

# Neural Correlates of the Automatic and Goal-Driven Biases in Orienting Spatial Attention

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**Fecteau, Jillian H., Andrew H. Bell, and Douglas P. Munoz.** Neural correlates of the automatic and goal-driven biases in orienting spatial attention. *J Neurophysiol* 92: 1728–1737, 2004. First published April 28, 2004; 10.1152/jn.00184.2004. How do stimuli in the environment interact with the goals of observers? We addressed this question by showing that the relevance of an abruptly appearing visual object (cue) changes how observers orient attention toward a subsequent object (target) and how this target is represented in the activity of neurons in the superior colliculus. Initially after the appearance of the cue, attention is driven to its locus. This capture of attention is followed by a second bias in orienting attention, where observers preferentially orient to new locations in the visual scene—an effect called inhibition of return. In the superior colliculus, these two automatic biases in orienting attention were associated with changes in neural activity linked to the appearance of the target—relatively stronger activity linked to the capture of attention and weaker activity linked to inhibition of return. This behavioral pattern changes when the cue predicts the upcoming location of the target—the benefit associated with the capture of attention is enhanced and inhibition of return is reduced. These goal-driven changes in behavior were associated with an increase in pretarget- and target-related activity. Taken together, the goals of observers modify stimulus-driven changes in neural activity with both signals represented in the salience maps of the superior colliculus.

## INTRODUCTION

In this article, we explored three questions. How do distinct objects in the environment influence spatial attention? How are these automatic influences modified through the goals of observers? How are these automatic and goal-driven influences represented in the brain?

A distinct object in the visual scene has dramatic influences on spatial attention. This statement can be understood through a simple example. After a bolt of lightning strikes on a hot summer's evening, observers reflexively orient to its locus in the night sky. This compulsion that we have to inspect abrupt changes in the visual scene (hereafter, referred to as salient events) has been called the *capture of attention* (Jonides 1981; reviewed in Egeth and Yantis 1997; Klein 2000; Wright and Ward 1998). The capture of attention is short-lived but has a lingering influence. After attention has been removed from the locus of the salient event, observers are slower to return attention to this previously inspected location (Maylor 1985; Posner and Cohen 1984; Wright and Ward 1998). This later effect has been called *inhibition of return* (Posner et al. 1985), and it represents the tendency of observers to favor orienting attention toward new locations (see Klein 2000). Both the

capture of attention and inhibition of return represent the automatic consequences of a stimulus on orienting spatial attention.

Important changes to these biases in orienting attention occur when the salient event can be used to guide behavior. In this case, observers respond faster to the locus of the salient event, which further enhances the attentional benefit produced through the capture of attention and weakens inhibition of return (Richard et al. 2003; Wright and Richard 2000).

We investigated how these automatic and goal-driven influences on spatial attention are evidenced in the activity of visuomotor neurons in the superior colliculus. The cue-target task was used to produce these biases in orienting attention (Fig. 1) (reviewed in Egeth and Yantis 1997; Klein 2000; Wright and Ward 1998). In brief, a flash of light in the peripheral visual field (the cue) is followed by a second visual stimulus (the target) that appears at the same location as the cue or at the opposite location. The cue serves as the salient event. Responding to the target probes the consequences of the salient cue on orienting attention toward a new object (i.e., the target). Manipulating the time between the cue and target reveals the capture of attention and inhibition of return when the cue does not predict the upcoming location of the target (Fig. 2A). Comparing predictive and non-predictive versions of the cue-target task addresses how the “relevance” of the cue modifies its influence (Fig. 2, B and C).

As two monkeys performed this task, 36 visuomotor neurons in the intermediate layers of the superior colliculus were monitored. The superior colliculus is an ideal structure to monitor for these purposes because it is critically involved in initiating saccadic eye movements (the response required by the cue-target task used in this study), it receives input from every brain region that has been implicated in orienting attention, its neurons produce distinct sensory-, motor-, and attention-related signals (e.g., Goldberg and Wurtz 1972a,b; Kustov and Robinson 1996; Mays and Sparks 1980; Wurtz and Goldberg 1972; reviewed in Munoz and Fecteau 2002; Sparks and Hartwich-Young 1989), and lesion studies have implicated the superior colliculus in inhibition of return (Posner et al. 1985; Sapir et al. 1999). Recently, the neural correlates of the capture of attention and inhibition of return have been identified in the intermediate layers of the superior colliculus. The capture of attention was linked to relatively strong target-related activity when the cue and target appeared at the same location (Bell et al. 2004), whereas inhibition of return was associated with relatively weak target-related activity (Bell et al. 2004; Dorris et al. 2002).

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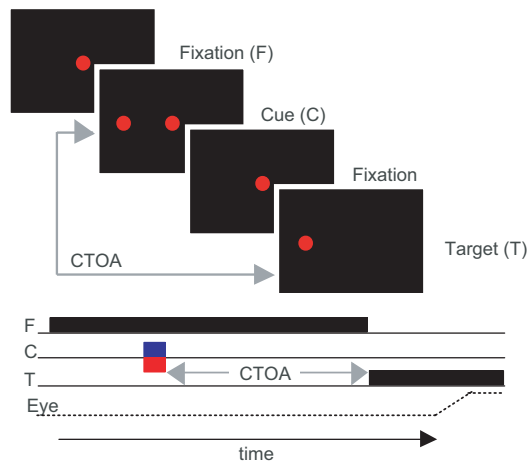


FIG. 1. Overview of the cue-target task. Note that the color of the light-emitting diodes (LEDs) changed between the non-predictive (red, as shown), and predictive (green, not shown) cases.

By monitoring the same neurons in the non-predictive and predictive versions of the cue-target task, we show how the automatic consequences of a salient event are evidenced in neural activity (see also Bell et al. 2004; Dorris et al. 2002), and we show how and when the goals of observers influence this.

## METHODS

### Participants

Two male rhesus monkeys (weighing between 7 and 10 kg) participated in this study. The techniques used to present stimuli, collect

behavioral data, and obtain physiological recordings have been described previously (Munoz and Istvan 1998) and were approved by the Queen's University animal care committee.

### Behavioral task.

As illustrated in Fig. 1, each trial began with the participants maintaining gaze at a central fixation marker for 500–1,000 ms. A visual cue appeared to the left or right field for 30 ms. A target followed, either appearing in the same or opposite location as the cue. Five cue-target onset asynchronies (CTOAs) were used (50, 100, 200, 500, or 1,200 ms) that were equally probable and randomly selected. When the target appeared, the fixation marker disappeared simultaneously to inform the participants to generate a saccade to the target's location. One of the cue-target locations appeared in the response field of the neuron being monitored, and the other cue-target location appeared at its mirror position (across the horizontal and vertical meridians). Visual stimuli consisted of light-emitting diodes (LEDs) that were matched in luminance ( $0.03 \text{ cd/m}^2$ ). Red LEDs were used when the cue did not predict the upcoming location of the target (50% of the time it appeared at the same location as the target and 50% of the time it appeared opposite the target), and green LEDs were used when it did (cue predicted the target's upcoming 75% of the time). Non-predictive and predictive versions of the cue-target task were run in consecutive blocks. In most instances, the non-predictive task was performed first. Changing the order in which the tasks were performed, however, did not change the obtained results (all  $P$ 's  $> 0.1$ ). In addition, no-cue trials, in which no cue preceded the appearance of the target, were interleaved with the cued trials and accounted for 9% of the trials in the non-predictive version and 4% of the trials in the predictive version. The data obtained from these no-cue trials were used to classify the neuron. The monkeys received a liquid reward for initiating a saccade to the target's location within 500 ms of its appearance. As the behavioral consequences of non-predictive and

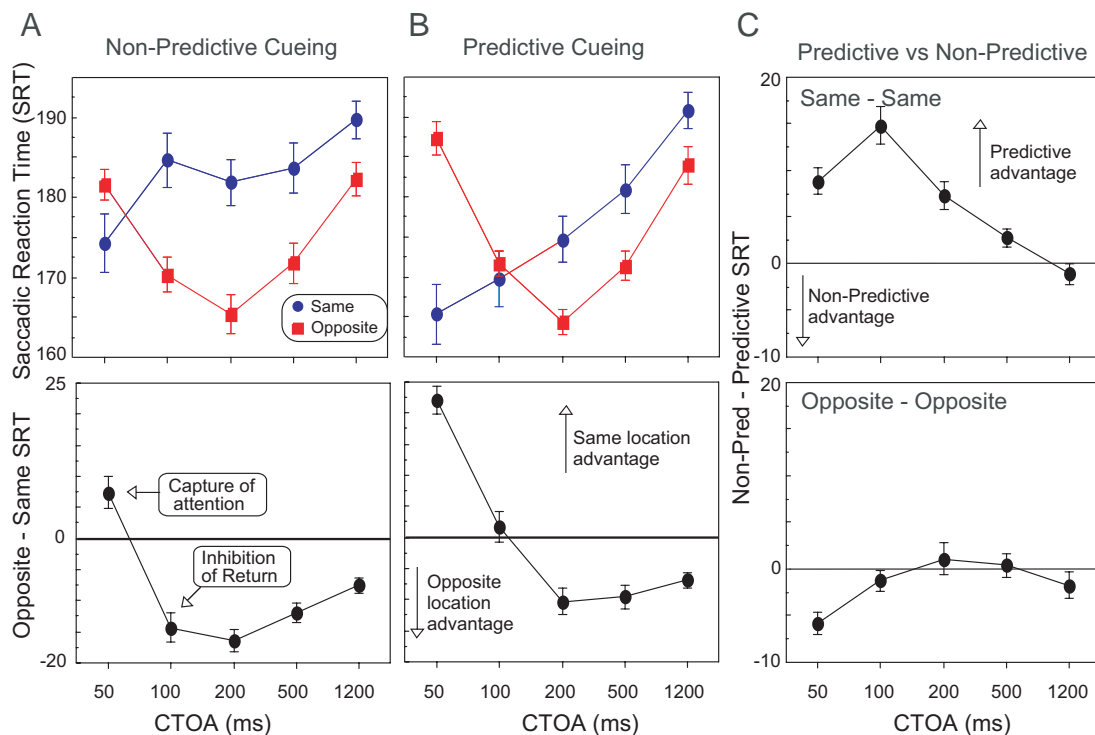


FIG. 2. *A* and *B*, top: mean correct saccadic reaction time (SRT) for the non-predictive (*A*, top) and predictive cue-target tasks (*B*, top). *A* and *B*, bottom: difference in saccadic reaction time when the cue and target appeared at the same and opposite locations for non-predictive (*A*, bottom) and predictive (*B*, bottom) cue-target tasks. *C*: difference in saccadic reaction time for the predictive and non-predictive cue-target tasks when the cue and target appeared at the same (top) or opposite (bottom) locations. Error bars represent  $\pm 1$  SE. NonPred, non-predictive.

predictive cues were similar for both monkeys, the data were collapsed across observers.

### *Behavioral and neural analyses.*

Saccadic reaction time was used as the behavioral estimate of spatial attention for two reasons. First, it encourages the immediate applicability of our findings to previous human studies as many have used reaction time as the primary dependent measure (e.g., Jonides 1981; Maylor 1985; Posner and Cohen 1984; Wright and Richard 2000). Second, it permits the relationship between neural activity and behavior to be determined on a trial-by-trial basis. Other behavioral measures, such as contrast sensitivity (Bisley and Goldberg 2003) do not allow this correspondence to be made as easily because the behavioral and neural data are obtained in separate sessions and even under separate stimulus conditions as these techniques require more trials than is suitable for neurophysiological investigation (Bisley and Goldberg 2003; see also Ignashchenkova et al. 2004). Only the reaction times from correct trials are presented in this paper. It should be noted, however, that errors were very rare.

Thirty-six neurons that yielded visual (>50 spikes/s)- and saccade (>80 spikes/s)-related responses (obtained on no-cue trials), provided at least four observations per condition (i.e., in the factorial breakdown of the experimental design;  $\geq 10$  observations was more common) and produced similar target- and saccade-related activity in the no-cue trials for predictive and non-predictive conditions,  $F(1,35) < 1$ , were included in this study. The action potentials on each trial were convolved into spike density waveforms (Gaussian kernel,  $\sigma = 10$ ). The peak activity was obtained for the target (75–125 ms, target-aligned) and saccade (–30–10 ms, saccade-aligned) epochs, and the mean activity was obtained for the pretarget epoch (50–70 ms, target-aligned). The target-related epoch was established on the basis of the visual response latency of the neurons for the no-cue trials and captured the peak target-related response in all instances. The mean values taken from each epoch were entered into the population analyses for each neuron in every condition. The only trials included in the neural and behavior analyses were those in which a saccade was correctly initiated to the target's location within 90–300 ms of its appearance. Population analyses of neural and behavioral data were analyzed with repeated-measures ANOVA, including the variables *relevance* (non-predictive vs. predictive) *cue-target relationship* (same location vs. opposite location), and *CTOA* (50, 100, 200, 500 vs. 1,200). An alpha of 0.05 was adopted as significant for all statistical analyses in this study.

Correlation analyses were obtained by comparing the saccadic reaction time on a specific trial to the neural activity obtained on the same trial. For non-predictive cueing, the correlations involving target- and saccade-related activity included both same and opposite location cues across all cue-target onset asynchronies. For pretarget activity, only trials when the cue and target appeared at the same location were included in the correlation analysis because of the low, if not absent, pretarget activity that occurred when the cue appeared at the opposite location (see Fig. 3). For predictive cueing, because half of the comparisons involved pretarget activity (and only permitted the inclusion of trials when the cue and target appeared at the same location), all of the correlations were limited to same location cues so as to keep the statistical power of these analyses equivalent across neural epochs. The significance of the correlation for each neuron was determined with a *t*-test.

To compare the time at which the pretarget activity diverged between the predictive and non-predictive conditions (Fig. 5), the Gaussian kernel used to create the spike density waveform was decreased ( $\sigma = 4$ ) to reduce the spread of neural activity backward in time. Mean predictive and non-predictive population spike densities were compared in 1-ms nonoverlapping time bins with a running *t*-test. Fifteen consecutive comparisons needed to achieve significance ( $P < 0.05$ ) to be considered meaningful. By chance alone, this

criterion has a probability of occurring  $1$  in  $3 \times 10^{19}$ . In addition, the difference in fixation related activity (350–450 ms, after the eye was in the fixation window, before the cue appeared) and postcue activity (115–135 ms after the cue appeared, cue-aligned) between the predictive and non-predictive conditions was assessed for each neuron. The significance of these comparisons was determined with a *t*-test ( $P < 0.05$ ).

## RESULTS

In describing the results of this study, we first show the behavioral consequences and the neural correlates of non-predictive cueing. These data replicate what has been shown in previous studies (Bell et al. 2004; Dorris et al. 2002) but provide the necessary backdrop for revealing how these behavioral and neural patterns change when the salient cue predicts the upcoming location of the target, which we describe in the subsequent section.

### *Behavioral and neural consequences of non-predictive cues*

Akin to findings in the human literature (e.g., Maylor 1985; Posner and Cohen 1984; Wright and Richard 2000), the influence of the non-predictive cue changed depending on its location relative to the target and the time that elapsed between the cue and target (cue target onset asynchrony, CTOA), as evidenced in the interaction between cue-target relationship (same location versus opposite locations) and CTOA,  $F(4,140) = 38.3$ ,  $P < 0.05$ . At the 50 ms CTOA, saccadic reaction times were faster when the cue appeared at the same, as opposed to the opposite, location as the target (Fig. 2A, *top*, blue below red). This *same location advantage* quantifies the reflexive capture of attention by the salient cue (Jonides 1981; Posner and Cohen 1984). At longer CTOAs, saccadic reaction times were slower when the cue and target appeared at the same location (red below blue). This *same location disadvantage* (opposite location advantage) quantifies inhibition of return (Posner and Cohen 1984; Posner et al. 1985). Because it is the relative difference in saccadic reaction time that reveals the capture of attention and inhibition of return, plotting this difference shows these biases directly (Fig. 2A, *bottom*; positive values signify the advantage in saccadic reaction time when the cue and target appear at the same location, whereas negative values signify the disadvantage when cue and target appear at the same location).

Figure 3 shows the correspondence between changes in orienting behavior and neural activity for the non-predictive cue-target task. At the 50 ms CTOA (Fig. 3B, *top*), there were two distinct bursts of neural activity when the target appeared in the response field of the neuron (cue opposite, red trace). The first represents the volley of activity associated with the appearance of the target (target-related activity), and the second represents the volley of activity preceding the initiation of the saccade to the target's location (saccade-related activity; saccade-alignment not shown). This pattern changed when the cue and target appeared in the response field of the neuron (blue trace)—the peak response to the target (gray box in Fig. 3B) was stronger because it built on the residual activity originating from the cue (white box; Fig. 3B). The peak saccade-related response did not change depending on the location of the cue (saccade-aligned spike densities are not shown, but see saccade-related epoch, Fig. 3A, *bottom*). By

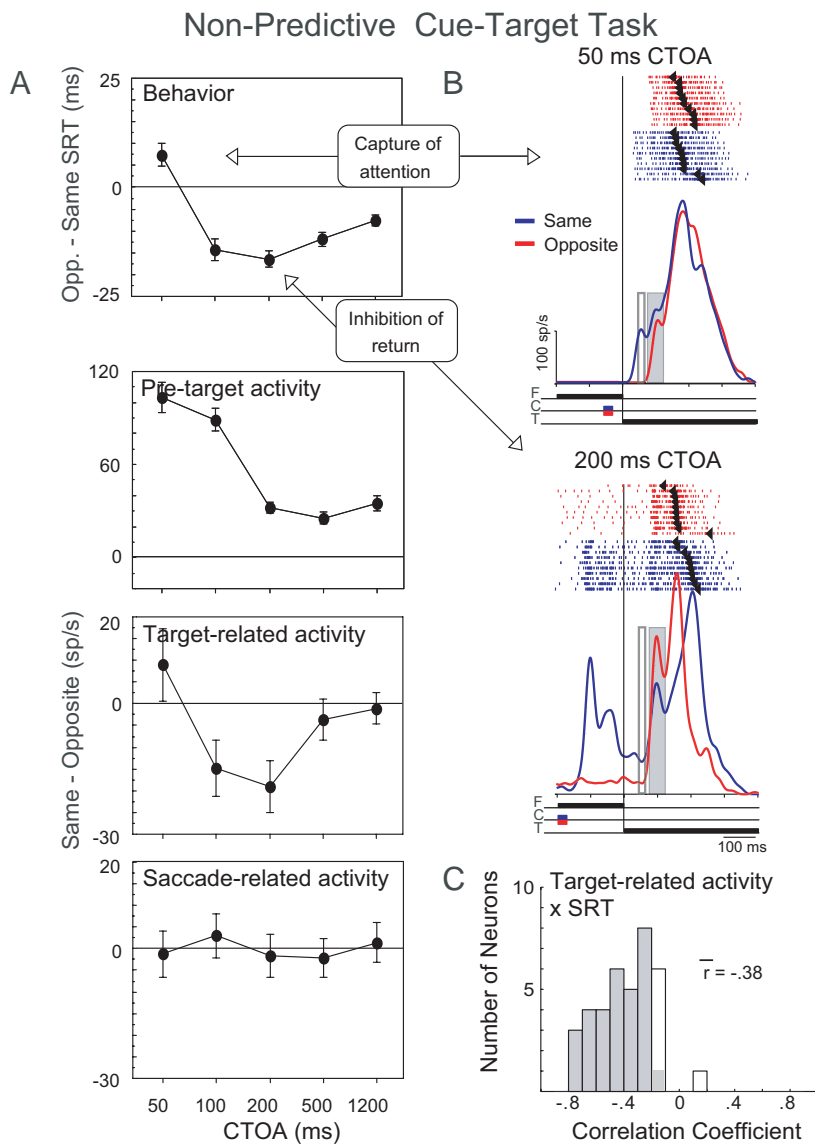


FIG. 3. *A*: population averages for saccadic reaction time, pretarget activity, target-related activity, and saccade-related activity across the 5 cue-target onset asynchronies (CTOAs) tested (top to bottom). *B*: neural activity when the cue and target (blue line) or the target alone (red line) appeared in the response field of a representative neuron at the 50 ms CTOA (*top*) and a 2nd representative neuron at the 200 ms CTOA (*bottom*). Black triangles, onset of the saccade for each trial; white bars, the pretarget epoch; gray bars, target-related epoch. *C*: histogram showing the correlation between target-related activity and saccadic reaction time obtained for every neuron in the sample. Gray bars, the neurons that produced a significant correlation ( $P < 0.05$ ).

contrast, the 200 ms CTOA (Fig. 3*B*, *bottom*) produced a different pattern of neural activity as shown in the example of another neuron. After the cue was registered by the neuron, there was an increase in low-frequency neural activity (white box; hereafter, referred to as elevated pretarget activity), but the incoming target-related activity was weaker. Again the saccade-related activity did not change depending on the location of the cue.

On the basis of these single neuron examples then, there are three neurophysiological signals that can be measured and compared to orienting behavior—the low-frequency activity that precedes the target's appearance (pretarget activity), the sensory response registering the target (target-related activity), or the motor burst associated with the initiation of the saccade (saccade-related activity; the pretarget and target-related epochs are highlighted in Fig. 3*B*, see also METHODS). In Fig. 3*A*, neural activity linked to the pretarget and target- and saccade-related epochs obtained across the population of neurons monitored are presented in a comparable way as behavior (positive values signify stronger neural activity when the cue and target appeared at the same location, whereas negative values signify

weaker neural activity when the cue and target appeared at the same location). Like behavior, the influence of the cue changed depending on the time that elapsed between the cue and target for pretarget activity and target-related activity,  $F(4,140) = 68.5$ ,  $F(4,140) = 5.3$ ,  $P < 0.05$ , respectively. Saccade-related activity did not change across these manipulations,  $F(4,140) < 1$ ,  $P > 0.1$ .

When comparing these graphs, the pattern obtained for target-related activity and orienting behavior is quite similar—stronger target-related activity was obtained when monkeys were faster to respond to a target appearing at the cued location (the capture of attention), whereas weaker target-related activity was obtained when monkeys were slower to respond to a target appearing at the cued location (inhibition of return). This relationship was not observed for pretarget activity. Albeit suggestive, a stronger test of the relationship between neural activity and behavior was obtained when correlating these measures on a trial-by-trial basis for each neuron (see METHODS). Figure 3*C* illustrates that greater target-related activity was associated with shorter reaction times, and weaker target-related activity was associated with longer reaction times

across the population of neurons in this study (average  $r = -0.38$ ; shaded bars represent the neurons for which this correlation was significant,  $P < 0.05$ ). Collapsing across CTOAs was not responsible for this relationship, as similar correlations were obtained at every CTOA tested (50 ms,  $r = -0.34$ ; 100 ms,  $r = -0.43$ ; 200 ms,  $r = -0.41$ ; 500 ms,  $r = -0.35$ ; 1200 ms,  $r = -0.24$ ). By contrast, weaker correlations between pretarget activity and saccadic reaction times (average  $r = -0.15$ ) and between saccade-related activity and saccadic reaction times (average  $r = -0.14$ ) were obtained.

#### *Comparing the consequences of non-predictive and predictive cues*

Up to now, we have shown that the presentation of a salient cue results in relatively stronger or weaker target-related activity depending on the time that elapsed between the cue and the target. These changes in target-related activity correlate with distinct biases in orienting behavior.

Different results were obtained when the cue predicted the upcoming location of the target. Predictive cues exaggerated and lengthened the benefit associated with the capture of attention and reduced inhibition of return (non-predictive, Fig. 2A, top; predictive, B, top) as evidenced in the three-way interaction involving relevance (predictive vs. non-predictive), cue-target relationship, and CTOA,  $F(4,140) = 18.7$ ,  $P < 0.05$ . To illustrate the difference between predictive and non-predictive cues, we plotted the difference between these conditions when the cue and target appeared at the same location (Fig. 2C, top; positive values signify faster reaction times for predictive than for non-predictive cues). Comparing saccadic reaction times across these conditions revealed that monkeys initiated saccades faster when the cue predicted the target's location, as evidenced in the main effect of relevance,  $F(1,35) = 58.2$ ,  $P < 0.05$ , and that this advantage was more prominent at shorter CTOAs than at longer CTOAs as evidenced in the interaction between relevance and CTOA,  $F(4,140) = 22.7$ ,  $P < 0.05$ . This difference between predictive and non-predictive cueing conditions was specific to when the cue and target appeared at the same location. By contrast, when the cue and target appeared at opposite locations, saccadic reaction times were faster for non-predictive cues at the 50 ms CTOA, which resulted in a two way interaction between relevance and CTOA,  $F(4,140) = 50.1$ ,  $P < 0.05$ .

Figure 4 shows the correspondence between the behavioral data and neural activity when comparing predictive and non-predictive cueing. Plotting the pretarget, target-related, and saccade-related activities in a similar way as behavior (Fig. 4A; positive values signify stronger neural activity for predictive than for non-predictive cues) shows that pretarget and target-related activity were elevated for predictive cues compared with non-predictive cues,  $F(4,140) = 23.6$ ,  $P < 0.05$  and  $F(4,140) = 4.9$ ,  $P < 0.05$ , respectively. Much like behavior (Fig. 2C), few differences were obtained between predictive and non-predictive cueing when the cue and target appeared at opposite locations,  $F(4,140) < 1$ ,  $P > 0.1$ , as is shown for target-related activity in Fig. 4D.

Similar to the non-predictive cueing task, correlation analyses revealed a strong relationship between target-related activity and saccadic reaction time on a trial-by-trial basis across CTOAs (average  $r = -0.43$ ; Fig. 4C) and at every CTOA tested (50 ms,  $r = -0.53$ ; 100 ms,  $r = -0.56$ ; 200 ms,  $r =$

$-0.44$ ; 500 ms,  $r = -0.32$ ; 1,200 ms,  $r = -0.28$ ). Pretarget activity also produced a moderate correlation with saccadic reaction times in this analysis (average  $r = -0.32$ ; Fig. 4C). No such relationship was observed for saccade-related activity (average  $r = -0.13$ , not shown). On the basis of Fig. 4B, showing an increase in pretarget activity and a corresponding increasing in target-related activity may suggest that the elevated pretarget activity augmented the target-related response. Consistent with this observation, a moderate correlation between pretarget and target-related activity was obtained for predictive cueing (average  $r = 0.27$ , Fig. 4C).

Finally, testing the same neurons in the predictive and non-predictive conditions allows us to show when the signal of relevance was registered in neural activity. To do this, we generated population spike densities for predictive and non-predictive cues to see when this upward shift in neural activity became significant across the population of neurons studied (see METHODS). At the 500 ms CTOA illustrated in Fig. 5A, predictive cues were associated with significantly stronger activity 116 ms after the appearance of the cue (or  $\sim 45$  ms after the cue was registered by the neurons), and this elevated activity was maintained throughout the rest of the CTOA. Figure 5B highlights this difference with a subtraction plot of the predictive and non-predictive population spike densities (positive values signify stronger neural activity for predictive cues).

Similar values were obtained across all CTOAs measured—on average, predictive cues resulted in significantly greater neural activity 112 ms after cue appeared (range: 103–118 ms) or  $\sim 41$  ms after the cue was registered by the neurons. As shown in Fig. 5C, the increase in neural activity at this postcue epoch (in red, Fig. 5A) was significantly stronger in 18/36 neurons with another 9 neurons showing a trend in the same direction. Only five neurons produced a significant effect in the opposite direction. Although the fixation-related epoch also produced significantly stronger activity in the predictive cueing condition at the 500 ms CTOA shown in Fig. 5A, this effect was not observed consistently. As shown in Fig. 5C (left), significantly stronger fixation-related activity was observed for only two neurons across all CTOAs.

#### DISCUSSION

Understanding the interplay between automatic influences and the goals of observers is a central question in cognitive neuroscience. Here we have explored this question by exploiting the biases in orienting attention that originate from the abrupt appearance of an irrelevant peripheral cue (e.g., Jonides 1981; Posner and Cohen 1984), noting how these biases are modulated when this cue becomes relevant to the participant (Richard et al. 2003; Wright and Richard 2000) and observing how these differences are evidenced in neural activity.

The appearance of an irrelevant peripheral cue has powerful influences on attentional orienting that correlate to notable changes in neural activity. The initial capture of attention is linked to a strong target-related signal that originates from the summation of target-related activity and residual cue-related activity (Fig. 3) (see also Bell et al. 2004). The subsequent inhibition of return effect corresponds to a weak neural representation of the target (see also Bell et al. 2004; Dorris et al. 2002).

These automatic consequences of the salient cue on biasing attention undergo important changes when the cue predicts the

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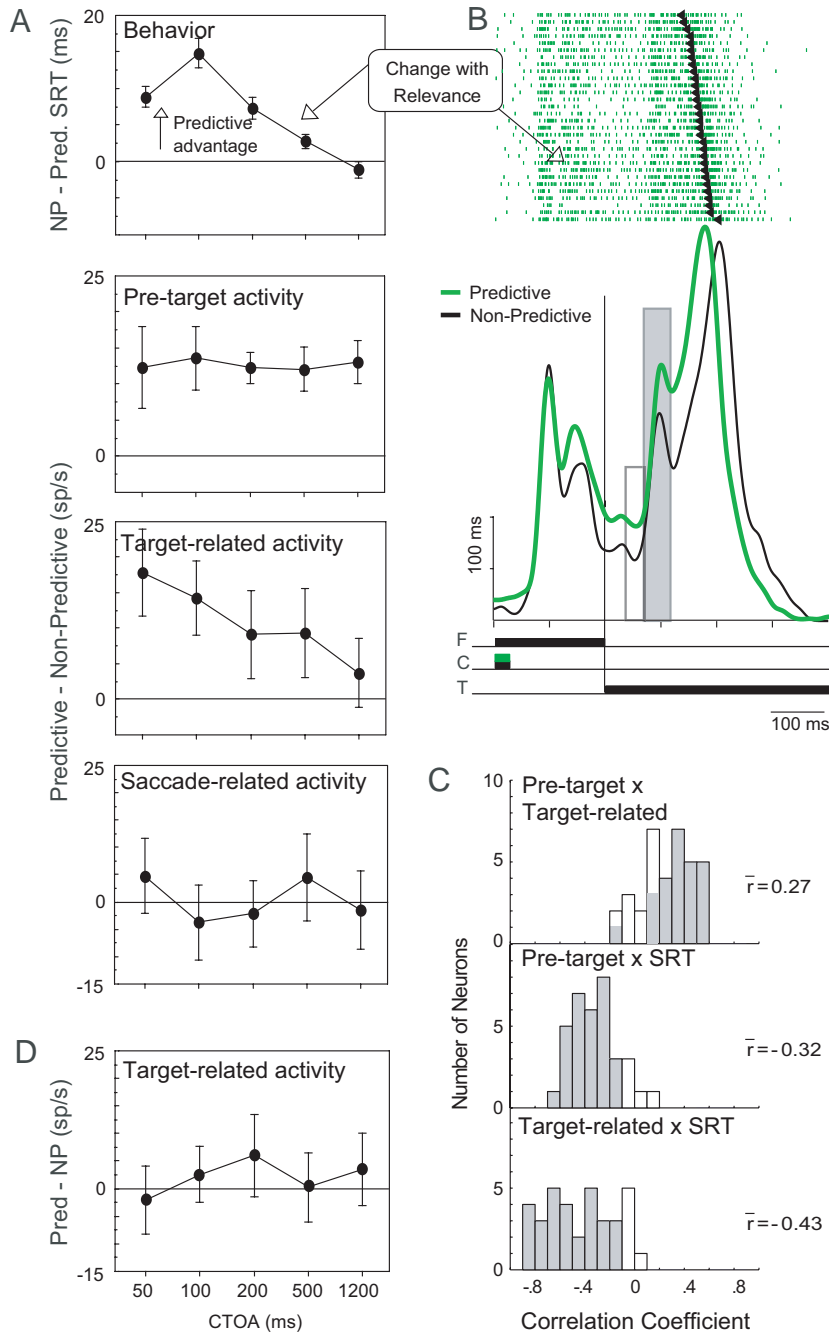


FIG. 4. A: population averages for saccadic reaction time, pre-target activity, target-related activity, and saccade-related activity that show the difference between predictive and non-predictive cues when the cue and target appeared at the same location (top to bottom). B: activity of a single neuron at the 200 ms CTOA, when predictive cues (green line) resulted in faster reaction times than non-predictive cues (black line). Rasters for non-predictive condition shown in Fig. 3B. White bar, pre-target epoch; gray bar, target-related epoch. C: histograms showing correlation between pre-target activity and target-related activity (top), pre-target activity and saccadic reaction time (middle), and target-related activity and saccadic reaction times (bottom). Gray bars, the neurons that produced a significant correlation ( $P < 0.05$ ). NP, non-predictive; Pred, predictive. D: population average of target-related activity when cue and target appeared at opposite locations; contrast with behavior shown in Fig. 2C (bottom).

upcoming location of the target—the attentional benefit linked to the capture of attention is enhanced and inhibition of return is diminished (see Fig. 4) (Richard et al. 2003; Wright and Richard 2000; A. von Muhlenen, personal communication). These changes between predictive and non-predictive cueing were correlated with elevated pre-target activity, occurring only 112 ms after the appearance of the cue (~41 ms after the cue was registered by the neuron), which enhanced the target-related response (for related findings see Basso and Wurtz 1998; Dorris and Munoz 1998; Glimcher and Sparks 1992; Kustov and Robinson 1996). Taken together then, the neural representation of the target is modulated by all of the manip-

ulations used in this study—the location, the time, and the relevance of the preceding cue.<sup>1</sup>

<sup>1</sup> It is important to consider whether the changes in target-related activity originated from the inclusion of saccade-related activity when saccadic latencies were short. The range of saccadic latencies included in the analysis ranged from 90 to 300 ms, whereas target-related activity was defined as the peak response occurring 75–125 ms after the appearance of the target. This means that, for short-latency saccades (<140 ms), motor activity may contaminate the target-related signal. Albeit a potential concern, this alone cannot explain the data obtained in this study. The number of short-latency saccades ( $\leq 140$  ms) was extremely small, accounting for <4% of the data set (1.3% non-predictive, 3.4% predictive). Using the median target-related activity, rather than the mean, as one way to remove outliers, produced the same pattern of data (not

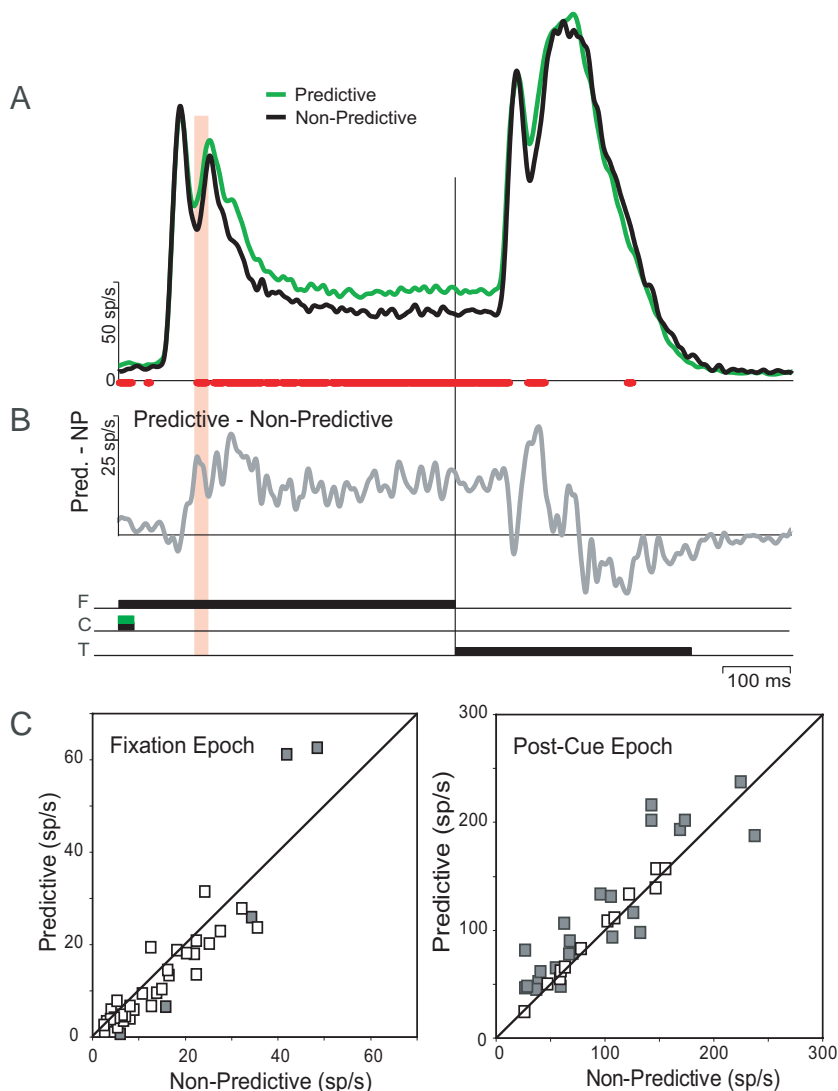


FIG. 5. *A*: population spike density comparing neural activity obtained for predictive (green) and non-predictive (black) cues at the 50 ms CTOA. Red lines at bottom indicate significant difference in neural activity between these conditions ( $P < 0.05$ ). Red bar, the postcue epoch. *B*: subtraction plot revealing the difference in neural activity between predictive and non-predictive spike densities. *C*: comparison of fixation-related activity (*left*) and postcue related activity (*right*) for every neuron in the sample. Gray squares, neurons that produced a significant correlation ( $P < 0.05$ ).

#### Relationship with previous studies

As a whole, our findings have important consequences for interpreting the inconsistent outcomes of the previous studies exploring the neural correlates of salient events in the dorsal visual pathway (Milner and Goodale 1995). Like this study, the correlate of “salience” was linked to changes in neural response to the target (Bell et al. 2004; Constantinidis and Steinmetz 2001b; Dorris et al. 2002; Gottlieb et al. 1998; Kusunoki et al. 2000; Robinson and Kertzman 1995; Robinson et al. 1995; Steinmetz et al. 1994; reviewed in Colby and Goldberg 1999; Gottlieb 2002; Goldberg et al. 2002; but see Bisley and Goldberg 2003). The important difference across these studies was *how* this signal was modified: sometimes target-related activity was strong (Bell et al. 2004; Gottlieb et al. 1998; Kusunoki et al. 2000), whereas in other instances, it was weak (Bell et al. 2003; Constantinidis and Steinmetz 2001b; Dorris et al. 2002; Robinson and Kertzman 1995;

shown). Finally, similar changes in target-related activity have been observed in neurons that have only visual responses (Fecteau and Munoz 2003b; Robinson and Kertzman 1995). In this case, contamination from saccade-related activity is impossible. Therefore, although saccade-related activity could contaminate our measures of target-related activity on some trials, it alone does not account for the findings.

Robinson et al. 1995; Steinmetz et al. 1994). No explanation for these opposite, but otherwise replicable, changes in target-related activity had been provided.

Despite many potential sources for the discrepancies across these studies (e.g., tasks used, brain region scrutinized, etc.), we have shown that these inconsistent findings are *complementary*: strong target-related activity links to the capture of attention, whereas weak neural activity corresponds to inhibition of return. Indeed separating the previous studies on the basis of those that have explored consequences of a salient event shortly after it appeared from those that probed the consequences of a salient event after more time elapsed segregates the outcomes of these studies quite well: relatively strong neural activity was obtained in the short term (Gottlieb et al. 1998; Kusunoki et al. 2000; see also Bisley and Goldberg 2003) and weak neural activity was obtained in the long term (Constantinidis and Steinmetz 2001b; Dorris et al. 2002; Robinson and Kertzman 1995; Robinson et al. 1995; Steinmetz et al. 1994).

Of more immediate importance to this study were the inconsistent findings associated with predictive and non-predictive cues. Weak target-related activity was obtained in both instances (Bell et al. 2004; Dorris et al. 2002; Robinson and

Kertzman 1995; Robinson et al. 1995; see also Steinmetz et al. 1994), even though there are important differences between these two conditions (Richard et al. 2003; Wright and Richard 2000).

Here, we have shown that predictive cues produce important differences when compared with non-predictive cues—the attentional benefit linked to the capture of attention is enhanced and inhibition of return is diminished. Important changes in neural activity occur also—elevated pretarget activity appears to enhance the target-related response. However, this influence of relevance is subtle when compared with the large changes in neural activity that originate from the salient event alone (non-predictive cue). Had we not established the consequences of non-predictive and predictive cues in the same neurons, this important change would have been impossible to see.

#### *Toward a generalized understanding of the neural basis of orienting attention*

Up to now, we have focused on the consequences of salient events—the abrupt appearance of an object in the visual scene—on biasing attention. However, static objects that contain a unique feature (e.g., a single red rose on a green bush) profoundly influence the orienting behavior of observers as well. Visual search, the task used to explore the consequence of salient static objects in the scene (Treisman and Gelade 1980; reviewed in Wolfe 1998), also produces the same biases in attention that we have explored here—the capture of attention by a unique feature (Treisman and Gelade 1980; reviewed in Wolfe 1998; but see Yantis and Egeth, 1999), inhibition of return to prevent repeated inspection of the same spatial location (Klein 1988; reviewed in Shore and Klein 2000), and the important changes in this pattern when the explicit or implicit goals of the observers guide their searching strategies (e.g., Caputo and Guerra 1998; Wolfe 1994; Wolfe et al. 1989, 2003).

These biases in visual search have been incorporated in theoretical models that describe the orienting behavior of observers. The salience model of visual attention is of particular note because it provides a simple way to describe these biases in attention across tasks (Bichot and Schall 1999; Fecteau and Munoz 2003b; Itti and Koch 2001; McPeck and Keller 2002; Thompson et al. 2001). The salience map is a two-dimensional topographical map that represents each object in the visual scene. The most distinct object produces the strongest peak of activity and demarcates the location to which attention is oriented. Relative differences in the height of this peak produce graded differences in how quickly attention is oriented with greater activity producing faster orienting. To avoid repeated selection of the same location, inhibition of return decreases the salience of previously inspected locations (reviewed in Itti and Koch 2001; see also Itti et al. 1998; Koch and Ullman 1984; Treisman and Gelade 1980; Wolfe 1994).

In visual search, the neural correlate that represents the bottom-up salience of an object is not observed in initial registration of the target but in the later evolution of neural activity that differentiates the target from distractors (Schall and Hanes 1993; Thompson et al. 1996; see also McPeck and Keller 2002; Schall et al. 1995; Thompson et al. 1997): the capture of attention is associated with rapid selection of the salient target (Bichot and Schall 1999; Sato et al. 2001),

whereas inhibition of return is associated with a delay in its selection (Bichot and Schall 2002). By contrast, the goals of observers lead to a speeding up of this selection process (Bichot and Schall 2002).

Although visual search and the cue-target task produce the same attentional effects, it may appear as if there is little to compare between these two tasks in neurophysiology—visual search is associated with changes in the evolution of neural activity differentiating the target from distractors, whereas the cue-target task (used in this study) is associated with changes in the initial registration of the target. Focusing on these differences across tasks turns us away from what is common, though. It is the relative difference in the target-related response across task manipulations, either evolving across time or immediately apparent, that comprises the automatic neural correlates of a salient object or event, and it is the further enhancement of the target's neural representation that signifies the goals of observers.

These changes in the neural representation of the target appear to have access to motor planning as a strong relationship between target-related activity and saccadic reaction times have been reported in many studies (Bell et al. 2004; Bichot and Schall 1999, 2002; Dorris et al. 2002; Sato et al. 2001; but see Thompson et al. 1996, 1997). At the level of the superior colliculus, changes in target-related activity are evidenced in the activity of visuomotor neurons. One property of these neurons is that the accumulation of activity before the motor burst may help determine when threshold for initiating an action is achieved (Hanes and Schall 1996) and may provide a simple solution for linking the salience map with the planning and initiation of actions (Itti and Koch 2001).

Showing a relationship between these neural signals of salience and saccadic behavior does not mean that these signals should be interpreted as saccadic plans. On the contrary, when the observers do not respond immediately to the target—for instance, when the task makes them hesitant to indicate their decision—no relationship between the neural correlate of target salience and reaction times is found (Murthy et al. 2001; Sato and Schall 2003). Similarly, sensory information can be dissociated from saccadic eye movements (Mays and Sparks 1980). This promotes the intriguing possibility that the mental set of the observer (respond immediately versus respond with hesitancy) dictates how closely these signals of attention are linked to motor acts.

#### *Adopting a network view*

Whenever the neural correlates of a cognitive behavior are revealed in one brain structure, one erroneous conclusion that can be made is that the brain structure under scrutiny is the one producing the behavior. On the basis of single-cell recording, this conclusion is not justified because similar patterns of neural activity may be observed across the network of brain regions connected to the one being monitored (Schall 2002). The studies we have drawn on support this contention because neurons in the frontal eye fields (Bichot and Schall 1999, 2002; reviewed in Schall and Thompson 1999), the superior colliculus (Dorris et al. 2002; McPeck and Keller 2002; Robinson and Kertzman 1995), the lateral intraparietal area (Bisley and Goldberg 2003; Gottlieb et al. 1998; Robinson et al. 1995), and area 7a (Constandinidis and Steinmetz 2001a,b) have shown



these neural correlates of orienting attention. Thus by recording the activity of neurons in one structure, we observe the characteristics of that structure *and* the properties of the network of which it is a member (see also Schall 2002, 2004).

Showing the same signals in 7a (Constandtinidis and Steinmetz 2001b; Steinmetz et al. 1994) has important implications because this structure is not, strictly, a member of the oculomotor network (Andersen et al. 1990; Clower et al. 2001). This finding indicates that changes in target-related activity are distributed across multiple networks and, perhaps, may be used to guide and trigger the actions of other effectors, such as the hand, as well (Cisek and Kalaska 2001; Murata et al. 2000; Shen and Alexander 1997a,b). Consider the ramifications of this observation. The widespread distribution of the same signals across the brain would produce the appearance of a unified attentional network (biases in attention that are independent of the effector used to respond) (Posner and diGirolamo 2000) and, at the same time, produce the important differences that have been observed across effectors (e.g., the hand and the eye code biases of attention in different frames of reference) (e.g., Abrams and Pratt 2000). Perhaps, then a resolution to the ongoing attention/intention debate that has dominated the field of orienting visual attention for some decades is in view (e.g., Chelazzi and Corbetta 2000; Colby and Goldberg 1999; Corbetta et al. 1998; Goldberg et al. 2002; Mesulam 1999; Nobre et al. 1999; Posner and diGirolamo 2000; Rizzolatti et al. 1987; Snyder et al. 1997). Can distinct cognitive signals nonetheless be used to guide actions? Future studies should see.

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