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A R T I C L E I N F O

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ABSTRACT

The human brain is able to process information flexibly, depending on a person's task. The mechanisms underlying this ability to initiate and maintain a task set are not well understood, but they are important for understanding the flexibility of human behavior and developing therapies for disorders involving attention. Here we investigate the differential roles of early visual cortical areas in initiating and maintaining a task set. Using functional Magnetic Resonance Imaging (fMRI), we characterized three different components of task set-related, but trial-independent activity in retinotopically mapped areas of early visual cortex, while human participants performed attention demanding visual or auditory tasks. These trial-independent effects reflected: (1) maintenance of attention over a long duration, (2) orienting to a cue, and (3) initiation of a task set. Participants performed tasks that differed in the modality of stimulus to be attended (auditory or visual) and in whether there was a simultaneous distractor (auditory only, visual only, or simultaneous auditory and visual). We found that patterns of trial-independent activity in early visual areas (V1, V2, V3, hV4) depend on attended modality, but not on stimuli. Further, different early visual areas play distinct roles in the initiation of a task set. In addition, activity associated with maintaining a task set tracks with a participant's behavior. These results show that trial-independent activity in early visual cortex reflects initiation and maintenance of a person's task set. Published by Elsevier Inc.

Introduction

The ability to process identical information differently depending on the information's relevance to a particular task is an integral component to many human behaviors. For example, your response to a ringing cell phone is different while attending a seminar vs. sitting at your desk. A task set is the configuration of cognitive processes that is actively maintained for subsequent task performance (Sakai, 2008) and is one component of cognitive control or executive function (Diamond. 2013). A classic and well-studied example in which task set influences stimulus processing is attention. Attention enhances accuracy and reaction time (Bashinski and Bacharach, 1980; Posner et al., 1980), improves acuity and contrast sensitivity (Carrasco et al., 2004; Herrmann et al., 2010; Montagna et al., 2009; Pestilli and Carrasco, 2005) and reduces interference from distracters (Shiu and Pashler, 1995). Humans can flexibly switch and maintain task sets with remarkable accuracy (Chiu and Yantis, 2009; Sakai, 2008). Thus, the nervous system transforms identical inputs into drastically different outputs as a function of the individual's task set.

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Understanding how the brain initiates and maintains these task sets will allow the field to better understand what goes wrong in disorders in which task sets are disrupted (e.g., Attention Deficit Hyperactivity Disorder, Alzheimer's disease (Perry, 1999), and other disorders). Here we examine the role of early sensory cortex in switching and maintaining a task set. In these experiments, the participant's task set is modulated through instructions to attend to stimuli of different modalities (visual vs. auditory). We find different patterns among the different early visual areas, and also find that task set-related activity predicts performance.

It is well known that attention to a visual stimulus or a location in space can modulate trial-driven activity in early visual cortex (reviewed in Carrasco, 2011). A cue to anticipate a visual stimulus, even in the absence of the stimulus, modulates visual cortical activity (Kastner et al., 1999), and the level of that modulation predicts the level of modulation of trial-driven activity (Murray, 2008; Sylvester et al., 2009). Silver et al. (2007) found that this modulation was sustained throughout the time that a participant anticipated a near-threshold stimulus. Aspects other than spatial attention can also modulate activity in early visual cortex. For example, activity in V1 can be modulated by attention to an auditory stimulus (Swallow et al., 2012), or by task structure (Jack et al., 2006). Thus it is clear that the visual cortex plays roles in addition to processing visual stimuli. In contrast to previous experiments, here we examine the differential role of early visual cortical areas in configuring a task set and maintaining that task set over a period of time.





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The mechanisms that underlie different aspects of a task set should follow different temporal patterns (Donaldson et al., 2001; Konishi et al., 2001; Petersen and Dubis, 2011). These distinct temporal patterns reflect the function of the activity being measured. Activity associated with processing information needed on individual trials (trial-driven activity) should be time-locked to the presentation of the trials, and should be transient, dying out after the information processing for that trial is complete. On the other hand, activity associated with components of a task that are not driven by a trial should show different temporal patterns. For example, activity associated with maintaining a task set may be sustained throughout the time a participant maintains a task set, despite the fact that individual trials occur only briefly and intermittently. Activity initiating a task set should be transient and time-locked to the beginning of the task. Activity that processes a cue should be transient and follow presentation of the cue. Functional Magnetic Resonance Imaging (fMRI) can be used to dissociate different timecourses of neural activity, and can separate activity associated with processing individual stimuli, maintaining a task set, initiating a task set, or responding to a cue. The role(s) that a brain area plays in cognition are reflected in the timecourses of activity observed there. Several experiments have used this approach of dissociating the function of neural activity based on its timecourse; most of these have focused on the role of frontal cortical areas in executive control (Braver et al., 2003; Chawla et al., 1999; Donaldson et al., 2001; Dosenbach et al., 2006; Velanova et al., 2003; Wenger et al., 2004). Here we use a similar approach, but we examine the role of early visual cortex in these distinct aspects of setting up and maintaining a participant's task set. No previous work has directly compared task-maintenance, cue-driven, and task-initiation related signals in retinotopically mapped early visual cortical areas.

Materials and methods

Participants

Twenty healthy right-handed participants took part in this study. Participants included 8 males and 12 females with a mean age of 26 years (range 19–32 years) who had normal hearing as measured using an Earscan 3 manual Audiometer (MicroAudiometrics Corp., Murphy, North Carolina, USA) and normal or corrected-to-normal vision (as measured with a Snellen eye chart). Participants were recruited through a campus wide advertisement. Recruitment procedures adhered to ethical standards as set and reviewed by the IRB at the University of Alabama at Birmingham. All participants provided a written consent prior to admission to the study. The study consisted of a total of 3 sessions: an initial behavioral measurement and two subsequent MRI sessions.

Task

During the fMRI experiment, participants performed attention demanding discrimination tasks in which they had to correctly discriminate between two successive auditory or visual stimuli. The four task conditions differed in attended modality (attend to Auditory vs. Visual) and whether or not auditory and visual stimuli were presented simultaneously. The tasks are described in Fig. 1A. Participants indicated with a button press whether two successively presented stimuli were the same or different. During the Auditory Unimodal (AU) and Visual Unimodal (VU) conditions, either auditory or visual stimuli were presented alone. During the Auditory Bimodal (AB) and Visual Bimodal (VB), conditions, both the auditory and visual stimuli were presented simultaneously and the participant discriminated between the stimuli of only the cued modality. During these bimodal conditions, the unattended stimuli followed a random pattern so that the participant could not gain an advantage by paying attention to the irrelevant stimulus.

Throughout the task, participants were instructed to keep central vision fixed on the location of the fixation mark in the middle of the screen. In order to monitor compliance with these instructions (and to confirm participants did not adopt a strategy of, e.g., closing eyes during presentation of irrelevant visual stimuli), participants' eye movements were monitored during the experiment using an Eyelink 1000 fMRI eye tracking system (SR Research Ontario, Canada). Eye position was calibrated at the beginning of each run, and monitored throughout.

Stimuli and trials

The auditory and visual stimuli were chosen based on previous work, suggesting that cortical information processing (such as topographic mapping and lateral inhibition) is analogous between visual and auditory stimuli (Shamma, 2001; Visscher et al., 2007). Trials contained two successive stimuli, either identical or different. Auditory stimuli varied sinusoidally in time and tone; these stimuli are often referred to as "ripple sounds" (Shamma, 2001). Stimuli that were 'different' were modulated with different temporal frequencies, while the identical trials contained exactly the same temporal frequencies. Visual stimuli varied sinusoidally in luminance over space. The stimuli were gray-scale horizontal gratings often called Gabor patches and were presented centrally. Visual stimuli that were 'different' varied from each other in the width of the gratings, while the identical trials contained exactly the same grating width. The Gaussian window defining the contrast of the bars in the Gabor patch had a standard deviation of 2.71° visual angle. Stimuli were the same as those used in a previous behavioral study (Visscher et al., 2007).

Four different cues were used to indicate the upcoming task. A small white central fixation cross remained on screen during all runs when no other stimuli or cues were present. The cues appeared at the location of the fixation cross and were small and of similar luminance, in order to minimize bottom-up sensory processing in response to the cue. A blue circle indicated the Visual Unimodal task while a blue circle with a cross within it indicated the Visual Bimodal task. A yellow cross indicated the Auditory Unimodal task, while a yellow circle with a cross within it indicated the Auditory Bimodal task.

The timeline of a trial is schematized in Fig. 1A. First, the cue was presented, indicating which task was to be performed. The cue was followed by two stimuli, each with a duration of 500 ms. The two stimuli were separated by a noise mask for 500 ms. For the auditory stimuli, the mask was white noise, filtered to include similar temporal frequencies to the range of auditory stimuli. For the visual stimuli, the mask was a white noise pattern filtered to include spatial frequencies similar to the range of frequencies of the visual stimuli. A question mark replaced the fixation mark during the two seconds during which the participant could make a response.

Threshold estimation and stimulus parameters

In order to standardize the perceptual difficulty of the task across participants, each participant's just noticeable difference (JND) threshold for auditory and visual stimuli was measured prior to the scanning sessions. Thresholds were defined using the QUEST algorithm (Watson and Pelli, 1983) as the stimulus difference (in units of % difference between two stimulus values) at which participants could correctly perform a forced choice paradigm 70% of the time. For Auditory tasks, participants were asked to identify which of two sequentially presented 500 ms stimuli had a faster temporal frequency. For visual stimuli, participants were asked to identify which of two sequentially presented 500 ms stimuli had a finer ('thinner') spatial frequency. The threshold estimation procedure was repeated in the scanner at the beginning of the fMRI session in order to control for the different presentation hardware used in the scanner. For logistical reasons and in order to save time, this was done with the gradient noise of the scanner off. JND values did not differ significantly between in-scanner and out-ofscanner measurements (data not shown). Auditory stimuli were presented at sound levels that were well discriminable over the sound of Download English Version:

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