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Saccades actively maintain perceptual continuity

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People make saccades—rapid eye movements to a new fixation—approximately three times per second. This would seemingly disrupt perceptual continuity, yet our brains construct a coherent, stable view of the world from these successive fixations. There is conflicting evidence regarding the effects of saccades on perceptual continuity: some studies report that they are disruptive, with little information carryover between saccades; others report that carryover is substantial. Here we show that saccades actively contribute to perceptual continuity in humans in two different ways. When bistable stimuli are presented intermittently, saccades executed during the blank interval shorten the duration of states of ambiguous figures, indicating that saccades can erase immediately past perceptual states. On the other hand, they prolong the McCollough effect, indicating that saccades strengthen learned contingencies. Our results indicate that saccades help, rather than hinder, perceptual continuity.

Saccades are often viewed as obstacles to perceptual continuity. They lead to suppression of the magnocellular visual pathway[1], and during a saccade, the perceived position of objects in visual space is compressed[2–6] as if memory for position were lost. However, there is evidence that some trans-saccadic memory is preserved[7,8], and memory for scenes is built up over time across saccades[9]. There is also evidence that the mechanisms involved in programming an eye movement are involved in deployment of attention[10–13].

These results are seemingly contradictory—saccades seem at once to help and to hinder the maintenance of perceptual continuity. Here we present work that reconciles these findings. Our results indicate that saccades are actively involved in regulating the flow of visual information.

It has recently been shown, using bistable patterns, that the persistence of one view (or state) is stabilized by intermittent presentation of the visual stimulus[14]. It has also been suggested that there is a type of store for visual representations, akin to a kind of visual short-term memory[15]. We investigated the possibility that saccades act as a trigger in maintaining perceptual continuity. They might erase recent visual input, but maintain and strengthen learned contingencies that is learned associations among stimulus attributes. For example, in the McCollough effect, the learned contingency refers to the learned association between a certain color and a certain orientation.

We displayed an ambiguous figure intermittently and asked observers to look away from the ambiguous figure when it disappeared, and then to look back to it when it reappeared. For this saccade condition, subjects reported even less persistence for a particular state of the ambiguous figure than during continuous viewing. This result indicates that saccades wipe out perceptual states that would otherwise persist.

On the other hand, we found that the McCollough effect[16] persists much longer during a saccade condition in which observers made a saccade away from then back to a target that was intermittently presented, as compared to conditions in which the target was presented continuously or intermittently without saccades. This indicates that

saccades maintain, and even strengthen, learned stimulus contingencies. These learned stimulus contingencies could help people to re-establish their position in the world after a saccade by providing information about context.

RESULTS

We used three stimuli to measure the rate of alternation of ambiguous, perceptually bistable configurations: (i) the well-known Necker cube[17] (**Fig. 1a**) (ii) orthogonal oblique gratings that cause binocular rivalry when shown separately to each eye[18] (**Fig. 1b**) and (iii) sequences of patterns made up of circularly arranged line segments that appear to alternate between clockwise and counter-clockwise rotation (**Fig. 1c**). The first two are almost identical to stimuli recently used to study the effects of intermittent presentation on perceptual stability[14]. The third is new and based on stimuli recently used to show how information about form can result in motion perception[19].

Experiment 1

In experiment 1, each stimulus was viewed under three conditions. In the 'continuous' condition, subjects kept their gaze on the center of the stimulus, which remained continuously in view. In the 'intermittent' condition, subjects again fixated the center of the stimulus, which alternately appeared and disappeared at 5-s intervals. In the 'saccade' condition, subjects fixated the center of the stimulus when it appeared, but when it disappeared as in the intermittent condition, they made a saccade to a spot that appeared in the periphery (**Fig. 1d**). When the central stimulus appeared again, subjects were instructed to make a saccade back to it. In all conditions, the ambiguous stimulus was foveated during the time that subjects indicated, by pushing a button on a response box, whenever a state change occurred.

In experiment 1, mean duration of state times (excluding time when the stimulus was absent from the screen) was slightly greater for intermittent than for continuous presentation (**Fig. 2**). Reversal rates
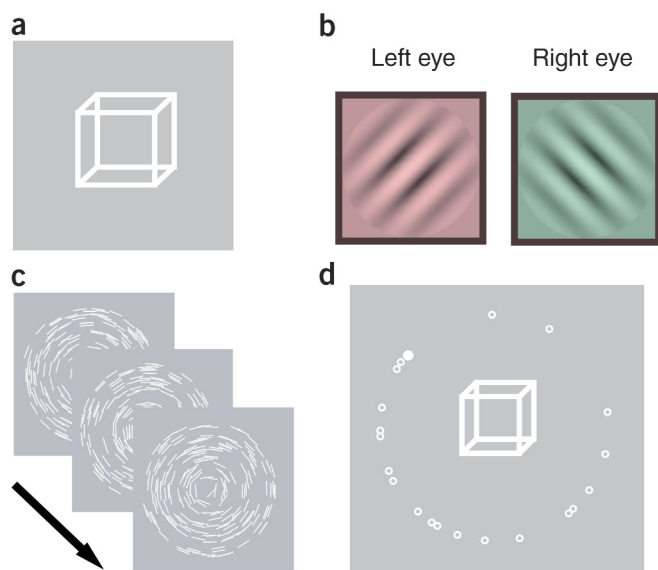
Figure 1 Bistable stimuli used in experiment 1. (**a**) Necker cube; (**b**) binocular rivalry; (**c**) a sample of 3 typical patterns of 20 that form the 'Glass line' stimulus, with an arrow showing the direction of time; (**d**) the position of the stimulus, illustrated by the Necker cube. The peripheral fixation spot (filled circle) used in the saccade condition is shown in one of its possible positions; ghost spots (open circles) show a sample of other possible positions.

were therefore slower for the intermittent condition compared to the continuous condition, replicating earlier results[14]. Mean duration for the saccade condition was strikingly smaller (and hence reversal more rapid) for each figure and for each subject than for continuous or intermittent presentation without saccades. The effects of viewing conditions in experiment 1 were highly significant ($P < 0.001$). A repeated-measurements ANOVA (linear model, balanced design, using randomly sampled subsets from each cell of state duration data, no correction to distributions) shows that the effect of viewing condi-

tion was highly significant ($P < 0.001$), as is the effect of stimulus type. There was a highly significant subject × stimulus type interaction ($P < 0.001$); the interaction of subjects with viewing conditions was not significant ($P > 0.05$).

Eye movements were not monitored, as all subjects were experienced in making voluntary saccades and in maintaining fixation between saccades. Although it is possible that subjects made microsaccades while maintaining fixation, the effects would have been small and, if present, would have reduced differences between the saccade condition and other conditions. The effects of small saccades are weaker than those of larger-amplitude saccades[5].

Experiment 2

In the McCollough effect, after adapting to black-and-color gratings, observers see the white bars of black-and-white gratings in a color complementary to that of the colored bars in the original grating[16]. Though this illusion is not fully understood, there is broad agreement that the link between pattern and color established in the adaptation period is a form of conditioning—laying down information that can lie dormant for substantial periods of time until an appropriate stimulus revives it[20,21]. The pattern-color link is orientation-specific so that orthogonal black-and-white test gratings can be made to appear differently colored, allowing the effect to be tested as shown in **Figure 3a**. Experiment 2 was designed to measure the influence of saccades on the persistence of the McCollough effect after mild conditioning.

Subjects first adapted to vertical green-and-black and horizontal red-and-black gratings (**Fig. 3a**, left) shown alternately for 5 s, each five times. Adaptation was repeated before each test trial. On test trials, subjects viewed a compound stimulus made from the halves of two white-and-black gratings, one vertical and the other horizontal (**Fig. 3a**, right). They were asked to hold down a response button

Figure 2 State durations for bistable stimuli. Mean times that a bistable stimulus remains in one or the other of its two possible states are shown for each subject in each condition for (**a**) the Necker cube (**b**) binocular rivalry and (**c**) Glass lines. Error bars represent s.e.m. For every subject and every stimulus, mean state durations are less (and hence rates of reversal higher) in the saccade condition than in either the continuous or the intermittent conditions. (**d**) Distributions of AMW's state times in the three conditions for the Necker cube stimulus. The data have been fitted with gamma distributions, which gave a good fit to the data of all subjects for all three stimuli in all three conditions. The shape parameter of the gamma distribution for the intermittent condition ($\gamma = 3.91$) was less than those for the continuous ($\gamma = 11.30$) and saccade ($\gamma = 8.85$) conditions, reflecting the relatively longer tail of the distribution of state times for the intermittent condition. This difference held for the other subjects and the other bistable figures as well (average values: continuous, $\gamma = 7.26$; intermittent, $\gamma = 3.71$; saccade, $\gamma = 4.99$). (**e**) Mean times for the two alternative states of each bistable stimulus averaged over subjects and viewing conditions. Error bars represent s.e.m. Differences are small, indicating the equal attractiveness, on average, of the two states for each figure. Equal attractiveness of alternative states held generally: the ratio of the longer to the shorter mean state time exceeded 1.25 in only 5 of 27 cases, and the maximum given by any subject for any stimulus in any condition was 1.81 (AMW, Glass line stimulus, continuous: a preference for counter-clockwise motion).
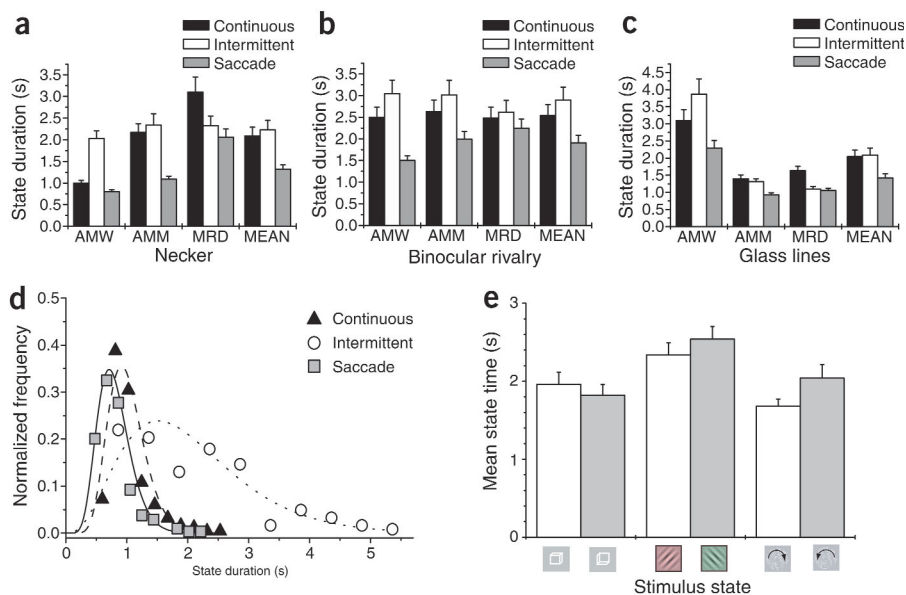
Figure 3 Persistence of the McCollough effect. (**a**) Adapting and test stimuli used in experiment 2. The adapting gratings are shown sequentially (see Methods). (**b**) Persistence times of the McCollough effect (means of three trials) for each subject. Persistence was measured as the time from the start of the presentation of the test stimulus to the last recorded button depression, averaged over three trials for each condition. It was longer in the intermittent than in the continuous condition. It was longer again in the saccade condition, on average almost three times as long as in the continuous condition. (**c**) A count of hits (response button found to be depressed when polled once per second) for AMW when observing the McCollough test stimulus in the continuous and saccade conditions. Results for the intermittent condition (not shown) were intermediate between these two. Counts were summed over three trials and binned in successive intervals, each 5 s long. The maximum possible count per bin is 15, when the button is depressed within an interval for the full 5 s on every trial. No hits are permitted in stimulus-off times in the saccade conditions, so even-numbered bins are empty in that condition. In the continuous condition the hit count fell with time, indicating that the McCollough effect was fading. In the saccade condition it revived with each saccade.
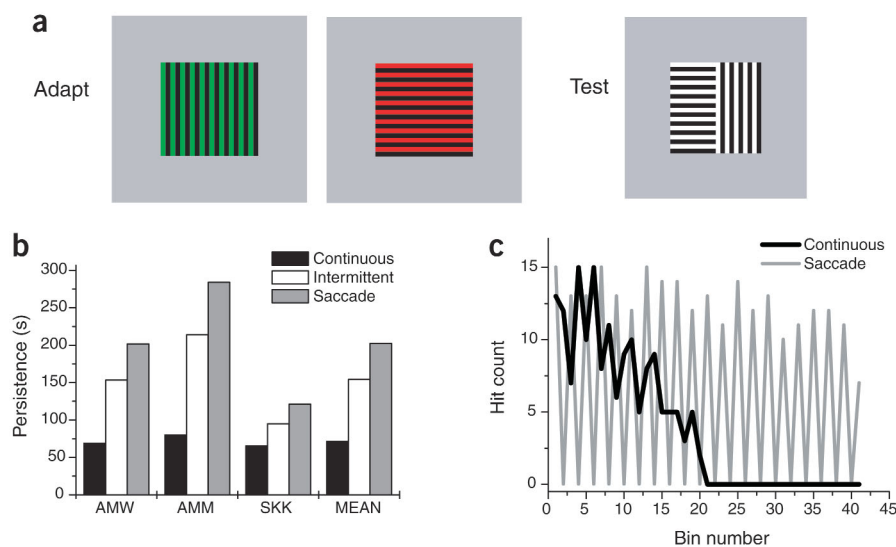
whenever the two grating components of the test stimulus appeared to be differently colored. In all conditions, the test stimulus was foveated during the time in which subjects indicated changes in its color. The response button was polled once per second. A trial terminated after 5 min or earlier if no hit had been recorded for 10 s.

As in experiment 1, there were three conditions: continuous, intermittent and saccade. The McCollough effect persisted much longer in the saccade condition than in the other two (**Fig. 3b**). Intermittency itself increases persistence, but saccades make it even longer (roughly three times longer) than in continuous viewing.

Saccades also made the illusory colors more vivid while the effect persisted (**Fig. 3c**). As in experiment 1, the effects of saccades in experiment 2 were large, but in the opposite direction: they reduced the time for which the states of ambiguous figures persist but increased the persistence of the McCollough effect. There was a significant effect of viewing condition in experiment 2 ($P < 0.001$).

DISCUSSION

Our results indicate that saccades eradicate immediately past perceptual states that could inhibit visual analysis, and they strengthen learned contingencies. Both effects may be due, at least in part, to attention being drawn to the objects that are the targets of saccades[10–13,22–24].

There is evidence to suggest that vision has little or no trans-saccadic memory. Substantial shifts of the position of saccadic targets during saccades go unnoticed[25], and we are blind to many changes made to objects in a scene while saccades are in progress[26]. There is also evidence that trans-saccadic visual memory is substantial. Humans and monkeys can make accurate saccades in the dark from memory[27]; humans can also point accurately in the dark to the very stimuli that they mislocate perceptually[28–30]. Furthermore, it has been shown that recollection for the structure of a scene builds up over several seconds while subjects make saccades to examine its details[7,9]. The key to the apparent contradictions in the evidence about the effects of saccades may be the existence of two different representations of visual space, one disrupted by saccades, the other not[28–30].

Some parietal neurons shift their receptive fields before eye movements, anticipating the consequences of saccades[31]. In doing so, they might disrupt existing visual representations but facilitate remapping after saccades[32]. Neurons in another area, the frontal eye field (FEF), seem to maintain a memory of the visual world in the absence of visual stimulation[33], and neurons in the lateral intraparietal area (LIP) seem to highlight stimuli that are behaviorally significant at the time of saccades[34]. Recent evidence shows that cells in primate FEF respond when a stimulus is present in their receptive fields in the encoding stage of a delayed matching-to-sample experiment, not while the eyes are shifted to a position eccentric to the stimulus during the delay stage[35]. It seems that the FEF is not only coding for eye position, but also possibly acting as a memory buffer for a saccade plan of earlier origin. This evidence indicates that saccades can affect both memory and the mapping of space. Saccades have also been shown to modulate levels of activity in frontoparietal areas within the cortex[4,36] that have been implicated in the alternation of the states of ambiguous figures by recordings of neural activity[37] and by fMRI studies[38]. Recent work shows that subsets of neurons in dorsal region MT/V5 seem to signal one or the other of the two configurations of bistable stimuli[39].

The results reported here suggest that saccades disrupt one type of visual representation—the temporary states of unstable figures—while enhancing another representation that preserves learned stimulus contingencies. A flexible representation for visual analysis would be useful when gaze is constantly shifting to examine parts of a scene. Yet it would be computationally expensive for the brain to rebuild the whole scene from scratch after each saccade.

Saccades could also have another functional benefit. A representation of space that is built up over time, and is strengthened by saccades, could act as a map representing spatial relationships within a scene. This map could be used to guide behavior when immediate visual information is degraded. Recent work indicates that while visual sensitivity is compromised at the time of a saccade, and gross errors are made in the perception of spatial position, it is still possible to (blindly) point with high accuracy to the location of a target in space[28–30].

METHODS

Subjects. The same three subjects (2 female, ages 26 and 32, and one male, age 44) participated in all three conditions of experiment 1. The two female

subjects also participated in experiment 2, but the male subject, who had a strong resting McCollough effect from conditioning some years earlier, was replaced by another (SKK, age 25). All subjects had normal vision except SKK whose vision was corrected to normal. One author (AMW) served as a subject. All other subjects were experienced psychophysical observers who were naive to the purpose of the experiments. Subjects were not informed of their results until the completion of all experiments, to avoid speculation and discussion. All subjects gave informed, written consent before participating in the experiment.

Stimuli. Stimuli were generated on a Cambridge Research Systems VSG2/4 graphics card and presented on a 52-cm Hitachi Accuvue color monitor with a spatial resolution of 800×600 pixels at a non-interlaced frame rate of 120 Hz. Stimuli were presented in the center of a gray screen ($11.4 \mathrm{~cd~m}^{-2}$), with no fixation spot, and viewed binocularly from a distance of 78 cm. Subjects were asked to keep their gaze fixed on the center of the screen except when required to transfer it to a peripheral fixation spot in condition 3 (saccade) of experiments 1 and 2, which appeared when the stimulus disappeared and vanished when it reappeared.

The Necker cube stimulus was drawn with white lines ($27 \mathrm{~cd~m}^{-2}$), the sides of the squares being 3.2° and the connecting struts 1.3° in length; all lines were 6′ in width. The binocular rivalry stimulus consisted of two Gabor patches on square backgrounds presented dichoptically by displaying them on alternate frames while subjects viewed the screen through liquid-crystal goggles (Cambridge Research Systems FE-1), toggled in synchrony with the display screen. The radius of both Gabor patches was 3.1°, their spatial frequency 1.4 c.p.d., their mean luminance $6.9 \mathrm{~cd~m}^{-2}$, and their maximum contrast 0.54. The left eye's patch was greenish and tilted clockwise, the right eye's patch reddish and tilted counter-clockwise.

The 'Glass line' stimulus consisted of a cycle of 20 patterns shown repeatedly in sequence at a rate of 30 Hz. Each pattern was made independently by positioning 200 points at random within a circular disc of radius 6.6° (except within a central area of radius 33′). A $27 \mathrm{~cd~m}^{-2}$ white line 1.3° in length and 3.6′ in width was then centered on each point, orthogonal to the radius connecting it to the center of the disc. A fresh set of patterns was used on each trial. Though the motion signals arising from such a sequence are incoherent, subjects see circular spin that reverses direction from time to time[19].

The stimuli to establish adaptation for the McCollough Effect consisted of two high-contrast squarewave gratings, each 6.4×6.4°, one horizontal with black and red bars, the other vertical with black and green bars. Each had a spatial frequency of $1.4 \mathrm{~c~d}^{-2}$. The test stimulus was composed of two halves, one containing a black and white horizontal squarewave grating, the other a black and white vertical squarewave grating.

Procedure. Subjects used a chin rest to view all displays. They were alerted to the two possible phases for each bistable stimulus. Subjects were given a response box with three buttons. Two of the buttons were assigned to states; one for each state in the bistable figure. In experiment 1, subjects were asked to press the button corresponding to the state, whenever a state change occurred. These buttons were polled by the computer and the button-press times were recorded.

They were instructed to press the appropriate button whenever a change of state occurred; in case of uncertainty they were also at liberty at any time to press the button appropriate to the state currently in view: the computer ignored button presses that did not indicate a change of state. In condition 1 (continuous) of experiment 1, the stimulus remained continuously in view for 250 s. In condition 2 (intermittent), it remained on for 5 s and disappeared for 5 s of each. The total time the stimulus was on display was again 250 s. In condition 3 (saccade), the stimulus was presented intermittently as in condition 2, but in the stimulus-off times, a fixation point appeared randomly at a distance of 6.2° from the center of the screen. Subjects made a saccade to transfer their gaze to the fixation point when the stimulus disappeared and another back to the center of the screen when the stimulus reappeared. The stimulus was therefore foveated when subjects indicated state changes. Eye movements were not monitored, as all subjects were experienced in making voluntary saccades. The computer ignored any button presses during stimulus-off times in conditions 2 and 3, and ignored stimulus-off periods in calculating the durations of state times.

In experiment 2, each trial began with an adapting period. The two adapting gratings were shown alternately, each five times for 5 s. The test stimulus was then displayed for a maximum 300 s. As in experiment 1, there were three conditions: continuous, intermittent and saccade. The test stimulus was alternately on for 5 s and off for 5 s as in conditions 2 and 3 of experiment 1 and, as in experiment 1, a remote fixation point appeared in the stimulus-off times of condition 3 (saccade). Subjects were required to hold down a response button whenever the two half gratings of the test stimulus appeared differently colored and to release it when they appeared the same. The response button was polled every second. A trial expired when 300 s had elapsed, or earlier if no button press had been recorded for 10 s. The duration of the McCollough effect was calculated from the time of the last button press registered. There were three trials for each condition, and condition order was randomized within each triplet of conditions.

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