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Fecteau JH, Munoz DP. Warning signals influence motor processing. *J Neurophysiol* 97: 1600–1609, 2007. First published November 29, 2006; doi:10.1152/jn.00978.2005. When observers initiate responses to visual targets, they do so sooner when a preceding stimulus indicates that the target will appear shortly. This consequence of a warning signal may change neural activity in one of four ways. On the sensory side, the warning signal may speed up the rate at which the target is registered by the brain or enhance the magnitude of its signal. On the motor end, the warning signal may lower the threshold required to initiate a response or speed up the rate at which activity accumulates to reach threshold. Here, we describe which explanation is better supported. To accomplish this end, monkeys performed different versions of a cue-target task while we monitored the activity of visuomotor and motor neurons in the superior colliculus. Although the cue target task was designed to measure the properties of reflexive spatial attention, there are two events in this task that produce nonspecific warning effects: a central reorienting event (brightening of central fixation marker) that is used to direct attention away from the cue, and the presentation of the cue itself. Monopolizing on these tendencies, we show that warning effects are associated with several changes in neural activity: the target-related response is enhanced, the threshold for initiating a saccade is lowered, and the rate at which activity accumulates toward threshold rises faster. Ultimately, the accumulation of activity toward threshold predicted behavior most closely. In the discussion, we describe the implications and limitations of these data for theories of warning effects and potential avenues for future research.

INTRODUCTION

The study of warning effects is one of the oldest topics in the field of psychology. Wundt (1881) observed that participants initiate responses sooner when a stimulus (the warning signal) indicates that the target will appear shortly (cited in Hackley and Valle-Inclán 2003; James 1890) (Fig. 1A). Since this time, many different ideas have circulated regarding how warning signals exert their effect. Some researchers have proposed that warning signals influence sensory or perceptual processing, whereas others have proposed that warning signals influence response selection or the execution of action. In this study, our goal was to translate these different models into direct predictions that could be tested in single neuron neurophysiology (Fig. 1B).

The sensory/perceptual accounts propose that a warning signal modifies how the target is processed in the brain. There are two views on how this might occur. The *speed of transmission* hypothesis, originally proposed by Wundt (1881), suggests that a warning signal allows the target to be registered in the brain faster (e.g., Wundt 1881). Alternatively, the *magnitude of registration* hypothesis (see e.g., Hackley and Valle-Inclán 2003) proposes that the transmission time is the same,

but the magnitude of the sensory evoked response is stronger after a warning signal has appeared.

By contrast, response selection/motor execution accounts suggest that a warning signal affects how the motor act is produced. There are two views on how this might occur. The *variable threshold* hypothesis suggests that a warning signal lowers the amount of activity that is needed to initiate a response (Fernandez-Duque and Posner 1997; Grice 1968; Reddi and Carpenter 2003; Reddi et al. 2003). Alternatively, the *variable rise to threshold* hypothesis proposes that a warning signal speeds up the rate at which information accumulates to trigger an action (Carpenter and Williams 1995; Reddi et al. 2003).

Human behavioral and psychophysiological investigations have not been able to ascertain which of these four hypotheses is more meritorious. Sanders (1980, 1983) used additive factors logic (Sternberg 1969) to assess whether warning effects modified perceptual or motor stages of processing. He found that response measures, such as the velocity of an action, interacted with warning effects, whereas perceptual manipulations did not. From this evidence, he concluded that warning signals influence motor processing. By contrast, psychophysiological studies have indicated that warning signals influence sensory/perceptual processing. For instance, Hackley and Valle-Inclán (1998) compared different components of the lateralized readiness potential (LRP) to determine whether the warning signal modified sensory/perceptual processing (stimulus-locked LRP) or late stages of motor processing (response-locked LRP). They observed that only the stimulus-locked LRP was affected by the warning signal, supporting a perceptual basis of warning effects. No explanation for the discrepancies among these studies has been offered.

This study was designed to bring critical neurophysiological evidence to this debate. Each theory can be translated directly into predictable changes in neural activity, observable in visuomotor and motor neurons of the superior colliculus (see Fig. 1C) (Sparks 1978). The sensory/perceptual accounts will be reflected in neural activity related to the registration of the visual target (Fig. 1C, left). Accordingly, if the speed of transmission hypothesis garners support, then the target-related response will be registered sooner after the appearance of a warning signal (Fig. 1, C, orange arrow, and D, orange bar graph), whereas if the magnitude of registration hypothesis garners support, then the target-related burst will be stronger after a warning signal (Fig. 1, C, blue arrow, and D, blue bar graph). By contrast, the response selection/ motor execution accounts hold that warning effects will be evidenced as changes in saccade-related activity (Fig. 1C, right). Namely, the variable threshold hypothesis predicts that less activity will be

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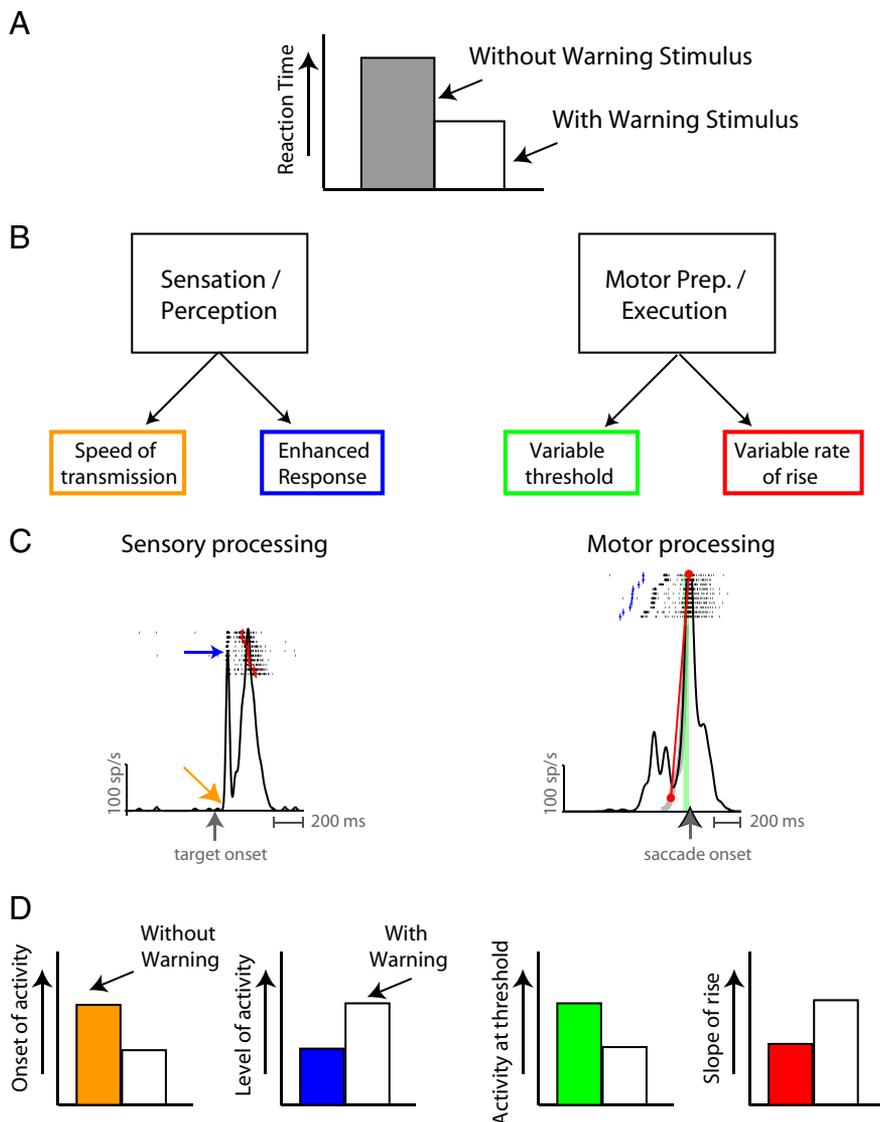


FIG. 1. Theoretical consequences of a warning signal in behavior and neural activity. *A*: change in reaction time with and without a warning stimulus. *B*: overview of possible mechanisms responsible for warning effects (see text for greater detail). Color scheme used in this figure maintained throughout rest of document. *C*: representative visuomotor neuron in the superior colliculus highlighting the neural correlates for each hypothesized mechanism of warning effects. *Left*: target-aligned raster shows onset of target-related activity (orange arrow) and peak target-related response (blue arrow). *Right*: saccade-aligned raster shows accumulation of activity toward threshold (red line) and threshold activity (green bar). Visuomotor neurons elicit a volley of activity that is time-locked to the presentation of a visual stimulus within the response field of the neuron (*C*, *left*) and a 2nd volley of activity that is time-locked to the generation of a saccade to the same spatial location. *D*: predicted change for each neural correlate for trials with and without a warning signal.

observed in the epoch marking saccadic threshold because less activity is necessary to trigger the action (Fig. 1, *C*, epoch high highlighted by green bar, and *D*, green graph). Finally, the differential variable rise to threshold hypothesis predicts that the warning signal will result in the faster accumulation of activity toward threshold. This neural correlate can be estimated in the slope of this change (Fig. 1, *C*, red line, and *D*, red graph).

Warning signals can be produced in many different ways and are observed in a wide range of contexts (see e.g., Hackley and Valle-Inclan 2003; Niemi and Näätänen 1981; Posner 1978; Posner et al. 1976). Here we monopolized on two features of the cue-target task (Fig. 2) that are thought to serve as warning signals. The nonpredictive cue-target task was developed to explore the reflexive properties of spatial attention (Posner and Cohen 1984). In addition to the usefulness of this task in the arena of reflexive orienting, many studies have now reported that features of this task act as warning signals (see Coull and Nobre 1998; Correa et al. 2004; Fernandez-Duque and Posner 1997; Milliken et al. 2003; Posner and Cohen 1984; Pratt and Fischer 2002; Reuter-Lorenz et al. 1996; Exp. 1 of Spence and Driver 1998; Tipper and Kingstone 2005). In the next few pages, we describe how warning signals,

produced through the cue-target task, lead to changes in the neural measures listed in the preceding text.

METHODS

Two male rhesus monkeys (weighing ~6 and 10 kg) participated in this study. The techniques used to collect behavioral data and to obtain physiological recordings have been described previously (Fecteau et

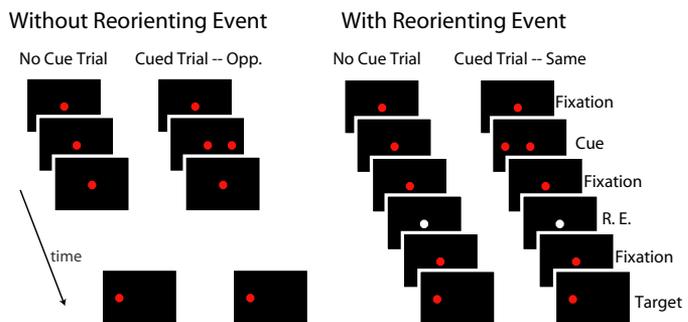


FIG. 2. Warning signals in the reflexive cue-target task. *A*: overview of the cue-target task without a reorienting event (*left*) and with a reorienting event (*right*) for cue and no-cue trials. RE, reorienting event; Opp., opposite.

al. 2004b; Munoz and Istvan 1998) and were approved by the Queen's University Animal Care committee.

Behavioral task

The nonpredictive cue-target task was developed to explore the reflexive properties of spatial attention (Posner and Cohen 1984). In this task, the observers begin each trial by maintaining gaze on a central fixation marker. A visual stimulus (the cue) is presented briefly. This cue is irrelevant and the observers must continue to maintain gaze at center. Next the target appears to which the observers initiate a response—in this study, a saccadic eye movement was generated to the target's location.

We monopolized on two features of this cue-target task (Fig. 2), which act as warning signals. First, the presence of a central reorienting event—a brief flash of light at the central fixation marker—acts as a warning signal (Posner and Cohen 1984; Pratt and Fischer 2002; Exp. 1 of Spence and Driver 1998). Importantly, this change in reaction time produced by a warning signal is additive, meaning that it does not affect the mechanisms responsible for inhibition of return directly (Pratt and Fischer 2002; see also Sternberg 1967).

Second, the appearance of a cue also acts as a warning signal because it provides temporal information indicating that the target will appear soon (see e.g., Fernandez-Duque and Posner 1997; Tipper and Kingstone 2005).

The behavioral task consisted of six conditions originating from the combination of two factors: reorienting event (reorienting event present vs. absent conditions) and cueing condition (no cue, cue and target at same location, vs. cue and target at opposite locations). Examples of these conditions are illustrated in Fig. 2.

Every trial began with the monkeys maintaining gaze on a central fixation marker for 500–1,000 ms (randomized among 5 values: 500, 625, 750, 875, and 1,000 ms). For the cued trials (cue same or cue opposite) without a reorienting event, the cue appeared briefly (30 ms) in the left or in the right visual field. The fixation marker remained in view until the target appeared. The cue-target interval was fixed at 200 ms. For the trials consisting of a cue and a reorienting event, the timing of events was identical except the fixation marker was flashed 100 ms after the onset of the cue. For the no-cue trials, the timing of events was identical to the cued trials. No-cue trials with and without a reorienting event were presented.

The monkeys' received a drop of water or juice for initiating a saccade to the target's location within 500 ms of its appearance.

The visual stimuli consisted of red light-emitting diodes (LEDs, 0.03 cd / m^2) that were rear projected onto a tangent screen in front of the observer. One of the cue-target locations was positioned to elicit the optimal response from the neuron being monitored and the second appeared at its mirror position (across the vertical and horizontal axes). The central reorienting event was produced by the 30 ms presentation of a red laser (5 cd/m^2) that was aligned perfectly with the central fixation marker. The cue and fixation stimuli were different intensities to allow the central reorienting event to be perceptible.

In each recording session, the experimenter attempted to obtain ≥ 10 trials for each condition, yielding a total of 120 trials: 80 cued trials originating from the combination of *reorienting event* (present vs. absent), *cue-target relationship* (same vs. opposite), and *target location* (in response field vs. out of response field); and 40 no-cue trials originating from the combination of *reorienting event* (present vs. absent), and *target location* (in response field vs. out of response field). This was achieved in most sessions. However, there were sessions in which the full number of trials was not achieved because the isolation of the neuron was lost or because the monkey was satiated. A minimum of four observations per condition were required to be included in the analysis.

Saccadic reaction time was used to index changes in behavior because most studies of warning effects have used reaction time as the primary dependent measure.

Behavioral and neural analyses

The behavioral data included in this study were obtained at the same time as the neural data were collected. Only the reaction times from correctly performed trials were included in the behavioral analyses. Only the data from these trials were used in the neural analyses. A correctly performed trial was defined as a single saccade initiated to the target's location within 125–300 ms of the target's appearance. Errors were rare, occurring on $< 2\%$ of the trials. The reaction time data were collapsed across the location of the target (within the response field versus opposite the response field) for the means comparisons, as this factor does not affect the manipulations of interest.

Of the 49 neurons monitored in the intermediate layers of the superior colliculus during this task, 26 visuomotor and 6 motor neurons met the criteria for inclusion in this study. At least four observations were obtained per condition (i.e., in the factorial breakdown of the experimental design; ≥ 10 observations were more common), the average peak saccade-related burst exceeded 80 spike/s. Visuomotor and motor neurons were separated on the basis of the presence of a target-related response (maximum activity occurring 70–120 ms, target-aligned raster) that exceeded 70 spike/s in the no-cue condition without a reorienting event. The action potentials on each trial were convolved using a Gaussian kernel ($\sigma = 10$); this sigma value provided adequate smoothing of the discharge profile without changing the time of the peak visual and peak saccade related discharges.

Each hypothesis of warning effects predicts that a specific change in neural activity will be observed (Fig. 1, C and D). For the speed of transmission hypothesis, the onset of target-related activity was assessed for visuomotor neurons across all conditions when the target appeared in the response field of neuron. The onset of activity was defined as a 3 standard deviation increase in activity above baseline (-300 to -150 ms target-aligned) occurring between 60 and 120 ms after the onset of the target. On the basis of this criterion, one value of target onset was obtained from the average spike density waveform for each neuron in every condition. The experimenter verified the reliability of these criteria for every neuron in the sample. The use of a Gaussian kernel for this analysis has the negative consequence of underestimating the onset of neural activity (Thompson et al. 1996). However, for this analysis, we were not interested in the true onset of neural activity but rather the differences in the onset of neural activity across conditions. The Gaussian kernel is well suited for this comparison.

For the magnitude of registration hypothesis, the average peak target-related activity was obtained for all visuomotor neurons in the sample. This correlate was defined as the maximum activity obtained 70–120 ms after the onset of the target (target-aligned spike density). A value was obtained for every trial and then combined into an average value for each neuron in every condition.

For the variable threshold hypothesis, we tested two epochs of neural activity before the onset of the saccade -20 to -10 and -50 to -30 ms. The -20 - to -10 -ms window is identical to that used in previous studies (e.g., Everling et al. 1999; Hanes and Schall 1996). This criterion was chosen for two reasons: the latency of electrically evoked saccades is ~ 10 ms in some studies (e.g., Robinson 1972; see arguments in Everling and Munoz 2000; Hanes and Schall 1996) and omnipause neurons in the brain stem turn off at this time before the onset of the saccade (e.g., Everling et al. 1998). This value has been supported by a more recent study that has shown that the estimated time it takes to cancel a planned saccade can be observed between 30 and 5 ms faster in the neural data than in the behavioral data (Pare and Hanes 2003). Therefore this 20- to 10-ms epoch is a reasonable choice because it marks the time at which the saccade is about to be initiated.

However, there is also some reason to believe that differences in threshold to trigger an action may occur before this -20 - to -10 -ms window. First, the latency of electrically evoked saccades is > 20 ms

when different stimulation parameters are used (Corneil et al. 2002; Stanford et al. 1996). Second, the -20 - to -10 -ms epoch often contains the peak of the saccade-related response when the vector of the saccade has been properly mapped (Sparks 1978; Sparks et al. 1976). The magnitude of this signal is highly stereotyped for visually-guided saccades and changes in the magnitude of this signal correspond to changes in the dynamics of the ensuing saccade (Munoz et al. 1991; Stanford and Sparks 1994). These qualities do not capture what is meant by threshold in theoretical discussions (e.g., Carpenter 2004; Reddi et al. 2003), where threshold is the set criterion for choosing one response over another as opposed to the forgone commitment to one choice. Third, neural evidence of threshold, as measured during the countermanding task, places threshold earlier in time. The magnitude of saccade-related activity of neurons in the superior colliculus was less than half on canceled trials than on noncanceled trials for the majority of neurons in the sample (average $\sim 1/3$ maximal) (Pare and Hanes 2003). This result indicates that threshold is reached at sometime after $1/3$ activity and before maximal activity. The -50 - to -30 -ms window captures this intermediate range (see green bar in Fig. 1C).

Because it is fair to conclude that we do not know the exact instant at which threshold is achieved, we describe the data originating from two epochs of *near* threshold activity, one early (-50 to -30 ms, saccade-aligned) and one late (-20 to -10 ms, saccade-aligned).

For the variable rise to threshold hypothesis, the speed at which neural activity accumulated was assessed with a slope function [change in activity across time]. To obtain a reliable measure of this activity that was not affected by the visual response (visuomotor neurons); the activity preceding this rise of activity (≤ 130 ms target-aligned) was removed from the spike-train.¹ The remaining activity was realigned to the onset of the saccade.

From the average spike density of each neuron, the onset of the rise in activity was defined as the moment when neural activity achieved 20 spike/s. The end of the rise was defined as 30 ms before the onset of the saccade—the estimated time at which the threshold of the response has been achieved (see preceding text). Although these values may seem arbitrary, changing these onset and offset values to values that were earlier, later, higher or lower had no impact on the pattern of results that were obtained. We report the data originating from the first parameters that were applied.

The neural and reaction time data were subjected to statistical analyses using repeated-measures ANOVA. The grand means from every neuron and corresponding behavioral data were treated as a subject in the analysis. This tactic equalizes the neural and behavioral data as much as possible as it keeps the degrees of freedom the same.

Two separate analyses were conducted. To maximize the ability to observe the consequences of a warning effect, ANOVA consisted of the factors *reorienting event* (present vs. absent) and *cueing condition* (no cue, cue same, cue opposite). A second ANOVA considered whether systematic changes were obtained across the *number of warning signals* (0, 1, or 2) the different trial types contained. This analysis was conducted separately for trials when the cue did (cue same) or did not (no cue, cue opposite) appear at the same location as the target because of the presence of inhibition of return at this cue-target onset asynchrony (see Fecteau and Munoz 2005; Fecteau et al. 2005). Simple effects were also compared with the *F*-distribution with the alpha adjusted appropriately (Bonferroni correction).

The data were then subjected to multiple stepwise regression analyses. Only the conditions that yielded a significant effect in the ANOVA were included. To assure that the statistical power remained the same for every comparison, each neuron (session) contributed 1 value for every experimental condition (combination of the reorienting event and cueing condition). From these analyses, the coefficient of determination (R^2) is described for the regression containing all

factors and for each predictor independently. An alpha of 0.05 was adopted as significant for all statistical analyses in this study. Because these statistical comparisons were two-tailed, and the predictions were directional, marginal effects were also considered ($P < 0.1$) when the effect was of theoretical interest and in the predicted direction (equivalent to a 1-tailed test).

RESULTS

Two analyses were conducted to establish the presence of warning signals in this study. First, comparing the data from trials that did or did not contain a reorienting event (as a main effect; Fig. 3A, *left*) allows us to assess the consequences of a warning signal in neural activity with the greatest amount of power. Second, a systematic change in performance should be observed across conditions that contain zero, one, or two warning events during the course of the trial (Fig. 3A, *right*). The second analysis was designed to make these comparisons possible.

As can be seen in Fig. 3A, the appearance of a reorienting event resulted in faster reaction times and systematic changes were obtained across conditions.

To confirm these observations, the first analysis considered the role of the reorienting event (present vs. absent) on performance across the different cueing conditions (no cue, cue same, cue opposite). This analysis revealed that a robust warning effect was obtained: reaction times were 28 ms faster when a reorienting event preceded the target compared with when it did not, $F(1,31) = 149.1$, $P < 0.05$ (Fig. 3A, *left*). Two additional effects were significant in this analysis. Baseline differences in reaction time were obtained across the different cueing conditions, $F(2,62) = 113.0$, $P < 0.05$: saccadic reaction times were fastest when the cue and target appeared at opposite locations (177.8 ms), of intermediate latency during the no-cue trials (194.5 ms), and slowest when the cue and target appeared at the same location (201.2 ms). Finally, the interaction involving these two factors was significant, $F(2,62) = 61.9$, $P < 0.05$, indicating that reorienting event had less influence when the cue and target appeared at opposite locations compared with the other two cueing conditions (Fig. 3A). Although the presence of this interaction appears to speak against the independence of warning signals and biases in selective attention (Fernandez-Duque and Posner 1997), drawing this conclusion would be inappropriate because the condition producing this interaction also yielded the shortest reaction times (i.e., a floor effect).

The second analysis assessed the changes in performance depending on the number of warning signals presented (Fig. 3B, *right*). When the cue did not appear at the same location as the target, performance was slowest when no warning signal preceded the target (no cue, without a reorienting event), of intermediate latency when one warning signal event appeared (no cue with reorienting event, cue opposite without reorienting event), and fastest when two warning signals appeared (cue opposite with reorienting event). Importantly, however, performance was not equivalent for the two intermediate conditions but was significantly faster for the no-cue trials with a reorienting event, $F(1,31) = 7.6$, $P < 0.05$. When the cue and target appeared at the same location (conditions of inhibition of return, highlighted with gray box), reaction times were faster after the appearance of the reorienting event $F(1,31) = 146.2$, $P < 0.05$.

¹ This cut-off was chosen because it removed the target-related burst of activity for every neuron in the sample.

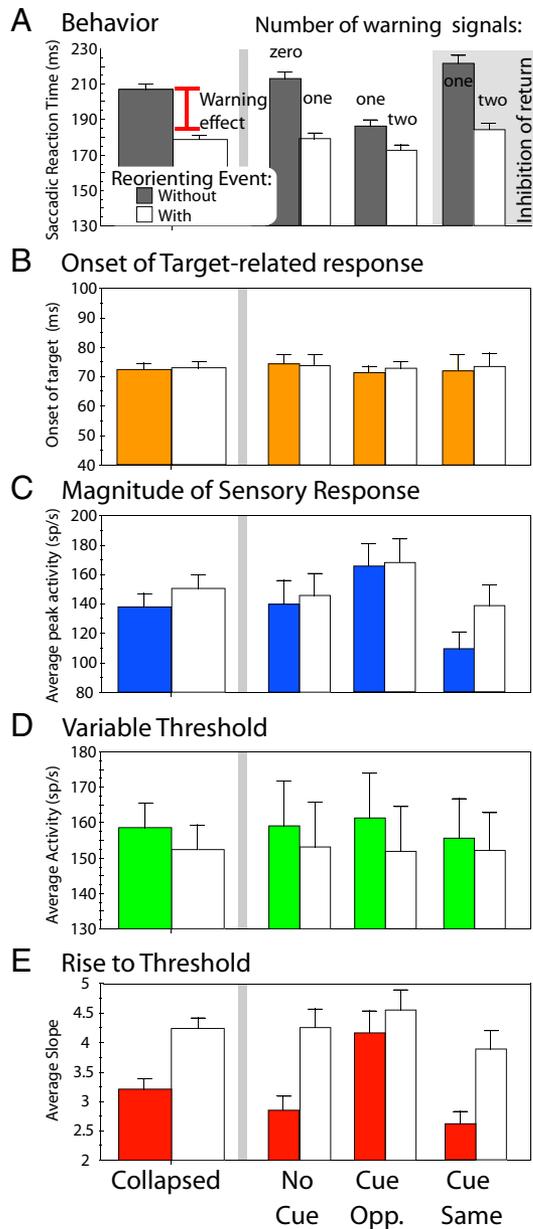


FIG. 3. Population averages for saccadic reaction time (A), the onset of the target-related response (B), the magnitude of the target related response (C), threshold activity (D; -50 to -30 ms saccade aligned data), and slope value estimate rate of rise (E). Error bars represent ± 1 standard error of the mean. In A, the number of warning signals each condition contains is listed and the condition producing inhibition of return (cue and target at same location) is highlighted in gray.

Four different neural correlates were analyzed in the same way as behavior; each one chosen for its unique ability to either support or deny one the four hypotheses described in the INTRODUCTION (Fig. 1, C and D). The outcomes of these analyses are described in turn.

Speed of transmission

The average onset latencies of target-related activity are illustrated in Fig. 3B and follow the same layout as that shown for behavior. The population spike densities are shown in Fig. 4A. As evident in these figures, no systematic differences in the onset of

target-related activity were obtained across conditions. The reorienting event had no influence, $F(1,25) < 1$. The same was true for the different cueing conditions, $F(1,25) < 1$. Finally, the interaction of these factors yielded no effect, $F(1,25) < 1$. As might be expected, this outcome did not change when focusing on the number of warning signals presented during the course of the trial, F 's < 1 . Therefore the speed of transmission hypothesis was not supported by the data.

Magnitude of Registration

The average peak target related activity for trials with and without the reorienting event are illustrated in Fig. 3C. The population spike densities are shown in Fig. 4A. The ANOVA consisting of the factors reorienting event (present vs. absent) and cueing condition (no cue, cue same, vs. cue opposite)

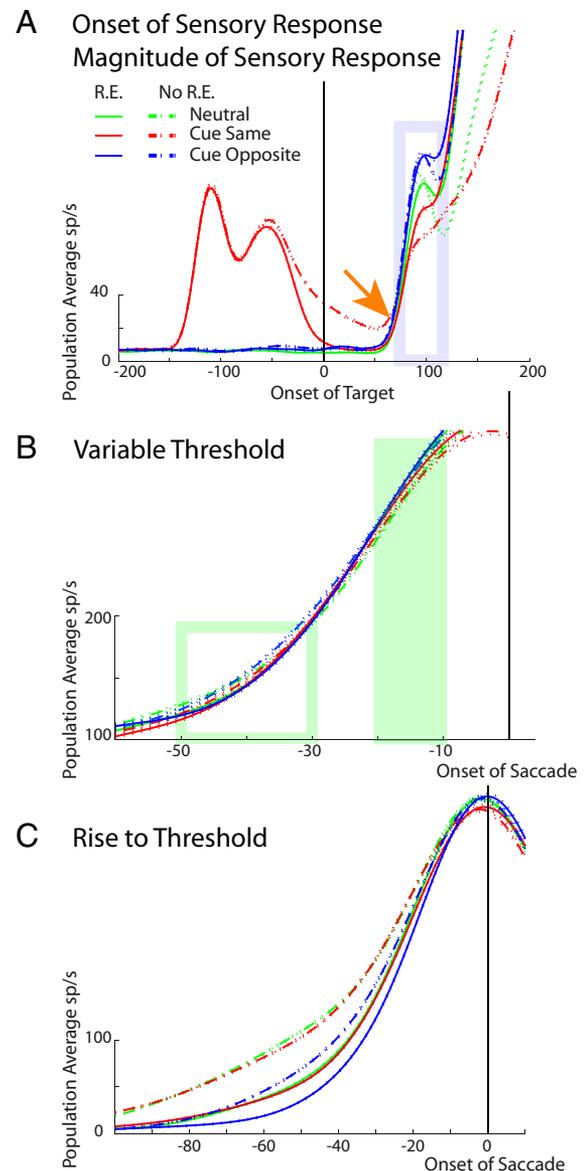


FIG. 4. Population spike density waveforms showing differences in the onset (orange arrow) and magnitude of the sensory response (blue rectangle; A), differences in the threshold for the -50 to -30 epoch (hollow rectangle) and the -20 to -10 epoch (filled rectangle; B), and differences in the slope (C). Dotted lines represent ± 1 SE.

revealed that the peak target-related response was stronger after the reorienting event, $F(1,25) = 3.7$, $P < 0.07$. The main effect of cueing condition followed the same pattern as behavior in which target-related activity was weakest when the cue and target appeared at the same location, intermediate for no-cue trials, and greatest when the cue and target appeared at opposite locations, $F(2,50) = 26.0$, $P < 0.05$. Finally, the interaction of these factors was significant, $F(2,50) = 5.8$, $P < 0.05$, which indicated that the reorienting event influenced target-related activity only when the cue and target appeared at the same location, $F(1,25) = 10.8$, $P < 0.05$. The other cueing conditions did not produce this difference, F 's < 1 . Therefore despite systematic changes in target-related activity across cueing conditions, the warning signal only influenced the target-related response when the cue and target appeared at the same location.

We have obtained an important difference between the neural correlates of warning signals and cueing effects. The results indicate that warning signals do not consistently affect the magnitude of the target-related response. Indeed, only one condition (cue same) was responsible for the apparent relationship between warning signals and target-related activity. Yet cueing effects systematically change the magnitude of the target-related response. Indeed, the relationship between the magnitude of the target-related response and saccadic reaction time exists a trial-by-trial basis as well: when the cue and target appeared at the same location (average $r = -0.63$), when the cue and target appeared at opposite locations (average $r = -0.56$), and when no cue appeared (average $r = -0.62$). Taken together then, warning signals do not appear to affect sensory processing in any meaningful manner even though different cueing conditions do. Both outcomes are consistent with previous studies: warning signals do not affect sensory and perceptual processing (Posner 1978; Sanders 1980, 1983), whereas inhibition of return does affect sensory and perceptual processing (e.g., Fecteau and Munoz 2005; Handy et al. 1999; Posner 1978; Reuter-Lorenz et al. 1996; Sanders 1980, 1983; see also Fecteau et al. 2004).

Variable threshold

Figure 3D illustrates the average near threshold activity of the visuomotor and motor neurons monitored in this study from the -50 - to -30 -ms epoch. The population spike density for the -50 to -30 epoch and -20 to -10 epoch are shown in Fig. 4B. As evidenced in Fig. 3D, *left*, threshold activity was weaker after the appearance a reorienting event, $F(1,31) = 4.0$, $P < 0.06$. This pattern is consistent with the idea that warning signals change the threshold needed to generate a response (Posner 1978). However, this change in threshold was not modified by any other factor—no difference was obtained across cueing conditions, $F(2,62) < 1$, and no interaction was obtained between factors, $F(2,62) < 1$. Therefore although it appears that threshold may be set to a lower level after a reorienting event, this change bears little relationship to the idiosyncrasies obtained across conditions.

As to be expected on the basis of these results, no changes in the average threshold activity were obtained depending on the number of warning signals presented during the course of the trial when the cue did not appear at the same location as the

target, $F(3,93) < 1.6$, $P > 0.1$, or when it did, $F(1,31) < 1$, $P > 0.1$.

We show on the population spike density for the data originating from the -20 - to -10 -ms epoch (Fig. 4B) because the same average values were obtained across all conditions (more on this issue in the following text), all F 's < 1 , all P 's > 0.1 . Taken together then, although the early (-50 to -30 ms) epoch of near threshold activity produced reliable differences, the later epoch of near threshold activity (-20 to -10 ms) did not. We discuss the consequences of these findings in greater detail in the DISCUSSION.

Variable rise to threshold

The slope data used to evaluate the variable rise to threshold hypothesis are illustrated in Figs. 3E and 4C. As evidenced in these figures, the slope data corresponded most closely to behavior. The slopes were steeper after a reorienting event, $F(1,31) = 20.1$, $P < 0.05$. Across the different cueing conditions, the slopes were steepest when the cue and target appeared at opposite locations, intermediate for the no-cue condition, and most shallow when the cue and target appeared at the same location, $F(2,62) = 12.0$, $P < 0.05$. Finally, the interaction reflecting the reduced warning effect when the cue and target appeared at opposite locations was observed in the slope data as well, $F(2,62) = 4.4$, $P < 0.05$. This outcome indicated that the reorienting event resulted in a significantly steeper slope for no-cue trials, $F(1,31) = 20.8$, $P < 0.05$, and cue-same trials, $F(1,31) = 18.9$, $P < 0.05$, but not cue opposite trials, $F(1,31) < 1.4$, $P < 0.05$.

A second analysis assessed the changes in slope values across the number of warning signals presented. The ANOVA indicated that the number of warning signals affected the estimated rise to threshold (0, 1, or 2), $F(3,93) = 10.2$, $P < 0.05$, when the cue did not appear at the same location as the target. The comparison when the cue and target appeared at the same location was also significant, $F(1,31) = 18.9$, $P < 0.05$. As illustrated in Fig. 3E, the slope values followed the same, albeit inverted, pattern as reaction times, although not all pair-wise comparisons were significant.

Summary of Neural Data

Taken together, three of the four neural correlates tested in this study were modified by the appearance of the warning signal: after the reorienting event, the magnitude of the sensory response was stronger (Fig. 3C), the near threshold neural activity was lower² (Fig. 3D), and activity accumulated toward threshold faster (Fig. 3E, see also Fig. 4C). This relationship fell apart when more detailed analyses were conducted. The apparent relationship between warning signals and the magnitude of the target-related response originated from trials in which the cue and target appeared at the same location: no other cueing conditions produced this relationship. However, this *inability* of the target-related response to reflect the consequences of warning effects existed alongside the *ability* of this correlate to reflect cueing effects: a stepwise increase in the target-related response was obtained across the cue-same, no-cue, and cue opposite conditions. This may suggest that not all changes in performance can be attributed to warning effects

² This difference was limited to one epoch being tested.

when the cue appears opposite the target (see Pratt et al. 1999; Snyder et al. 2001). By contrast, the activity near the threshold of the saccade was weaker after the appearance of a reorienting event; however, this main effect did not translate into systematic changes originating from the number of warning signals presented. Moreover, this effect was observed only for one measure of near threshold activity (-50 to -30 ms) not the other (-20 to -10). Taken together, these observations indicate that near threshold activity cannot be the only mechanism responsible for differences in reaction time. Finally, the slope analysis, estimating the rise of activity toward threshold, yielded a pattern of changes that was similar to all aspects of behavior: it revealed the consequences of the reorienting event, the cueing effects, and the systematic changes in reaction time originating from the number of warning signals presented. However, not all pair-wise comparisons achieved statistical significance. Thus although three of the four neural correlates produce some similarity to the changes observed in reaction time, none matched behavior perfectly.

To get a better understanding of the relationship between these neural correlates and behavior, we used regression analyses to gauge the capacity of each neural correlate to predict changes in saccadic reaction time across conditions. Figure 5, A–C, shows the scatter plots of the relationship of each neural correlate and reaction time. Figure 5D summarizes the coefficients of determination (percentage of variance the regression can predict) for the regression containing all factors (Fig. 5D, top) and each factor alone (Fig. 5D, bottom). Several trends from these analyses are noteworthy. The slope values were the best predictor of reaction time overall, accounting for 45% of the variance (47% no target analysis). Threshold activity was the worst predictor of reaction time, accounting for 5% of the variance (4% no target analysis). Finally, the magnitude of target-related activity was intermediate in its predictive capacity, accounting for 19% of the variance.

This basic outcome remained the same when the analysis was limited to different conditions. Focusing first on trials when the cue did not appear in the response field of the neuron, the target-related activity accounted for 15% of the variance, the threshold activity accounted for 6% of the variance (5%, no target analysis), and the slope values accounted for 35% of the variance (45%, no target analysis). When the cue and target appeared in the response field of the neuron, the target-related activity accounted for 21% of the variance, the threshold activity accounted for 4% of the variance (5%, no target analysis), and the slope analysis accounted for 64% of the variance (47%, no target analysis).

As evident in Fig. 5D, the predictors were correlated because the variance accounted for by the full regression (top) was less than the sum of the values from each regressor when considered alone (bottom). The data from the slope analysis dominated the regression fit. This outcome is not a violation of regression modeling; it simply means that the factors included in the analysis do not account for unique portions of the variance. Importantly, conducting partial correlations to assess the unique contribution of each predictor yielded very few differences with the correlation values reported in Fig. 5, A–C; at most, the values were moved a couple points in either direction (not shown).

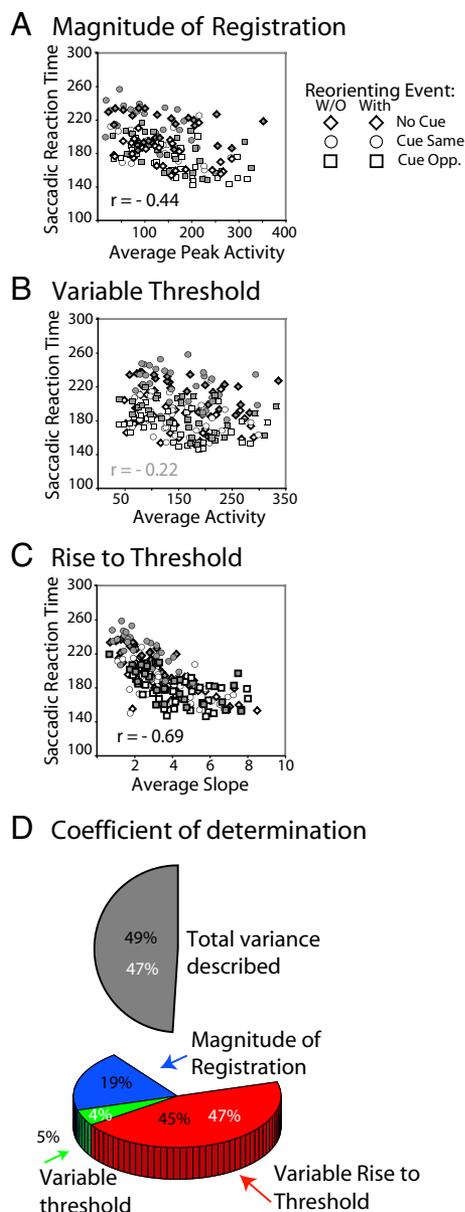


FIG. 5. Scatter plots showing the relationship between saccadic reaction time and the magnitude of the target related response (A), threshold activity (B), and slope values (C). D: coefficients of determination for full regression (top) and for each correlate separately (bottom).

DISCUSSION

The presentation of a warning signal speeds up the reaction time of observers. Over the years, this effect has been attributed to different neurophysiological mechanisms: the speed of transmission hypothesis predicted that warning signals would cause the sensory stimulus to be registered faster in the brain (e.g., Wundt 1881), the magnitude of registration hypothesis predicted that sensory and perceptual processing would be enhanced after the warning signal (Hackley and Valle-Inclán 1998), the variable threshold hypothesis predicted that the threshold necessary to trigger an action would be set to a lower level (Carpenter 2003; Fernandez-Duque and Posner 1997; Grice 1968; Posner 1978; Reddi and Carpenter 2001), and finally, the variable rise to threshold hypothesis predicted that the warning signal would speed up the rate at which informa-

tion accumulates to trigger an action (Carpenter and Williams 1995; Carpenter 2003; Hanes and Schall 1996; Reddi and Carpenter 2001; Reddi et al. 2003). In this study, we have determined that the variable rise to threshold best predicts the behavior. In the following paragraphs, we briefly summarize the outcomes of this study and the consequences of these findings for our understanding of warning effects.

Multiple sources of warning effects?

The first take-home message of this study is that warning signals can have multiple influences on neural activity. Here we observed that the magnitude of sensory activity was enhanced, the threshold needed to trigger an action was lowered, and activity rising toward threshold accumulated sooner. Albeit present to some degree, these correlates were not equally effective in predicting behavior. The rise of activity toward threshold was the best overall predictor of changes in performance originating from the warning signal.

SENSORY BASIS OF WARNING EFFECTS? Contrary to the first postulated mechanism of warning effects (Wundt 1881), we observed no change in the speed with which sensory information was processed. This outcome is in good standing with behavioral evidence indicating that observers respond sooner after the appearance of a warning signal but appear to do so on the basis of less information (Posner 1978). In fact, there is no evidence that sensory signals are registered faster in the brain across manipulations affecting attentional or cognitive processing (e.g., Bisley et al. 2004; Fecteau et al. 2004b; Ignashchenkova et al. 2004). The only manipulation that changes the speed with which targets are registered (of which we are aware) is the luminance of the stimuli, in which stimuli of high luminance can be registered 30 ms faster than stimuli of low luminance in the visuomotor neurons of the superior colliculus (Bell et al. 2006; Marino and Munoz 2005). Therefore the speed of transmission hypothesis is not supported.

By contrast, the magnitude of registration hypothesis did generate some support in this study. This statement is accompanied by a caveat, however—the warning signal enhanced the target-related response only when the cue and target appeared at the same location. No change in sensory activity was evident for the other two conditions even though large changes in saccadic reaction time were obtained. Importantly, this consequence cannot be attributed to the inability to see changes in this signal because differences in the magnitude of the target-related response were obtained across the different cueing conditions. Therefore the data clearly indicate that a change in sensory processing is not the general mechanism by which warning effects operate. This conclusion is supported by the mixed results from the ERP literature—changes in the magnitude of perceptual processes have been observed in some studies but not in all (reviewed in Hackley and Valle-Inclán 2003).

MOTOR BASIS OF WARNING EFFECTS AND THE LATER MODEL OF SACCADIC REACTION TIME. We have tested two plausible mechanisms by which warning signals may affect response selection and motor processing: changes in threshold needed to trigger a response and changes in the accumulation of information toward threshold. The variable threshold hypothesis was weakly supported. One estimate of near threshold activity (−50 to −30 ms before saccade onset) was lower after the

appearance of a reorienting event, but it was a poor predictor of differences in reaction time. The second estimate of near threshold activity (−20 to −10 ms before saccade onset) did not produce a difference. By contrast, the variable rise to threshold hypothesis was *strongly* supported: it followed a similar pattern as behavior and was the strongest predictor of differences in reaction time.

If we assume for a moment that the early epoch of near threshold activity can be used to identify threshold, then this is the first study to show that both threshold and rise to threshold mechanisms may be occurring at the same time. This finding contrasts previous neurophysiological investigations that have pitted these plausible mechanisms against each other (Hanes and Schall 1996). For instance, when the countermanding task has been used to produce large variations in saccadic reaction time, systematic changes in the rate of rise of activity toward threshold (assessed through slope) have been observed when the responses were binned into short-, medium-, and long-latency saccades (Hanes and Schall 1996; Hanes et al. 1998). By contrast, no differences were obtained for neurophysiological measures of near threshold activity. Therefore on the basis of previous neurophysiological investigations, these two processes are considered to be mutually exclusive and only the variable rate of rise mechanism has obtained empirical support (Hanes and Schall 1996; Hanes et al. 1998).

From a theoretical perspective, however, changes in threshold and the rate of rise may be considered as complementary processes. According to the LATER model (Carpenter 2003; Reddi and Carpenter 2001; Reddi et al. 2003), variability in saccadic reaction time originates from two sources: the threshold that must be surpassed to trigger an action and the rate of rise toward this threshold. Within the context of this theory, threshold can be manipulated through the demands of the experiment, such as forcing the participants to respond quickly or accurately (Reddi and Carpenter 2001; Reddi et al. 2003). By contrast, the rate of rise is a normally distributed process and without a specific manipulation of threshold is the sole factor that determines the variability in saccadic reaction time.

The findings can be interpreted with the theoretical framework of the LATER model. Consistent with its proposal, we observed less activity at the threshold of the response after the warning signal had appeared. This effect was weak—it was observed only as a main effect and had limited ability to predict the full pattern of saccadic reaction time across conditions (accounting for 4–5% of the variance as a unique predictor). Importantly, the LATER model predicts this outcome—threshold should be evidenced only when the demands of the experiment change the criterion the observers use to trigger a response. In this study, the appearance of the reorienting event served this role (see also Posner 1978). Also consistent with the LATER model, we observed strong changes in the accumulation of activity toward threshold across conditions (accounting for 45–47% of the variance as a unique predictor). This strong effect is also predicted by the LATER model—the variable accumulation of activity toward threshold is the factor that dominates differences in reaction time.

Importantly, the LATER model can also account for the findings of previous studies when cast in the appropriate manner. The countermanding task may yield a wide range of reaction times; yet no feature of this task instructs the observers to adopt a higher or lower criterion for generating a response. Without such a manip-

ulation, the rate of rise is the only factor that contributes to the variability in reaction time. This perfectly summarizes what Schall and his colleagues have reported.

One limitation of this synopsis is that it depends on the epoch that is chosen to reflect threshold. We have focused on a measure of threshold (-50 to -30 ms) that is quite different from other investigations (Everling and Munoz 2000; Hanes and Schall 1996). However, when we use the same measure of threshold as previous investigations (-20 to -10 ms, saccade-aligned), no change in threshold is observed. As described in METHODS, there are several reasons to question whether the "typical" measure of threshold is the correct measure to use; the main reason being that the -20 - to -10 -ms window corresponds to a region of the spike density where the commitment to initiate one action may have already past (Pare and Hanes 2003; Sparks et al. 1976; Sparks 1978). Accordingly, we do not offer the LATER model as a conclusive account for the data provided here, rather we suggest that it may provide one way to interpret the results of this study and other studies probing the consequences of a warning signal.

Reorienting events, cueing effects, and warning signals

One critical premise of this study is that the presentation of the reorienting event and the appearance of the cue act as warning signals. If this is true, then we should have showed the longest reaction time for trials with no warning signal (no-cue condition), intermediate and equivalent reaction times for trials with one warning signal (no cue with reorienting event and cue opposite without reorienting event), and the fastest reaction time for trials with two warning signals (cue opposite with reorienting event). We did not obtain this outcome because reaction times were not equivalent for trials containing one warning signal (Fig. 3A). There are two reasons why the observers responded faster in the no-cue condition with a reorienting event compared with the cue opposite condition without a reorienting event: the reorienting event may have been a more effective warning signal or the opposite side advantage might not represent a warning effect.

The suggestion that the reorienting event was a more effective warning signal has intuitive appeal because the cue and reorienting event were different intensities. There is no empirical evidence supporting this intuition, however—the warning effect produced by visual stimuli remains the same across a wide range of intensity and size when reaction time is used as the dependent measure (Niemi and Näätänen 1981). Therefore on the basis of previous studies, there is little reason to believe that the reorienting event was somehow a more effective warning signal.

By contrast, there is some reason to believe that the opposite side advantage does not represent a warning effect, in particular when studying the properties of inhibition of return. Previous studies have suggested that the opposite side advantage observed in the reflexive cue target task originates from the momentum that attention has to travel toward the location opposite the cue (e.g., Pratt et al. 1999). To provide evidence for this notion, a four-location cue-target task was designed that has important consequences for this discussion. Namely, if the appearance of a cue acted only as a warning signal, then performance should be equivalent whenever the cue and target do not appear at the same location. Instead performance was slowest when the cue appeared at the same location as the target, intermediate when the cue

appeared adjacent to the target, and fastest when the cue and target appeared at opposite locations. Therefore on the basis of previous behavioral investigations, the appearance of a cue cannot be considered only as a warning signal. In this study, we may have provided neurophysiological evidence that is consistent with this distinction: different cueing conditions produce large differences in the magnitude of the sensory response (see also Fecteau and Munoz 2005), whereas the appearance of a reorienting event does not have this consequence. This matter requires further exploration.

Present limitations and future considerations

We used the reflexive cue-target task to elicit warning effects because we have observed outcomes interpretable as warning effects in our own data (described in Fecteau and Munoz 2005; Fecteau et al. 2004b), which we wished to explore further, and because many other investigations have also observed warning effects when using the cue-target task (see e.g., Correa et al. 2004; Coull and Nobre 1998; Fernandez-Duque and Posner 1997; Griffin and Nobre 2005; Milliken et al. 2003; Nobre 2001; Posner and Cohen 1984; Pratt and Fischer 2002; Reuter-Lorenz et al. 1996; Exp. 1 of Spence and Driver 1998; Tipper and Kingstone 2005). We have also been careful to consider the data in which attention has been directed to the location of the target (i.e., inhibition of return when the cue and target appear at the same location) separately from conditions in which attention was not directed to the location of the target. Our conclusions have been based entirely on the conditions in which attention was not directed to the location of the target during the trial. On the basis of these analyses, we have shown behavioral effects interpretable as temporal warning effects (see e.g., Correa et al. 2004; Coull and Nobre 1998; Fernandez-Duque and Posner 1997; Griffin and Nobre 2005; Milliken et al. 2003; Nobre 2001; Posner and Cohen 1984; Pratt and Fischer 2002; Reuter-Lorenz et al. 1996; Exp. 1 of Spence and Driver 1998; Tipper and Kingstone 2005), and we have shown the neural correlates of these changes in behavior.

Now, albeit well placed in this context, one must keep in mind that the neural correlates described here might not be the same when eliciting warning effects through other means. We have shown the neural correlates of warning effects in the context of the cue-target task. Future studies should examine the neural correlates of warning effects, produced through other means, to further uncover the neural basis of this long-studied phenomenon.

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