中国科学: 生命科学 2014 年 第 44 卷 第 5 期: 450 ~ 462
SCIENTIA SINICA Vitae www.scichina.com life.scichina.com
《中国科学》杂志社
SCIENCE CHINA PRESS

评 述

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: 2013-11-08; : 2014-02-14
(: 31230029) (: 2011CBA00400, 2010CB833903)
doi: 10.1360/052013-314

摘要 ,
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关键词

, ,
, . Parkes [5]
(crowding)[1]. , Gabor ,
. , Gabor
, [2,3]; Gabor . Greenwood [6]
, [4]. ,
1923 , Korte : “ ,
, , .
, ‘ ,
”[2]. .
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引用格式: , , . . : , 2014, 44: 450–462
Fan Z Z, Fang F, Chen J. Neural mechanisms of visual crowding effect. SCIENTIA SINICA Vitae, 2014, 44: 450–462, doi: 10.1360/052013-314

[7,8],

. , ,

[9~16].

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2007 , (*Journal of vision*)

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1.1

1 .

, R (target), S Z (flanker),

(eccentricity),

.

(critical spacing)

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; ( )

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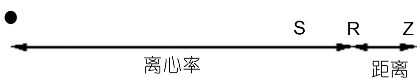
1.2

[17],

,

[3] [18~21]

[22] [6] [23,24]



1

[25] [26]. ,

[17] [27,28]

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,

,

(ordinary masking) (lateral interaction)

(surround suppression) .

,

.

. Pelli [29] ,

, .

,

[21,29],

[30]. Kooi [31] ,

, . Levi [32]

,

. Petrov [33] , ,

(inner-outer anisotropy).

, Whitney Levi[1]

6 ,

: ( )

; ( )

,

; ( )

.

, , . Bouma[34,35]

,

0.4~0.5 ,

Bouma .

Bouma [17,25]; ( )

(anisotropy). ,

[36], , ,

. ,

[20]. ,

,

[37]. 2

;

( ) (inner-outer asymmetry),

2

;

,

[24,34,38]. 2 ,

;

( ) (temporal tuning).

, [39,40],

. ,

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Whitney Levi[1] 6

(diagnostic criteria), 6

. , ,

[41,42]. Petrov [33] ,

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2

, 2 : ( )

, .

,

[10,14,18,20,43~45]; ( )

,

[19,46~49].

,

[5,50]. [51]

(event-related potentials, ERPs) (functional magnetic resonance imaging, fMRI) ,

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2.1

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. Flom [52] ,

(Landolt C) ,

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, .

“ ”[3].

[4,53]. Motter Simoni[54]

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, .

[55]. , ,

(V1: * (*Cebus albifrons*), * 1.5 1[56]; * , 3 1[57] ; V2: , 1.5 1[58]; V4: , 2 1[59]),

.

(long-range horizontal connections).

[60,61]. (*Catus*)

6~8 mm[62~65] .

, [66].
,
[31],
[63,67~69].
Orbach Wilson[70], Wilkinson [71] Parkes
[5] ,
(texture),
,
[29,36].

. ,

( ) (
) [4,31,52,72].

,
, [69].
, ,
[73],
.

. Blake [18] Ho
Cheung[20]
, ,
V1 .
, Millin [74] fMRI
. ,

(blood oxygen level dependent, BOLD)
, ,
,
. , V1
, , V1
; , (lateral
occipital complex, LOC), .
, ,
,
. V1
, Arman [75] Bi
[76] fMRI V1
, V2.
, V4

* , V4
2 1[59],
[36]; V4
0.5 , Bouma .
V4
[77,78], Chung [10]

,
. Liu [21] ,
1/4 ,

,
,
.
V2 V3,
, , V2 V3
.
, V1
. V1, V2 V3 ,
V4 LOC.

, ,
V1.
,
. Chakravarthi Cavanagh[79]
,
. , metacontrast
.
, metacontrast
,
[80~86];
(object substitution mask) ,
,
,
[87,88].
, metacontrast
,
, ,
LOC[89],
, LOC .
Ho Cheung[20] (contin-
uous flash suppression technique)

, , , . Ho
. Wallis Bex[90] “ Cheung[20]
”(adaptation-induced blindness) .
, ,
. , .
, , ,
. Chakravarthi Cavanagh[40]
, , ,
,
, Shin Tjan[91] Gabor 2 6~8 Hz , 6~8 Hz
, “ ”2 ,
. , . Petrov Meleshkevich[38] ,
Gabor , , ,
, ,
, . , Tripathy
; Gabor , Cavanagh[49] ,
“ ”
, ,
, ,
. , [93],
, . ,
“ ” . , ,
. Nador

2.2 [94] (steady state visually evoked potential, SSVEP)
,
; . 2 Gabor 36 Gabor
. , ,
1996 , He [19] , ,
( ) ( );
, , Gabor,
. ( ).
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, , ;
[92]. 2 22 , ,
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, , .
. He [19] ,
Blake [18] , Blake [18] , He , ,
[19] . Fischer [95] ,
, , Gabor Gabor , Gabor

? . h

(drift),
. ,

, ,
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. Yeh [96] ,
. Faivre [97]
Faivre Kouider[98] ,

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( ) . ,
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, .
(lateral interaction) ,
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[9,119~124].
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Chung[9] 8 3
, 6000 .
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34% 64%,
(3),
. , Hussain
[121] ,
, ,
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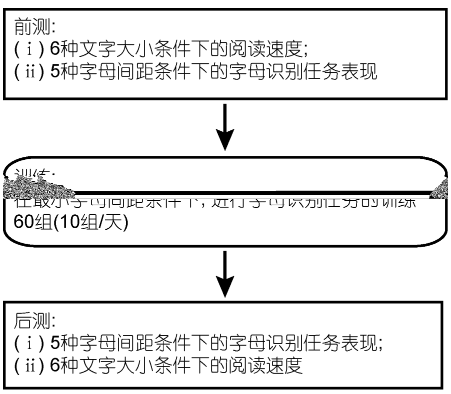
Huckauf Nazir[120] ,



3 Chung[9]

Maniglia [123] ,
Gabor Gabor ,
Gabor . ,
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,
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Huang Watanabe[119]
10° . 6
, ,
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, ,
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, ,
.
Sun [124] (ideal observer analysis) ,
. , ,
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, 2 ,
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(perceptual window) ,
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. .
[51] . ,
. (vision-for-perception)
(vision-for-action)

5

[128]. Chen [129]
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, ;
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, , [23,24] ,
[26] [25] [97] . ,
[97,98] . ,

, , .
, . , ,
, , : ( )
. , [51] (,),
, V1 , ? ( )
, ?
, . ? ( )
, . , ,
, ? ( ) ,
, ?
. ( ) ,
Harrison [125~127] ?
, , ,
, (ERPs)
[126]. , (fMRI) ,
( ) (transcranial magnetic stimulation, TMS)
, . ,
, ,
. .

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1 Whitney D, Levi D M. Visual crowding: a fundamental limit on conscious perception and object recognition. Trends Cogn Sci, 2011, 15: 160–168

2 Levi D M. Crowding—an essential bottleneck for object recognition: a mini-review. Vision Res, 2008, 48: 635–654

3 Levi D M, Waugh S J. Spatial scale shifts in peripheral vernier acuity. Vision Res, 1994, 34: 2215–2238

4 Levi D M, Klein S A, Aitsebaomo A P. Vernier acuity, crowding and cortical magnification. Vision Res, 1985, 25: 963–977
5 Parkes L, Lund J, Angelucci A, et al. Compulsory averaging of crowded orientation signals in human vision. Nat Neurosci, 2001, 4: 739–744
6 Greenwood J A, Bex P J, Dakin S C. Positional averaging explains crowding with letter-like stimuli. Proc Natl Acad Sci USA, 2009, 106: 13130–13135
7 Alvarez G A. Representing multiple objects as an ensemble enhances visual cognition. Trends Cogn Sci, 2011, 15: 122–131
8 Joo S J, Boynton G M, Murray S O. Long-range, pattern-dependent contextual effects in early human visual cortex. Curr Biol, 2012, 22: 781–786
9 Chung S T. Learning to identify crowded letters: does it improve reading speed? Vision Res, 2007, 47: 3150–3159
10 Chung S T, Li R W, Levi D M. Crowding between first- and second-order letters in amblyopia. Vision Res, 2008, 48: 788–798
11 Chung S T, Mansfield J S, Legge G E. Psychophysics of reading. XVIII. The effect of print size on reading speed in normal peripheral vision. Vision Res, 1998, 38: 2949–2962
12 Pelli D G, Tillman K A, Freeman J, et al. Crowding and eccentricity determine reading rate. J Vision, 2007, 7: 20
13 Williamson K, Scolari M, Jeong S, et al. Experience-dependent changes in the topography of visual crowding. J Vision, 2009, 9: 15
14 Yu D, Akau M M, Chung S T. The mechanism of word crowding. Vision Res, 2012, 52: 61–69
15 Zhang J Y, Zhang T, Xue F, et al. Legibility variations of Chinese characters and implications for visual acuity measurement in Chinese reading population. Invest Ophthalmol Vis Sci, 2007, 48: 2383–2390
16 Zhang J Y, Zhang T, Xue F, et al. Legibility of Chinese characters in peripheral vision and the top-down influences on crowding. Vision Res, 2009, 49: 44–53
17 van den Berg R, Roerdink J B, Cornelissen F W. On the generality of crowding: visual crowding in size, saturation, and hue compared to orientation. J Vision, 2007, 7: 14
18 Blake R, Tadin D, Sobel K V, et al. Strength of early visual adaptation depends on visual awareness. Proc Natl Acad Sci USA, 2006, 103: 4783–4788
19 He S, Cavanagh P, Intriligator J. Attentional resolution and the locus of visual awareness. Nature, 1996, 383: 334–337
20 Ho C, Cheung S H. Crowding by invisible flankers. PLoS One, 2011, 6: e28814
21 Liu T, Jiang Y, Sun X, et al. Reduction of the crowding effect in spatially adjacent but cortically remote visual stimuli. Curr Biol, 2009, 19: 127–132
22 Westheimer G, Truong T T. Target crowding in foveal and peripheral stereoacuity. Am J Optom Physiol Opt, 1988, 65: 395–399
23 Farzin F, Rivera S M, Whitney D. Holistic crowding of Mooney faces. J Vision, 2009, 9: 18
24 Louie E G, Bressler D W, Whitney D. Holistic crowding: selective interference between configural representations of faces in crowded scenes. J Vision, 2007, 7: 24
25 Moutoussis K, Zeki S. Seeing invisible motion: a human FMRI study. Curr Biol, 2006, 16: 574–579
26 Ikeda H, Watanabe K, Cavanagh P. Crowding of biological motion stimuli. J Vision, 2013, 13: 20
27 Vidyasagar T R. Gating of neuronal responses in macaque primary visual cortex by an attentional spotlight. Neuroreport, 1998, 9: 1947–1952
28 Vlaskamp B N, Hooge I T. Crowding degrades saccadic search performance. Vision Res, 2006, 46: 417–425
29 Pelli D G, Palomares M, Majaj N J. Crowding is unlike ordinary masking: distinguishing feature integration from detection. J Vision, 2004, 4: 1136–1169
30 Thomas J P. Detection and identification: how are they related? J Opt Soc Am A, 1985, 2: 1457–1467
31 Kooi F L, Toet A, Tripathy S P, et al. The effect of similarity and duration on spatial interaction in peripheral vision. Spatial Vision, 1994, 8: 255–279
32 Levi D M, Hariharan S, Klein S A. Suppressive and facilitatory spatial interactions in peripheral vision: peripheral crowding is neither size invariant nor simple contrast masking. J Vision, 2002, 2: 167–177
33 Petrov Y, Popple A V, Mckee S P. Crowding and surround suppression: not to be confused. J Vision, 2007, 7: 12
34 Bouma H. Interaction effects in parafoveal letter recognition. Nature, 1970, 226: 177–178
35 Bouma H. Visual interference in the parafoveal recognition of initial and final letters of words. Vision Res, 1973, 13: 767–782
36 Toet A, Levi D M. The two-dimensional shape of spatial interaction zones in the parafovea. Vision Res, 1992, 32: 1349–1357
37 Feng C, Jiang Y, He S. Horizontal and vertical asymmetry in visual spatial crowding effects. J Vision, 2007, 7: 13
38 Petrov Y, Meleshkevich O. Locus of spatial attention determines inward-outward anisotropy in crowding. J Vision, 2011, 11: 1
39 Bex P J, Dakin S C, Simmers A J. The shape and size of crowding for moving targets. Vision Res, 2003, 43: 2895–2904
40 Chakravarthi R, Cavanagh P. Temporal properties of the polarity advantage effect in crowding. J Vision, 2007, 7: 11

41 Andriessen J J, Bouma H. Eccentric vision: adverse interactions between line segments. Vision Res, 1976, 16: 71–78
42 Levi D M, Carney T. The effect of flankers on three tasks in central, peripheral, and amblyopic vision. J Vision, 2011, 11: 10
43 Bernard J B, Chung S T. The dependence of crowding on flanker complexity and target-flanker similarity. J Vision, 2011, 11: 1
44 Chung S T, Tjan B S. Shift in spatial scale in identifying crowded letters. Vision Res, 2007, 47: 437–451
45 Nandy A S, Tjan B S. Saccade-confounded image statistics explain visual crowding. Nat Neurosci, 2012, 15: 463–469
46 Intriligator J, Cavanagh P. The spatial resolution of visual attention. Cogn Psychol, 2001, 43: 171–216
47 Leat S J, Li W, Epp K. Crowding in central and eccentric vision: the effects of contour interaction and attention. Invest Ophth

80 Alpern M. Metacontrast. J Opt Soc Am, 1953, 43: 648–657
81 Anbar S, Anbar D. Visual masking: a unified approach. Perception, 1982, 11: 427–439
82 Breitmeyer B G, Ganz L. Implications of sustained and transient channels for theories of visual pattern masking, saccadic suppression, and information processing. Psychol Rev, 1976, 83: 1–36
83 Bugmann G, Taylor J G. A model of visual backward masking. Biosystems, 2005, 79: 151–158
84 Macknik S L, Livingstone M S. Neuronal correlates of visibility and invisibility in the primate visual system. Nat Neurosci, 1998, 1: 144–149
85 Rolls E T, Tovee M J. Processing speed in the cerebral cortex and the neurophysiology of visual masking. Proc Biol Sci, 1994, 257: 9–15
86 Sperling G. A model for visual memory tasks. Hum Factors, 1963, 5: 19–31
87 Enns J T. Object substitution and its relation to other forms of visual masking. Vision Res, 2004, 44: 1321–1331
88 Tata M S. Attend to it now or lose it forever: selective attention, metacontrast masking, and object substitution. Percept Psychophys, 2002, 64: 1028–1038
89 Carlson T A, Rauschenberger R, Verstraten F A. No representation without awareness in the lateral occipital cortex. Psychol Sci, 2007, 18: 298–302
90 Wallis T S, Bex P J. Visual crowding is correlated with awareness. Curr Biol, 2011, 21: 254–258
91 Shin K, Tjan B S. Crowding with invisible flankers a reexamination. J Vision, 2013, 13: 578–578
92 He S, Cavanagh P, Intriligator J. Attentional resolution. Trends Cogn Sci, 1997, 1: 115–121
93 Mullen K T. The contrast sensitivity of human colour vision to red-green and blue-yellow chromatic gratings. J Physiol, 1985, 359: 381–400
94 Nador J, Petrov Y, Quian J. SSVEPs indicate that grouping limits resolving power of attention inducing crowding. J Vision, 2013, 13: 626–626
95 Fischer J, Spotswood N, Whitney D. The emergence of perceived position in the visual system. J Cogn Neurosci, 2011, 23: 119–136
96 Yeh S L, He S, Cavanagh P. Semantic priming from crowded words. Psychol Sci, 2012, 23: 608–616
97 Faivre N, Berthet V, Kouider S. Nonconscious influences from emotional faces: a comparison of visual crowding, masking, and continuous flash suppression. Front Psychol, 2012, 3: 129
98 Faivre N, Kouider S. Increased sensory evidence reverses nonconscious priming during crowding. J Vision, 2011, 11: 16
99 Freeman J, Donner T H, Heeger D J. Inter-area correlations in the ventral visual pathway reflect feature integration. J Vision, 2011, 11: 15
100 Freeman J, Pelli D G. An escape from crowding. J Vision, 2007, 7: 22
101 Nazir T A. Effects of lateral masking and spatial precueing on gap-resolution in central and peripheral vision. Vision Res, 1992, 32: 771–777
102 Scolari M, Kohnen A, Barton B, et al. Spatial attention, preview, and popout: which factors influence critical spacing in crowded displays? J Vision, 2007, 7: 7
103 Shiu L P, Pashler H. Spatial attention and vernier acuity. Vision Res, 1995, 35: 337–343
104 Felisberti F M, Zanker J M. Attention modulates perception of transparent motion. Vision Res, 2005, 45: 2587–2599
105 Huckauf A, Heller D. Spatial selection in peripheral letter recognition: in search of boundary conditions. Acta Psychol (Amst), 2002, 111: 101–123
106 Yeshurun Y, Rashal E. Precueing attention to the target location diminishes crowding and reduces the critical distance. J Vision, 2010, 10: 16
107 Balas B, Nakano L, Rosenholtz R. A summary-statistic representation in peripheral vision explains visual crowding. J Vision, 2009, 9: 13
108 Oliva A, Torralba A. The role of context in object recognition. Trends Cogn Sci, 2007, 11: 520–527
109 Clark V P, Fan S, Hillyard S A. Identification of early visual evoked potential generators by retinotopic and topographic analyses. Hum Brain Mapping, 1994, 2: 170–187
110 Di Russo F, Martínez A, Sereno M I, et al. Cortical sources of the early components of the visual evoked potential. Hum Brain Mapp, 2002, 15: 95–111
111 Martinez A, Anllo-Vento L, Sereno M I, et al. Involvement of striate and extrastriate visual cortical areas in spatial attention. Nat Neurosci, 1999, 2: 364–369
112 Fan Z, Fang F. Learning to discriminate crowded orientations. J Vision, 2013, 13: 565
113 Solomon J A, Felisberti F M, Morgan M J. Crowding and the tilt illusion: toward a unified account. J Vision, 2004, 4: 500–508
114 van den Berg R, Roerdink J B, Cornelissen F W. A neurophysiologically plausible population code model for feature integration explains visual crowding. PLoS Comput Biol, 2010, 6: e1000646
115 van den Berg R, Johnson A, Martinez Anton A, et al. Comparing crowding in human and ideal observers. J Vision, 2012, 12: 13

116 Karklin Y, Lewicki M S. Emergence of complex cell properties by learning to generalize in natural scenes. Nature, 2009, 457: 83–86
117 Sigman M, Cecchi G A, Gilbert C D, et al. On a common circle: natural scenes and Gestalt rules. Proc Natl Acad Sci USA, 2001, 98: 1935–1940
118 Deubel H, Schneider W X. Saccade target selection and object recognition: evidence for a common attentional mechanism. Vision Res, 1996, 36: 1827–1837
119 Huang T R, Watanabe T. Association of perceptual learning to reduce spatial crowding with shrinkage of receptive fields. J Vision, 2011, 11: 1006
120 Huckauf A, Nazir T A. How odgcrnwi becomes crowding: stimulus-specific learning reduces crowding. J Vision, 2007, 7: 18
121 Hussain Z, Webb B S, Astle A T, et al. Perceptual learning reduces crowding in amblyopia and in the normal periphery. J Neurosci, 2012, 32: 474–480
122 Le Dantec C C, Melton E E, Seitz A R. A triple dissociation between learning of target, distractors, and spatial contexts. J Vision, 2012, 12: 5
123 Maniglia M, Pavan A, Cuturi L F, et al. Reducing crowding by weakening inhibitory lateral interactions in the periphery with perceptual learning. PLoS One, 2011, 6: e25568
124 Sun G J, Chung S T, Tjan B S. Ideal observer analysis of crowding and the reduction of crowding through learning. J Vision, 2010, 10: 16
125 Harrison W, Remington R, Mattingley J. Visual crowding is altered during smooth pursuit eye movements. J Vision, 2013, 13: 581
126 Harrison W J, Mattingley J B, Remington R W. Eye movement targets are released from visual crowding. J Neurosci, 2013, 33: 2927–2933
127 Harrison W J, Retell J D, Remington R W, et al. Visual crowding at a distance during predictive remapping. Curr Biol, 2013, 23: 793–798
128 Bulakowski P F, Post R B, Whitney D. Visuomotor crowding: the resolution of grasping in cluttered scenes. Front Behav Neurosci, 2009, 3: 49
129 Chen J, Sperandio I, Goodale M A. The influence of crowding on grip scaling during grasping. J Vision, 2013, 13: 336

Neural Mechanisms of Visual Crowding Effect

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When a target is presented with nearby flankers in the peripheral visual field, it becomes difficult to be identified, which is a phenomenon termed crowding. Studying crowding not only facilitates understanding of object recognition, but also benefits the remedy of macular degeneration, amblyopia and dyslexia. Since the concept of crowding was put forward, researchers have studied it extensively and gained much knowledge. Here, we provide an overview of the advances in this research field, including the properties of crowding, the existing theories and computational models that were proposed to explain the underlying neural mechanisms of crowding and how to alleviate crowding with perceptual learning. Although there has been tremendous growth of this topic, controversies remain. Further studies with elaborate designs and advanced technologies are required to address these controversies.

visual crowding, neural mechanisms, computational models, perceptual learning

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