



评述

\*,  
 ,  
 , 100871;  
 - , 100871;  
 , 100871;  
 The Brain and Mind Institute, The University of Western Ontario, London N6A 5B7, Canada  
 \* , E-mail: chenjuan033@163.com

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

摘要

关键词

(crowding)<sup>[1]</sup>.

1923 , Korte

”[2]

Gabor

Gabor

Gabor

Greenwood

Parkes

[5]

[6]

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], [25] [26], [17] [27,28], [9~16] (ordinary masking) (lateral interaction) (surround suppression)

2007, (Journal of vision), Pelli [29],

[21,29], [30] Kooi [31],

1, Levi [32]

1.1, Petrov [33], (inner-outer anisotropy).

R (target), S Z, Whitney Levi<sup>[1]</sup>

(flanker), (eccentricity), 6 : ( ) ; ( )

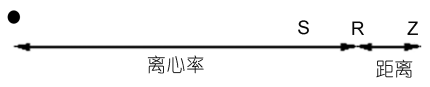
(critical spacing) ; ( )

: ( ) ; ( ) , Bouma<sup>[34,35]</sup>

0.4~0.5, Bouma

1.2, Bouma [17,25]; ( ) (anisotropy).

[3] [18~21] [22] [6] [23,24] [17], [36], [20],



1, [37], 2 (inner-outer asymmetry),

[5,50] [51]  
(event-related potentials, ERPs) (functional magnetic resonance imaging, fMRI)

2

2.1

[24,34,38] 2

Flom [52]  
(Landolt C)

( ) (temporal tuning).

[39,40]

Whitney Levi<sup>[1]</sup> 6  
(diagnostic criteria), 6

[41,42] Petrov [33]

[4,53] Motter Simoni<sup>[54]</sup>

[55]

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

2

(long-range horizontal

connections).  
[60,61] (*Catus*)

6~8 mm<sup>[62~65]</sup>

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

[66]. V4

2: 1<sup>[59]</sup>,  
 [36]; V4

Orbach<sup>[5]</sup>, Wilson<sup>[70]</sup>, Wilkinson<sup>[71]</sup>, Parkes<sup>[63,67-69]</sup> 0.5, Bouma<sup>[77,78]</sup>, V4, Chung<sup>[10]</sup>

(texture),

[29,36]. Liu<sup>[21]</sup> 1/4

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

V2 V3, V2 V3

[69]. V1

[73], V1, V2 V3, V4 LOC.

Cheung<sup>[20]</sup>, Blake<sup>[18]</sup>, Ho<sup>[18]</sup>, V1.

, Chakravarthi<sup>[79]</sup>, Cavanagh<sup>[79]</sup> metacontrast

(blood oxygen level dependent, BOLD), metacontrast

[80-86]. (object substitution mask)

; V1, V1 (lateral occipital complex, LOC), [87,88]. metacontrast

[76] fMRI, Arman<sup>[75]</sup>, Bi<sup>[75]</sup>, LOC<sup>[89]</sup>, LOC, V2. Ho<sup>[76]</sup>, Cheung<sup>[20]</sup> (continuous flash suppression technique)

Wallis Bex<sup>[90]</sup>  
”(adaptation-induced blindness)

“ Cheung<sup>[20]</sup>

Chakravarthi Cavanagh<sup>[40]</sup>

, Shin Tjan<sup>[91]</sup>

Gabor 2

6~8 Hz

6~8 Hz

“ ”2

. Petrov Meleshkevich<sup>[38]</sup>

Gabor

, Tripathy

; Gabor

Cavanagh<sup>[49]</sup>

“ ”

[93]

“ ”

. Nador

## 2.2

[94]

(steady state visually

evoked potential, SSVEP)

;

. 2

Gabor

36

Gabor

1996 , He

[19]

( )

( );

Gabor,

( ).

3

[92]

2

22

He [19]

Blake [18]

, Blake [18]

, He

. Fischer [95]

[19]

Gabor

Gabor

Gabor

(drift),

, , .

. Yeh <sup>[96]</sup> ,  
. Faivre <sup>[97]</sup>

Faivre Kouider<sup>[98]</sup> ,

. ,  
.

:

---

,

,

,

.

,

( )

(lateral interaction)

Maniglia [123]  
Gabor Gabor  
Gabor

4

[9,119-124]

Huang Watanabe [119]  
10° 6

Chung [9] 8 3  
6000

34% 64%,  
( 3),

[121]

Hussain

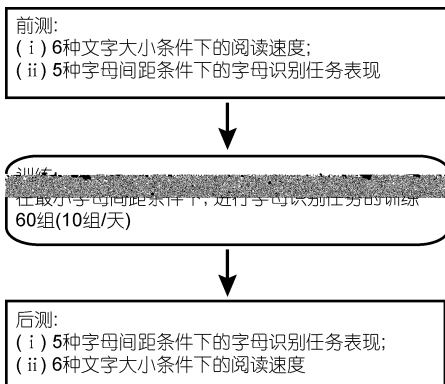
Sun [124] (ideal observer  
analysis)

6

2

Huckauf Nazir [120]

(perceptual window)



3 Chung [9]



[51]

(vision-for-perception)

(vision-for-action)

5

[128]. Chen

[129]

[23,24]

[26]

[25]

[97]

[97,98]

[51]

V1

? ( )

(ERPs)

(fMRI)

(transcranial magnetic stimulation, TMS)

- 
- 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—implications for object recognition: a mini-review. Vision Res, 2008, 48: 635–654
  - 3 Levi D M, Waugh S. Visual crowding. 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 peripheral vision: the effect of interaction and distance. *Optom*, 2010, 71(4): 45–71

- 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 Martínez 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, Martínez 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 odgerwi 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

FAN ZhenZhi<sup>1</sup>, FANG Fang<sup>1,2,3</sup> & CHEN Juan<sup>4</sup>

*1 Key Laboratory of Machine Perception (Ministry of Education), Department of Psychology, Peking University, Beijing 100871, China;*

*2 Peking-Tsinghua Center for Life Sciences, Beijing 100871, China;*

*3 IDG/McGovern Institute for Brain Research, Peking University, Beijing 100871, China;*

*4 The Brain and Mind Institute, The University of Western Ontario, London N6A 5B7, Canada*

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**

10.1360/052013-314