Predictive feature remapping before saccadic eye movements

Dongjun He
School of Psychological and Cognitive Sciences and Beijing Key Laboratory of Behavior and Mental Health, Beijing, China
Key Laboratory of Machine Perception, Ministry of Education, Beijing, China
Peking-Tsinghua Center for Life Sciences, Beijing, China
IDG/McGovern Institute for Brain Research, Peking University, Beijing, China

Ce Mo
Peking-Tsinghua Center for Life Sciences, Beijing, China
IDG/McGovern Institute for Brain Research, Peking University, Beijing, China

Fang Fang
School of Psychological and Cognitive Sciences and Beijing Key Laboratory of Behavior and Mental Health, Beijing, China
Key Laboratory of Machine Perception, Ministry of Education, Beijing, China
Peking-Tsinghua Center for Life Sciences, Beijing, China
IDG/McGovern Institute for Brain Research, Peking University, Beijing, China

Saccadic eye movements cause rapid and dramatic displacements of the retinal image of the visual world, yet our conscious perception of the world remains stable and continuous. A popular explanation for this remarkable ability of our visual system to compensate for the displacements is the predictive feature remapping theory. The theory proposes that, before saccades, the representation of a visual stimulus can be predictively transferred from neurons that initially encode the stimulus to neurons whose receptive fields will encompass the stimulus location after the saccade. Visual adaptation aftereffect experiments performed by Melcher (2007) provided psychophysical evidence for this theory. However, it was argued that the visual aftereffects were not measured at the "appropriate" remapped location (Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). Therefore, whether the remapped representation contains feature information (e.g., orientation, motion direction, or contrast) is still a subject of intense debate. Here, to explore the nature of the predictive transfer during trans-saccadic perception, we measured visual aftereffects (tilt aftereffect, motion aftereffect, and threshold elevation aftereffect) at the appropriate remapped location of adapting stimuli before saccades. We observed a significant tilt aftereffect and motion aftereffect, but little threshold elevation aftereffect. Furthermore, the tilt aftereffect and motion aftereffect exhibited spatial specificity. These findings provide strong evidence for the predictive feature remapping theory and suggest that intermediate visual processing stages (i.e., extrastriate visual cortex) might be critical for feature remapping. Finally, we propose that the feature remapping process might also contribute to the spatiotopic representation of visual features.

Introduction

[illegible] ë, 2001; [illegible], 2000), [illegible], 1982), [illegible], 1991),

Citation: He, D., Mo, C., & Fang, F. (2017). Predictive feature remapping before saccadic eye movements. *Journal of Vision*, *17*(5):14, 1–12, doi:10.1167/17.5.14.

10.116 /1 .5.14 , 201 24, 201 1534- 362 201

(’A ., 2006; , B , B , & , 1997). (, C , & , 1992; & , 2006), (C , , A , & , 2010; & C , 2008). (C , , & , 1995; ., 1992; ., 2016), (& B , 1990; & , 2006), (, , & , 1995), (- & C , 2002). (. .,).

A (C ., 2010; , C , & , 2011; & B , 2012, 2016; , , , & C , 2011).

(, , , & , 2013; , 2007; & C , 2008; & C , 2014; , , , C , & , 2016). (. ., , ,) (2007) (A)

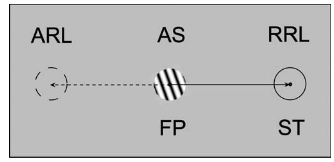

Figure 1. Appropriate remapped location of visual adaptor. In Melcher’s study (2007), subjects adapted to a tilted grating presented at the initial fixation point. Then they were asked to make a saccade and judge the orientation of a test grating briefly presented at either the initial fixation point or the saccadic target location. According to Rolfs et al. (2011), the visual adaptor (i.e., the tilted grating) at the initial fixation point activates neurons that encode the adaptor’s expected retinal location after the saccade. The remapping vector (dashed arrow) actually opposes the saccade vector (solid arrow). Therefore, the appropriate remapped location of the adaptor corresponds to the retinal position that the adaptor will have only following the saccade. FP: fixation point; ST: saccadic target; ARL: appropriate remapped location; AS: adapting stimulus; and RRL: reversed remapped location.

A , A ( ), A ( ), (A , , & , 1998; & , 2001; , 2005). A A ( ) (. .,) . . (2011) , A ( ) (1), (, , , & , 2014; & , 2014). A , A , A

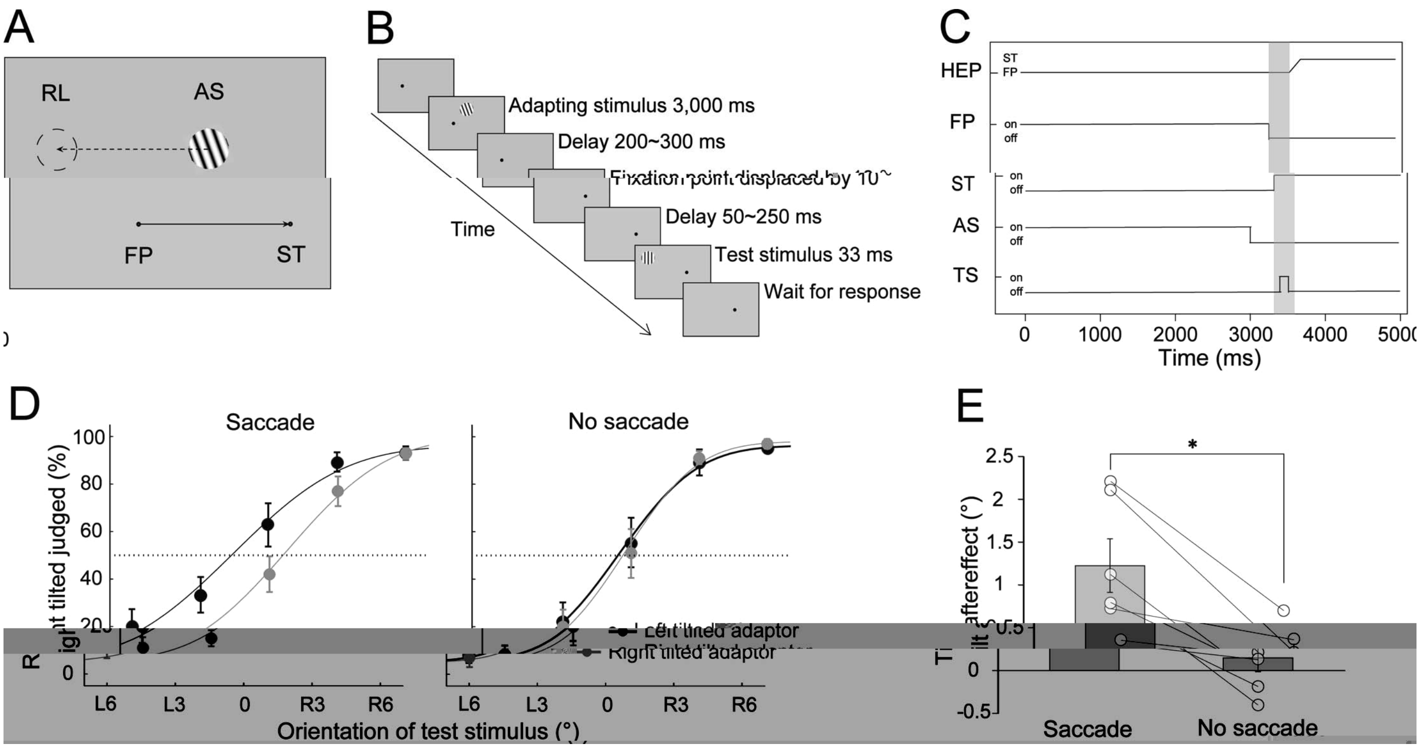

Figure 2. Stimuli, procedure, time course of events, and results in Experiment 1. (A) The spatial location and the remapped location of the grating adaptor. Subjects made a saccade from the fixation point to the saccadic target. The saccade direction and the remapping direction are shown by the solid arrow and the dashed arrow, respectively. Test stimuli were presented at the remapped location before saccades. (B) Schematic description of a trial for measuring the TAE. (C) Time course of events in a trial. RL: remapped location; HEP: horizontal eye position; FP: fixation position; ST: saccadic target; AS: adapting stimulus; and TS: test stimulus. (D) Psychometric functions showing orientation judgments after adapting to the left or right tilted adaptor. The abscissa refers to the orientation of test stimuli. L and R indicate that a test stimulus was left or right tilted. The ordinate refers to the percentage of trials in which subjects indicated that a test stimulus was right tilted. (E) TAE magnitudes in the saccade and no-saccade conditions. Data are plotted for each subject (lines and circles) as well as the group means (bars). The asterisk indicates a statistically significant difference between the two conditions (*$p < 0.05$). Error bars denote 1 *SEM* calculated across subjects for each condition.

(2011; 2A). (, ,) , , 2004; , 2007; , 2015),

20 30.

Methods

Subjects

A (18 16) 1 6

Apparatus and stimuli

57 . 43.4 / 2 4 10.5 / 2 . A A (: 204 ; : 60 ; : 1024 × 768; : 22 .). 4, 8- 14- C

Design

n n 10 40 (
). n 3
n 2
n n . n
n, 2-A C
n n n n
(n).

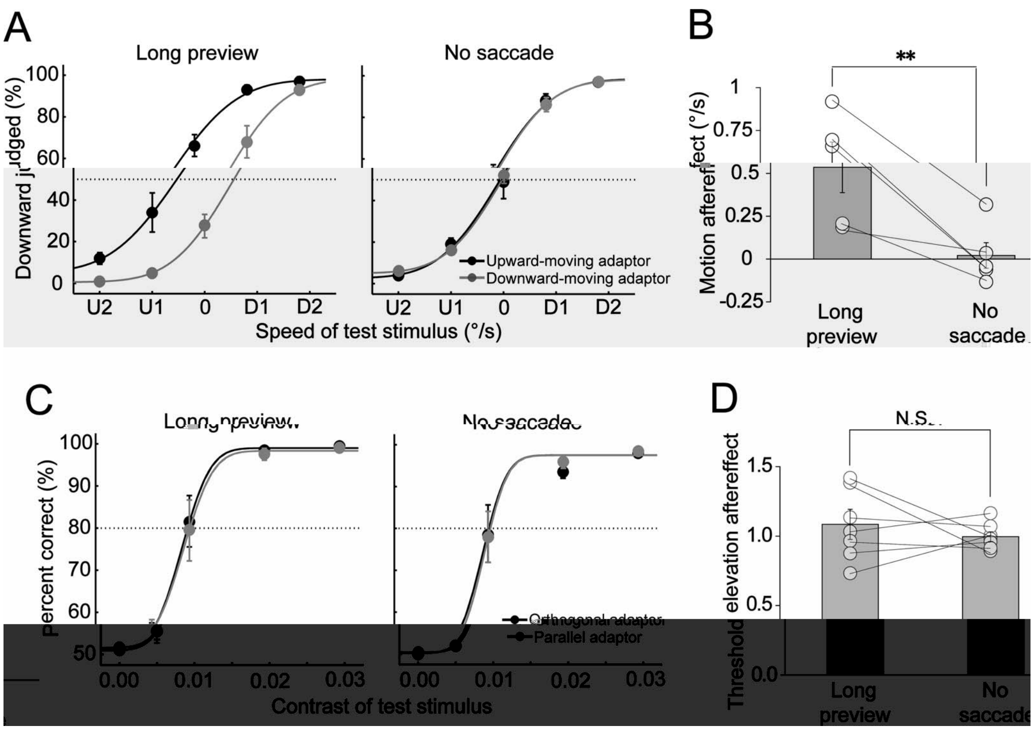

Figure 4. Results of Experiments 3 and 4. (A) Psychometric functions showing motion direction judgments after adapting to the upward- or downward-moving adaptor. The abscissa refers to the direction of test stimuli. U and D indicate that a test stimulus moved upward or downward. The ordinate refers to the percentage of trials in which subjects indicated that a test stimulus moved downward. (B) MAE magnitudes in the long-preview and no-saccade conditions. (C) Psychometric functions showing contrast detection performance after parallel or orthogonal adaptation. (D) TEAE magnitudes in the long-preview and no-saccade conditions. Data are plotted for each subject (lines and circles) as well as the group means (bars). Asterisks indicate a statistically significant difference between two conditions (**$p < 0.01$). Error bars denote 1 *SEM* calculated across subjects for each condition.

Data analysis

±20°

80% (

4B).

Results

Experiment 1: Predictive remapping of orientation before saccade

$t(5) = 3.92$, p

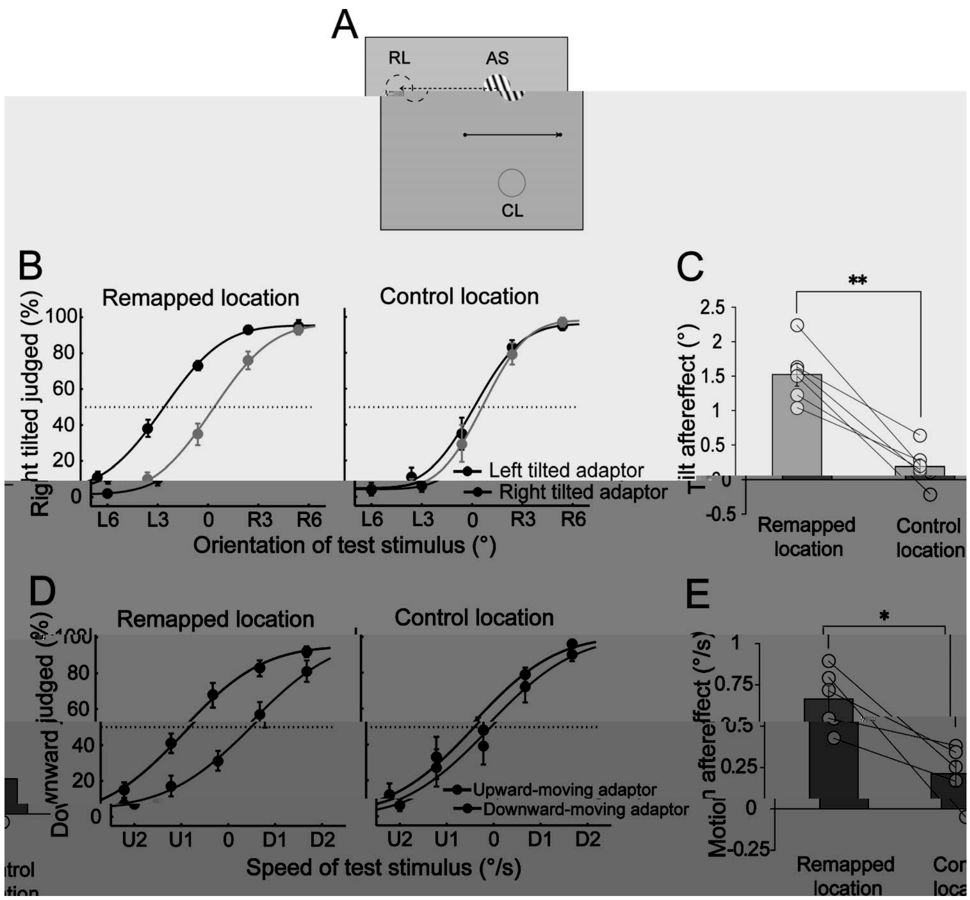

Figure 5. Results of Experiments 5 and 6. (A) The spatial location and the remapped location of the grating adaptor and the control location. RL: remapped location; AS: adapting stimulus; and CL: control location. (B) Psychometric functions showing orientation judgments after adapting to the left or right tilted adaptor. The abscissa refers to the orientation of test stimuli. L and R indicate that a test stimulus was left or right tilted. The ordinate refers to the percentage of trials in which subjects indicated that a test stimulus was right tilted. (C) TAE magnitudes at the remapped location and the control location. (D) Psychometric functions showing motion direction judgments after adapting to the upward- or downward-moving adaptor. The abscissa refers to the direction of test stimuli. U and D indicate that a test stimulus moved upward or downward. The ordinate refers to the percentage of trials in which subjects indicated that a test stimulus moved downward. (E) MAE magnitudes at the remapped location and the control location. Data are plotted for each subject (lines and circles) as well as the group means (bars). Asterisks indicate a statistically significant difference between two conditions (*$p < 0.05$; **$p < 0.01$). Error bars denote 1 *SEM* calculated across subjects for each location.

= 0.011, A n n - n n, $t(5)$ = 0.92, $p = 0.398$. , t n A n n n n n n n n - n - n, $t(5) = 3.82$, $p = 0.012$ (2 n 2). n n n n n . n n n A n n n (B & C , 1969; B n n & nn , 2003; n , , n, & , 2005; , n n , & B , 1973; n & nn , 1979), n n n n n - n n .

Experiment 2: Time-dependent predictive remapping of orientation

A n 1 n n n n n n , n n n n n n . n n , n n (3A). A n n , n - t n n A n n - n n, $t(4) = 8.14$, $p < 0.01$, n - n n, $t(4) = 3.97$, $p = 0.017$, A n n n n, $t(4) = 0.16$, $p =$ 0.878. , t A n n n n n n

: $t(4) = 7.05, p < 0.01$; : $t(4) = 3.67, p = 0.021$ (3C 3). , A , $t(4) = 6.08, p < 0.01$.

Experiment 3: Predictive remapping of motion direction before saccade

A . 3 6, 2 A . t A , $t(4) = 3.62, p = 0.022$, A , $t(4) = 0.28, p = 0.791$. , t A , $t(4) = 4.58, p = 0.01$ (4A 4B). . A (& , 2003; , , & , 2003; ., 1995; & B , 2003). , .

Experiment 4: Contrast information cannot be predictively remapped

A . t A , $t(6) = 0.779, p = 0.465$, , $t(6) = 0.105, p = 0.919$. , t , $t(6) = 0.723, p = 0.497$ (4C 4). . A (1) (., 2005; , & , 1989; , , , & , 2004), 1 .

Experiments 5 and 6: Location specificity of predictive feature remapping

A , . , A A (5A). 5, t A , $t(5) = 9.07, p < 0.001$, , $t(5) = 1.67, p = 0.155$. , t A , $t(5) = 6.66, p < 0.001$ (5B 5C). 6, t A , $t(4) = 8.20, p < 0.001$, , $t(4) = 2.88, p = 0.045$. , t A , $t(4) = 3.95, p = 0.017$ (5 5). .

Discussion

(A , A , A) (, ,) . A , A A , A . , A A . , . (2011)

n & , 1997; ., 1995; n ., 2016; n , n , , , & , 2014), n n n n n n n n n n n n (n n n & C , 2014, n n q). n , n n n n (. ., n n).

Keywords: feature remapping, saccade, psychophysics, adaptation, visual aftereffect

Acknowledgments

C 31230029, 2015CB351800, C 31421003, C 61621136008, C 61527804, n C 31671168. n n n n - n C n n n C n n n n (2016 590006).

C n : n n .
C n n : n n .
: n @ . . n .
A : n C n
n , n n , B n , C n .

References

An , ., n , . A. ., & , . (1998). n . *Trends in Cognitive Sciences*, *2*(3), 111 117.

B , . ., n , . ., & n , . (1991). n n n n n q . *Journal of Neuroscience*, *11*(1), 168 190.

B , C. ., & . C , (1969). n n n n n n n n n n . *Journal of Physiology*, *203*(1), 237 260.

B , . ., An n , . A., & n , . . (1990). n n n - nn n n ( ) n q . *Journal of Comparative Neurology*, *299*(4), 421 445.

B n n , . ., & nn , . . (2003). n n - n n n . *Journal of Neuroscience*, *23*(25), 8781 8787.

C , C., & n - , . . (1989). n n : . n n n n n n n . *Journal of Comparative Neurology*, *287*(4), 422 445.

C n , ., n , A. ., A , A., & , . (2010). n n n n n . *Trends in Cognitive Sciences*, *14*(4), 147 153.

C n , ., B n , . A., n , . ., & , . . (2016). C n n . *Journal of Neuroscience*, *36*(1), 31 42.

C , C. ., , . ., & , . . (1995). n n n n - . *Cerebral Cortex*, *5*(5), 470 481.

'A , ., , ., C , ., B , ., B , . C., & n , . C. (2006). B n n n n . *Nature Neuroscience*, *10*(2), 249 255.

, . ., B , ., B n , ., & , . (1997). n n n n n . *Nature*, *389*(6653), 845 848.

, . ., C , C. ., & , . . (1992). n n n n n n n . *Science*, *255*(5040), 90 92.

n , ., , . ., n , ., & , . (2005). n n - n n n n . *Journal of Neurophysiology*, *94*(6), 4188 4195.

n , . (2004). : C n n n n . *Current Biology*, *14*(18), 751 753.

, . ., & B , C. . (1990). n . . n n n n . *Journal of Neurophysiology*, *64*(2), 489 508.

n , . ., , . ., n n , . ., & n , . B. (2013). n n n n . *Current Biology*, *23*(9), 793 798.

, ., & , . . (2001). n n - n n - n n . *Nature*, *411*(6836), 473 476.

n , . . (1991). n n n n n . *Cognitive Psychology*, *23*(23), 420 456.

n , . ., C n , ., & , . . (2011). n n n

n n . *Journal of Neurophysiology*, *106*(3), 1179 1190.

n , ., n, . ., & n , . (1982). n n n n n . *Science*, *215*(4529), 192 194.

n , ., & n , . (2005). n n n n n n. *Nature Neuroscience*, *8*(5), 679 685.

n n, ., , ., , ., & C n , . (2010). n . *Journal of Vision*, *10*(1):8, 1 13, :10.1167/10.1.8.

A n, A. (2007). n: , n , n n n n . *Journal of Neurophysiology*, *97*(5), 3155 3164.

n, A., & n, . A. (2003). n n n n q . *Neuron*, *39*(4), 681 691.

, ., n n , A., & B , . (1973). n n . *Science*, *182*(4116), 1036 1038.

, . (2005). n - n n . *Current Biology*, *15*(19), 1745 1748.

, . (2007). n n . *Nature Neuroscience*, *10*(7), 903 907.

, ., & C , C. . (2008). n - n. *Trends in Cognitive Sciences*, *12*(12), 466 473.

, . ., n , C. ., & C , C. . (2007). n n n . *Journal of Neurophysiology*, *97*(2), 1738 1755.

, ., & B , . . (2012). An n n n n . *Journal of Neuroscience*, *32*(46), 16449 16457.

, ., & B , . . (2016). n , , n n n : n n n . *Cerebral Cortex*, *26*(7), 3138 3195.

n, . A., & nn , . (1979). n- n n n n . *Nature*, *278*(278), 850 852.

, ., & C , C. . (2002). n n n n n - n . *Proceedings of the National Academy of Sciences, USA*, *99*(6), 4026 4031.

n, . ., & ë, A. (2001). A n n n n n n . *Behavioral & Brain Sciences*, *24*(5), 973 1031.

n n , . A. (2000). n n n n . *Visual Cognition*, *7*(1), 17 42.

n n, . A. (1964). n n n . *Journal of Physiology*, *174*(2), 245 264.

, ., n , ., , ., & C n , . (2011). n n n n . *Nature Neuroscience*, *14*(2), 252 256.

, . ., , A., n , . ., & B , . (1995). nn n n n q : C n n n n n . *Journal of Neuroscience*, *15*(6), 4464 4487.

, ., nn , ., & , . . (1989). C n n n q . *Vision Research*, *29*(7), 747 755.

, A. ., , . C., , A. ., & , . B. (2003). n n n n n: , n n , n n n - . *Cerebral Cortex*, *13*(4), 340 349.

n, . ., , . ., , . ., & nn , . (2004). n n n n . *Neuron*, *42*(1), 155 162.

, . A., & , . . (2006). n n n n n n . *Nature*, *444*(7117), 374 377.

n n, ., B , C., & , . (1995). n q n . *Journal of Comparative Neurology*, *353*(2), 291 305.

n n, ., & C , C. . (2014). n n n . *Journal of Neurophysiology*, *111*(3), 613 627.

n , ., n , ., , ., C n , ., & , . (2016). - n n n n n n n n . *Journal of Neurophysiology*, *116*(4), n .00171.02016.

, . B. ., , . B., , A. ., , . B., n , . ., , ., & n, B. . (1995). n n n n n n n n n . *Nature*, *375*(6527), 139 141.

n , . ., & , . . (1997). n n n n . . n . *Journal of Neurophysiology*, *78*(3), 1373 1383.

n , . ., & B n , . . (2003). n n n . *Journal of Neurophysiology*, *88*(6), 3469 3476.

, . ., n, . ., & , . . (1995). n n n n n. *Journal of Neurophysiology*, *73*(5), 1988 2003.

n , ., n , C. C., n, ., , ., , . ., & n , . (2016). n n n n . *Neuron*, *90*(2), 400 409.

, . A. (2015). n. *Annual Review of Vision Science*, *1*(1), 547 567.

, ., n , ., , ., & n , . (2016). n n n n n n n n . *Current Biology*, *26*(23), 3176 3182.

nn, ., n , . C., n , . ., & B , . (2013). n n n . *Current Biology*, *23*(5), 193 194.

nn, ., n , ., A , . ., & n , . . (2016). n n . *Journal of Neuroscience*, *36*(37), 9526 9534.

n , ., & , . (2014). n n : An n n q n n ? *Trends in Cognitive Sciences*, *18*(12), 621 628.

n , ., n , . A., , ., , . ., & , . (2014). n n n . *Nature*, *507*(7493), 504 507.