hours a day in the laboratory. The animal is taken from its cage to the laboratory and returned at the end of the recording session. We observe no evidence of discomfort in the animals. They quickly learn to move into the experimental apparatus in anticipation of the behavioral task and its associated rewards. During the session the monkey sits in a box-like primate chair with its head restrained by means of a skull attachment. It can otherwise move within the chair and assume a comfortable sitting posture. Microelectrodes are inserted into the brain through the intact dura mater and removed again after recording. Visual stimuli are presented while the monkey performs the behavioral task that it has learned and while we record electrical activity of single neurons in its visual cortex. After each recording session, dexamethasone (drops for ophthalmic use) is applied locally and the recording chamber is sealed.

3iii. Postprocedural care and medication. The same care and controls as described above (3i) for the training phase are applied after each recording session. In general, no special treatment is necessary. Occasionally, granular tissue is removed carefully from the dura. This is done under ketamine anesthesia as specified above using sterilized

instruments and linens. This procedure takes approximately 10 minutes. After this minor surgery the animal is observed continuously until it has regained full consciousness whereupon it is returned to its cage. Sometimes antibiotics ointments are applied on the wound margins to control infections, as indicated by a veterinarian.

3iv. Frequency of repeated experimental manipulations. Recording experiments, six days a week, for periods of 2-3 weeks. After a pause of one week or more, during which the animal is kept under normal conditions of alimentation in its cage, another hole is drilled and recording started again. This is repeated for up to 10 recording periods per animal.

4. Procedures designed to minimize discomfort and pain. None of the procedures excepting the surgical procedure described previously seem to cause the animal pain or discomfort. Indeed, it is common for the animal to come to the door of the cage so that it can be helped into the animal chair. We assume that it does so in anticipation of the behavioral task and the other activities in the laboratory. During the training and experimental period care is taken that the animal receives a sufficient amount of water. Each animal is trained by a single person to minimize the stress of human contact. During the training and experimentation periods the monkey is fed raisins, nuts, and fruits of various kinds by the people with whom it is working in order to make it more comfortable.

5. Method of euthanasia. Euthanasia is accomplished with an initial dose of ketamine (20 mg/kg, i.m.) followed by a large dose of intravenous sodium pentobarbital (50 mg/kg). This method is consistent with the recommendations of the Panel on Euthanasia of the American Veterinary Medical Association.

B. Alternatives. All of the procedures that might produce pain or distress are described above. I follow the recent literature and regularly attend scientific meetings, such as the Meeting of the Society for Neuroscience, with sessions on the use of animals in research in order to see where our methods can be improved.

C. Duplication. None of the experiments unnecessarily duplicates experiments. Among the checks and balances is the fact that each animal represents many man years of effort when the direct experimental time and indirect efforts (data analysis, development of methods and equipment, etc.) are added up. This factor as much as any other weeds out unnecessary duplication. To be sure, I follow the recent literature and regularly attend scientific meetings such as the Meeting of the Society for Neuroscience and the Meeting of the Vision Sciences Society.

Bibliography

1. Marr,D. *Vision. A computational investigation into the human representation and processing of visual information* Freeman, San Francisco (1982).
2. Qiu,F.T. & von der Heydt,R. Figure and ground in the visual cortex: V2 combines stereoscopic cues with Gestalt rules. *Neuron* 47, 155-166 (2005).
3. von der Heydt,R., Qiu,F.T. & He,Z.J. Neural mechanisms in border ownership assignment: motion parallax and gestalt cues. *J. Vision* 3/9, 666 (2003).
4. Zhou,H., Friedman,H.S. & von der Heydt,R. Coding of border ownership in monkey visual cortex. *J. Neurosci.* 20, 6594-6611 (2000).
5. von der Heydt,R., Zhou,H. & Friedman,H.S. Representation of stereoscopic edges in monkey visual cortex. *Vision Res.* 40, 1955-1967 (2000).
6. Qiu,F.T., Sugihara,T. & von der Heydt,R. Figure-ground mechanisms provide structure for selective attention. *Nat. Neurosci.* doi:10.1038/nn1989, (2007).
7. Sugihara,T., Qiu,F.T. & von der Heydt,R. Border-ownership coding in monkey area v2: dynamics of image context integration. *Soc. Neurosci. Abstr.* 29, 819.12 (2003).
8. Craft,E., Schuetze,H., Niebur,E. & von der Heydt,R. A neural model of figure-ground organization. *J. Neurophysiol.* 97, 4310-4326 (2007).
9. Angelucci,A. & Bullier,J. Reaching beyond the classical receptive field of V1 neurons: horizontal or feedback axons? *J. Physiol Paris* 97, 141-154 (2003).
10. von der Heydt,R., Macuda,T.J. & Qiu,F.T. Border-ownership dependent tilt aftereffect. *J. Opt. Soc. Am. (A)* 22, 2222-2229 (2005).
11. Friedman,H.S., Zhou,H. & von der Heydt,R. The coding of uniform color figures in monkey visual cortex. *J. Physiol. (Lond)* 548, 593-613 (2003).
12. Lamme,V.A.F. The neurophysiology of figure-ground segregation in primary visual cortex. *J. Neurosci.* 15, 1605-1615 (1995).
13. Zipser,K., Lamme,V.A.F. & Schiller,P.H. Contextual modulation in primary visual cortex. *J. Neurosci.* 16, 7376-7389 (1996).
14. Lee,T.S., Mumford,D., Romero,R. & Lamme,V.A.F. The role of the primary visual cortex in higher level vision. *Vision Res.* 38, 2429-2454 (1998).
15. Ito,M. & Gilbert,C.D. Attention modulates contextual influences in the primary visual cortex of alert monkeys. *Neuron* 22, 593-604 (1999).
16. Roelfsema,P.R., Lamme,V.A.F. & Spekreijse,H. Object-based attention in the primary visual cortex of the macaque monkey. *Nature* 395, 376-381 (1998).

17. Treue,S. & Maunsell,J.H. Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* 382, 539-541 (1996).
18. Super,H., Spekreijse,H. & Lamme,V.A.F. A neural correlate of working memory in the monkey primary visual cortex. *Science* 293, 120-124 (2001).
19. Fuster,J.M. Network memory. *Trends Neurosci.* 20, 451-459 (1997).
20. Zhang,N.R., von der Heydt,R. & Qiu,F.T. A reverse correlation method for studying the neural mechanisms of visual context integration in border ownership assignment. *Soc. Neurosci. Abstr.* (2006).
21. Zhang,N.R. & von der Heydt,R. The contribution of T-junctions and L-junction to neural border ownership signals. *Soc. Neurosci. Abstr.* 506.12/NN19 (2007).
22. Qiu,F.T. & von der Heydt,R. Neural representation of transparent overlay. *Nat. Neurosci.* 10, 283-284 (2007).
23. Schuetze,H., Niebur,E. & von der Heydt,R. Modeling cortical mechanisms of border ownership coding. *J. Vision* 3/9, 114 (2003).
24. Zhaoping,L. Border ownership from intracortical interactions in visual area V2. *Neuron* 47, 147-153 (2005).
25. O'Herron,P.J. & von der Heydt,R. Onset, persistence and reset of border ownership signals. *Soc. Neurosci. Abstr.* (2006).
26. von der Heydt,R. & Pierson,R. Dissociation of color and figure-ground effects in the watercolor illusion. *Spat. Vis.* 19, 323-340 (2006).
27. Sugihara,T., Qiu,F.T. & von der Heydt,R. Border-ownership coding in monkey area V2: dynamics of image context integration. *Soc. Neurosci. Abstr.* 29, 819.12 (2003).
28. Qiu,F.T. & von der Heydt,R. Neural selectivity for three-dimensional shape of edges. *Journal of Physiology-London* (subm) (2007).
29. von der Heydt,R. & Qiu,F.T. Stereoscopic mechanisms for structural depth in macaque visual cortex. *Journal of Physiology-London* (submitted) (2007).
30. Dong,Y., von der Heydt,R. & Niebur,E. Synchrony and the binding problem in macaque visual cortex. *Soc. Neurosci. Abstr.* (2006).
31. Mihalas,S., Dong,Y., von der Heydt,R. & Niebur,E. A spiking neuronal model for border ownership assignment. *Soc. Neurosci. Abstr.* 394.18/JJ27 (2007).
32. Gilbert,C.D. & Sigman,M. Brain states: top-down influences in sensory processing. *Neuron* 54, 677-696 (2007).
33. Angelucci,A. *et al.* Circuits for local and global signal integration in primary visual cortex. *J. Neurosci.* 22, 8633-8646 (2002).

34. Nakayama,K., Shimojo,S. & Silverman,G.H. Stereoscopic depth: its relation to image segmentation, grouping, and the recognition of occluded objects. *Perception* 18, 55-68 (1989).
35. Goldberg,M.E., Bisley,J.W., Powell,K.D. & Gottlieb,J. Saccades, salience and attention: the role of the lateral intraparietal area in visual behavior. *Prog. Brain Res.* 155PB, 157-175 (2006).
36. Dong,Y., Mihalas,S., Qiu,F.T., von der Heydt,R. & Niebur,E. Synchrony and the binding problem in macaque visual cortex. *J. Vision* (under review) (2007).
37. Takeichi,H., Watanabe,T. & Shimojo,S. Illusory occluding contours and surface formation by depth propagation. *Perception* 21, 177-184 (1992).
38. Mitchell,J.F., Sundberg,K.A. & Reynolds,J.H. Differential attention-dependent response modulation across cell classes in macaque visual area V4. *Neuron* 55, 131-141 (2007).
39. Julesz,B. Binocular depth perception of computer-generated patterns. *Bell System Technical Journal* 39, 1125-1161 (1960).

PHS 398 Checklist

OMB Number: 0925-0001

Expiration Date: 9/30/2007

1. Application Type:

From SF 424 (R&R) Cover Page. The responses provided on the R&R cover page are repeated here for your reference, as you answer the questions that are specific to the PHS398.

* Type of Application:

New Resubmission Renewal Continuation Revision

Federal Identifier:

2. Change of Investigator / Change of Institution Questions

Change of principal investigator / program director

Name of former principal investigator / program director:

Prefix:

* First Name:

Middle Name:

* Last Name:

Suffix:

Change of Grantee Institution

* Name of former institution:

3. Inventions and Patents (For renewal applications only)

* Inventions and Patents: Yes No

If the answer is "Yes" then please answer the following:

* Previously Reported: Yes No

4. * Program Income

Is program income anticipated during the periods for which the grant support is requested?

Yes No

If you checked "yes" above (indicating that program income is anticipated), then use the format below to reflect the amount and source(s). Otherwise, leave this section blank.

*Budget Period *Anticipated Amount (\$)

*Source(s)

--	--	--

--	--	--

--	--	--

--	--	--

--	--	--

5. Assurances/Certifications (see instructions)

In agreeing to the assurances/certification section 18 on the SF424 (R&R) form, the authorized organizational representative agrees to comply with the policies, assurances and/or certifications listed in the agency's application guide, when applicable. Descriptions of individual assurances/certifications are provided at: <http://grants.nih.gov/grants/funding/424>

If unable to certify compliance, where applicable, provide an explanation and attach below.

Explanation:

Attachments

CertificationExplanation_attDataGroup0

File Name

Mime Type