Modeling the time course of attention signals in human primary visual cortex

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ABSTRACT

Previous neuroimaging studies have documented the existence of attention signals in human visual cortex, but little is known about the time course of these signals. A recent study reported persistent activity in early visual cortex whose duration was correlated with the duration of sustained attention[1]. The present study extends these findings by modeling the time course of sustained attention signals with a linear function with duration equal to the period of sustained attention but with variable amplitude and slope. Subjects performed a visual detection task in which a variable-duration delay period occurred before every target presentation. This design required the subjects to allocate visuospatial attention throughout the delay period. Functional magnetic resonance imaging (fMRI) was used to record activity in primary visual cortex (cortical area V1) during performance of the task. There were significant individual differences in the time course of attention signals, with some subjects displaying time courses consistent with constant amplitude attention signals, while others showed decreasing amplitude of attention-related activity during the delay period. These individual differences in time course of attention signals were correlated with behavioral response bias, suggesting that they may reflect differences in the types of attention used by the subjects to perform the detection task. In particular, those subjects who had constant amplitude sustained attention signals may have been employing relatively more endogenous, or top-down attention, while the subjects who exhibited attention signals that decreased over time may have been using relatively more exogenous, or bottom-up attention.

Keywords: attention, fMRI, neuroimaging, primary visual cortex, V1, top-down, sustained attention, endogenous attention, visuospatial attention, delay period

INTRODUCTION

In humans, allocation of spatial attention to a location in the visual field increases accuracy and decreases reaction time for detecting visual targets within the attended region[2,3]. A number of studies have employed fMRI to investigate neural correlates of this enhancement of visual perception by spatial attention. Cues that direct spatial attention to a particular visual field location (in the absence of eye movements) cause increases in the blood oxygenation level dependent (BOLD) fMRI signal in visual cortex, including primary visual cortex (area V1)[1,4,5]. This cue-related activity occurs even in the absence of a visual stimulus, suggesting that it is a top-down attention signal. This is consistent with the finding that the amplitude of this V1 signal is correlated with performance on a visual detection task[5].

These attention signals in V1 are retinotopically specific. V1 contains a map of the visual field on its surface, and the visual field is represented in retinotopic coordinates. The attention signals are confined to the portion of V1 that represents the attended visual field locations[4,5,6]. In addition, portions of V1 that represent more peripheral, unattended, visual field locations show a decrease in fMRI signal[1,6]. This spatial correlation between visual attention and activity in V1 is also evident in the temporal domain. The duration of maintained activity in V1 is correlated with the duration of sustained attention, even for individual trials[1]. In addition, there is a transient off-response that occurs at the termination of a period of sustained readiness[7,8] or attention[1]. Unlike the sustained attention signals, the off-response is not retinotopically specific[1,8] and occurs in parietal and frontal cortex as well as occipital cortex[7].

Attention-related increases in V1 activity occur in the absence of visual stimulation and can even be evoked by the presentation of an auditory stimulus that signals the subject to allocate visual attention[1,5]. Presentation of this auditory stimulus alone, in the absence of any task demands, does not cause any change in V1 activity (David Ress, personal communication). Together, these results suggest that the attention signals are unlikely to be generated in V1. Rather, they are probably initiated in higher cognitive areas that contain abstract representations of the rules of the task. These areas are likely to send signals to early visual cortex to enhance processing in portions of these cortical areas that

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represent the attended parts of the visual field. The sources of these top-down signals are not known, although a variety of studies using electrophysiology[9], neuropsychology[10], and neuroimaging[11] have implicated parietal cortex. Recently, two novel parietal cortical areas have been discovered[12]. These areas, named IPS1 and IPS2 based on their location in the intraparietal sulcus, each contain topographic maps of visuospatial attention signals, yet they respond poorly to passive viewing of visual stimuli. This suggests that IPS1 and IPS2 may be involved in the transmission of spatially-specific top-down attention signals to early visual cortex.

Improvements in perception or changes in activity following voluntary allocation of attention are examples of the effects of top-down, or endogenous spatial attention. This type of attention occurs as the result of a conscious decision to attend to a particular location in the visual field. Endogenous attention is often contrasted with bottom-up, or exogenous attention[13]. Shifts in exogenous visuospatial attention are involuntary and are driven by the appearance of salient stimuli. The functional networks underlying endogenous and exogenous attention in the brain are distinct[14].

The present study has employed a visual detection task with a variable-duration delay period to measure the time course of sustained endogenous attention signals in human cortical area V1. Modeling of these attention signals demonstrated individual differences in their time courses. Specifically, subjects differed in the slope of the amplitude of estimated sustained activity. Some subjects' data were well fit by a model in which attention signals were maintained at a constant level, while other showed a decrease in signal amplitude for longer periods of sustained attention. These individual differences were correlated with a behavioral measure of response bias based on performance of the visual detection task. In addition, individual differences in response bias were correlated with the magnitude of the off-response associated with the termination of attention. Overall, the results suggest that subjects may have employed different strategies to perform the visual detection task. Modeling of the time course of attention signals and correlating these measures with behavioral indices may provide important information concerning individual differences in cognition and the neural bases of these differences.

METHODS

All methods describing the visual detection task and acquisition of fMRI data have been described elsewhere[1]. Four healthy subjects participated in this study, and all of them provided written consent. Experiments were carried out in compliance with safety guidelines for MR research, and the experimental protocol was approved by the human subject Institutional Review Board of Stanford University.

Time courses of activity during performance of the visual detection task were measured in portions of cortical area V1 that retinotopically represented the attended portion of the visual field. The boundaries of V1 were determined for each subject using well-established retinotopic mapping methods[15,16,17]. Area V1 was retinotopically restricted based on fMRI responses to a high-contrast visual stimulus that was the same shape and size as the attended annulus. This restriction procedure has been previously described in detail[1].

The fMRI time courses during sustained visual spatial attention were fit using a model of the underlying neural activity and a model of the hemodynamics. Initially, neural activity during the delay period was modeled as a step function whose duration was equal to the duration of sustained attention for each trial. These step functions were convolved with a canonical hemodynamic response function as defined in the SPM99 software package (http://www.fil.ion.ucl.ac.uk/spm/software/spm99) to generate an estimate of the BOLD signal measured with fMRI. The amplitude of activity for each trial was estimated using an iterative optimization algorithm (implemented as the function fmincon in MATLAB (The MathWorks, Inc., Natick, MA)). The transient off-response associated with the termination of sustained attention was modeled as a positive transient (100 msec duration) response at the end of the response period. The amplitudes of the off-response for each trial were estimated at the same time as the amplitudes of sustained neural activity during the delay period. A more complete description of the procedures used to estimate amplitudes of sustained activity and off-responses can be found elsewhere[1].

After estimation of amplitudes based on the assumption of constant (step function) amplitude of sustained activity, a second optimization was carried out in which the slope of the amplitude of sustained activity was a free parameter. The duration and mean amplitude were fixed, but the slope was allowed to increase or decrease from its starting value of zero for each trial if this improved the fit to the measured fMRI time courses. The estimates of slope were normalized by the mean amplitude for each trial, resulting in slope units of (proportion of delay-period amplitude/second). The optimization included upper and lower bounds for the slope parameter corresponding to

+/- (2 * delay-period amplitude) / 9 seconds

Thus, for the average duration of sustained attention (from auditory cue to the end of response period, or 9 seconds), the slope estimate was constrained such that it could not exceed twice the absolute value of the mean amplitude and did not change sign at any point during the delay period. Because it was previously shown that sustained attention signals are positive in the attended portion of V1[1], only those trials that had positive signal amplitudes during the delay period were included in the analysis of the slope of sustained activity.

RESULTS

Subjects performed a visual detection task that was designed to isolate sustained top-down attention signals in cortical area V1, primary visual cortex (Figure 1). The key elements of the task were 1) the use of a threshold-contrast target that was difficult to detect and therefore required significant attention resources, 2) a variable-duration delay period preceding target presentation, 3) the absence of any changes in visual stimulation during the delay period, 4) the use of an auditory cue to initiate each trial and to instruct subjects to allocate their attention to the portion of the visual field where the target could be presented, and 5) a long intertrial interval to allow the fMRI response to return to baseline before the beginning of the subsequent trial. Details of the task can be found elsewhere[1].

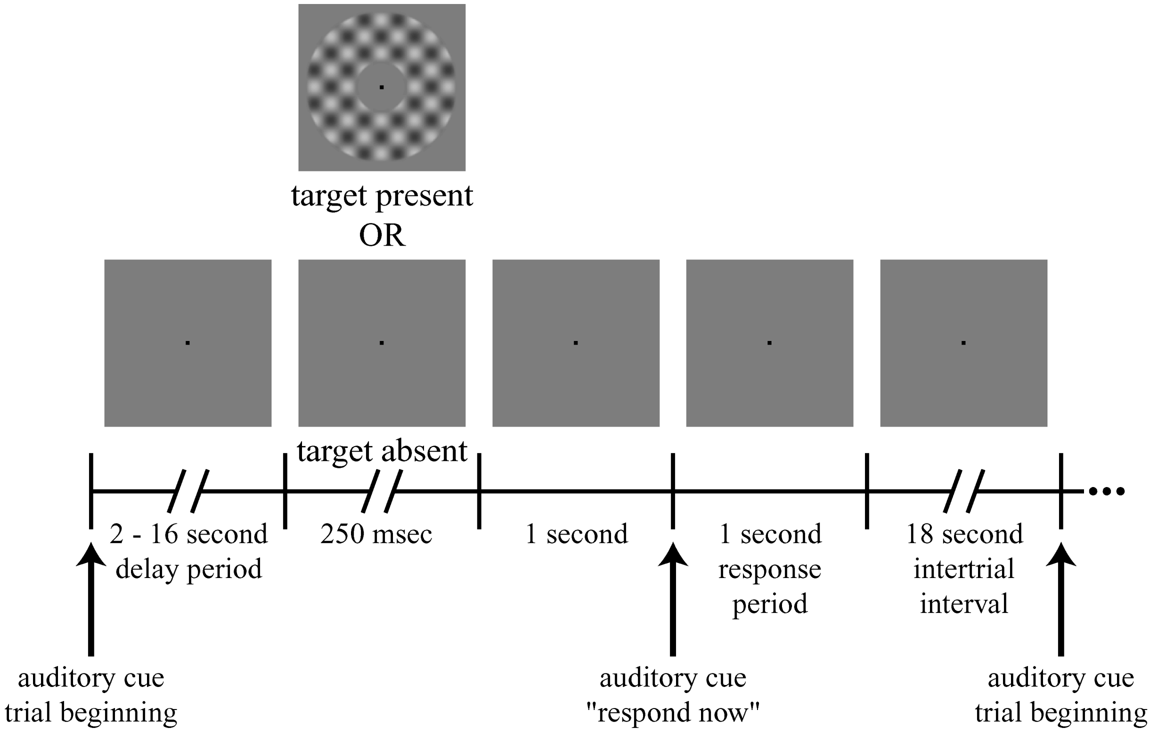

Figure 1. Schematic of visual detection task used in this study. Targets were presented with 50% probability for each trial, and target presentation always occurred following the end of the delay period (for target-prsent trials). In this schematic, the target is shown at high contrast. However, during actual performance of the task, the target was presented at a contrast corresponding to the detection threshold for each subject.

All subjects practiced the detection task extensively before the acquisition of fMRI data. This allowed the accurate determination of contrast thresholds for each subject. Practice also caused the subjects to develop a perceptual template corresponding to the size, shape, and visual appearance of the target. The existence of this template allowed the subjects to allocate spatial attention to the appropriate part of the visual field (corresponding to where the target could be presented), even though there was no visual stimulus used to label this region during the delay period.

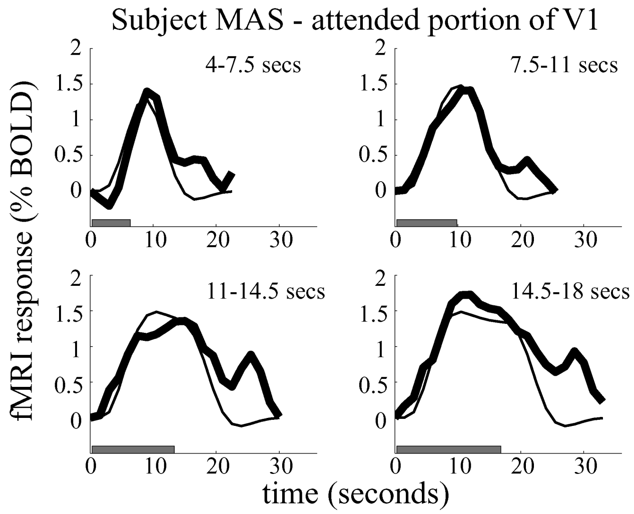

Figure 2. Modeling of fMRI responses during sustained visuospatial attention. Responses were binned into four groups based on delay-period duration. *Gray boxes*, model of neural activity as a step function with onset and offset times corresponding to the beginning of the delay period and the end of the response period, respectively. *Thin lines*, predicted fMRI responses corresponding to a convolution of the step functions with a hemodynamic response function. *Thick lines*, actual fMRI responses in the attended portion of cortical area V1 for subject MAS.

fMRI responses were measured in cortical area V1 for each subject during performance of the visual detection task. Trials were aligned to the time of the auditory cue signaling the beginning of each trial, and they were binned based on the duration of the delay period. Previous work has shown a strong correlation between the duration of sustained activity in the attended portion of V1 and the delay period duration for individual trials[1]. Therefore, sustained neural activity was modeled as a step function which began at the onset of the trial and persisted until the end of the response period. This step function was convolved with a hemodynamic response function to generate a predicted fMRI response (% BOLD signal change). Amplitudes of sustained activity were estimated using an iterative optimization procedure (see Methods and ref. 1).

This step-function model fit the observed fMRI responses quite well, especially for some subjects (Figure 2). However, for other subjects (Figure 3A), there were systematic differences between the estimated and actual time courses, indicating that the assumption of constant amplitude of sustained activity during the delay period was not met. Specifically, the actual time courses had shorter onset latencies than the model's predictions, and they returned to baseline more quickly than the model time courses.

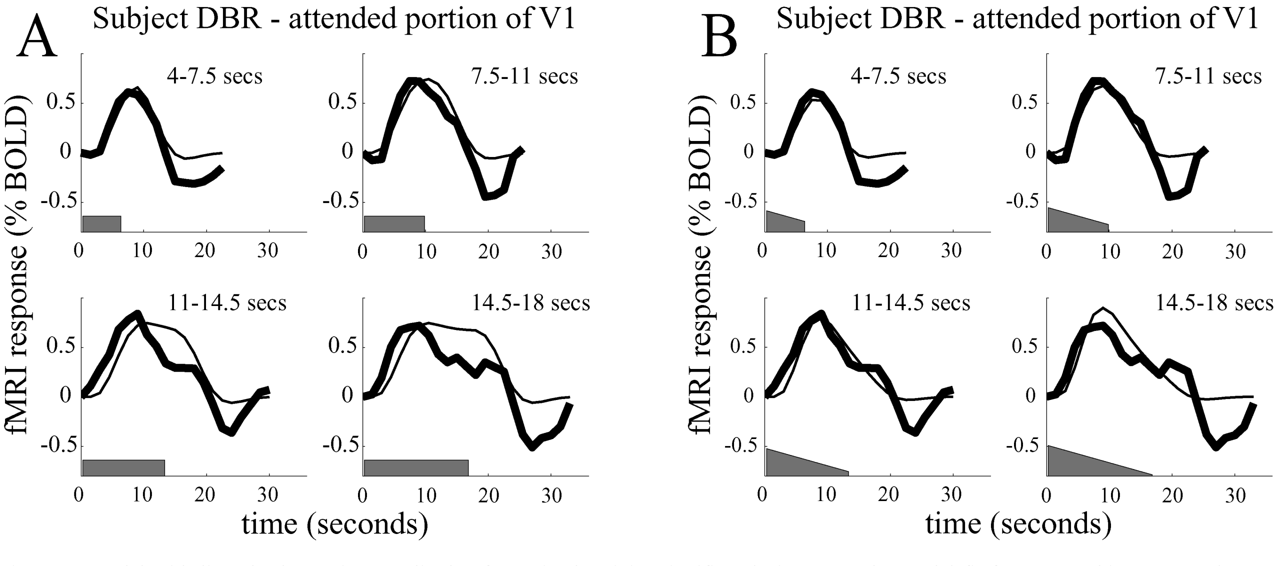

Figure 3. Model with linearly decreasing amplitude of sustained activity significantly improves the model fit for some subjects. *Gray boxes*, model of neural activity. *Thin lines*, predicted fMRI response. *Thick lines*, actual fMRI responses in the attended portion of cortical area V1 for subject DBR. **A**, step-function model in which neural activity was assumed to be maintained at a constant level throughout the delay period. The actual response onset was earlier than the model predicted, and the actual response decayed over time, unlike the model response. **B**, sustained neural activity was assumed to linearly decrease thoughout the delay period. This model accounts for the observed time course much better than the step-function model.

To improve the model, an additional free parameter was added. Following the initial optimization to generate estimates of the amplitude of sustained activity for each trial, a second optimization was performed in which the signal was allowed to linearly vary over the duration of the delay period for each trial (Figure 3B). The duration and mean amplitude of estimated neural activity were held constant during this second optimization, but the slope of the activity was allowed to vary until the best possible fits of the data (minimum mean square error between the observed and measured fMRI time courses) were obtained.

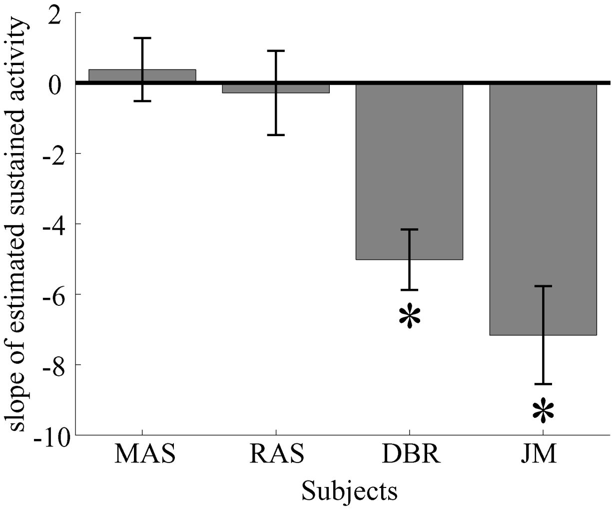

Figure 4. Slopes of estimated sustained neural activity reveal individual differences in time course of attention signals. Two subjects (MAS, RAS) exhibited slopes that were not significantly different from zero, while the remaining subjects (DBR, JM) had significantly negative slopes, indicating a decrease in signal amplitude during the delay period. *Asterisks,* $p < 10^{-5}$.

For two subjects (MAS and RAS), the slopes of the estimated sustained activity were not significantly different from zero, indicating that the step-function model effectively described the time course of attention signals in area V1 for these subjects (Figure 4). For the remaining subjects (DBR and JM), the slopes were significantly less than zero, suggesting that a model in which attention signals linearly decreased during the delay period provided a substantially better description of the data than the step-function model.

The magnitude of the slope of estimated neural activity in V1 during the delay period was correlated with behavioral response bias for individual subjects (Figure 5). Specifically, large slopes (rapidly decreasing delay-period activity) were associated with conservative response bias (tendency to respond “target absent” more often than “target present”). Response bias was computed as the sum of the z-transformation of the hit rate and false alarm rate divided by two[18]. All subjects showed positive response bias measures, indicating that they were more likely to respond “target absent” than “target present”. However, subjects DBR and JM had unusually large response bias measures. For example, subject JM responded “target absent” for 97% of

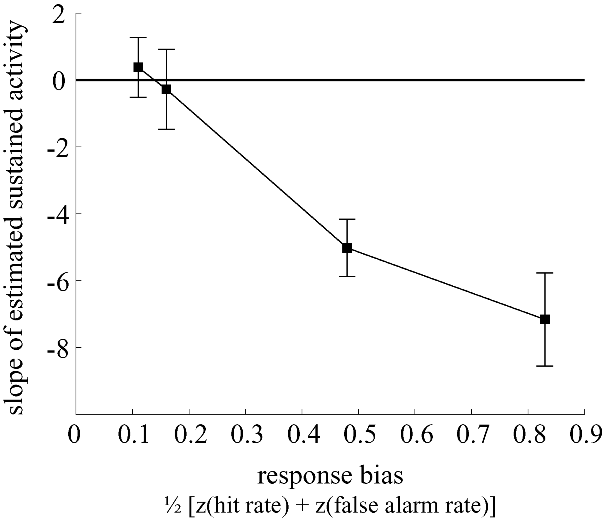

Figure 5. The slope of estimated sustained neural activity is correlated with behavioral response bias for individual subjects. This measure of response bias will be equal to zero if subjects were equally likely to respond "target present" as "target absent". Positive values indicate a more conservative response criterion.

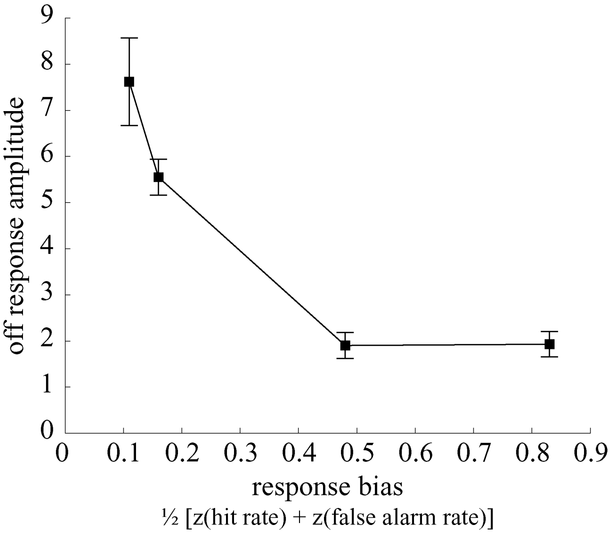

Figure 6. The amplitude of the transient off-response that follows a period of sustained attention was correlated with behavioral response bias for individual subjects. Response bias measures are identical to those displayed in Figure 5.

the trials when no target was shown and for 43% of the trials when a target had been presented. Large response bias values (and the associated large negative slopes of estimated activity) may indicate that subjects were using proportionately more exogenous attention to perform the visual detection task (see Discussion).

The optimizations described above used to generate estimates of amplitude and slope also included a transient off-response (100 msec duration) at the end of the delay period. This off-response occurs following termination of a period of sustained readiness[7,8] or attention[1]. The amplitude of the off-response was estimated for each trial during the initial optimization, simultaneous with the estimation of amplitude of the sustained delay-period activity. Like the slopes of estimated activity during the delay period, the mean off-response amplitude for individual subjects was correlated with behavioral response bias (Figure 6).

DISCUSSION

The present study used an iterative optimization method to model the time course of fMRI activity in cortical area V1 during sustained visuospatial attention in the absence of visual stimulation. Specifically, the slope of estimated neural activity during sustained attention was allowed to vary, and the value that provided the best fit of the measured fMRI responses was computed for each trial of a visual detection task.

There were significant individual differences in slope across the sample of four subjects. Two subjects had slopes very close to zero. Their pattern of activity is consistent with a step-function model in which attention signals persisted with constant amplitude throughout the delay period. The other subjects had slopes that were significantly less than zero. The time course of attention signals in area V1 for these subjects is described much better by a linear decrease in neural activity during the delay period than by the step-function model.

The estimated slope values were correlated with two other factors that were measured during performance of the visual detection task: behavioral response bias and off-response amplitude. Taken together, this set of results suggests that some of the individual differences in behavior and fMRI responses may be due to the relative levels of endogenous and exogenous attention used by each subject (Figure 7). Specifically, those subjects with high response bias measures required a very vivid visual percept of the threshold-contrast target in order to meet their response criterion for reporting “target present”. It is possible that such a strong visual perception would activate exogenous, or stimulus-driven, attention systems in the brain. Reliance on exogenous attention for target detection would have allowed those subjects to reduce their level of endogenous attention. This is consistent with the fact that response bias was correlated with negative slope of estimated sustained activity, because subjects that were using proportionately more exogenous attention would not be expected to maintain top-down attention signals as well as subjects that employed relatively more endogenous attention.

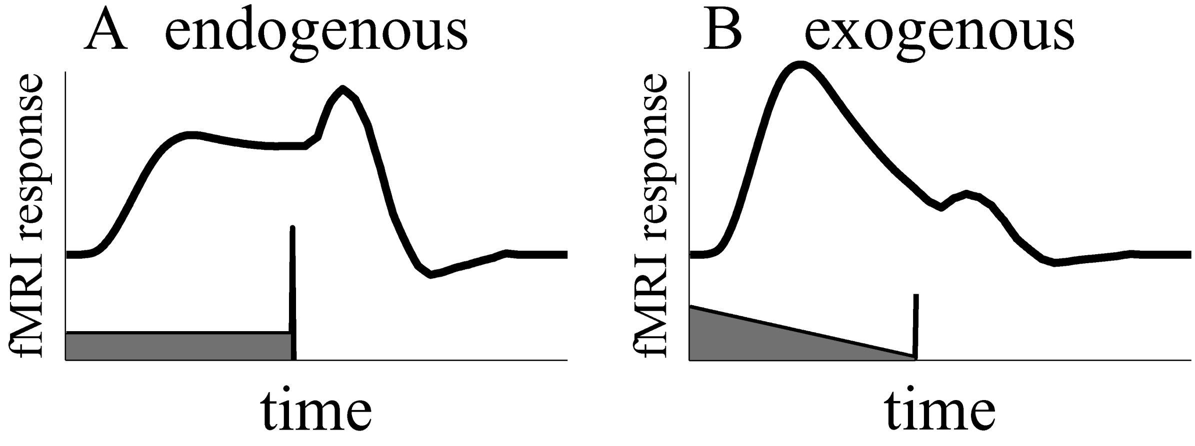

Figure 7. Schematic depiction of fMRI delay-period activity. **A**, time course for relatively more endogenous attention. Neural activity is maintained at a constant level throughout the entire delay period, followed by a large transient off-response. **B**, time course for relatively more exogenous attention. Neural attention signals decrease in amplitude during the delay period, followed by a smaller off-response.

It should be noted that although the endogenous and exogenous attention systems are often opposed, both systems are active at all times. For example, a sufficiently salient stimulus will always attract attention, regardless of how focused a person is on the task at hand. Similarly, humans are able to employ endogenous attention and maintain their attentional spotlight on a region of interest even in the presence of visual distractors. Thus, the distinction between endogenous and exogenous attention displayed in Figure 7 should be considered to represent a difference in the relative amounts of endogenous and exogenous attention, not the presence of one form of attention to the exclusion of the other.

The same subjects that exhibited large response bias and negative slopes of estimated activity also had smaller off-responses. Very little is known about the off-response, but it has been described as a transient response occurring after a prolonged state of readiness[7]. Unlike the sustained attention signals, the off-response is present in portions of V1 representing both attended and unattended visual field locations[1,8], and it has also been reported to occur in parietal and frontal cortex[7]. If the off-response amplitude is related to the amplitude of sustained attention signals that occurred in the preceding interval, then those subjects that maintain attention signals at a constant level should have exhibited larger off-responses than the subjects whose activity decreased during the delay period. This is exactly the pattern of results that was observed.

While these correlations between fMRI attention signals and visual detection behavior are intriguing, they are based on a sample of four subjects. Therefore, any conclusions from this data set should be taken as provisional. However, the general approach of quantitative modeling of the components of attention signals in the brain combined with behavioral measures based on signal detection theory holds great promise in the study of the neural substrates of attention. Recent discoveries of top-down attention signals in early visual cortex[4,5], parietal cortical areas containing topographic maps of spatial attention[12], and functional integration among attention signals in multiple visual areas[19] have laid the foundation for the identification of top-down attention pathways. Progress has also been made in defining the networks subserving exogenous visual attention[20]. These methods will provide valuable information concerning individual differences in attention and their correlates in the brain.

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