Spatiotopic Transfer of Visual-Form Adaptation across Saccadic Eye Movements

David Melcher[1,2,*]
[1]Faculty of Psychology
San Raffaele University
Via Olgettina 58
20132 Milan
Italy
[2]Department of Psychology
Oxford Brookes University
Gipsy Lane
Oxford OX3 OBP
United Kingdom

Summary

Although conscious perception is smooth and continuous, the input to the visual system is a series of short, discrete fixations interleaved with rapid shifts of the eye. One possible explanation for visual stability is that internal maps of objects and their visual properties are remapped around the time of saccades, but numerous studies have demonstrated that visual patterns are not combined across saccades. Here, we report that visual-form aftereffects transfer across separate fixations when adaptor and test are presented in the same spatial position. The magnitude of the transsaccadic adaptation increased with stimulus complexity, suggesting a progressive construction of spatiotopic receptive fields along the visual-form pathway. These results demonstrate that basic shape information is combined across saccades, allowing for predictive and consistent information from the past to be incorporated into each new fixation.

Results

To investigate the mechanisms involved in visual stability, we chose to examine perception of visual-form aftereffects [1–4]. Adaptation aftereffects hold several advantages for studying transsaccadic perception. First, adaptation can persist over time periods longer than a typical fixation, allowing the adaptor and test stimuli to be separated by one saccade. Second, aftereffects are thought to involve the selective adaptation of a specific set of anatomically circumscribed neurons along the visual processing stream [5–7]. Contrast adaptation, for example, depends on cells in early visual areas such as the lateral geniculate nucleus and primary visual cortex [8–10], whereas face adaptation is contrast independent and is thought to involve specialized areas, such as the fusiform gyrus, at a more advanced stage of the visual hierarchy [11–13]. Four different adaptation aftereffects were chosen to represent lower and higher stages of visual-form processing (Figure 1). This made it possible to study the nature of visual representations along the processing stream, ranging from those closely tied to exact pictorial quali-

ties (contrast) to more-abstract visual properties related to object identification (faces).

In order to be useful, integration of information across saccades should be confined to the same object or location. Four basic conditions were tested to measure the magnitude of the transsaccadic aftereffect and its spatial specificity. In the baseline condition, responses were measured with fixation and without any adaptor. In the second condition, both the adaptor and test stimuli were viewed peripherally from central fixation in the same retinal position (retintopically matched adaptation). These first two conditions allowed for measuring the magnitude of the basic adaptation effect in the periphery. In the remaining two conditions, the adaptor was fixated in one of two lateral locations, and this was followed by a saccade to the center of the screen (Figure 2). Then, the test stimulus was presented in either the same spatial location as the adaptor (statiotopically matched) or in the opposite side of the display at the same retinal eccentricity. Thus, the retinal distance between the adaptor and test was identical in the two saccade conditions. These four conditions made it possible to measure a basic adaptation effect (retinotopic) and to compare this to the spatially specific and nonspecific aftereffects found across saccades.

Overall, the spatially specific adaptation aftereffect increased with stimulus complexity (Figure 3, circles). Contrast adaptation did not occur across saccades, consistent with earlier studies that used similar stimuli [14]. Tilt and shape adaptation, however, resulted in a specific, spatiotopically modulated aftereffect. When the adaptor and test were shown in the same spatial location across saccades, a strong aftereffect was found, equal to more than half the effect found with full retinotopic adaptation without saccades. There was little or no influence of the tilt or shape adaptor on the test stimulus shown at the same retinal distance in the opposite side of the display of the adaptor (Figure 3, squares). For face adaptation, complete spatiotopic transfer of adaptation was found across saccades, along with a spatially nonspecific effect of smaller size. Presumably this nonspecific aftereffect reflects the relative positional and size invariance of face adaptation [11–13]. This nonspecific effect occurred despite the presentation of a second stimulus (house) in the opposite hemifield during the adaptation phase.

Interestingly, the difference in aftereffect size between the spatially matched and unmatched locations was similar in magnitude across the three form conditions (Figure 3, squares). This implies that both spatiotopic and nonspecific adaptation increase as stimulus complexity grows and as the locus of the relevant adaptation moves from early to later visual-form processing areas.

Discussion

The current findings show that visually detailed information can persist across saccades and influence sub-

*Correspondence: david.melcher@psy.ox.ac.uk
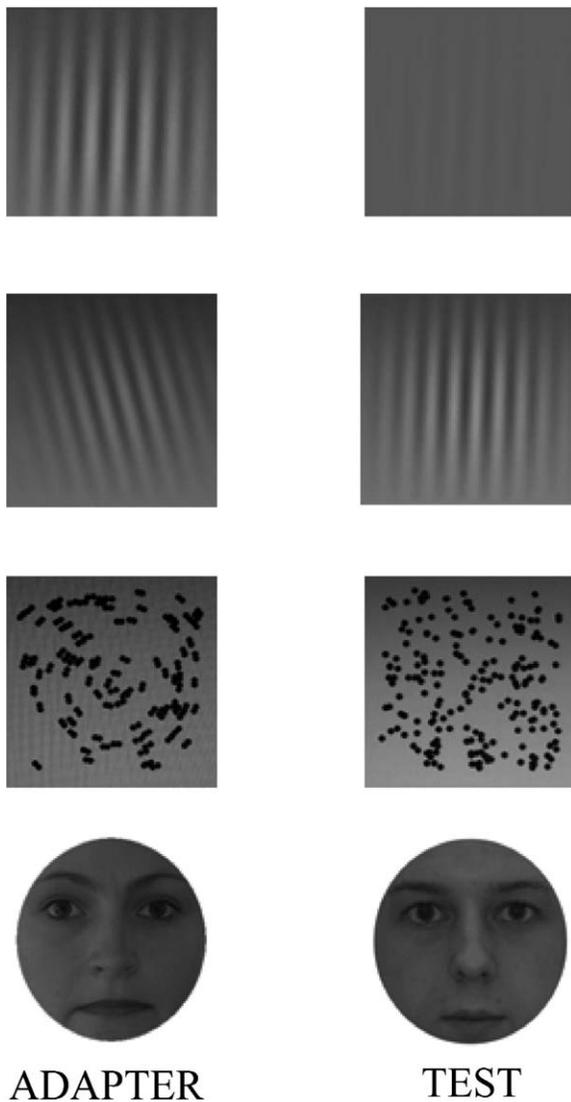
ADAPTER   TEST

Figure 1. Stimuli Used to Measure Form-Adaptation Aftereffects

Adaptation effects can be observed by fixating the adaptor on the left for 5 s and then the test stimulus on the right. In the case of tilt adaptation (second row), for example, the perceived tilt of the test is shifted stimulus away from the orientation of the adaptor. The contrast and tilt stimuli (top two rows) were Gaussian-windowed sinusoidal luminance patterns that subtended 4° visual angle. The dynamic form adaptor (third row) was made up of 100 dark dots that were oriented in a radial or circular pattern. The face and form stimulus both subtended 6° visual angle.

sequent perception of an object in the same spatial location. The transsaccadic-adaptation effect found here suggests that analysis and recognition of even simple forms—such as circles and squares—are mediated by neurons whose receptive fields are not only retinotopic but are also linked to external space.

The finding that an increase in stimulus complexity resulted in a corresponding increase in transsaccadic adaptation suggests a progressive construction of receptive fields that are neither retinotopically defined nor spatially invariant. In the case of tilt and shape adapta-
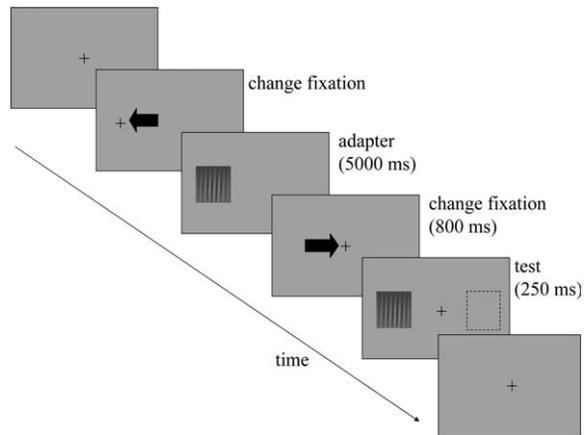

Figure 2. Experimental Events for Saccade Trials

The adaptor was presented for 5 s, followed by a change in fixation position (10°). After a 800 ms delay, the test was presented for 250 ms in either the same spatial location as the adaptor or in the opposite side of the screen at the same distance from fixation.

tion, which have been correlated with activity in areas such as V2 and V4 [7, 15], the effect of the adaptor was less than that found with full retinotopic adaptation. This intermediate level of adaptation transfer might be mediated by a mixture of retinotopic and spatiotopic receptive fields in the same population of neurons. This idea is supported by a study of the response of neurons to stimuli in the location where their receptive field would be after an imminent saccade [16]. Around half (52%) of the V3A cells responded to the stimulus in their "new" receptive field, whereas only around 10% of V2 cells responded to the new stimulus. It is important to note, however, that the transient shift of receptive fields lasted for only 100 ms around the time of the saccade [16], whereas adaptor and test in the present study were separated by 800 ms.
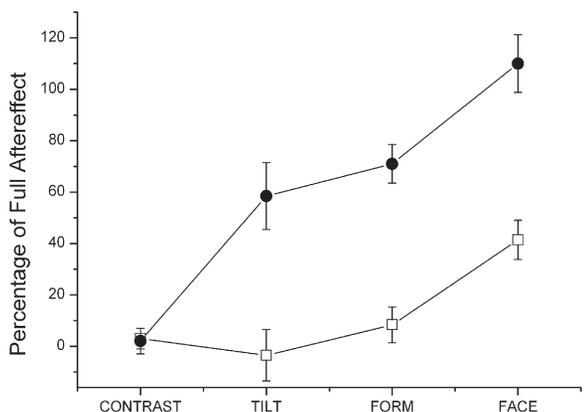
A second potential explanation for the intermediate

Figure 3. Adaptation Aftereffect for the Four Stimulus Types Tested

For five subjects, average data showing aftereffect magnitude for spatiotopically matched (red circles) and unmatched stimuli (non-specific aftereffects: black squares). Error bars indicate standard error.

effects found here is gaze modulation, which could serve a role in the transition from retinotopic to head-centered coordinates [17, 18]. Eye-position modulation has been found in areas such as V5/MT+ and in V4 [19]. A small but significant effect of gaze direction has been reported for visual adaptation [20]. In the present study, however, gaze direction was similar in the spatiotopically matched and unmatched conditions, excluding gaze direction per se as an explanation.

In order to show integration across saccades, a spatiotopic receptive field must retain sensitivity to the same location in external space. For some groups of cells, such as those in V3A, this change is transient and contingent to the saccade [16], such that the cell effectively remains retinotopic. Other neurons in areas of parietal cortex [21, 22], V6 [23], and possibly MT+ [18, 24] appear to show true spatiotopy. One interesting possibility is that the first group of cells, which show transient and incomplete spatial remapping, could serve as the intermediate stage in a process that uses gaze information to build eye-independent receptive fields [22]. However this selectivity is achieved, the current results imply that form processing is not a simple feedforward system of retinotopic receptive fields defined by the combination of outputs from earlier visual neurons.

Evidence for the integration of visual-form information across saccades was initially reported in a study of visual pattern integration [25], suggesting the existence of a metric transsaccadic memory buffer. These results, however, were later shown to be an artifact of phosphor persistence on the display screen [26]. Subsequently, a number of studies have demonstrated that patterns are not spatiotopically fused across saccades, arguing against transsaccadic integration of form [27, 28]. On closer consideration, however, metric pattern integration might not be a useful strategy for the visual system because double images could result if the orientation or position of objects changed with respect to the observer across saccades. A truly metric memory buffer might also be disrupted by the spatial compression and visual suppression found around the time of saccadic eye movements [29]. The current results imply that there is no need to fuse together separate snapshots of the world. Instead, the progressive transformation from retinotopic to eye-independent receptive fields may provide a simple and elegant strategy to maintain visual stability while incorporating useful and predictive information from previous fixations.

Experimental Procedures

The author and four naïve observers took part in the experiments. All had normal or corrected-to-normal vision. Stimuli were displayed on a Sony F520 monitor and viewed from a distance of 60 cm. Experiments were run with MATLAB software (Mathworks) and VSG graphics (Cambridge Research Graphics). Adaptor and test stimuli subtended six degrees of visual angle.

There were four conditions for each stimulus type. Each trial was begun with a button press. In the baseline condition, observers fixated centrally and were presented with the test stimulus in one of two peripheral locations. In the remaining three conditions, the trial began with a 5 s adaptation period, followed by a 800 ms delay, a 250 ms test stimulus, and, finally, a blank screen for response. In the "full adaptation" condition, both adaptor and test were presented in the same peripheral location.

Whereas fixation was maintained in the center for the first two conditions, the second two conditions involved a series of eye movements (Figure 2). At the beginning of the trial, the fixation cross moved to one of the two eccentric positions (chosen randomly on each trial). After the button press, the adaptation stimulus was presented at the lateral fixation point. The second eye movement was triggered by the simultaneous disappearance of the adaptor and appearance of the fixation cross at the center of the screen. While observers fixated the central cross, the test stimulus was shown either to the right or to the left of fixation. In the spatially matched condition, the adaptor and test were shown in the same location, and in the unmatched condition, the test was shown in the opposite side of the screen from where the adaptor had been presented. Note that the retinal distance between the adaptor (displayed at the fovea) and the two test conditions was identical for spatially matched and unmatched conditions.

After two blocks of practice trials with the first (no adaptor) condition and a single block of practice trials with the remaining three conditions, the separate conditions were run in an interleaved, randomized order. Each block contained 50 trials, with the first two conditions run in separate blocks and the two saccade conditions run (randomly interleaved) in the same blocks of 50 trials.

Eye position was monitored with a ViewPoint video-based eye tracker (Arrington Research). Average saccadic latency across all observers was less than 400 ms, signifying that saccades tended to be made within the first half of the delay period. Only one observer made an error in the pattern of eye movements during the experimental trials, at which point data collection was stopped until the observer completed an additional block of practice trials.

Contrast thresholds and adaptation effects were calculated for each observer with standard procedures (see the Supplemental Data available with this article online). The magnitude of the tilt aftereffect was measured by comparing baseline tilt judgments for gratings tilted from −4° to 4° to judgments for the same stimulus after presentation of a grating tilted 15° to the right or left. As found previously, perceived tilt was biased in the opposite direction of the adaptor [30, 31]. The magnitude of this effect was estimated by fitting a curve to the data from each condition and estimating the 50% point at which the stimulus was perceived on an equal number of trials to be tilted to the right or the left (see Supplemental Data). Shape adaptation was measured with a dynamic form stimulus, a variant on previous studies of circular/radial adaptation [32, 33]. The adaptor contained random pairs of oriented dots that could be aligned in either a radial or concentric pattern at 100% coherence, whereas the test stimulus contained either a weakly (30%) radial, random, or weakly circular pattern (see Figure 1). The percentage of trials in which subjects judged the stimulus to be radial versus concentric was tested with and without a dynamic radial or concentric adaptor. The magnitude of the adaptation effect was measured by comparing the average difference in responses for trials containing a radial adaptor and those with a concentric adaptor. As expected, observers were more likely to respond that the stimulus was radial after they were shown a concentric adaptor, and vice versa [32, 33].

Face adaptation was measured with conventional methods [11–13]. In this experiment, observers identified each test stimulus as one of three possible targets. All three targets, which were male faces, were morphed with a female adaptor. Overall, the percentage of correct discrimination increased as the percentage of male target was augmented (see Supplemental Data). Presentation of the female adaptor increased discrimination performance, leading to a measurable face-adaptation aftereffect [11–13].

Supplemental Data

Supplemental Data, including two figures, are available at http://www.current-biology.com/cgi/content/full/15/19/1745/DC1/.

Acknowledgments

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