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Recurrent Processing of Contour Integration in the Human Visual Cortex as Revealed By fMRI-Guided TMS

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Abstract

Contour integration is a fundamental visual process that allows us to perceive the shape of objects from fragmented information. We used fMRI-guided TMS to investigate the role of the human visual cortex in contour integration. We found that TMS to the primary visual cortex (V1) disrupted contour integration performance, and that this disruption was associated with increased activity in the visual cortex. These findings suggest that contour integration is a recurrent process that involves the visual cortex.

Key words: contour integration, fMRI, TMS, visual cortex, recurrent processing

Introduction

Contour integration is a fundamental visual process that allows us to perceive the shape of objects from fragmented information. This process is thought to involve the visual cortex, and recent work has shown that TMS to the visual cortex can disrupt contour integration performance (Brewer & Lau, 2017). This finding suggests that contour integration is a recurrent process that involves the visual cortex.

1. (1995; 2006).
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 1- 1
). , 4, 1
)
 k
 fi
 A (A 2002; 2002; 2003; 2006, 2008; 2007; 2013; 2013; 2014; 2016).
 k
 fi (2006; 2008;) k. 2011).
 () (A 2003; 2003; 2016).)
 fi 1
 (2014)
 1 4 k,
 4 1,
 k 4.)
 4
 k 1.
 (), fi
 (1/ 2) (3)
 k. 3
 k, 4
 () k. 2001; 2003),
 (k 2009; 2010; 2016)
 2008; 2009; 2014). ()
 1, 1/ 2 3
 4 (A)
 fi (A)
 90–110. 3 120–140.
 1/ 2, 2
 2, fi 2
 fi A 2
 2. fi fi
 1
 3 1/ 2. fi
 k

Materials and Methods

Experiment 1

Participants

(10. , 10 = 21, ; = 18–25)

k
 A.
 k

Stimuli and Aperture

k
 100} 3 (1997; 1997; 2007) A A (k, A)
 k. fi. (12.66° × 12.66°)

(k : 6.62 / , σ: 0.10°, : 100%). A. fi.

11
 ()
 fi () (1
 1A).

fi
 k. fi
 fi 0.86°

Procedure

1. 3 : 2
 fi. ()
 (2008; 2015).

1 3
 fi 1 3
 k.

fMRI Session

(1 3)
 ,
 k

fi
 fi ()
 (2005). A
 k.

fi. fi

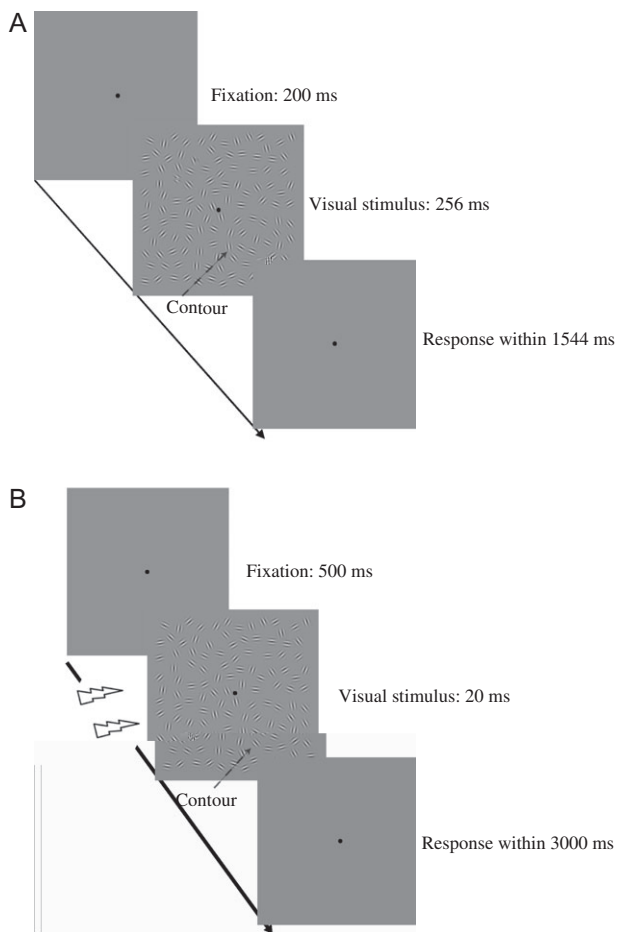


Figure 1. (A) Contour detection task. (B) pRF mapping task. **Data acquisition:** 20 trials per condition. (1) Contour detection task: Fixation (200 ms), Visual stimulus (256 ms), Response within 1544 ms. (2) pRF mapping task: Fixation (500 ms), Visual stimulus (20 ms), Response within 3000 ms. **pRF mapping task:** (1) 1, 2, 3; (2) 1, 2, 3.

5
: 1
(), 4 fl. k.
k. (100%)
(1).
8 k
308 . A fl. k. (10.35°, 100%)
4 , 32 k.
8 k
4 k k k 36 A
(: 2.14°)
(: 10.22°). 18 (: 1.07°). k.
(0°, 45°, 90°, 135°). A 8-
k. 12- k
k. fi
fi
Contour detection task:
k, 4
81 (.
2), k.
(8) (12) (-
fi) (-
(. 2002). A
1A, 200. fi ,
fi.
256.
fi.
k. k.
k.

TMS Sessions

2 3
1/ 2 3
1/ 2, 1
k.
2 1 (2011; ,
2005; 2012.) , 1
1 (1995;
2006; 2014).

TMS protocol:

2 ()
70- fi -8 (2A).
fi
(1/ 2 3)
(2; A
)
k.
2
60%

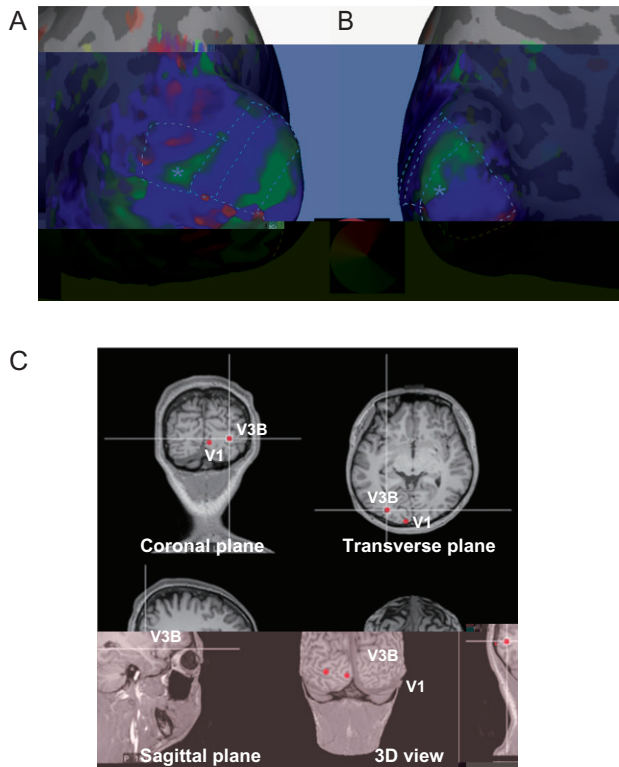


Figure 2. ... (A) 3 ... (B) 1. ... (A) ... (C) ... 1/ 2 ... 3

(... 2005; ... 2012). ... (60/80, 90/110, 120/140, 150/170. ... 1/ 2 ... 3

(... 2003; ... 2005) ... (... 2003). A.

Contour detection task with TMS:

1/ 2 ... 3 ... A ... 3 ... 1/ 2 ... 16 ... 2 ... (... : 60/80, 90/110, 120/140, 150/170. ; ...) ... 96 ... 12.

fi ... fi ... A ... 1B, ... 500. fi ... 20. ... k ... 3 ... fi ... k.

Data Analysis:

A ... (...) ... (A ... A), ... 3 ... fi ... (...) ... (... 2006, 2009; ... 2008; ... 2010; ... 2012; ... 2014). A.

fi ... fi ... t- ... (... 0). ... A, ... A ... fi ... t- ...

Experiment 2

Participants

(11 ... , 9 ... ; ... = 20-26 ...) ... 8 ... 1. ... A.

Stimuli and Aperture

2 ... 1, ... k. fi ... fi ... 2 ... fi.

Procedure

1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100

Psychophysics Session

1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100

fMRI Session

1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100

TMS Sessions

1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100

fMRI Data Analysis

Data preprocessing: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100

Results

Experiment 1

1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100

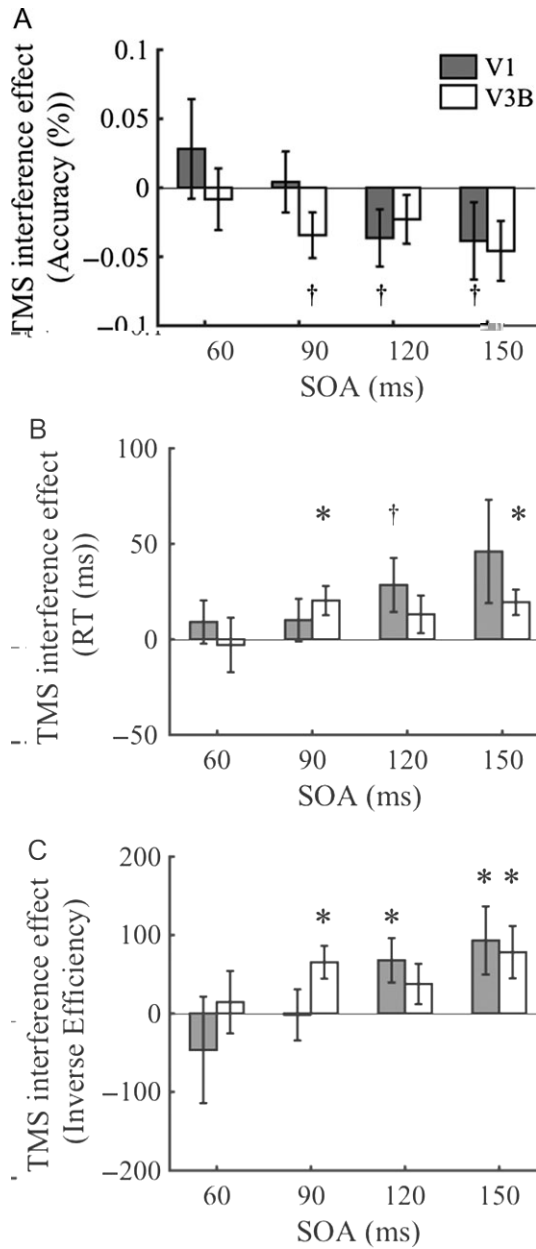


Figure 3. (A) TMS interference effect on accuracy (%), (B) TMS interference effect on RT (ms), (C) TMS interference effect on Inverse Efficiency. Error bars represent SEM. *P < 0.05; †P < 0.05.

(F(1,19) = 0.64, P = 0.42, $\eta_p^2 = 0.03$)
 (F(3,57) = 0.83, P = 0.48, $\eta_p^2 = 0.04$).
 (P > 0.1).
 (F(3,57) = 3.22, P < 0.05, $\eta_p^2 = 0.15$).
 (F(1,19) = 0.42, P = 0.52, $\eta_p^2 = 0.02$).
 (F(3,57) = 1.19, P = 0.31, $\eta_p^2 = 0.06$).
 (P = 0.05, = 0.0083).
 (t(19) = -1.76, P = 0.05, d = -0.39),
 (t(19) = 2.02, P = 0.03, d = 0.45),
 (t(19) = 2.40, P = 0.01, d = 0.54).
 (t(19) = -2.07, P = 0.03, d = -0.46),
 (t(19) = 2.66, P = 0.008, d = 0.60),
 (t(19) = 3.18, P = 0.002, d = 0.71).
 (t(19) = 1.46, P = 0.08, d = 0.33).
 (t(19) = -1.38, P = 0.09, d = -0.31); (t(19) = 1.70, P = 0.05, d = -0.38); (t(19) = 2.17, P = 0.02, d = 0.49); (t(19) = -2.12, P = 0.02, d = -0.47); (t(19) = 2.91, P = 0.004, d = 0.65); (t(19) = 2.37, P = 0.01, d = 0.53).
 (F(1,19) = 7.37, P = 0.014, $\eta_p^2 = .28$).

(F(1,19) = 0.64, P = 0.42, $\eta_p^2 = 0.03$)
 (F(3,57) = 0.83, P = 0.48, $\eta_p^2 = 0.04$).
 (P > 0.1).
 (F(3,57) = 3.22, P < 0.05, $\eta_p^2 = 0.15$).
 (F(1,19) = 0.42, P = 0.52, $\eta_p^2 = 0.02$).
 (F(3,57) = 1.19, P = 0.31, $\eta_p^2 = 0.06$).
 (P = 0.05, = 0.0083).
 (t(19) = -1.76, P = 0.05, d = -0.39),
 (t(19) = 2.02, P = 0.03, d = 0.45),
 (t(19) = 2.40, P = 0.01, d = 0.54).
 (t(19) = -2.07, P = 0.03, d = -0.46),
 (t(19) = 2.66, P = 0.008, d = 0.60),
 (t(19) = 3.18, P = 0.002, d = 0.71).
 (t(19) = 1.46, P = 0.08, d = 0.33).
 (t(19) = -1.38, P = 0.09, d = -0.31); (t(19) = 1.70, P = 0.05, d = -0.38); (t(19) = 2.17, P = 0.02, d = 0.49); (t(19) = -2.12, P = 0.02, d = -0.47); (t(19) = 2.91, P = 0.004, d = 0.65); (t(19) = 2.37, P = 0.01, d = 0.53).

Experiment 2

87.3 ± 2.8% (k = 120/140)
 89.1 ± 4.0%; (k = 90/110)
 85 ± 5.2% (k = 150/170)
 (F(1,19) = 7.37, P = 0.014, $\eta_p^2 = .28$).

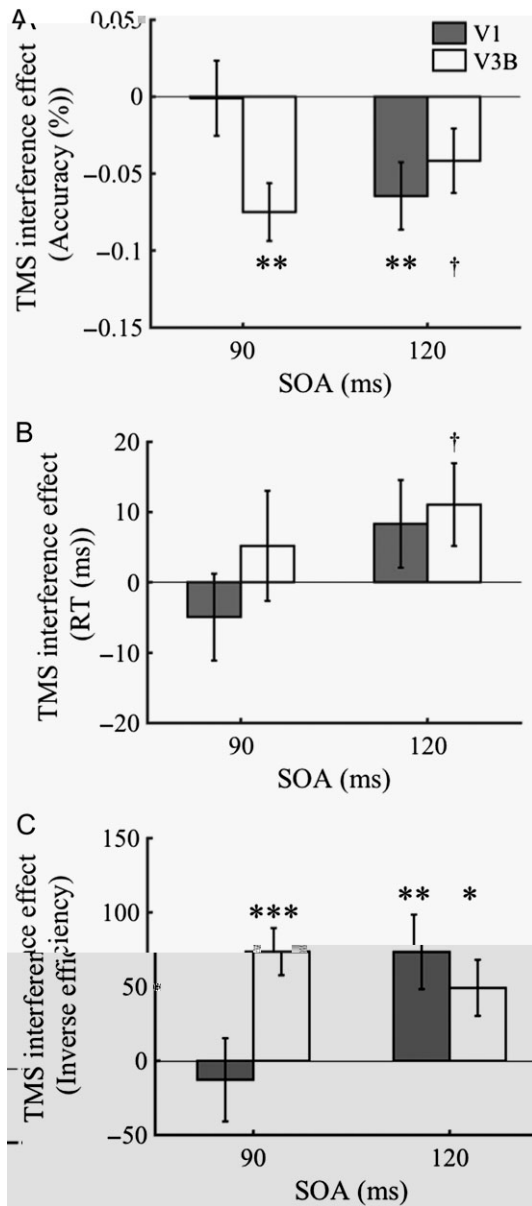


Figure 4. (A) TMS interference effect on accuracy (left), (B) TMS interference effect on RT (middle), and (C) TMS interference effect on inverse efficiency (right) for V1 (dark grey) and V3B (light grey) conditions at 90 ms and 120 ms SOA. Error bars represent standard error. Significance markers: ***P < 0.001, **P < 0.01, *P < 0.05, †P < 0.05.

($F(1,19) = 7.34, P = 0.01, \eta_p^2 = 0.28$).
 ($F(1,19) = 2.37, P = .14, \eta_p^2 = 0.11$) A ($F(1,19) = 3.07, P = 0.10, \eta_p^2 = 0.14$).
 ($F(1,19) = 7.67, P = 0.01, \eta_p^2 = 0.29$).
 ($F(1,19) = 1.23, P = 0.28, \eta_p^2 = 0.06$).

($t(19) = -2.95, P = 0.004, d = 0.66$)
 ($t(19) = 2.92, P = 0.004, d = 0.65$)
 ($t(19) = -3.99, P < 0.001, d = -0.89$)
 ($t(19) = 4.64, P < .001, d = 1.04$).

($t(19) = -1.99, P = 0.03, d = -0.45$)
 ($t(19) = -1.88, P = 0.04, d = 0.42$)
 ($t(19) = 2.60, P = 0.009, d = 0.58$)

($t(19) = 2.60, P = 0.009, d = 0.58$)

Discussion

(1995; 2006; 2013)

(1993) (A 2003; k 2009; 2010). (2014)

(3)

(1/2 3 4 k 3 90/110 3)

(1/2 3 90/110 3)

2015.
 (A) (.)
 35(2):731-738.
 2016.
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 9(4):
 594-600.
 A,
 2014.
 51:46-55.
 k } , fi . k 1997.
 17(6):
 2112-2127.
 } . 1997. 10:
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 A. 105(14):5644-5648.
 2002. fi .
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 801-813.
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 82(3):682-694.
 A 1999.
 1949:179-194.
 } , k , A 2014.
 24: 66- 67.
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 36(1):
 185-192.
 A. 2008. fi .
 39:647-660.
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 105:14298-14303.
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 A 1999.
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 9(9):195-207.
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 142(1):139-150.
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 78(2):389-402.
 A , } . 2016. fi .
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 97:105-119.
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 1157(1):167-176.
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15:843-856.
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 31(7):2488-2492.
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 2003.
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 2014. A .
 26(3):621-634.
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 2008. k
 57:442-451.
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 50:951-962.
 2015.
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 8637-8642.
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 9(6):740-742.
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 21(6):1204-1214.
 } , 2014.
 88:10-21.
 2008.
 99:
 2456-2469.
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 31(102(/ 2)-5 1790. A , 2001.
 292(5516):510-512.
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2006. A 29:203–227.
) k. 2011. A 73(8):
 2542–2572.
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 2012. ? } 33:652–665.
 k , A } ,
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 1854–1867.
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 69:146–156.
 A, 2005. (1)
 8(2):143–144.
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 (11):1736–1741.
 A, 2002.
 36:739–750.

,) k. 2001. “ 4”
 ?
 11:298–311.
) , 2003.
 “ ”
 23(10):3981–3989.
) k , A . 2005. 27:95–105.
 2014. k
 5:
 264.
 A. 2003.
 (A):
 A, AA. 2007.
) 56(2):366–383.
 A, 2015. fi. 19(6):
 349–357.
 k k A , } , A . 2013.
 : k. 24:63–71.
 2010.
 A
 A. 107(30):13503–13508.