Current Biology 24, 2926–2929, December 15, 2014 http://dx.doi.org/10.1016/j.cub.2014.10.041

Report

Age-Related Declines of Stability in Visual Perceptual Learning

Li-Hung Chang,[1,2] Kazuhisa Shibata,[1] George J. Andersen,[3] Yuka Sasaki,[1] and Takeo Watanabe[1,*]
[1]Department of Cognitive, Linguistic, and Psychological Sciences, Brown University, Providence, RI 02912, USA
[2]Education Center for Humanities and Social Sciences, National Yang-Ming University, Taipei 112, Taiwan
[3]Department of Psychology, University of California, Riverside, CA 92521, USA

Summary

One of the biggest questions in learning is how a system can resolve the plasticity and stability dilemma [1–3]. Specifically, the learning system needs to have not only a high capability of learning new items (plasticity) but also a high stability to retain important items or processing in the system by preventing unimportant or irrelevant information from being learned. This dilemma should hold true for visual perceptual learning (VPL), which is defined as a long-term increase in performance on a visual task as a result of visual experience [4–18]. Although it is well known that aging influences learning [19–24], the effect of aging on the stability and plasticity of the visual system is unclear. To address the question, we asked older and younger adults to perform a task while a task-irrelevant feature was merely exposed. We found that older individuals learned the task-irrelevant features that younger individuals did not learn, both the features that were sufficiently strong for younger individuals to suppress and the features that were too weak for younger individuals to learn. At the same time, there was no plasticity reduction in older individuals within the task tested. These results suggest that the older visual system is less stable to unimportant information than the younger visual system. A learning problem with older individuals may be due to a decrease in stability rather than a decrease in plasticity, at least in VPL.

Results

To address characteristics of learning with older individuals, we took advantage of interesting aspects of perceptual learning as a result of mere exposure to a feature. It has been found at least in some cases that mere exposure to a visual feature that is not relevant to a given task with younger individuals does not lead to learning of the feature if it is suprathreshold and/or conspicuous [7–9, 25, 26]. This suggests that if an exposed task-irrelevant feature is detected, the brain of a younger individual should filter out or suppress the feature to avoid replacing existing important information or processing with task-irrelevant and therefore usually insignificant information. That is, the younger brain makes itself stable as well as plastic. If it holds true that older individuals simply have less plasticity than younger individuals, then a smaller magnitude of visual perceptual learning (VPL) should occur with older compared to younger adults, irrespective of whether the learned feature is task relevant or task irrelevant.

*Correspondence: takeo_watanabe@brown.edu

Note that it has been pointed out that the plasticity and stability dilemma cannot be resolved merely by changes in local circuits, including synaptic weight changes, without changes at a more global system level that include interactions between different types of processes that could include attention [1, 2]. Thus, here, we define plasticity as changes resulting from involvement of global processing associated with learning, and we discuss the ability to prevent unimportant or irrelevant information from being learned as a result of different types of processing at a global system level as an aspect of stability.

To test the hypothesis that older individuals are simply less plastic at a global system level, two groups of ten older adults (between the ages of 67 and 79) and ten younger adults (between the ages of 19 and 30) participated in the experiment with the same procedure, which was approved by the Institutional Review Board at Boston University or Brown University and by the Elder Rights Review Committee, the Executive Office of Elder Affairs, and the Massachusetts Councils on Aging (for details, see Supplemental Experimental Procedures available online). The experiment consisted of 1 day of pretesting, 8 days of training, and 1 day of posttesting, respectively. In each trial of the training stage, subjects were presented with a sequence of six letters and two digits at the center of the display. After the offset of the sequence, subjects were asked to report the two digits as targets in the sequence of otherwise letters (Figure 1). During the presentations of the letters and digits, a motion display was exposed in the background as a task-irrelevant feature. The display consisted of a certain ratio of dots moving coherently from frame to frame and the other dots moving randomly [9, 25, 27, 28]. The coherent motion level (signal strength) was varied in four steps (0.3×, 0.6×, 1.0×, and 4.0× the individual 80% coherent motion detection threshold). The multiplicative values of the individual threshold were used to adjust individual differences in perception of coherent motion, particularly between older and younger subjects [29]. Coherent motion with each coherent level moved in a different direction (see Table S1 for details).

We measured subjects' performance on a coherent motion discrimination task in the pretest and posttest stages. Because coherent motion was irrelevant to the given task during the training stage, the amount of performance increase in the posttest stages as compared to the pretest stages, if any, is regarded as the magnitude of task-irrelevant perceptual learning. As shown in Figure 2, for the younger group, the amplitude of task-irrelevant learning was highest around the threshold, and no learning was observed when the coherent motion level was 4× the threshold, which is suprathreshold. This result is in accord with the previous study and is regarded as a typical profile of younger adults [28]. However, the results of the older group were different than the results of the younger group. With the increasing coherent motion level, the amplitude of learning did not decline. The results of the following statistical analyses are in accord with this observation.

In order to compare the overall task-irrelevant learning amplitudes between older and younger adults (see Figure 2), we conducted a three-way ANOVA, with age (older versus younger groups) and coherent motion level (0.3×, 0.6×, 1.0×, and 4.0× the threshold) as between-subject factors and test (pretest versus posttest) as a within-subject factor.

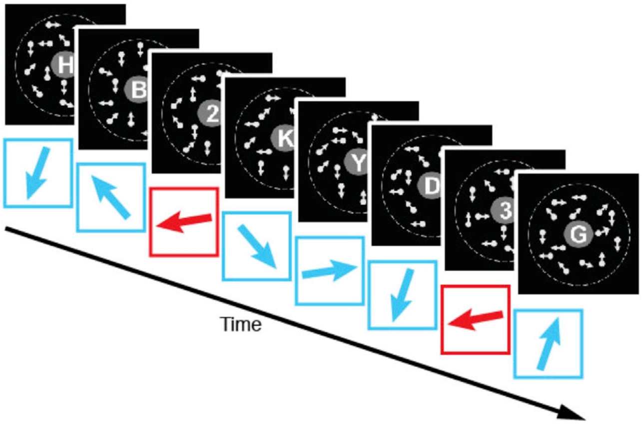

Figure 1. The Procedure of a Trial in the Training Stage

Red arrows represent the coherent motion direction that was paired with digits as targets (paired direction). Cyan arrows represent coherent motion directions that were not paired with digits (unpaired directions). Arrows are for illustrative purposes and were not presented in the training.

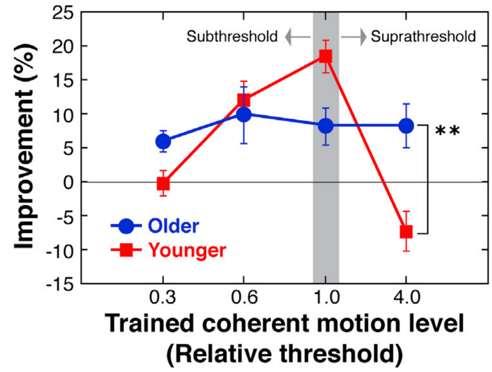

Figure 2. Mean, ±SEM, Performance Improvement in Motion Discrimination

The y axis represents the mean percent correct across displays, with four coherent motion levels (0.3×, 0.6×, 1.0×, and 4.0× the individual threshold) in the pretest stage subtracted from those in the posttest stage. The x axis represents the coherent motion levels (0.3×, 0.6×, 1.0×, and 4.0× the individual threshold) exposed in the training stage. The gray area indicates the threshold level. $^{**}p < 0.01$.

The results showed significant main factors of age ($F(1, 32) = 5.194$, $p = 0.0295$) and test ($F(1,32) = 18.26$, $p = 0.0002$) and also indicated significant interactions between coherent motion level and test ($F(3,32) = 3.613$, $p = 0.0236$). A t test applied to performance improvements (performance in the pretest subtracted from performance in the posttest) for the suprathreshold coherent level (4.0× the threshold) showed that performance improvement in the older group was significantly greater than in the younger group ($t(10) = 3.566$, $p = 0.0051$), as shown in Figure 2. These results indicate that a greater magnitude of VPL of task-irrelevant coherent motion occurred with the older individuals than with the younger individuals when a coherent motion level was suprathreshold.

We further conduced two-way ANOVA with coherent motion level (0.3×, 0.6×, 1.0×, and 4.0× the threshold) as a between-subject factor and test (pretest versus posttest) as a within-subject factor for each of the older and younger groups. For the older subjects, only the main factor of test ($F(1,16) = 17.316$, $p = 0.0007$) was significant, indicating that performance improvement was constant across the coherent motion levels. For the younger subjects, the main factor of test ($F(1,16) = 4.952$, $p = 0.0408$) and the interaction between test and coherent motion level ($F(3,16) = 5.033$, $p = 0.0121$) were significant, indicating that performance improvement was not constant across the coherent motion levels.

Why did task-irrelevant VPL at such a high signal level (4× the coherent motion level threshold) occur for older subjects but not for younger subjects? A series of studies with younger individuals has suggested the following mechanisms: when a task-irrelevant feature is above threshold or conspicuous, it is detected and suppressed by an attentional system [28, 30, 31], but when it is below threshold, it fails to be detected and therefore to be filtered out by the attentional system [31]. As a result, task-irrelevant VPL of a suprathreshold feature is less likely to occur [28], as shown in the results of the younger group of the current experiment. If this model is true, the occurrence of task-irrelevant VPL of suprathreshold motion in the older group results from the failure of the attentional system to suppress task-irrelevant feature signals. Note that previous studies have found less suppressive control for older as compared to younger adults [32, 33]. Thus, the degree of suppression on a task-irrelevant signal should be smaller with older individuals if the signal is suprathreshold. This may allow task-irrelevant VPL of a suprathreshold feature to occur. That is, task-irrelevant VPL of a suprathreshold motion may have occurred with older adults because older individuals have a decreased capacity to filter out irrelevant signals. If so, this may make older individuals' visual system more plastic in a harmful way and therefore less stable. That is, the decreased capacity to filter out irrelevant signals may lead the visual system in older individuals to resolve the plasticity-stability dilemma less effectively than the visual system in younger individuals.

To test the hypothesis mentioned above, we measured the useful field of view (UFOV) tests [34]—standard tests for attentional processing in older adults [34]—before and after the training in the current experiment for both age groups. The UFOV tests have three subtests for three different attentional abilities: subtest 1 for processing speed, subtest 2 for divided attention, and subtest 3 for selective attention. The selective attention measure in subtest 3 is to assess the ability to filter out task-irrelevant information. Note that a lower score in a UFOV test represents higher performance. If the hypothesis that task-irrelevant VPL with the suprathreshold coherent motion level occurred only with the older group because of their lower ability to filter out task-irrelevant signals is true, the score of subtest 3 should be higher (performance being lower) in the older group than in the younger group.

A three-way ANOVA, with age (older versus younger) as a between-subject factor and UFOV subtest (1, 2, and 3 versus one another) and test (pretest versus posttest) as within-subject factors, was conducted. The results showed significant main effects of age ($F(1,18) = 15.958$, $p = 0.001$) and UFOV subtest ($F(2, 36) = 49.48$, $p < 0.0001$) and significant interaction between age and UFOV ($F(2,36) = 21.884$, $p = 0.00001$). However, no significant main effect of test (pretest versus posttest) was found ($F(1,18) = 1.793$, $p = 0.197$), suggesting that none of the tested attention abilities were changed due to the training.

Based on the significant interaction between age and UFOV subtest, we applied a two-way ANOVA (age [older versus

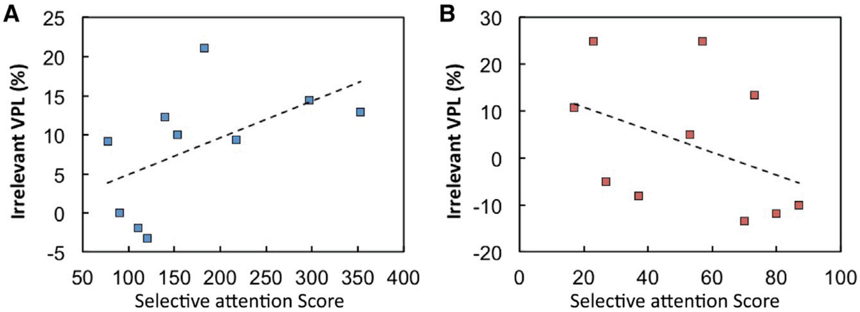

Figure 3. Correlation between Performance Improvement and Filtering

Correlation between post-UFOV subtest 3 scores (the lower the score, the higher the ability to filter out) and performance improvement, resulting from exposure to suprathreshold (4.0× the threshold) coherent motion level across older subjects for the older (A) and younger (B) groups.

younger] × test [pretest versus posttest]) to each of the results from three UFOV subtests. Main effect of age was significant ($F(1,18) = 30.634$ $p = 0.00003$) only for UFOV subtest 3 (selective attention).

These results indicate that older subjects have significantly lower ability for filtering task-irrelevant signals than younger subjects. If task-irrelevant VPL of a suprathreshold motion occurred with older adults because they have lower ability to filter out irrelevant signals, then one could predict that the lower ability should result in a greater amplitude of task-irrelevant VPL of suprathreshold motion. Figure 3 shows the correlation between the score of UFOV subtest 3 (filtering) and the amplitude of task-irrelevant VPL in the older (A) and younger (B) groups. A significant positive correlation was obtained for the older group ($r = 0.735$, $p = 0.048$), but not for the younger group ($r = -0.46$, $p = 0.179$). Almost all the UFOV scores for younger subjects were lower (higher filtering ability) than those for older subjects. These results are in accord with the hypothesis that task-irrelevant VPL of a suprathreshold motion occurred with older individuals because older adults have a decreased ability to filter out irrelevant signals, resulting in the undesirable development of task-irrelevant VPL.

Discussion

In the present study, we examined how task-irrelevant learning occurs in older and younger individuals. We found that older individuals learned highly weak and strong task-irrelevant coherent motion directions that younger people did not learn. The amplitude of task-irrelevant VPL in the older individuals was negatively correlated with the degree of ability to filter out task-irrelevant signals.

Task-irrelevant VPL with 0.3× the coherent motion threshold in older individuals indicates that plasticity of older individuals is not lower than that of younger individuals. Is this tendency specific for task-irrelevant VPL? To address this question, we analyzed the accuracy of the rapid serial visual presentation (RSVP) task during the training stage of the current experiment. No significant difference was found between the performance improvements of the RSVP task in the older and younger groups. A three-way ANOVA (age, training session, and coherent motion level) indicated that the main effect of training session was significant ($F(7,224) = 10.321$, $p < 0.000001$), but neither the main effect of age ($F(1,32) = 1.983$, $p = 0.169$) nor the coherent motion level ($F(3,32) = 1.058$, $p = 0.381$) was significant. None of the interactions were significant (age × coherent motion level: $F(3,32) = 0.941$, $p = 0.432$; age × training day: $F(7,224) = 2.429$, $p = 0.05$; training session × coherent motion level: $F(21,224) = 0.584$, $p = 0.855$; age × training session × coherent motion level: $F(21,224) = 0.738$, $p = 0.715$). These results indicate that older subjects as well as younger subjects showed significant amounts of task-relevant learning. No evidence that indicates that older individuals have a problem with plasticity was obtained. This tendency is in accord with previous studies that showed that older individuals' efficiency in learning visual tasks is not significantly different from younger individuals' efficiency in learning visual tasks [35–40].

Is there any possibility that the older subjects learned between the two tests (pretest and posttest) as a result of the repeated testing in the test stage(s) and that this resulted in the rather flat curve for the older group in Figure 2? To test this possibility, we compared performance (accuracy) of the pretest and posttest on the motion that was ±60° apart from both of the directions that were paired with targets during training. The mean improvements (performance in the pretest subtracted from performance in the posttest) were −0.047 (±0.043 SE) for the older group and −0.015 (±0.056 SE) for the younger group. We applied a two-way ANOVA (age [old versus young] and test [pretest versus posttest]). None of the main effects of age ($F(1, 18) = 0.007$, $p = 0.933$), test ($F(1, 18) = 0.771$, $p = 0.391$), or interaction of age × test ($F(1,18) = 0.206$, $p = 0.655$) were significant. These results do not support the possibility that the older subjects learned in the test stage(s).

For the visual system to efficiently adapt to a new environment, the plasticity-stability dilemma needs to be resolved. Our results indicate that older individuals learn strong task-irrelevant signals that younger people do not learn, whereas the results of task-irrelevant and task-relevant VPL show no evidence that older individuals are less plastic than younger individuals. From this viewpoint, the results of the present study suggest that older individuals have a problem with stability at the global system level (to avoid task-irrelevant signals from being learned) rather than with plasticity.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and one table and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.10.041.

Acknowledgments

This study was supported by grants from the NIH (R01EY019466, R01AG031941, and R01MH091801). We also acknowledge and thank the experiment site for support and the subjects that were recruited from the Brookline Senior Center.

Received: July 27, 2014
Revised: September 30, 2014
Accepted: October 14, 2014
Published: November 26, 2014

References

1. Grossberg, S. (2013). Adaptive resonance theory: how a brain learns to consciously attend, learn, and recognize a changing world. Neural Netw. *37*, 1–47.
2. Abraham, W.C., and Robins, A. (2005). Memory retention—the synaptic stability versus plasticity dilemma. Trends Neurosci. *28*, 73–78.
3. Sasaki, Y., Nanez, J.E., and Watanabe, T. (2010). Advances in visual perceptual learning and plasticity. Nat. Rev. Neurosci. *11*, 53–60.
4. Szpiro, S.F., Wright, B.A., and Carrasco, M. (2014). Learning one task by interleaving practice with another task. Vision Res. *101*, 118–124.
5. Carmel, D., and Carrasco, M. (2008). Perceptual learning and dynamic changes in primary visual cortex. Neuron *57*, 799–801.
6. Watanabe, T., and Sasaki, Y. (2015). Perceptual learning: toward a comprehensive theory. Annu. Rev. Psychol. Published online September 10, 2014. http://dx.doi.org/10.1146/annurev-psych-010814-015214.
7. Seitz, A.R., and Watanabe, T. (2003). Psychophysics: is subliminal learning really passive? Nature *422*, 36.
8. Watanabe, T., Náñez, J.E., Sr., Koyama, S., Mukai, I., Liederman, J., and Sasaki, Y. (2002). Greater plasticity in lower-level than higher-level visual motion processing in a passive perceptual learning task. Nat. Neurosci. *5*, 1003–1009.
9. Watanabe, T., Náñez, J.E., and Sasaki, Y. (2001). Perceptual learning without perception. Nature *413*, 844–848.
10. Das, A., Demagistris, M., and Huxlin, K.R. (2012). Different properties of visual relearning after damage to early versus higher-level visual cortical areas. J. Neurosci. *32*, 5414–5425.
11. Li, J., Thompson, B., Deng, D., Chan, L.Y., Yu, M., and Hess, R.F. (2013). Dichoptic training enables the adult amblyopic brain to learn. Curr. Biol. *23*, R308–R309.
12. Xu, J.P., He, Z.J., and Ooi, T.L. (2010). Effectively reducing sensory eye dominance with a push-pull perceptual learning protocol. Curr. Biol. *20*, 1864–1868.
13. Xu, J.P., He, Z.J., and Ooi, T.L. (2012). Perceptual learning to reduce sensory eye dominance beyond the focus of top-down visual attention. Vision Res. *61*, 39–47.
14. Beste, C., Wascher, E., Güntürkün, O., and Dinse, H.R. (2011). Improvement and impairment of visually guided behavior through LTP- and LTD-like exposure-based visual learning. Curr. Biol. *21*, 876–882.
15. Dosher, B.A., and Lu, Z.L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. Proc. Natl. Acad. Sci. USA *95*, 13988–13993.
16. Gilbert, C.D., and Li, W. (2012). Adult visual cortical plasticity. Neuron *75*, 250–264.
17. Karni, A., and Sagi, D. (1993). The time course of learning a visual skill. Nature *365*, 250–252.
18. Law, C.T., and Gold, J.I. (2008). Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. Nat. Neurosci. *11*, 505–513.
19. Freitas, C., Farzan, F., and Pascual-Leone, A. (2013). Assessing brain plasticity across the lifespan with transcranial magnetic stimulation: why, how, and what is the ultimate goal? Front Neurosci *7*, 42.
20. Jones, S., Nyberg, L., Sandblom, J., Stigsdotter Neely, A., Ingvar, M., Magnus Petersson, K., and Bäckman, L. (2006). Cognitive and neural plasticity in aging: general and task-specific limitations. Neurosci. Biobehav. Rev. *30*, 864–871.
21. Lustig, C., Shah, P., Seidler, R., and Reuter-Lorenz, P.A. (2009). Aging, training, and the brain: a review and future directions. Neuropsychol. Rev. *19*, 504–522.
22. Mahncke, H.W., Connor, B.B., Appelman, J., Ahsanuddin, O.N., Hardy, J.L., Wood, R.A., Joyce, N.M., Boniske, T., Atkins, S.M., and Merzenich, M.M. (2006). Memory enhancement in healthy older adults using a brain plasticity-based training program: a randomized, controlled study. Proc. Natl. Acad. Sci. USA *103*, 12523–12528.
23. Verhaeghen, P., Marcoen, A., and Goossens, L. (1992). Improving memory performance in the aged through mnemonic training: a meta-analytic study. Psychol. Aging *7*, 242–251.
24. Yesavage, J.A., Sheikh, J.I., Friedman, L., and Tanke, E. (1990). Learning mnemonics: roles of aging and subtle cognitive impairment. Psychol. Aging *5*, 133–137.
25. Seitz, A.R., Kim, D., and Watanabe, T. (2009). Rewards evoke learning of unconsciously processed visual stimuli in adult humans. Neuron *61*, 700–707.
26. Seitz, A.R., and Dinse, H.R. (2007). A common framework for perceptual learning. Curr. Opin. Neurobiol. *17*, 148–153.
27. Newsome, W.T., and Paré, E.B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). J. Neurosci. *8*, 2201–2211.
28. Tsushima, Y., Seitz, A.R., and Watanabe, T. (2008). Task-irrelevant learning occurs only when the irrelevant feature is weak. Curr. Biol. *18*, R516–R517.
29. Gilmore, G.C., Wenk, H.E., Naylor, L.A., and Stuve, T.A. (1992). Motion perception and aging. Psychol. Aging *7*, 654–660.
30. Meteyard, L., Zokaei, N., Bahrami, B., and Vigliocco, G. (2008). Visual motion interferes with lexical decision on motion words. Curr. Biol. *18*, R732–R733.
31. Tsushima, Y., Sasaki, Y., and Watanabe, T. (2006). Greater disruption due to failure of inhibitory control on an ambiguous distractor. Science *314*, 1786–1788.
32. Betts, L.R., Taylor, C.P., Sekuler, A.B., and Bennett, P.J. (2005). Aging reduces center-surround antagonism in visual motion processing. Neuron *45*, 361–366.
33. Healey, M.K., Campbell, K.L., and Hasher, L. (2008). Cognitive aging and increased distractibility: costs and potential benefits. Prog. Brain Res. *169*, 353–363.
34. Ball, K.K., Beard, B.L., Roenker, D.L., Miller, R.L., and Griggs, D.S. (1988). Age and visual search: expanding the useful field of view. J. Opt. Soc. Am. A *5*, 2210–2219.
35. Andersen, G.J., Ni, R., Bower, J.D., and Watanabe, T. (2010). Perceptual learning, aging, and improved visual performance in early stages of visual processing. J. Vis. *10*, 4.
36. Mishra, J., Rolle, C., and Gazzaley, A. (2014). Neural plasticity underlying visual perceptual learning in aging. Brain Res. Published online September 8, 2014. http://dx.doi.org/10.1016/j.brainres.2014.09.009.
37. Bower, J.D., Watanabe, T., and Andersen, G.J. (2013). Perceptual learning and aging: improved performance for low-contrast motion discrimination. Front. Psychol. *4*, 66.
38. McKendrick, A.M., and Battista, J. (2013). Perceptual learning of contour integration is not compromised in the elderly. J. Vis. *13*, 5.
39. Polat, U., Schor, C., Tong, J.L., Zomet, A., Lev, M., Yehezkel, O., Sterkin, A., and Levi, D.M. (2012). Training the brain to overcome the effect of aging on the human eye. Sci Rep *2*, 278.
40. Yotsumoto, Y., Chang, L.-H., Ni, R., Pierce, R., Andersen, G.J., Watanabe, T., and Sasaki, Y. (2014). White matter in the older brain is more plastic than in the younger brain. Nat. Commun. Published online November 19, 2014. http://dx.doi.org/10.1038/ncomms6504.