Brief Communications

Attentional Cues Affect Accuracy and Reaction Time via Different Cognitive and Neural Processes

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We investigated whether symbolic endogenous attentional cues affect perceptual accuracy and reaction time (RT) via different cognitive and neural processes. We recorded magnetoencephalography in 19 humans while they performed a cued somatosensory discrimination task in which the cue–target interval was varied between 0 and 1000 ms. Comparing behavioral and neural measures, we show that (1) attentional cueing affects accuracy and RT with different time courses and (2) the time course of our neural measure (anticipatory suppression of neuronal oscillations in stimulus-receiving sensory cortex) only accounts for the accuracy time course. A model is proposed in which the effect on accuracy is explained by a single process (preparatory excitability increase in sensory cortex), whereas the effect on RT is explained by an additional process that is sensitive to cue–target compatibility (post-target comparison between expected and actual stimulus location). These data provide new insights into the mechanisms underlying behavioral consequences of attentional cueing.

Introduction

Cognitive processes are typically inferred from behavioral data such as accuracy and reaction time (RT). For example, through such data, it is now well accepted that perception is improved by knowledge of upcoming stimuli, through voluntary orienting of attention. This is inferred from both RT decreases (Posner, 1980; Coull and Nobre, 1998) and perceptual accuracy increases (Carrasco, 2011) to validly (compared with invalidly) cued stimuli.

It is often implicitly assumed that task-induced changes in accuracy and RT are a manifestation of the same underlying cognitive and neural process. An important question pertains to whether this common belief holds true. This is important because it is the cognitive and neural architecture that we are ultimately interested in. Dissociable influences of an experimental manipulation on accuracy and RT will inform us about the existence of distinct underlying cognitive and neural processes.

We investigated the effects on accuracy and RT of a symbolic cue, which allows for voluntary spatial orienting of attention. To address the dissociability of accuracy and RT effects, we looked for two types of evidence. First, we investigated the time course of the effect of a symbolic cue on both accuracy and RT. These time courses were extracted by presenting target stimuli at varying cue–target intervals. In case of dissimilar time courses for accuracy and RT, this implies distinct underlying causes. Second, we investigated the correspondence between these behavioral time courses and the time course of a recently proposed neurophysiological mechanism underlying voluntary attentional orienting: anticipatory suppression of neuronal oscillations in relevant sensory cortex (Worden et al., 2000; Thut et al., 2006; Jones et al., 2010; van Ede et al., 2011). If this neurophysiological time course corresponds to only one of the two behavioral time courses, this directly shows distinct underlying processes.

Our results show that (1) cueing affects accuracy and RT with different time courses and (2) the neurophysiological time course (indexing anticipatory suppression of neuronal oscillations) only accounts for the accuracy time course. At surprisingly short cue–target intervals, RT effects occur in the absence of both accuracy improvement and anticipatory suppression of neuronal oscillations. To explain these effects, we propose a model in which the accuracy effects are fully explained by a single process (preparatory excitability increase in relevant sensory cortex), whereas the RT effects are at least partly explained by another process (post-target comparison between expected and actual stimulus location).

Materials and Methods

Participants, design, and task. Nineteen right-handed healthy participants (13 male; mean age = 27.95 years, SD = 5.38 years) took part in the experiment. Two participants were excluded from the analyses because they performed at chance level. The experiment was conducted in accordance with guidelines of the local ethical committee (Committee on Research Involving Human Subjects, Region Arnhem-Nijmegen, The Netherlands).

Participants performed a cued somatosensory discrimination task that required discrimination of a tactile stimulus (20 ms duration) that was presented at either the lower or the upper part of the fingertips of all fingers of a single hand (Fig. 1). For tactile stimulation, we used a custom-built Braille device (Fig. 1) that has been described previously (van Ede et al., 2010). On 80% of the trials, this tactile stimulus was preceded by an auditory cue (25 ms duration) that indicated with 75% validity on which

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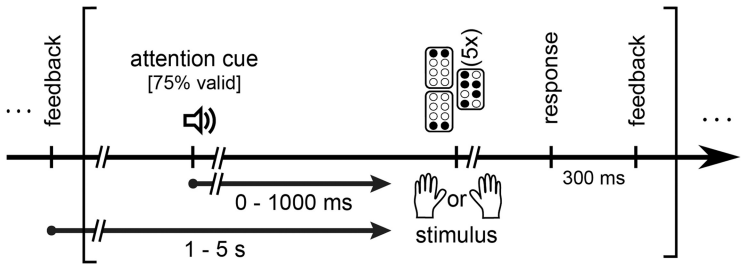

Figure 1. Task. A symbolic auditory cue indicates with 75% validity whether a tactile stimulus will occur on the left or the right hand. Between 0 and 1000 ms after this cue, the target stimulus is presented to the upper or lower part of all fingertips (using the upper or lower pins of the Braille-cells; black dots) of either hand. This is followed by five masks without spatial structure. The participant's task is to discriminate the target (upper or lower) and respond with the right (upper target) or left (lower target) button. After a response, feedback is presented.

hand the to-be-discriminated stimulus would occur. Cue type (white noise or a 750 Hz pure tone) was counterbalanced across participants. To investigate behavioral time courses, we varied the interval between auditory cue and tactile target. Per trial, this interval was randomly drawn from a uniform distribution with values between 0 and 1000 ms. The remaining trials consisted of two baseline conditions (tactile target presented without a preceding cue or simultaneously with a valid cue) and trials in which no stimulus followed the cue.

The tactile target was followed by five masks that contained no spatial structure (individual masks lasted 20 ms, intermask interval was 50 ms). Masking of the target was necessary to increase the difficulty of the discrimination, thus allowing attentional orienting to improve performance. For both hands, tactile stimulation by the upper (lower) pins required a right (left) hand button-press. Because of this, the side of the (expected) target and the side of the subsequently required button-press were uncorrelated. Responses were self-paced. Tactile feedback was presented 300 ms after the response. A correct (incorrect) response was followed by a single (double) 20 ms tap to both hands. The interval between feedback and the next stimulus was drawn from a truncated negative exponential distribution (range: 1–5 s). Because this distribution has a nearly flat hazard rate, the onset of the next cue could not be predicted on the basis of elapsed time since the last cue.

In two sessions of ~1 h each, we collected ~1500 trials.

Analyses of behavioral data. We calculated time-resolved measures of accuracy and RT, with the time pertaining to the different cue–target intervals. We calculated average behavioral performance for stimuli occurring within a 250 ms cue–target interval window. This window was advanced in 60 steps from 125 to 875 ms post-cue. For each participant, we then normalized these data in two ways: (1) we expressed performance on validly and invalidly cued stimuli as a percentage change from the average of our two baseline conditions (Fig. 2*A*,*C*); and (2) we contrasted validly and invalidly cued trials, and expressed this contrast as a percentage change (Fig. 2*B*,*D*). With this second normalization, we calculate so-called cue validity effect time courses.

Recording and analyses of neural data. Recordings and analyses of neural data were highly similar to previous reports from our lab (van Ede et al., 2010, 2011). Data were collected using a 275 axial gradiometers MEG system (CTF MEG TM Systems), and analyzed in FieldTrip (Oostenveld et al., 2011). From the axial gradiometer signal, we calculated the planar gradient (Bastiaansen and Knösche, 2000), which is maximal above the neuronal sources. Using the poststimulus data, we selected for each participant the 10 channels above left and right primary somatosensory cortex (S1) and the individual frequency band that showed the strongest stimulus-induced lateralization (left- vs right-hand stimulus). We estimated oscillatory amplitude using the multitaper method (Fig. 2*F*) (Percival and Walden, 1993). For both left and right channels, we contrasted contralateral and ipsilateral anticipation, then averaged left and right channels. This anticipatory neural lateralization was then analyzed with the same sliding time window that was used for the calculation of the behavioral time courses. We only used data from epochs without tactile stimulation.

Comparing time courses. We fitted three-parameter logistic functions to the observed behavioral (cue validity effect) and neural (anticipatory neural lateralization) time courses:

$$f(t) = \frac{p_1}{1 + e^{-(t-p_2)/p_3}}$$

This is a sigmoid function in which right and left asymptote are determined by p_1 and p_2, and the slope by p_3. Parameters were estimated using a nonlinear least-square algorithm in Matlab (Mathworks, http://www. mathworks.com).

We wanted to compare the cue-dependent time courses for accuracy, RT, and the anticipatory neural lateralization, which have different scales and different signs. We determined the effect size of each measure by calculating the right asymptote of the fitted logistic function. We then scaled the time course of each measure with respect to its maximal effect size. Accuracy increase, RT decrease, and stronger neural lateralization (i.e., lower contralateral minus ipsilateral amplitude) were expressed as positive effects, with their time courses increasing monotonically from 0 to 1 (Fig. 3).

To statistically compare the three time courses, we fitted and normalized logistic functions per participant and calculated the areas under these curves. Under the null hypothesis of identical normalized time courses, this metric does not differ. We evaluated this null hypothesis using paired sample *t* tests (alpha = 0.05).

Results

On average, participants correctly discriminated between the two tactile patterns (Fig. 1) on 70% ± 1.5 (mean ± 1 SEM) of the trials. Average reaction time was 931 ± 77 ms.

Figure 2 reveals accuracy and RT as a function of time after the attentional cue. These time courses are derived from responses to target stimuli occurring at various cue–target intervals (see Materials and Methods, above). For example, after a valid cue, perceptual accuracy increases between 200 and 600 ms after the cue (Fig. 2*A*, red line). This did not occur on invalidly cued trials (Fig. 1*A*, gray line), as there was no clear deviation from baseline (no cue or a target presented simultaneously with a cue).

Assuming that validly and invalidly cued trials differ only in the induced direction of spatial attention (contralateral vs ipsilateral to the upcoming target), contrasting the two time courses directly reveals the effect of this spatial orienting of attention. Figure 2*B* shows the time course of this cue validity effect for accuracy. This time course is well in line with several previous studies in the visual modality (Müller et al., 1998; Busse et al., 2008; Andersen and Müller, 2010). Following a symbolic cue, perceptual accuracy starts to improve ~200–300 ms, continues to increase until 500–700 ms, and then stabilizes.

If multiple behavioral consequences of a symbolic cue are all due to a single underlying process (spatial orienting of attention), then the time courses of these behavioral consequences (i.e., accuracy and RT) must be identical. However, this is not what we observe. The time course of the cue validity effect for RT (Fig. 2*D*) follows a distinct time course, starting much earlier after the cue and changing less rapidly. (This time course did not qualitatively differ between correct and incorrect responses, and therefore these responses were collapsed.) These data indicate that the time courses of the two behavioral consequences of cue validity must be caused, at least in part, by distinct underlying cognitive and neural processes.

In addition to the time courses of behavioral cue validity effects, we investigated the time course of a neural phenomenon

that has been proposed to underlie the behavioral consequences of attentional orienting: anticipatory suppression of alpha- and beta-band oscillations in the relevant (i.e., stimulus-receiving) sensory cortex (Worden et al., 2000; Thut et al., 2006; Jones et al., 2010; van Ede et al., 2011). Concurrently with the behavioral data, we collected MEG signals that were analyzed with the same time resolution (250 ms; see Materials and Methods, above). We analyzed an anticipatory neural lateralization time course by contrasting anticipation of contralateral and ipsilateral targets. Like the behavioral cue validity effects, this reflects a spatially specific (and thus comparable) measure. Figure 2*E* shows anticipatory neural lateralization with frequency resolution. Clearly, anticipation involves a lateralized modulation of oscillatory activity in the alpha- and the beta-bands (together, 8–30 Hz). The time course of this effect is depicted in Figure 2*F*. Because the time courses of alpha- and beta-band lateralizations were highly similar, they were considered together. Anticipatory neural lateralization starts ~200 ms, continues to increase up to 600–700 ms, and then stabilizes. This lateralization is the result of a contralateral suppression. In fact, the amplitude over contralateral MEG channels correlates negatively with the time following the cue (Fig. 2*F*, insets) (cf. van Ede et al., 2011).

We investigated whether the time course of this anticipatory neural lateralization could account for the time courses of the behavioral cue validity effects (accuracy and/or RT). To address this question, we fitted logistic functions to these behavioral and neural cue-dependent time courses (see Materials and Methods, above). Results are depicted in Figure 3. While the time course of the anticipatory neural lateralization is highly similar to the time course for cue validity effect on perceptual accuracy (Fig. 3*A*), the cue validity effect on RT precedes the neural lateralization (Fig. 3*B*). To quantify these phenomena, we fitted these logistic functions to single-subject data and calculated a single metric that allows for a comparison of the three time courses (see Materials and Methods, above). This showed that the cue validity effect on RT systematically preceded the cue validity effect on accuracy ($t_{(16)} = -2.337$, $p = 0.033$) as well as the anticipatory neural lateralization ($t_{(16)} = -7.2378$, $p < 10^{-5}$). Time courses of the cue validity effect on accuracy and the anticipatory neural lateralization did not differ significantly ($t_{(16)} = 1.148$, $p = 0.268$).

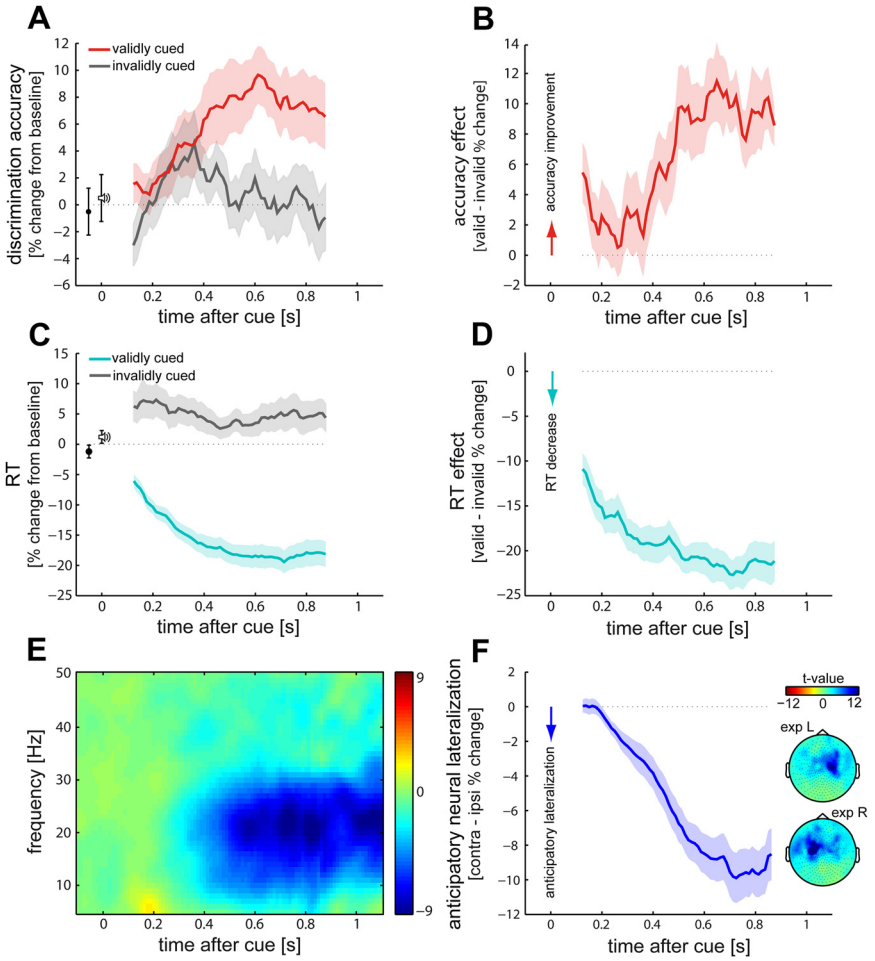

Figure 2. Behavioral and neural time courses following a symbolic attentional cue. ***A***, Tactile discrimination accuracy, as a function of cue–target interval and cue validity. Data are expressed as the percentage change from the average of two baseline conditions: stimulus occurring without a cue (depicted before $t = 0$) or simultaneous with a cue (depicted at $t = 0$). ***B***, Cue validity effect (valid minus invalid) on accuracy, expressed as a percentage. ***C***, ***D***, Similar to ***A*** and ***B***, for RT. ***E***, Anticipatory neural lateralization as a function of frequency and time after the cue. Colors denote the difference in amplitude between contralateral and ipsilateral primary somatosensory cortex with respect to the cued location. ***F***, Same as ***E***, except that data are extracted for a single frequency range (between 8 and 30 Hz; see Materials and Methods) containing the alpha- and/or beta-band. Insets depict *t*-valued topographies of the correlation between oscillatory amplitude and time-after-cue. Error bars and colored patches surrounding the time courses represent ±1 SEM.

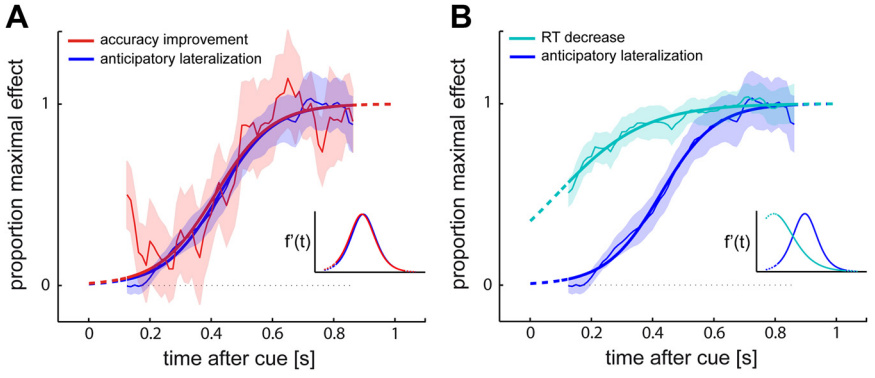

Figure 3. Anticipatory neural lateralization accounts for cue validity effect on accuracy but not RT. ***A***, Overlay of cue validity effect on accuracy and anticipatory neural lateralization. Plots include fitted logistic functions that are normalized to their maximal effect (see Materials and Methods). An effect of 0 signifies no difference between validly and invalidly cued stimuli (accuracy) or contralateral and ipsilateral S1 alpha- and beta-band amplitude (anticipatory neural lateralization). Inset shows rates of change of these functions. ***B***, Identical to ***A***, except RT is depicted instead of accuracy.

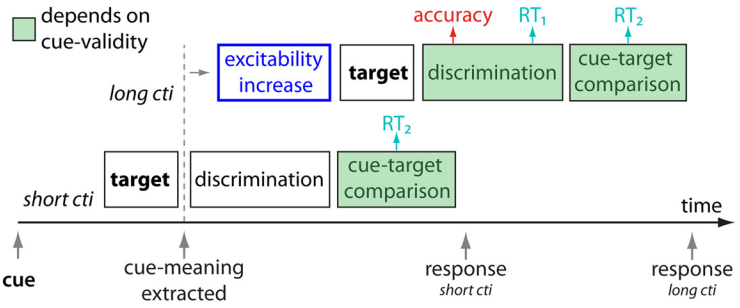

Figure 4. Schematic of processes underlying accuracy and RT consequences of symbolic attentional cueing. When stimuli occur at very short cue–target intervals (short cti), cue validity effects on RT (as the one we observed) must be explained by processes occurring post-target. This is because cue-meaning is only extracted post-target. One possibility is that, post-target, expected and actual location of the stimulus are compared (cue–target comparison), e.g., to update cue–target contingency. If this process occurs faster in valid compared with invalid trials (a compatibility effect), then this will lead to a cue validity RT effect (RT_2). (While this process is here depicted following discrimination, it might in reality occur parallel to the discrimination process.) When stimuli occur at longer intervals after the cue (long cti), spatially specific preparatory processes increase neuronal excitability in stimulus-relevant areas, affecting target discrimination in a cue validity-dependent manner. This will affect both accuracy and RT (RT_1). Because cue validity-dependent RT_1 and RT_2 effects cannot be disambiguated, it is problematic to infer preparatory processes solely on the basis of RT data.

Discussion

We observe that the two most-studied behavioral consequences of attentional cueing (perceptual accuracy increase, RT decrease) follow dissimilar time courses: the cue validity effect on RT precedes the effect on accuracy. This implies that distinct cognitive and neural processes underlie the different behavioral consequences of symbolic cueing. We investigated one such neural process, anticipatory suppression of alpha- and beta-band oscillations in contralateral primary sensory cortex, and observed that this accounts only for the cue validity effect on accuracy. To account for the cue validity effect on RT, at least one additional underlying process must be postulated.

Our results add to the existing literature in two important aspects. First, we show a dissociation between accuracy and RT following a manipulation of voluntary (endogenous) spatial attention (by comparing validly and invalidly cued stimuli). Previously, such a dissociation has only been reported between two different forms of attention, voluntary and involuntary (Prinzmetal et al., 2005). Second, our data reveal that the anticipatory suppression of neuronal oscillations is an important process underlying accuracy improvement with symbolic cueing. Previously this neural phenomenon has been associated with both accuracy (Thut et al., 2006; Yamagishi et al., 2008; Haegens et al., 2011a) and RT improvement (Thut et al., 2006; Haegens et al., 2011a; van Ede et al., 2011). Our results show that RT improvement can also occur in the absence of this neural phenomenon, namely at short cue-target-intervals. It is important to point out that this does not invalidate previous observations showing that anticipatory alpha- and beta-band modulation is related to RT. Instead, it shows that, to give a complete account of cue validity effects on RT, additional neural processes must be identified. An important goal for future research will be to quantify exactly how much of the cue validity effect on RT can be accounted for by the anticipatory suppression of alpha- and beta-band oscillations.

We propose that at least two processes are involved in the behavioral consequences of symbolic cueing. The first process is preparatory (occurs before the target) and affects both accuracy and RT. This is the process to which behavioral consequences of symbolic cueing are typically attributed. The second process is nonpreparatory (occurs after the target) and affects only RT. This process has not been postulated before.

Our model (Fig. 4) applies to tasks in which participants receive a symbolic cue that contains information about the likely spatial location of the upcoming target (e.g., Posner's cueing paradigm). Once the meaning of the cue has been extracted, participants can initiate spatially specific preparatory processes, such as an increase in neuronal excitability in the relevant (stimulus-receiving) sensory cortex. Arrival of validly cued stimuli leads to enhanced processing of sensory information, which in turn leads to more accurate and faster stimulus discrimination (Fig. 4, long cti, accuracy, and RT_1 effect). In our model, this process accounts for accuracy improvement with attentional orienting. Our main evidence for this claim is that the time course of the cue validity effect for accuracy is accounted for by the time course of the anticipatory amplitude suppression, which has been associated with increases in neuronal excitability (Romei et al., 2008; Sauseng et al., 2009; Haegens et al., 2011b).

To explain the cue validity effect for RT, an additional, nonpreparatory process is postulated. The nonpreparatory nature of this process is suggested by the reliable RT effect at very short cue–target intervals. In fact, the average response to stimuli that occurred within 250 ms after the cue was 10.98 ± 1.69% faster after a valid compared with an invalid cue. Moreover, extrapolation to a cue–target interval of 0 ms would indicate a substantial RT effect at this time point (Fig. 3*B*). Because it is unlikely that the meaning of the symbolic auditory cue is extracted at such short intervals, the early RT effect is unlikely accounted for by processes occurring between cue and target. (Note also that this early effect cannot be accounted for by concurrent processing of the cue and the target, because this occurs regardless of cue validity.) In addition, this early RT effect occurred in the absence of a neurophysiological signal of pretarget increase in neuronal excitability. The early RT effect must thus be explained by a post-target process.

To show the role of this post-target process, we consider trials with a very short cue–target interval (Fig. 4, short cti). Target stimuli occurring very shortly after the cue cannot benefit from spatially specific preparatory processes, and hence no spatially specific accuracy improvement occurs. However, if the extraction of the meaning of the symbolic cue continues beyond target presentation, then this information likely becomes available before the response and thus might still affect RT. One possible scenario is that, post-target, the cue information is compared with the actual target location, e.g., to update the cue–target contingency. This process may occur faster for valid compared with invalid stimuli (i.e., a compatibility effect; Fig. 4, RT_2 effect), and this then explains the observed cue validity effect on RT. Although speculative, this gives rise to the notion that such RT effects need not reflect an improvement in perception. As a consequence, at longer cue–target intervals, one cannot infer perception-improving preparatory processes from RT effects only, because these may also be due to a compatibility effect.

In addition to the post-target compatibility effect, also other post-target processes could explain our observed dissociation between accuracy and RT. In fact, it has also been put forward (Thut et al., 2006) that accuracy and RT might be differentially affected by reflexive reorienting of attention, occurring after unexpected

(i.e., invalidly cued) stimuli. While reorienting will improve accuracy, it increases RT. For this alternative explanation to be valid for our dataset, one would have to assume that anticipatory spatial orienting of attention does occur at short (<200 ms) cue–target intervals. No validity effect on accuracy is observed because the benefit due to anticipation (on valid trials) can be matched by the benefit obtained from attentional reorienting (on invalid trials). A validity effect on accuracy only becomes visible at longer cue–target intervals, when the anticipation has grown so much that attentional reorienting can no longer match its effect. Validity effects on RT occur, also at short cue–target intervals, because anticipatory processes facilitate target-processing on valid trials (decreasing RT), while attentional reorienting occurs on invalid trials (increasing RT). While this provides an alternative explanation, a number of aspects in our experimental setup and data make this scenario rather unlikely. First, reorienting of attention can only affect accuracy if the stimulus is still present or can be easily retrieved from memory following the reorienting. Our target-stimulus lasted only for 20 ms and was followed by a mask. Second, reorienting should increase RT (in invalidly cued trials) more at longer cue–target intervals. However, this was not observed (Fig. 2*C*). Third, under the notion that the anticipatory orienting of attention is indexed by the anticipatory neural lateralization, its time course is expected to follow the RT time course. This was clearly not the case (Fig. 3). Fourth, reorienting of attention requires that the meaning of the cue is extracted before target onset. However, as discussed above, our RT effect occurs at intervals after the cue for which it is unlikely that the meaning of the cue is extracted. Despite these arguments, reorienting of attention can be another source via which accuracy and RT might dissociate. This mechanism may be particularly important when cue–target intervals are long, and targets are salient or not masked, as in Thut et al. (2006).

In conclusion, symbolic attentional cues affect accuracy and RT in part via different cognitive and neural processes. While the effect of symbolic cueing on accuracy is likely explained by a single process (preparatory excitability increase), an additional, nonpreparatory, process likely underlies its effect on RT.

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