Report

Spatiotopic Visual Maps Revealed by Saccadic Adaptation in Humans

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Summary

Saccadic adaptation [1] is a powerful experimental paradigm to probe the mechanisms of eye movement control and spatial vision, in which saccadic amplitudes change in response to false visual feedback. The adaptation occurs primarily in the motor system [2, 3], but there is also evidence for visual adaptation, depending on the size and the permanence of the postsaccadic error [4–7]. Here we confirm that adaptation has a strong visual component and show that the visual component of the adaptation is spatially selective in external, not retinal coordinates. Subjects performed a memory-guided, double-saccade, outward-adaptation task designed to maximize visual adaptation and to dissociate the visual and motor corrections. When the memorized saccadic target was in the same position (in external space) as that used in the adaptation training, saccade targeting was strongly influenced by adaptation (even if not matched in retinal or cranial position), but when in the same retinal or cranial but different external spatial position, targeting was unaffected by adaptation, demonstrating unequivocal spatiotopic selectivity. These results point to the existence of a spatiotopic neural representation for eye movement control that adapts in response to saccade error signals.

Results

We modified the saccadic standard adaptation paradigm ([1]; for review, see [2, 3]) by creating a double-step saccade task to a remembered location. Adaptation was induced via a saccade-scanning paradigm (that transfers well to memory-guided saccades [8]): subjects saccaded upward to the first saccadic target (T1, black circle in Figure 1B) and then rightward to the second saccadic target (T2, black diamond). On initiation of the second saccade, T2 was displaced 4° in the direction of the saccade (outward adaptation, probably more effective in inducing visual changes [4–7]). After about 100 trials, the magnitude of the second saccade increased in the direction of the displaced position of T2 (see Figure S1 available online), demonstrating that adaptation does occur with this paradigm.

The test phase was a separate block of trials with intermingled top-up adaptation trials. While subjects fixated the fixation point (FP1), they memorized the second saccade target (T2), presented at screen center (with ±1° of jitter) for 1000 ms. Shortly after extinction of T2, the fixation point was extinguished and the primary saccade target (T1) appeared, to which subjects saccaded immediately and then saccaded again to the memorized position of T2 (Figure 1A). The main experimental manipulation was to move the starting fixation point (FP2) to the right of the screen (gray triangle, Figure 1B) and T1 to one of the six positions indicated by colored symbols in Figure 1B. All were to the right of T2 (which remained unchanged). For these six experimental conditions, the second saccade was in the opposite direction of adaptation training and therefore outside what is normally considered to be the adaptation field [9–11].

Figure 1C shows the average landing error for the various conditions (color coded as in Figure 1B). After adaptation, the landing points of all second saccades were to the right of the physical position of T2, both for the rightward second saccades (with the sequence starting from FP1) and for the leftward second saccades initiated from FP2 (filled symbols). Adaptation followed the visual signal, even though the saccade was in the opposite direction. And this meant that whereas the saccadic amplitude increased for saccades in the same direction as the training session, amplitude decreased when the direction was reversed. The bar graphs of Figures 1D and 1E show this effect, represented as the change in the horizontal amplitude vectors of the first and second saccades, averaged over all observers. Adaptation has no effect on either the horizontal or vertical component of the first saccade amplitudes (three-way analysis of variance [ANOVA]; $F = 0.681$, $p = 0.409$) but a large and systematic effect on the second saccade, increasing amplitudes of the rightward saccade and decreasing those of the leftward saccades. The effects on horizontal amplitude all cause a rightward displacement in landing position. The absolute size of the horizontal amplitude changes for the seven conditions is significantly different from before adaptation (two-way ANOVA; $F = 37.624$, $p < 0.001$).

We next examined the spatial specificity of the visual adaptation in eye-centered, head-centered, and external space. The adaptation training sequence was similar to that used in the first experiments: an upward-rightward saccade sequence, with the second saccadic target displaced 3° rightward on initiation of the second saccade (Figure 2A). During the test phase, the second saccade was memory guided as before. In the various conditions, the starting fixation point and saccadic targets changed position to dissociate retinal, cranial, and external coordinates. The "full adaption" condition was like that used for adaptation training. The "spatiotopic" condition was similar to the "full" condition, except that the fixation point was displaced 10° rightward, so that during fixation, the saccadic targets were in the same screen position as during adaptation, but in different retinal positions. For the "retinotopic" condition, all three points were displaced 10° leftward on the screen and therefore unchanged on the retina (which moves with fixation point). For the control, fixation point was the same as for adaptation training, but T1 and T2 shifted 10° leftward on both screen and retina. In all
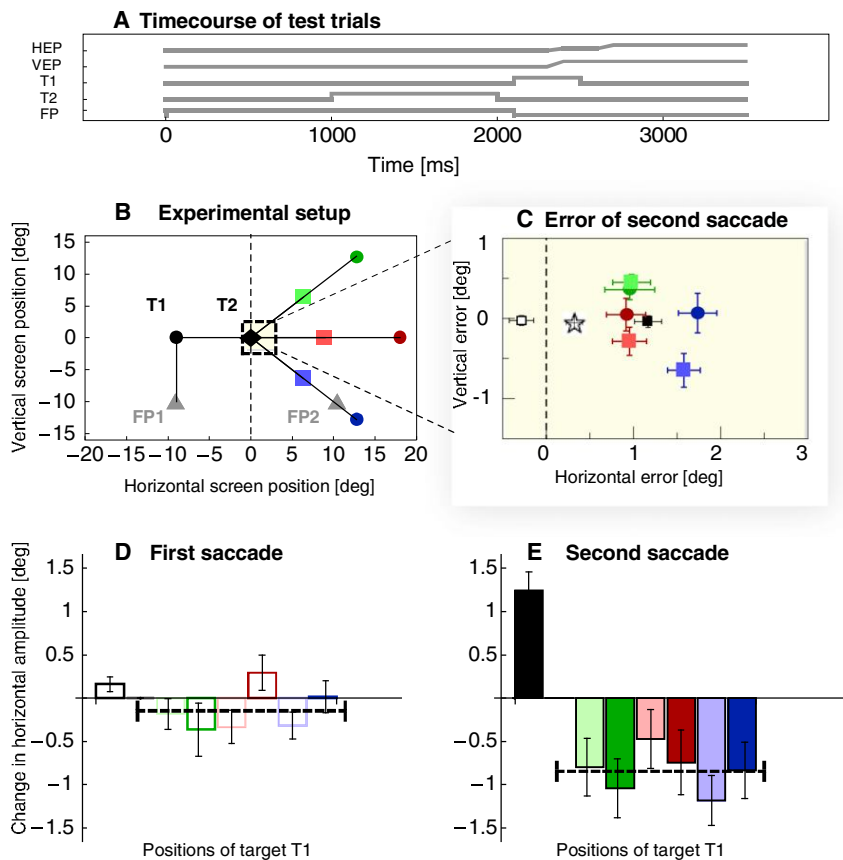
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Figure 1. Spatial Specificity of Outward Adaptation of Double-Step Memory-Guided Saccades

(A) Time course of events during tests trials. Subjects started each trial by fixating the fixation point (FP). After 1300–1500 ms, the secondary saccade target (T2) was shown for 1000 ms for the subject to memorize while keeping fixation. Both T2 and FP were then extinguished, and the primary saccade target (T1) was turned on, to which subjects saccaded immediately, followed by a second saccade to the remembered position of T2. VEP and HEP represent the vertical and horizontal eye movements.

(B) Experimental setup. At the beginning of each test trial, the subject fixated the fixation point, FP1 for rightward saccades and FP2 for leftward saccades. For rightward saccades to T2, target T1 (black circle) was presented in the left part of the screen. For rightward saccades to T2, target T1 (colored symbols) was shown in one of six possible locations. Saccade target T2 (black diamond) was presented in the screen center, jittered around a range of 2°.

(C) Error in second-saccade landing position in preadaptation trials for rightward (open square) and leftward saccades (black star), and error in second-saccade landing position in postadaptation trials for rightward (filled black square) and leftward saccades (colored symbols). The dashed line depicts the horizontal position of T2. Color coding of symbols is the same as in (B). Error bars in (C)–(E) indicate ±1 standard error of the mean.

(D) Change of amplitude of the horizontal vector of the first saccade, expressed as the difference in average amplitude before and after adaptation. The black-outlined bar refers to the rightward saccade condition, and the colored-outline bars refer to the leftward conditions (code as in C). The dashed line represents the average change in amplitude for all leftward saccades.

(E) As in (D), for the second saccade. Adaptation had clear effects on the second saccades in different directions for rightward and leftward saccades, resulting in similar landing positions.

trials, the actual position of T2 was jittered over a 2° range to prevent stereotyped saccading to a fixed position.

Figures 2B–2E report data for one typical subject, with different colors referring to different jitter positions. Before adaptation, saccadic landing of the second saccade clustered about the physical position of T2 (vertical dashed color-coded lines); saccades to the three different physical positions of T2 are clearly separated, showing that subjects encoded the position of the target on each trial rather than saccading to a constant position in a stereotyped manner. After adaptation, the landing sites are shifted rightward of the physical position of T2 by about 1° for the full and spatiotopic conditions, but not for the control and retinotopic conditions. The pattern of results is also evident from the eye traces (of another subject) and landing plots of Figure S2.

The gray bars of the lower panels of Figures 3A and 3B show results averaged over all subjects, expressed as adaptation-induced change in horizontal adaptation of the first saccade (to T1) and second saccade (to T2). The first saccade had no significant effect on either horizontal or vertical amplitude, similar for the four conditions (three-way ANOVA; $F = 0.31$, $p = 0.58$). However, adaptation caused large and significant changes in the horizontal amplitude of the second saccade for the full and spatiotopic adaptation conditions [Bonferroni-corrected t tests: full, $t(180) = 8.66$, $p < 0.001$; spatiotopic, $t(203) = 7.08$, $p < 0.001$], but not for the retinotopic [$t(196) = 1.37$, $p = 0.09$] or control conditions [$t(156) = 0.41$, $p = 0.34$].

The results reported so far do not distinguish spatiotopic (external) from craniotopic (head-centered) selectivity. However, it is important to distinguish between these two, because if the adaptation were modulated by eye position, one might expect the adaptation selectivity to be head centered (because the eyes are anchored in the head). To dissociate the two possibilities, we introduced a 9° head turn between adaptation and test trials, both leftward and rightward. A leftward head turn caused the retinotopic condition to become also head centered (see Figure 3C), while for both head turns, the spatiotopic condition (anchored in external coordinates) remained spatiotopic. The results (lower panels of Figures 3A and 3B) show that the second-saccade amplitude change remained strong and significant in the spatiotopic condition for both head turns [leftward: $t(136) = 0.03$, $p < 0.001$; rightward: $t(136) = 8.76$, $p < 0.001$]. The craniotopic condition, however, produced only weak changes in amplitude, one-quarter that of the average of the spatiotopic conditions, and not significantly different from zero [$t(83) = 1.18$, $p = 0.12$]. The other retinotopic condition also remained without adaptation effects [$t(108) = 0.10$, $p = 0.45$].

Discussion

We have created a saccadic adaptation paradigm where the saccadic errors clearly follow the visual signal. Changing completely the direction of the saccade vector had very little
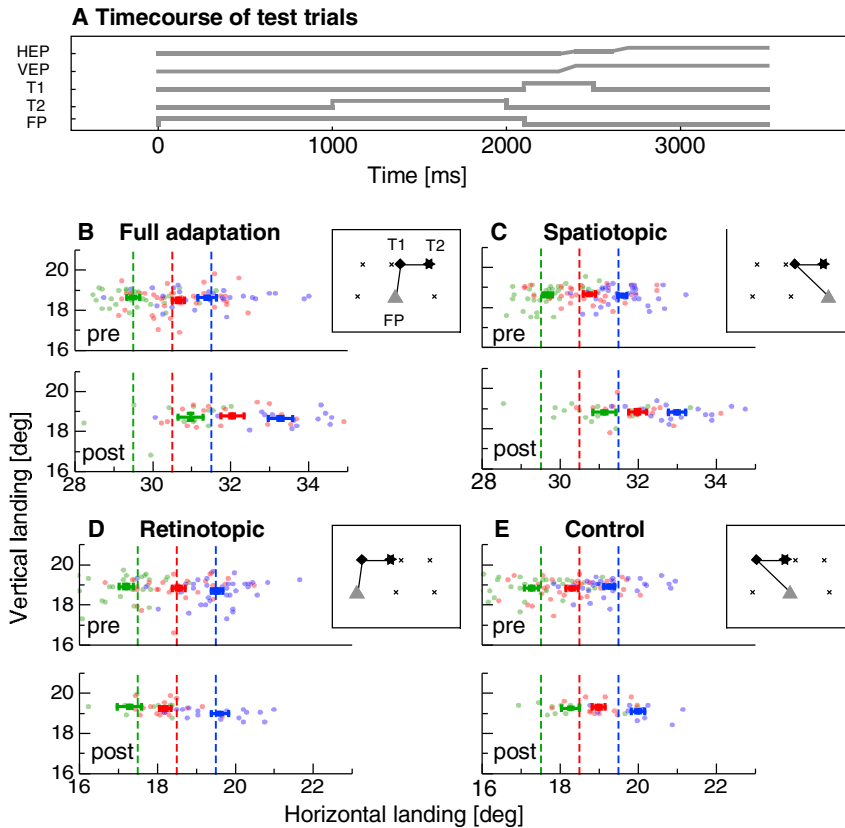
Figure 2. Head-Centered versus Eye-Centered Spatial Specificity of Saccadic Adaptation

(A) Time course of events during test trials (as in Figure 1A).

(B–E) Sample landing positions of the second saccade to the memorized target, for pre- and postadaptation sessions for a single subject for the four experimental conditions (illustrated by schematics at the upper right of each panel). The dashed lines (green, red, and blue) indicate the three positions of the memory saccade target, which was jittered around a range of 2°. The color code of the points refers to the physical target position of that trial. The larger rectangles with error bars represent the mean landing positions, with ±1 standard error of the mean; small filled dots indicate individual saccadic postadaptation landing positions.

effect. Our results suggest that, in our particular memory-guided paradigm, eye movements are guided by a spatiotopic visual map, which adapts to the error signals produced by adaptation.

The effects of saccadic adaptation are complex: saccade adaptation can be specific to the amplitude and vector of the saccade during adaption trials [1] or general to all directions and amplitudes [12]. Under most conditions, particularly for inward (gain-decreasing) adaptation, it is mainly the motor system that adapts [9, 13, 14]. Even for double-step saccades similar to ours (two-step memory-guided saccades), inward adaptation reveals no effect of a spatiotopic encoding of the saccade target position [15]. However, there is also evidence that saccadic adaptation can cause perceptual distortions [16–19, 11], even when the eye does not move [4–7], highlighting the relevance of motor signals for perceptual localization. Many studies suggest that the system assigns the saccadic adaptation error to either the visual representation of the target or the motor plan, depending on

effect on the magnitude of the adaptation; however, the adaptation was highly selective for visual position, in external rather than retinal or cranial coordinates. If the adaptation were motor based, we might expect it to be either spatially unspecific (resulting from a generalized correction to a presumed weakening of one set of rectus muscles) or possibly craniotopically specific, reflecting a map of eye position in the orbit. However, we found only weak craniotopically selective adaptation, about a quarter of the spatiotopically selective
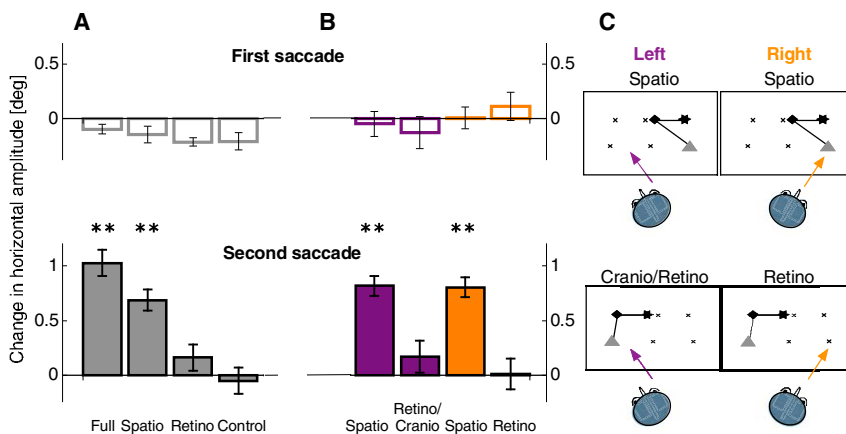

Figure 3. Allocentric versus Head-Centered Spatial Specificity of Saccadic Adaptation

(A) Effect of adaptation on the amplitude of the horizontal saccadic vector of the first saccade in the double-step sequence, expressed as the difference in average amplitude before and after adaptation. Error bars represent the standard error of the sample mean.

(B) Effect of head turn on adaptation-induced horizontal saccade amplitude changes of the second saccade in the double-step sequence. Horizontal saccades were adapted with the head facing the screen center, and test trials were collected with the head turned 9° leftward (purple) or rightward (orange). The adaptation remained spatiotopic with head turns. Error bars represent the standard error of the sample mean.

(C) Experimental setup. Saccade adaptation was induced with the head in a straight-ahead position in all sessions. In head-turn sessions, saccade amplitudes were then tested either for leftward (purple arrow) or rightward (orange arrow) head turns. For both head turns, the spatiotopic and the retinotopic conditions were tested. The leftward head turn causes the retinotopic sequence to become also craniotopic: in both adaptation and test conditions, the nose points to the fixation point at the beginning of the session, and the sequence is identical from there.

the timescale and on the size of errors [20, 21]: small saccadic errors are more likely to be attributed to fatigue or changes in saccade dynamics, whereas larger and long-lasting errors are attributed to changes in targeting representation [14]. Also under the conditions of our experiment, preliminary studies suggest that inward adaptation causes no spatiotopically selective effect, showing that the results reflect specific mechanisms activated by the outward adaptation condition rather than a general cognitive strategy.

Our results show that outward adaptation, combined with memory-guided saccades, can reveal a visual component encoded in a spatiotopic reference frame. Outward adaptation favors adaptation of the visual rather than the motor system, and the delayed motor response to the memorized target may invoke a gaze-invariant (spatiotopic) map to guide it. This is consistent with other evidence studying the dissociation between vision for action and for perception: delaying motor responses can change the reference frame from an online visuomotor relative metric to a perceptual, absolute, allocentric metric [22]. Interestingly, adaptation of saccades with longer latencies—like the scanning saccades used in our study—does not transfer well to stimulus-driven (reactive) saccades [8].

Under the conditions of our experiments, the adaption was spatially selective in external, not retinal or head-centered coordinates. Spatiotopicity is a hotly debated topic. There is clear evidence for spatiotopy in some cortical areas of the dorsal stream of monkey, particularly V6 and VIP [23, 24]. There is also good evidence for the existence of spatiotopic maps in the dorsal stream of human cortex ([25, 26], but see also [27]), and also selectivity to perceived rather than actual position [28]. Our paradigm does not at this stage distinguish between spatiotopy in true allocentric coordinates and object-centered selectivity relative to, for example, the screen frame. Future studies will attempt to disentangle these two alternatives. Interestingly, spatiotopicity seems to depend strongly on the allocation of spatial attention [26, 29], which is often linked with eye movements [30, 31].

To date, there is no clear consensus of how the visual system constructs a spatiotopic representation of the world. However, it is clear that doing so requires information about where the eyes are pointing, and most agree that this information is provided by a motor-related signal [32]. Distortion of this signal (by false feedback) could impact on the construction of the spatiotopic representation, resulting in distortions that are selective in external space. It is conceivable that under the particular procedure of our experiments, the delayed, memory-driven eye movements are guided by this spatiotopic map. But whatever the underlying neural mechanism, our results provide strong evidence for the existence of a spatiotopic map that serves the saccade system and show that it is plastic, continually modified by error signals from saccadic landing.

Experimental Procedures

Participants

Five subjects (author E.Z. and four naive subjects; mean age 29 years) participated in all of the experiments. All subjects had normal or corrected-to-normal vision, and all subjects gave informed consent. The experiments were carried out in accordance with the principles laid down in the Declaration of Helsinki.

Subjects were seated 57 cm from a 22-inch CRT color monitor (Barco Calibrator) with head stabilized by a chin- and headrest. The visible screen diagonal was 20 inches, resulting in a visual field of 40° × 30°. Stimuli were presented on the monitor with a vertical frequency of 120 Hz at a resolution of 800 × 600 pixels. Eye movements were monitored by the EyeLink 2000 system (SR Research), which samples gaze positions with a frequency of 2000 Hz. Viewing was binocular, but only the dominant eye was recorded. The system detected start and end of a saccade when eye velocity exceeded or fell below 22°/s and acceleration was above or below 4000°/s². All fixation points and saccade targets (red color) were 1° in diameter. The color of the fixation point was either green (62 cd/m²) or red (28 cd/m²), signaling to the subject the kind of trial: green meant that the trial was the double-step memory task and the subject had to keep fixation until the fixation point disappeared; red meant that it was the saccade adaptation trial, where the subject had to saccade directly to the targets. Adaptation trials lasted 1500 ms and test trials 2500 ms. Each trial started automatically after the completion of the previous trial.

Adaptation Trials

To induce modification of saccade amplitudes, we used a version of the saccade adaptation paradigm [1]. Subjects fixated a fixation point 5° below screen center. After 800 ms, two saccade targets appeared, to which the subject saccaded in a self-paced manner. As soon as the eye crossed an invisible border 3° to the right of saccade target T1, the fixation point and the first saccade target were turned off. In preadaptation trials, the second saccade target remained in its initial position. In adaptation trials, the second saccade target was displaced 4° in the direction of the saccade as soon as the eye crossed an invisible border 3° to the right of saccade target T1.

Test Trials

Subject fixated the fixation point until it was extinguished. After 1000 ms plus a randomly chosen delay between 300 and 500 ms, the secondary saccade target (T2) was shown in the screen center for 1000 ms. 100 ms after extinction of T2, the fixation point was also turned off and the primary saccade target was presented for 400 ms. The subject saccaded to the primary saccade target and then to the remembered position of the secondary target. In the head-turn conditions, subjects rotated their heads 9° leftward or rightward after adaptation, calibrated by a small laser fixed to the head. The eye tracker was briefly recalibrated in this new position before proceeding with the test trials.

Number of Trials

The experiment reported in Figure 1 had 84 test trials (12 for each of the 7 conditions), and the experiment reported in Figure 2 and Figure 3 had 72 test trials (18 for each of the 4 conditions). Adaptation sessions in all sessions started with 200 adaptation trials. The first 20 of these adaptation trials were baseline trials in which the saccade target was not displaced. In the next 180 adaptation trials, the saccade target was displaced to induce adaptation. In the postadaptation sessions, test trials were randomly intermingled with top-up adaptation trials (twice as many as test trials) to keep adaptation at a steady level. Each subject was tested in the pre- and postadaptation sessions at least twice. All sessions were counterbalanced within subjects. For every subject, there was a break of least 1 day between two successive adaptation sessions.

Data Analysis

To determine the amount of adaptation in all conditions, we calculated the distance between the saccade landing position and the physical target position for every trial. Data from the subjects were pooled together. These values were averaged for each condition separately. All trials went into analysis in which gaze position during the fixation period was within a window of 2.5° of the fixation point position and in which the first saccades to the primary saccade target landed within a window of 2.5° of the saccade target position. This was the case in 90% of all collected data. For all conditions, we checked whether the saccadic landing positions reflected the small jittering of the horizontal saccade target position. In all tested conditions, the slopes of the relationship between horizontal saccade target position and average landing positions were significantly different from zero.

For the experiments reported in Figure 1 and Figure 2, a three-way ANOVA was calculated for the amplitude errors of the first saccade in the double-step sequence with the factors pre- and postadaptation (horizontal saccade amplitude errors from before and after adaptation), directional component (horizontal and vertical), and conditions (one condition for rightward saccades and six conditions for leftward saccades). For the second saccade in the double-step sequence, a two-way ANOVA was calculated with the factors pre- and postadaptation (horizontal saccade amplitude

errors from before and after adaptation) and conditions (one condition for rightward saccades and six conditions for leftward saccades). Horizontal saccade amplitude errors were obtained by subtracting the actual saccade amplitude from the physical distance between targets T1 and T2.

Saccade latencies were determined by calculating the difference between saccade onset and onset of target T1. Latencies averaged over experimental sessions and over subjects for the first saccades (pre, 270 ± 3 ms; post, 297 ± 4ms) and the second saccades (pre, 366 ± 4 ms; post, 369 ± 3 ms) of the double-step sequence did not differ notably between pre- and postadaptation trials.

Supplemental Information

Supplemental Information includes two figures and can be found with this article online at doi:10.1016/j.cub.2011.06.014.

Acknowledgments

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