

Oculomotor adaptation of visuospatial memory

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Abstract

Visuospatial working memory enables the temporary retention and maintenance of visual spatial information. It involves both the content of a scene and the spatial locations of the scene elements. The mechanisms for the memory of spatial locations are potentially linked to the mechanisms of oculomotor planning, particularly the preparation of saccadic eye movements. In the present study, we show that adaptation of saccade control through oculomotor learning affects stored locations in visuospatial memory. Participants first encoded a complex visual scene with objects placed at various positions. Then, they completed a saccadic adaptation protocol with simple point targets on a blank screen in which saccades were either increased or decreased in amplitude. Thereafter, they were tested on recollection of scene locations. We found that increasing saccadic adaptation produced a change in the remembered spatial location of previously encoded objects that scaled with the amount of adaptation. This indicates that visuospatial memory relies on oculomotor processes.

Keywords: memory; eye movements; learning; vision

Introduction

Visuospatial working memory, attention, and saccade planning all assess the same spatial maps for prioritizing target locations in prefrontal or parietal cortex (Awh & Jonides, 2001; Jerde & Curtis, 2013; Ester, Sprague, & Serences, 2015; Bettencourt & Xu, 2016). This has led to the idea that the planning of saccadic eye movements is part of the maintenance and selection of spatial location in memory (Bays & Husain, 2008; Guerard, Tremblay, & Saint-Aubin, 2009; Belopolsky & Theeuwes, 2011; Pearson, Ball, & Smith, 2014; Hanning & Deubel, 2018; Ohl, Kroell, & Rolfs, 2024). To test this idea, we ask whether manipulation of saccade control affects the contents of memory.

Saccadic adaptation is an oculomotor learning mechanism for adjusting the eye movement control if systematic targeting errors are observed. When, for example, a saccade falls short of a target the next saccade to the same target will become slightly longer. Experimentally, saccadic adaptation can be induced by the double step paradigm, wherein, unbeknownst to the subject, the target of the saccade is stepped *during the saccade* from its original location (T1) to a new location (T2). If the step is consistently into the direction of the saccade the saccade amplitude will gradually increase adaptation. If the step is against the direction of the saccade the saccade will decrease. Increase and decrease adaptation differ in that increase adaptation more likely involves a change of saccade planning while decrease adaptation involves a change in motor control (Ethier, Zee, & Shadmehr, 2008). Saccadic adaptation, and in particular increase adaptation, has been shown to modify spatial perception such that visual targets appear shifted into the direction of adaptation (Bahcall & Kowler,

1999; Awater, Burr, Lappe, Morrone, & Goldberg, 2005; Zimmermann & Lappe, 2010). We ask whether they also affect spatial location in memory.

Methods

Participants (19 for decrease and 21 for increase adaptation) initially viewed and memorized a display of a rural scene containing 7 memory objects (Fig. 1a). Then, during a first recollection and localization phase (Fig. 1c) the memory items and 7 distractor items were presented in random sequence. If the participant rated an item as part of the memory display they subsequently indicated its remembered location.

Afterwards, participants underwent 100 trials of saccadic adaptation in a sequence of a vertical and a horizontal saccade, the latter of which was adapted (Fig. 1b). Saccade targets were luminous squares on a grey background, clearly different from the objects in the memory display, and initially placed at the positions of the lantern, the airplane and the flag (T1 of increase condition) or the cloud (T1 of decrease condition). When the eye tracker detected the onset of the saccade to T1, the targets stepped to the right (increase) or left (decrease) so that the target now occupied position T2, which was close to the cloud in the increase and the flag in the decrease condition. This procedure was to produce a gradual shortening or lengthening of the saccade over these 100 trials (Fig. 1d,e). The adaptation trials were preceded by ten trials without target step as baseline. After adaptation, participants were re-tested on recollection and localization of the memory items (Fig. 1c).

Results

Each participant's mean saccade amplitude over the last 10 adaptation trials was compared to their mean saccade amplitude in the 10 baseline trials to calculate individual adaptation strengths in percent (Fig. 1f,g left panels). We then determined whether the adaptation strength correlated with any change in spatial memory. We computed the shift in remembered item location as the horizontal difference between the post- and pre-adaptation localization of the item and calculated linear regressions with adaptation strength. We did this for the initial position T1, the adapted position T2 and a control position AF.

For increase adaptation (Fig. 1h), we found a positive relationship between localization shift and adaptation strength at position T1 ($R^2 = 0.26, F_{(1,17)} = 6.027, p = .03$, slope = 7.443, $p = .03$) indicating that the localization memory shifted in the direction of adaptation. At position T2, the regression showed a significant negative influence of saccadic adaptation ($R^2 = 0.21, F_{(1,18)} = 4.876, p = .04$, slope = -7.96, $p = .04$), indicating that the remembered positions shifted against the direction of adaptation. Position AF showed no significant regression. For decrease adaptation (Fig. 1i), none of these regressions were significant.

Thus, after increase adaptation, remembered location of items at position T1 shifted in adaptation direction while re-

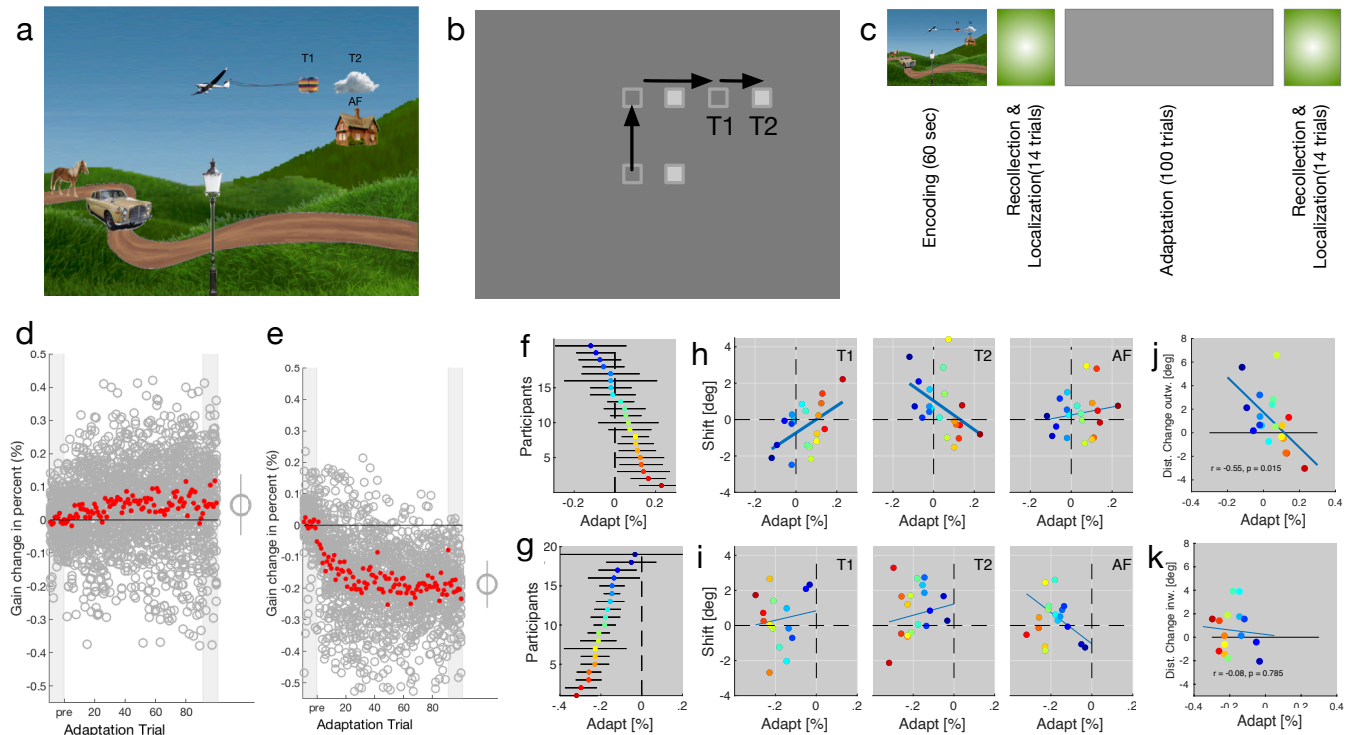


Figure 1: a) The memory display. b) Arrangements of targets and intra-saccadic target shifts during the adaptation procedure. c) Sequence of events. d) Example of increase adaptation over the course of the experiment. e) Example of decrease adaptation. f) Individual adaptation strengths for increase adaptation. g) Same for decrease adaptation. h) Regressions between adaptation strength and change in memory location for increase adaptation. i) Same for decrease adaptation. j,k) Change of distance in memory between T1 and T2 for increase and decrease adaptation.

membered location of items at position T2 shifted against saccade direction. Taken together, this indicates that the two remembered locations shift towards each other, as if the remembered space shrank. To quantify this directly, we computed the distance change (DC) between position T1 and position T2 from pre- to post-adaptation levels: $abs(T1_{post} - T2_{post}) - abs(T1_{pre} - T2_{pre})$. For increase adaptation (Fig. 1j) distance change showed a significant negative association to adaptation strength, as the remembered locations of T1 and T2 drew closer together with increasing amount of adaptation ($r = -.55, p = .015$).

Discussion

We found that increase saccadic adaptation affected the remembered location of items in visuospatial memory. This link existed at the spatial positions of the initial (T1) and final (T2) target of saccadic adaptation and brought these two locations closer together in memory. Increase adaptation relies on a change in saccade planning or target remapping (Ethier et al., 2008; Zimmermann & Lappe, 2010) whereas decrease adaptation is achieved by manipulating saccade dynamics (Chen-Harris, Joiner, Ethier, Zee, & Shadmehr, 2008). The latter process is more associated with the cerebellum (Xu-Wilson, Chen-Harris, Zee, & Shadmehr, 2009; Thier & Markanday, 2019) while the former, i.e. target remapping during increase

adaptation, likely involves cortical areas such as the frontal and parietal eye fields (Blurton, Raabe, & Greenlee, 2012; Gerardin, Miquee, Urquizar, & Pelisson, 2012; Panouilleres et al., 2014; Guillaume, Fuller, Simal, & Curtis, 2018), areas in the brain that are also involved in visuospatial memory. Our observation that manipulations of saccade planning can affect location of objects stored in memory shows the intricate link between these processes and has implication for the understanding and modeling of the mechanisms by which visuospatial memory is constructed.

Our results show that adaptation of saccade control modifies the remembered locations of a previously encoded scene. However, the direction of the memory shift at position T2 is opposite to the shift typically observed for visually presented targets. This suggests that the memory shift is not a simple copy of the adaptation. Instead, positions T1 and T2 become associated with each other as the subject repeatedly experiences a pre-saccadic target at position T1 in conjunction with a post-saccadic target at position T2. This repeated exposure may lead to a merging of the two positions in memory space. Effectively, then, the recollection of their positions moves closer together.

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