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Selective attention and the active remapping of object features in trans-saccadic perception

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ABSTRACT

When the same object is attended both before and after a saccadic eye movement, its visual features may be remapped to the new retinal position of the object. To further investigate the role of selective attention in trans-saccadic perception, the magnitude of the cross-saccadic tilt aftereffect was measured for both attended and unattended objects. The results show that both selective attention and saccadic eye movements influenced the magnitude of the tilt aftereffect, but in different ways. Dividing attention among multiple objects lead to a general decrease in the tilt aftereffect, independent of whether or not a saccade occurred. Making a saccade also resulted in a consistent reduction of the aftereffect, but this was due to incomplete transfer of form adaptation to the new retinal position. The influences of selective attention and saccadic remapping on the tilt aftereffect were independent and additive. These findings suggest that trans-saccadic perception is not limited to a single object but instead depends on the allocation of selective attention. Overall, the results are consistent with the hypothesis that the role of attention is to select salient objects, with trans-saccadic perception mechanisms acting to maintain information about those salient objects across eye movements.

1. Introduction

Visual perception in a complex environment requires numerous shifts of attention and gaze. Saccadic eye movements tend to change the location of the attended object on the retina, which raises a number of problems for visual perception. It is critical to keep track of the location of objects across saccades in order to guide goal-directed behavior (Hayhoe, Lachter, & Feldman, 1991; Heide et al., 2001; Land & Hayhoe, 2001; Medendorp, Goltz, Vilis, & Crawford, 2003; Vaziri, Diedrichsen, & Shadmehr, 2006). In addition, the displacement of an object on the retina interrupts the processing of visual features by neurons with retinally defined receptive fields. The existence of frequently gaze shifts raises the question of how it is possible that visual experience appears smooth and continuous despite the frequent occurrence of saccades.

This study examines two potential mechanisms that may work together to ensure that we perceive a stable world across eye movements: selective attention and trans-saccadic perception. One of the most important roles of selective attention may be to exclude irrelevant objects from influencing behavior. The lack of detailed processing of, and memory for, the vast majority of the environment at any given point in time ensures that we do not need to update the representations of objects that were never attended (O'Regan and Noë, 2001). One strategy to ensure that the world is perceived as stable may be to take advantage of the fact that the world is indeed stable. In laboratory studies, people are poor at noticing when non-salient objects in complex scenes appear and disappear without accompanying visual transients. In real life, the visual system is quite sensitive to such transients, which attract selective attention based on motion cues rather than memory (Kanai & Verstraten, 2004; O'Regan and Noë, 2001).

Although selective attention may eliminate the need to keep track of the location of non-salient objects across saccades, a further step is required to explain trans-saccadic perception of salient items. Two related mechanisms have been proposed to explain perceptual stability: active remapping and spatiotopy. In the former case, visual processing is thought to be anchored in retinotopic coordinates. Trans-saccadic perception results from the dynamic "remapping" of retinotopic receptive fields around the time of saccadic eye movement. Consistent with this hypothesis, a subset of neurons in areas associated with eye movement planning change their receptive fields around the time of saccades (Duhamel, Colby, & Goldberg, 1992; Kusunoki & Goldberg, 2003; Merriam, Genovese, & Colby, 2003; Sommer & Wurtz, 2006; Umeno & Goldberg, 1997). Some of these neurons respond to stimuli placed in their future receptive field, while others respond to the stimulus in the current receptive field or, in some cases, the neuron may be activated by stimuli in both the current and the future

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receptive field. In addition, after the saccade many neurons continue to respond to stimuli in the pre-saccadic receptive field (for review, see Colby & Goldberg, 1999). In addition to its role in updating spatial location, remapping may play a role in visual processing itself. The visual selectivity of neurons in areas showing remapping (Durand et al., 2007; Lehky & Sereno, 2007; Sereno & Maunsell, 1998; Toth & Assad, 2002)—areas which project to visual processing areas such as V4 and TEO (Baizer, Ungerleider, & Desimone, 1991; Webster, Bachevalier, & Ungerleider, 1994)—implies a close link between visual processing and the parietal saliency maps thought to underlie eye movements and dynamic remapping. Moreover, remapping has also been found in visual cortex (Merriam, Genovese, & Colby, 2007; Nakamura & Colby, 2002; Tolias et al., 2001).

Thus, there appears to be an important overlap between areas involved in spatial attention, eye movements and remapping. Posterior parietal cortex, which is considered part of the spatial attention network (Corbetta, 1998; Kastner & Ungerleider, 2000; Mesulam, 1981), may also play an important role in both remapping and in computing the saliency of objects in the scene (Colby & Goldberg, 1999; Gottlieb, 2007). This possible link between remapping and attention is also supported by experimental evidence showing that the saccadic programming itself can influence conscious perception of salient objects (Hafed & Krauzlis, 2006; Melcher, 2007; Ross & Ma-Wyatt, 2004; Wexler, 2005; Wexler, Panerai, Lamouret, & Droulez, 2001). In addition, deficits in both attention and in keeping track of objects across gaze shifts are found in neurological patients with parietal damage (Duhamel, Goldberg, Fitzgibbon, Sirigu, & Grafman, 1992; Sapir, Hayes, Henik, Danziger, & Rafal, 2004).

A contrasting set of proposals, grouped here under the umbrella term "spatiotopic", focus on a different explanation for trans-saccadic perception: non-retinotopic coordinate systems. According to this idea, visual stimuli are processed in coordinate systems tied to external space (Colby & Goldberg, 1999; Duhamel, Bremmer, BenHamed, & Graf, 1997; D'avossa et al., 2006; Galletti & Battaglini, 1989; Graziano, Yap, & Gross, 1994; Snyder, Grieve, Brotchie, & Andersen, 1998), to specific objects (Melcher, 2005; Melcher & Morrone, 2007; Olson, 2003; Olson & Gettner, 1995; Ward & Arend, 2007) or to a post-saccadic reference such as the saccade target (Deubel, Schneider, & Bridgeman, 2002; Hamker, Zirnsak, Calow, & Lappe, 2008; Lappe, Awater, & Krekelberg, 2000). Trans-saccadic integration, then, could reflect the ability of these non-retinotopic neurons to combine information across gaze shifts. It is important to note, however, that these theories are not necessarily mutually exclusive and may, instead, capture different aspects of a process that aligns—across saccades or other body movements—the network of spatial maps in the brain that encoded objects and actions in multiple coordinate systems (Crawford, Medendorp, & Marotta, 2004; Hamker et al., 2008; Melcher, 2008; Zipser & Andersen, 1988).

Critically, both types of explanations for perceptual stability suggest a link between trans-saccadic effects and attentional selection of a specific spatial location, salient object, or saccadic target. The exact role of selective attention in space or object-based matching across saccades, however, has not been fully explored. Previous studies examining visual remapping have typically used simplified displays with only one or a few objects and have not manipulated which, if any, object was selected by attention. What, then, is the role of selective attention in trans-saccadic perception?

1.1. Motivation of the current study

The main focus of this study was to measure a trans-saccadic adaptation aftereffect (Melcher, 2005; 2007) for attended and non-attended stimuli. One possibility, based on previous research, is that remapping might occur only for a single attended object. Performance across saccades in a variety of tasks tends to be better for the saccadic target (Kowler, Anderson, Dosher, & Blaser, 1995), with "bystander" stimuli showing little or no trans-saccadic memory (Germeys, De Graef, & Verfaillie, 2002; McConkie & Currie, 1996). Moreover, neurons in area LIP, which appears to be critical for dynamic remapping, do not strongly represent unattended objects in the saliency map (Gottlieb, Kusunoki, & Goldberg, 1998; Ipata, Gee, Goldberg, & Bisley, 2006). Thus, one might predict that an object receiving little focused attention would fail to show any trans-saccadic perceptual effects.

In contrast, a number of studies have suggested that trans-saccadic memory has a capacity of around 3–4 items (Irwin, 1992; Melcher, 2001; Prime, Tsotsos, Keith, & Crawford, 2007). It remains an open question, however, whether the number of objects that show trans-saccadic perceptual effects, studied here using adaptation aftereffects, is related to working memory capacity. Critically, the present study measures perception of an aftereffect rather than explicit memory. Orientation aftereffects do not depend on conscious awareness or recollection of the orientation of the tilted stimulus (He, Cavanagh, & Intriligator, 1996; He & MacLeod, 2001), while working memory depends on the comparison of a consciously perceived stimulus with one stored in memory. Despite these large differences in the task being studied, the fact that observers can typically report changes in orientation for three or four stimuli across a saccade (Prime et al., 2007) is at least suggestive that trans-saccadic aftereffects could occur for two or more stimuli.

The phenomenon of adaptation lends itself to studying perception across saccades for several reasons. First, adaptation persists longer than a typical fixation. Second, adaptation alters subsequent processing and thus reflects a change in visual processing based on previous experience (Bednar & Miikkulainen, 2000; Georgeson, 2004; Schwartz, Sejnowski, & Dayan, 2006; Wainwright, 1999). Third, adaptation is highly specific for a limited spatial location: there is typically no measurable aftereffect, at least for simple features such as contrast, tilt or curvature, when the test stimulus is shown at a distant retinal location. When the spatial location of the adapter and test is matched on the screen, however, form adaptation aftereffects across saccades can transfer to the new retinal position (Melcher, 2005; 2007). This transfer of the aftereffect occurs pre-saccadically, tied to the intention to make a saccade (Melcher, 2007), consistent both qualitatively and temporally with the pattern of remapping found in single neurons (Duhamel, Colby, et al., 1992; Kusunoki & Goldberg, 2003).

In this study, the magnitude of the trans-saccadic aftereffect was measured for both attended and unattended locations with a display of two objects. On each trial, either one or both of the objects were task-relevant and the test stimulus was presented at either an attended or unattended location. Neither object was the saccadic target. In separate blocks of trials, the participant either maintained fixation during the entire trial or was instructed to make a saccade to a new fixation point during the delay period between the adaptation and the presentation of the test stimulus. This manipulation allowed for separate measures of the influence of selective attention and to measure any interactions between attention and saccades on adaptation aftereffects.

2. Methods

2.1. Subjects

Five adults with normal vision participated in the experiment. All observers gave informed written consent.

2.2. Materials

Stimuli were presented on a Sony F520 monitor running at a refresh rate of 100 Hz, viewed from a distance of 60 cm. Experiments were run with MATLAB software (Mathworks, Inc.) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The adapter and test stimuli subtended 4° of visual angle.

Eye position was monitored during the experiment with the Viewpoint eye tracker (Arrington Research Ltd.). The calibrated eye position during the trial was recorded and analyzed offline to ensure that all observers followed the experimental protocol correctly. Trials in which the observer failed to make the saccade at the correct time or deviated gaze by more than 1° from fixation during the adapter or test period were excluded from further analysis (less than 1% of the trials).

2.3. Procedure

The experiment was preceded by a practice session of 20 trials with the test stimulus presented for 50 ms at the cued location. This practice session familiarized the participants with the basic task of orientation direction discrimination. The test stimulus was presented in one of seven orientations: −4°, −2°, −1°, 0°, 1°, 2° or 4°. After each trial, a written prompt was presented on the screen asking for a keypress to indicate whether the stimulus had been tilted to the left or to the right. The experiments were self-paced, with each trial begun by the observer pressing a key.

The basic design was similar across all experimental conditions (Fig. 1). After the keypress to begin the trial, a red dot appeared at a location in the periphery. This position was displaced horizontally by ±8° and vertically by ±4° from the fixation point and indicated the location where the observer should direct selective attention. The presentation of the red dot was a cue to shift attention to that location in order to concentrate on the adapter stimulus that would appear at that position. The attended adapter stimulus was shown for 3 s, during which time it briefly dimmed either four or five times. Subjects were instructed to count the number of dimming periods. Each participant was given a block of 20 practice trials with the counting task. The adapter was tilted 20° in orientation, with half of the trials containing a grating tilted to the left and half tilted to the right. The difficulty of the dimming task was adjusted, using a staircase procedure, by changing the magnitude of the contrast decrement in order to maintain performance at around 75% correct on the counting task. Across blocks, performance never fell below 68% and never exceeded 90%. After the disappearance of the adapting stimulus, there was a delay of 800 ms before the presentation of the test stimulus, followed by a 200 ms blank delay and then the prompt to indicate the number of dimming periods and the orientation of the test stimulus.

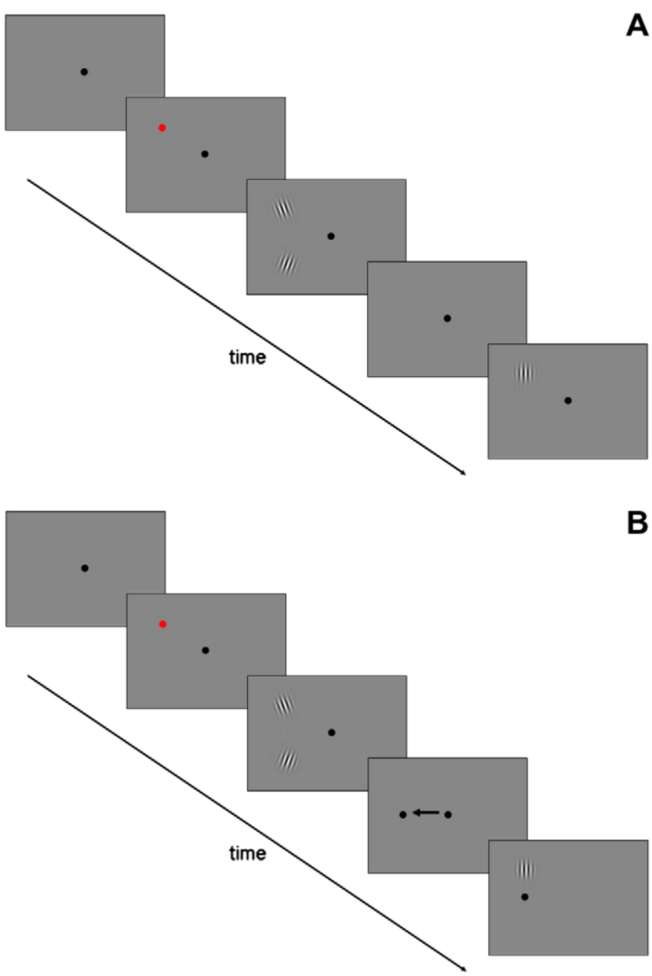

Fig. 1. Illustration of the order of events in trials. (A) Depiction of the order of events on trials with maintained fixation and with attention directed to only one adapting stimulus. This pattern of events represents the situation in which the test stimulus was shown at the attended location, which was the case on only 50% of trials. (B) Depiction of the order of events in trials in which the fixation point was displaced horizontally during the delay period between the adaptation period and the presentation of the test stimulus (see Section 2).

In the first condition ("baseline"), only one adapter stimulus was presented during the 3 s adaptation period. This condition was used to estimate the maximum possible tilt adaptation aftereffect for each observer, which served as a baseline for characterizing performance in the other conditions. This condition was run in separate blocks from the experimental condition, with the order of all blocks counterbalanced across observers.

In the main experimental conditions, two adapter stimuli were presented. As described above, the adapters were offset vertically from the center of the screen by ±4° and were of opposite orientations. In the "attend one" conditions, the presentation of the red circle served as a cue to the participant to focus attention on one adapter only, in order to count the number of dim periods (4 or 5), while ignoring the second grating shown nearby. The test stimulus was then shown at either the attended or unattended location, randomized across trials (Fig. 1A). In separate blocks of trials, observers were instructed to make an 8° horizontal saccadic eye movement during the trial. Following the disappearance of the adapter stimulus, the fixation point was displaced horizontally by 8° after a delay of 100–300 ms to a position at the center of where the two adapters had been displayed. This displacement served as a cue to make a saccade to the new fixation point, which was located between the two possible test locations (Fig. 1B).

In the other two conditions ("attend both"), subjects were instructed to pay attention to both adapters. On those blocks of trials, red circles to cue attention were shown at the location of both adapters and participants were told to discriminate which adapter showed more dimming periods. Each condition (one or two attended stimuli) was run in separate blocks. Trials with maintained fixation and trials with cued saccades were run in separate blocks of trials. Overall, there were seven conditions, each of which involved 280 trials (7 test orientations, 2 adapter orientations, 20 trials). The experiment was run in blocks of 70 trials, with the order of the experimental condition counterbalanced across subjects.

2.4. Data analysis

Proportion of trials in which the observer responded "Left" was calculated for each orientation of the test stimulus for each condition. The data from each subject was fit with a sigmoid Boltzmann function (Non Linear Least Squares Fitter, Origin 8 software, OriginLab, USA). Modeling the proportion of "Left" responses y, the function has the form $y = A2 + (A1 - A2)/(1 + \exp((x - x_0)/w))$, where x_0 is the midpoint of the function and w parameterizes the width of the psychometric curve. All functions fit the data significantly, with $R^2 >= 0.98$ and χ^2 values significant at the criterion $p < .01$. The midpoint of the Boltzmann function was used as the estimate of the point of subject equality (PSE) at which participants perceived the stimulus as tilted to the left on 50% of the trials. Confidence intervals for the value of x_0 were calculated using the Non Linear Least Squares Fitter and used to analyze within-subject differences. Leftward and rightward tilted adapters were plotted separately to measure the distance between the two psychophysical curves. The magnitude of tilt aftereffect (TAE) was calculated as the distance between the 50% point for rightward and leftward tilted adapters.

Performance on the baseline condition was used to estimate a "maximum tilt aftereffect" for each participant. This value varied across participants, ranging from 2.65° to 4.21°. Based upon this maximum value, the "proportion of full TAE" was calculated for each observer and each condition (Melcher, 2005; 2007). For example, a TAE of 2° in a particular condition, given a maximum TAE of 4° for that observer, would be recorded as a proportion of 0.5 out of a possible 1.0. The proportion of full TAE was used for all between subjects statistical analyses.

3. Results

As expected, the perceived tilt of the stimulus in the control condition with only one adapter was biased towards the direction opposite to that of the adapting grating (Fig. 2). Thus, all observers showed the classic tilt aftereffect (Blakemore & Campbell, 1969; Gibson & Radner, 1937). As expected, the tilt aftereffect (TAE) was strongest in the control condition with only one adapter and no saccadic eye movements.

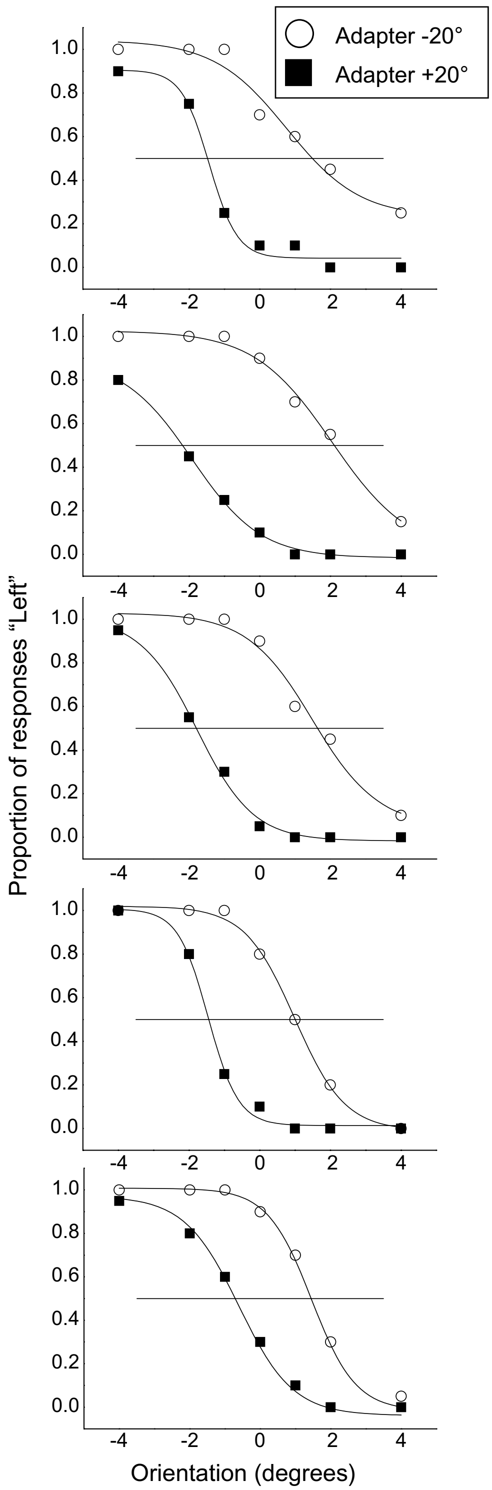

Fig. 2. These panels show the full tilt aftereffect in the baseline condition for each of the five observers. The proportion of trials in which the test stimulus was perceived as tilted leftward is plotted as a function of the orientation of the test stimulus. The two curves show average performance for the +20° and −20° oriented adapters in the baseline condition (single adapter). The magnitude of the tilt aftereffect for each observer and condition was calculated as the distance (in degrees of orientation) between the two curves when the observer responded "leftward" on 50% of the trials (horizontal line).

The allocation of attention influenced the magnitude of the TAE (Fig. 3, dark bars). The largest aftereffect, at 88.5% of the full TAE, was found when observers maintained fixation and selectively attended to only one adapter and the test stimulus was presented at that same attended location (Fig. 3A). Attending to two adapters simultaneously led to a reduction in the TAE in comparison to attending to only one adapter. The smallest TAE was found on trials in which the test stimulus was presented at an unattended location. There was a main effect of attention condition ($F[2,4] = 11.49$, $p = .039$), which was similar in fixation and the saccade trials (Fig. 4, light bars). Thus, selective attention led to both a "benefit" at the cued location ($F[1,4] = 38.12$, $p = .003$) and a "cost" at the unattended location ($F[1,4] = 56.33$, $p = .002$), compared to trials in which both adapters were attended.

There was also a significant main effect of eye movement condition, such that the TAE was smaller on trials with saccades ($F[1,4] = 42.92$, $p = .003$). There was a consistent reduction in the TAE compared to trials with maintained fixation (Fig. 3, white bars). The effect of making the saccade during the interval between the adapter and test was strikingly consistent, ranging from a 39.6% to a 41.9% average decrease in the full TAE in the various conditions in the group data (Fig. 3A). The decrease in TAE by 40% on saccade trials, found here, is similar the magnitude of reduction found in other recent studies of trans-saccadic tilt adaptation using different subjects and stimulus parameters, which reported reductions of 42% (Melcher, 2005) and 44% (Melcher, 2007) of the full TAE for saccade trials.

There was no significant interaction between saccade condition and attention condition ($F[2,4] = 0.17$, $p = .983$). This absence of an interaction is clear in the data from individual subjects as well (Figs. 3B–F and 4). The consistency of the two main effects across experimental conditions strongly suggests that the effects of attention and saccades on the TAE were independent and additive.

4. Discussion

The present results provide further evidence for spatiotopic adaptation aftereffects that persist across saccadic eye movements. This finding is consistent with other studies showing that body, head and eye movements can directly influence the interpretation of visual stimuli (Bompass & O'Regan, 2006; Hafed & Krauzlis, 2006; Ross & Ma-Wyatt, 2004; Wexler, 2005; Wexler et al., 2001). Given that the shape, location and identity of objects are unlikely to change as a result of an eye movement, it would be efficient to incorporate predictive and consistent information about stable properties of objects into visual processing itself across saccades (Melcher, 2005; 2007; Melcher & Morrone, 2003).

Trans-saccadic aftereffects were not limited to a single object, as might have been expected based on earlier studies which have found best performance at a single location across saccades (Germeys et al., 2002; Kowler et al., 1995; McConkie & Currie, 1996). Selective attention did influence the magnitude of the aftereffect. The test stimuli presented in the unattended location yielded the smallest spatiotopic TAE. Overall, selective attention increased or decreased the impact of the adapting stimulus (Spivey & Spirn, 2000), with or without saccades. The results imply additive and independent effects of both attention and saccades, rather than a specific suppression of unattended objects in trans-saccadic perception. Thus, the hypothesis that attention selects one, and only one, object for trans-saccadic perception was not supported. In practice, the main role of selective attention in trans-saccadic perception appeared to be to serve as a limiting factor on the visual processing of the objects in the display.

One intriguing mystery of trans-saccadic perception is the contrast between our naïve intuition—smooth and continuous perception of the world in sharp detail—and the striking limits

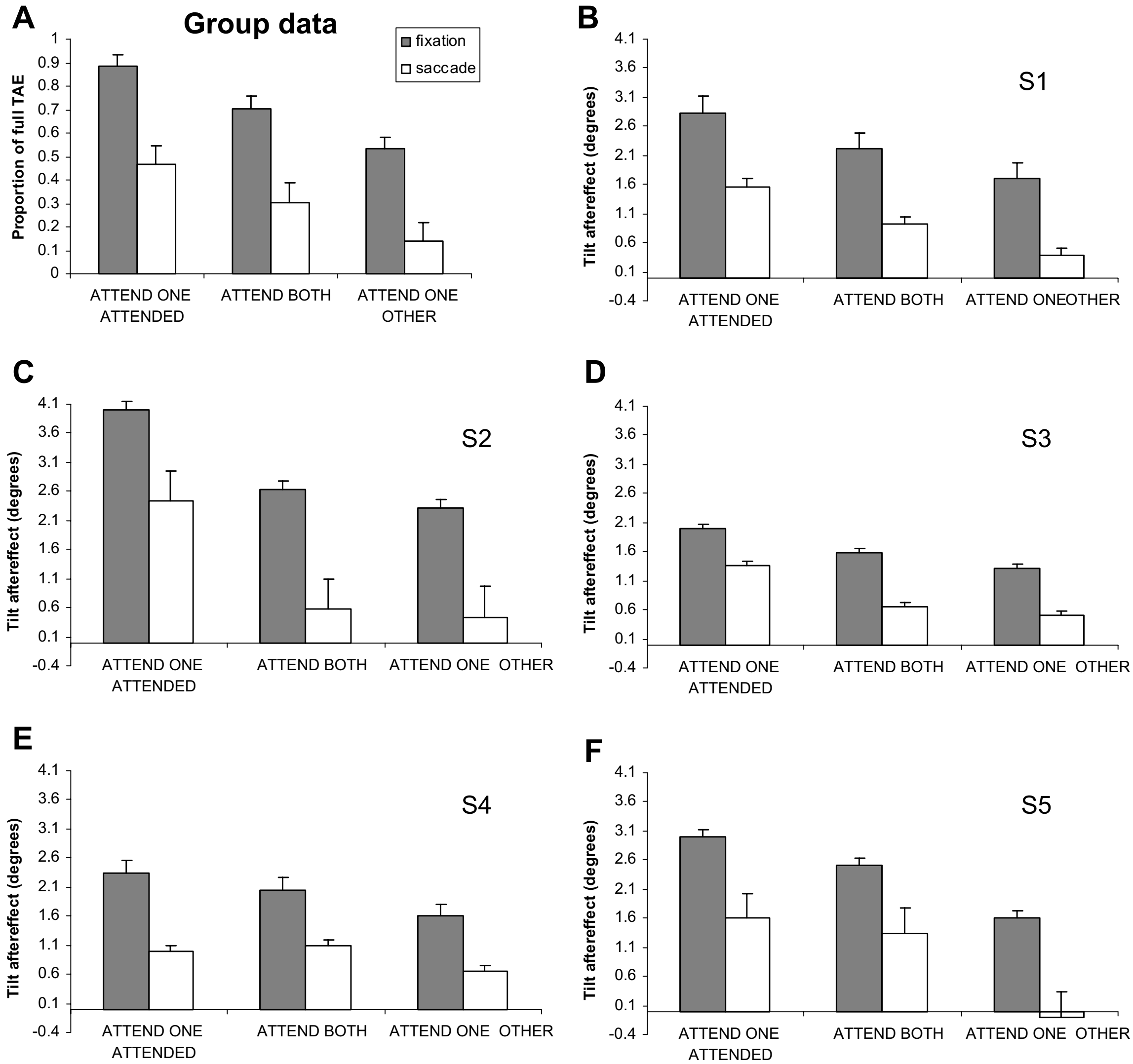

Fig. 3. The tilt adaptation aftereffect (TAE) for each experimental condition. The three attention conditions are shown as separate pairs of bars, with dark bars showing average performance on fixation trials and the white bars representing the TAE on saccade trials. (A) The proportion of full TAE averaged across all observers. (B–F) The average TAE, in degrees of orientation, is shown for each observer in each condition.

of visual acuity, attention and memory. Our conscious perception is tied to selective attention, which can be shifted at will giving the impression that all details of the scene are available to conscious perception (for review, see O'Regan and Noë, 2001). Selective attention influences which objects "win" the competition to be strongly represented in the saliency map. In practice, the need to guide behavior requires a limit in the number of salient objects. For example, detailed information about the form and size of an attended objects is used, across saccades, to guide behavior such as grasping (Crawford et al., 2004; Land & Hayhoe, 2001; Vaziri et al., 2006). The existence of interference effects in grasping make it clear the danger of keeping in mind the shape and size of multiple objects at the level required for accurate grasping (Gangitano, Daprati, & Gentilucci, 1998; Patchay, Castiello, & Haggard, 2003; Singhal, Culham, Chinellato, & Goodale, 2007). Thus, at least at the level of goal-directed behavior, the capacity limit for trans-saccadic perception of form in some tasks may, by necessity, be limited to one or, at most, a few objects.

At the same time, even information outside of the focus of attention is processed up to a certain level (Melcher, Papathomas, & Vidnyanszky, 2005; Melcher & Vidnyanszky, 2006; Wolfe, 1992). The processing of items outside the focus of attention is critical for a variety of abilities, including the ability to notice visual transients (Kanai & Verstraten, 2004), detecting a limited number of important features and stimuli (Eastwood, Smilek, & Merikle, 2001; Kirchner & Thorpe, 2006; Rousselet, Fabre-Thorpe, & Thorpe, 2002) and quickly gleaning the general layout and gist of the scene (Melcher, 2001; Potter, 1976; Torralba, Oliva, Castelhano, & Henderson, 2006). This "background activity" is necessary to determine which objects or events should enter into the saliency map that guides behavior. Until an object reaches the status of behaviorally salient, however, there may be no need to actively remap its spatial location and perceptual properties across the saccade.

In conclusion, the current results suggest that attention plays an important role in trans-saccadic perception by selecting which objects will be given preferential visual processing. Given the additive nature of the effects of attention and saccades, there may be no need for an oculomotor-specific mechanism to exclude unattended objects from feature remapping. Instead, the combination of these two effects may provide a simple and efficient strategy to ensure that only information about salient objects is remapped across saccades.

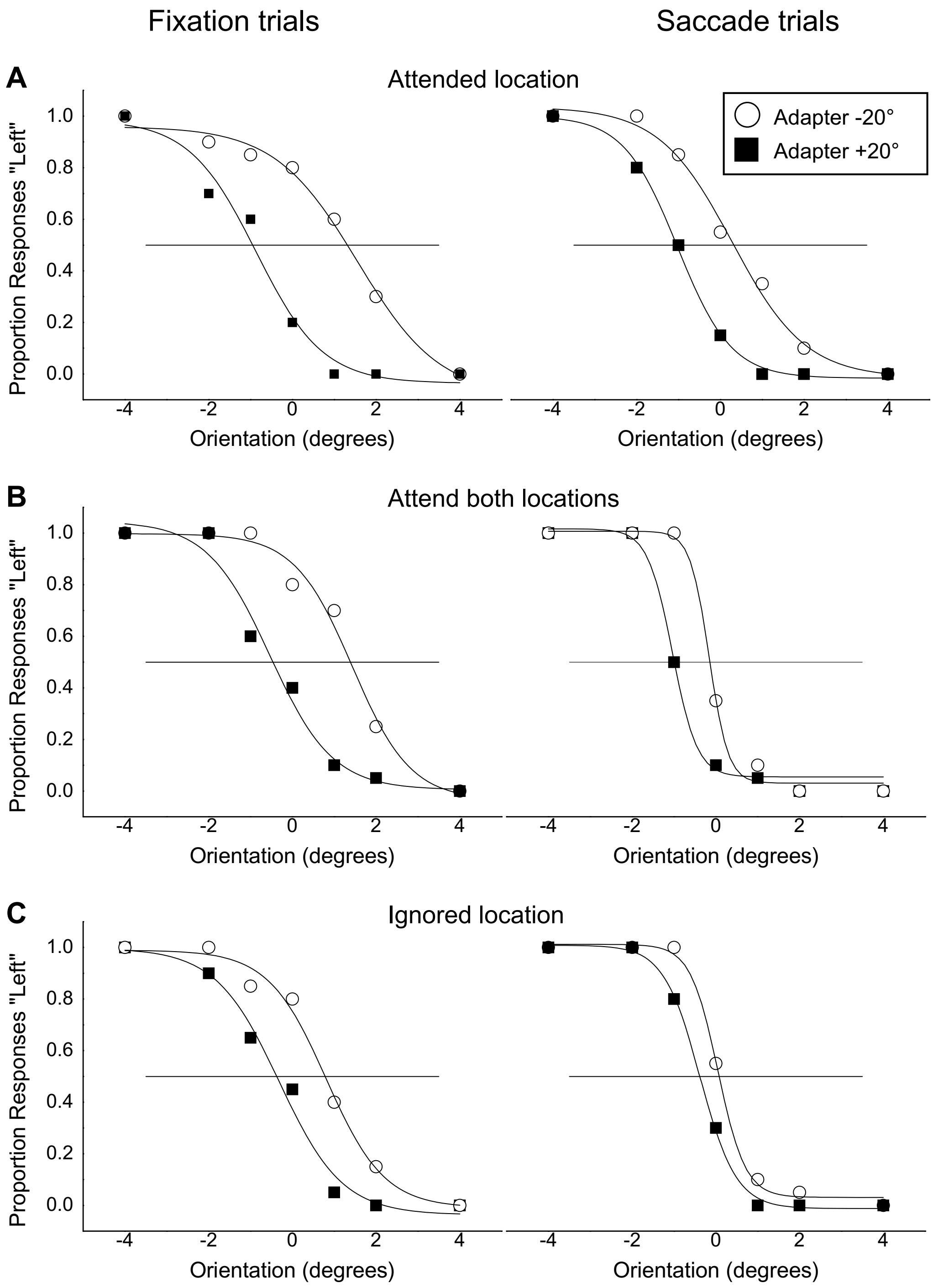

Fig. 4. Proportion of trials in which the observer responded "leftward" as a function of test orientation. Within each panel, the two curves show performance with +20° and −20° oriented adapters. Data is shown from one representative observer.

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