

The Influence of Alertness on Spatial and Nonspatial Components of Visual Attention

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Three experiments investigated whether spatial and nonspatial components of visual attention would be influenced by changes in (healthy, young) subjects' level of alertness and whether such effects on separable components would occur independently of each other. The experiments used a no-cue/alerting-cue design with varying cue-target stimulus onset asynchronies in two different whole-report paradigms based on Bundesen's (1990) theory of visual attention, which permits spatial and nonspatial components of selective attention to be assessed independently. The results revealed the level of alertness to affect both the spatial distribution of attentional weighting and processing speed, but not visual short-term memory capacity, with the effect on processing speed preceding that on the spatial distribution of attentional weighting. This pattern indicates that the level of alertness influences both spatial and nonspatial component mechanisms of visual attention and that these two effects develop independently of each other; moreover, it suggests that intrinsic and phasic alertness effects involve the same processing route, on which spatial and nonspatial mechanisms are mediated by independent processing systems that are activated, due to increased alertness, in temporal succession.

Keywords: alertness, TVA, attention, cueing

It is widely accepted that attention is a cognitive ability that consists of multiple components supported by overlapping, but independent, neural networks (Desimone & Duncan, 1995; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005; Fernandez-Duque & Posner, 1997; Posner & Boies, 1971). Current theoretical

accounts bridging the behavioral and neuroanatomical levels of analysis such as the theory of visual attention (TVA; Bundesen, 1990; 1998) or the attentional-networks theory (ANT; Fan, McCandliss, Sommer, Raz, & Posner, 2002) consider both spatial and nonspatial components of visual attention to be critical determinants of attentional performance. Although the term *spatial* pertains to differential processing of objects at different locations in the visual field (e.g., selective processing of objects within one hemifield), the term *nonspatial* refers to the allocation of processing resources in time, independently of object position (cf. Husain & Rorden, 2003). A current widely debated question concerns whether and, if they do, how these different components interact (Robertson, Mattingley, Rorden, & Driver, 1998; Robertson, Tegner, Tham, Lo, & Nimmo-Smith, 1995; Thimm, Fink, Kust, Karbe, & Sturm, 2006). One important line of research on this issue has focused on how varying levels of alertness influence spatial and nonspatial components of attention (Fimm, Willmes, & Spijkers, 2006; Manly, Dobler, Dodds, & George, 2005). We briefly review this research to provide the background for the present study, an investigation, based on Bundesen's (1990, 1998) TVA, of the nature and time course of alertness-related effects on visual processing capacity and spatial attention.

The general concept of alertness refers to basic intensity aspects of attention. It comprises the notion of a general level of response

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readiness (Posner & Petersen, 1990; Sturm et al., 1999; Sturm & Willmes, 2001), enabling an organism to respond to sensory stimuli faster and more efficiently due to self-initiated preparation or external signals indicating the imminent occurrence of a stimulus (Sturm & Willmes, 2001). Consequently, the state of alertness is thought to affect processing speed as a nonspatial component of attention, and a broad distinction is made between intrinsic (non-phasic) and extrinsic (phasic) alertness (e.g., Posner & Boies, 1971; Posner & Rafal, 1987; Sturm et al., 1999; Sturm & Willmes, 2001; van Zomeran & Brouwer, 1994). *Intrinsic alertness* refers to the internal (top-down) control of the level of arousal that can be observed in a simple reaction time (RT) task without a preceding warning stimulus. *Phasic alertness*, on the other hand, refers to a more short-lived change in the preparatory state of the cognitive system induced extrinsically, subsequent to external cues or “alerting stimuli” (Heilman, Watson, & Valenstein, 1993; Posner & Petersen, 1990). For example, several studies have shown that stimulus detection and discrimination can be enhanced by alerting or warning signals, which inform subjects that a target stimulus is imminent (e.g., Posner, 1978). Although alerting signals usually provide little or no information as to where or when a target will occur, the alerting effect confers a behavioral advantage over conditions without warning signals (Coull, Nobre, & Frith, 2001; Posner, 1978; Posner & Petersen, 1990).

Neuroimaging studies have revealed the intrinsic alertness system to be supported by a widely distributed, predominantly right-hemispheric cerebral network involving the frontal lobe, the inferior and superior parietal lobe, as well as thalamic and brain stem regions (Coull, Frackowiak, & Frith, 1998; Kinomura, Larsson, Gulyas, & Roland, 1996; Robertson et al., 1998; Sturm et al., 1999, 2006; Sturm & Willmes, 2001). With respect to phasic alertness, only few studies have explored the underlying neural substrate and their results are somewhat inconsistent. Thiel, Zilles, and Fink (2004) found higher activity mainly in extrastriate regions when trials with visual warning stimuli were compared to trials without, which they attributed to enhanced sensory processing as a result of top-down influences from higher order frontal and parietal areas. Weis et al. (2000) observed additional activations in the thalamus of the right hemisphere and in parts of the frontal gyrus and the parietal lobe of the left hemisphere in phasic alertness compared to intrinsic alertness conditions (additional evidence for left lateralized fronto-parietal activation is also provided by Coull et al., 2001). Konrad et al. (2005) reported left-sided superior parietal and right-sided ventral prefrontal activity, while Fan et al. (2005) and Thiel and Fink (2007) found the most extensive phasic alertness-related activation in the right temporo-parietal junction. Sturm and Willmes (2001) also suggested that phasic alertness activates a right-hemispheric network. They attributed a more extended activation of the left hemisphere under phasic alerting conditions to extrinsic activity generated by the warning stimulus, with the additional left frontal and parietal activation reflecting the need to select the target stimulus and inhibit a response to the warning stimulus. Alternatively, the noted discrepancy in left-versus right-lateralized neuroimaging indexes of alertness could reflect differences in the phasic (alerting cues operating within hundreds of milliseconds) versus intrinsic (alertness/arousal operating over a period of a minute or more during performance of vigilance tasks) measures of alertness used in the different studies.

In our (behavioral) investigation, we used variations of intrinsic and phasic alertness on a trial-by-trial basis.

Taken together, the neuroimaging results show a more complex and bilateral pattern of activation under phasic compared to intrinsic alertness conditions, but also confirm a significant overlap of both systems. One of the areas that is activated during both intrinsic and phasic alertness, namely the right parietal cortex, is also known to play a central role in spatial attention functions (e.g., Bundesen, 1998, 2005; Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Corbetta & Shulman, 2002; Schneider, 1995). Although parietal cortex is also heavily implicated in nonspatial aspects of attention (Kanwisher & Wojciulik, 2000) that may as well be affected by alertness (Coull et al., 1998), this overlap suggests that direct (neural) links between (intrinsic and phasic) alertness and spatial attention might exist. Therefore, alertness-related effects may not only affect processing speed, but also spatial attention.

Strong evidence in favor of this assumption comes from studies of patients suffering from a combination of a spatial-attentional asymmetry and a reduced level of (intrinsic) alertness. The most prominent example are patients with visual hemi-neglect who show a pathological ipsi-lesional spatial bias of attention almost exclusively following right parietal lesions (Bisiach & Vallar, 1988; Heilman et al., 1993; Karnath, Himmelbach, & Kuker, 2003; Mort et al., 2003; Vallar, Rusconi, Bignamini, Geminiani, & Perani, 1994). The strongest rightward deviation of spatial attention can be observed in those patients whose intrinsic alertness state is especially low (Bartolomeo & Chokron, 2002; Heilman et al., 1993; von Cramon & Kerkhoff, 1993). Conversely, phasically alerting neglect patients with a warning tone temporarily reduces their rightward bias (Robertson et al., 1998), and increasing intrinsic alertness by a computerized training procedure leads to an alleviation of spatial hemi-neglect symptoms, associated with increased activity within frontal and parietal brain regions of the right hemisphere (Thimm et al., 2006; see also Robertson et al., 1995).

Similar evidence comes from patients with attention deficit hyperactivity disorder (ADHD) who also show a combination of spatial and nonspatial attentional deficits, although less pronounced than neglect patients. Clinically, ADHD patients are known to suffer predominantly from deficits in maintaining an appropriate level of alertness (Antrop, Roeyers, Van Oost, & Buysse, 2000; George, Dobler, Nicholls, & Manly, 2005; Tucha et al., 2006). Consequently, the dominant pharmacological approach for treating ADHD symptoms consists of stimulant medication, which elevates the patients' intrinsic alertness state (Nigg, Swanson, & Hinshaw, 1997; Sheppard, Bradshaw, Mattingley, & Lee, 1999; Tucha et al., 2006). Recently, ADHD patients have been reported to favor the right visual hemifield, similar to visual hemi-neglect patients (Carter, Krener, Chaderjian, Northcutt, & Wolfe, 1995; Dobler et al., 2005; George et al., 2005; Nigg et al., 1997; Sheppard et al., 1999). This rightward spatial bias has been reported to increase with time-on-task, which lowers the intrinsic alertness level (George et al., 2005), and to disappear after successful stimulant medication (Sheppard et al., 1999; Tucha et al., 2006).

Additional support for the linkage between alertness and spatial attention also comes from healthy normal subjects. Normal subjects show a slight leftward spatial bias, referred to as *pseudoneglect* (Bowers & Heilman, 1980), that can be observed, for exam-

ple, in a line bisection task (for a review, see Jewell & McCourt, 2000). Bellgrove, Dockree, Aimola, and Robertson (2004) reported this leftward pseudoneglect bias to be significantly reduced (i.e., a stronger rightward shift of spatial attention) in a group of healthy participants who performed poorly on a (nonspatial) alertness task, compared to good performers. Another interesting line of studies used the method of sleep deprivation. Sleep deprivation lowers intrinsic alertness, observable, for instance, as prolonged response latencies in simple RT tasks (Dinges & Kribbs, 1997; Gillberg & Akerstedt, 1998). It is associated with decreased levels of global cerebral glucose metabolism especially in the alertness-related fronto-parieto-thalamic network (Kinomura et al., 1996; Thomas et al., 2000). In a within-subject design, Manly et al. (2005) found a significantly stronger rightward spatial lateralization of attention in sleep-deprived subjects compared to a normal alertness state (see also Dufour, Touzalin, & Candas, 2007). Moreover, a rightward shift of spatial attention was observed over the course of the testing session (time-on-task effect). Similarly, Fimm et al. (2006) reported a disproportionate slowing of responses to stimuli presented on the left side of fixation for subjects in a state of maximally lowered alertness. Therefore, it has been proposed (e.g., Bellgrove et al., 2004; Fimm et al., 2006; Manly et al., 2005) that a reduction in the level of alertness might suffice to induce a rightward bias in visuospatial attention even in subjects with a healthy attention system, who normally show a slight bias towards the left.

In summary, there is converging (neuroimaging, neuropsychological, and psychophysiological) evidence that the level of phasic and intrinsic alertness not only affects nonspatial attention functions such as processing speed (as reflected in RT performance), but also exerts a significant influence on spatial-attention functions, reflected in a modulation of the spatial bias; in particular, higher levels of alertness give rise to an enhancement of processing speed, whereas lower levels lead to a slowing of RTs as well as a weaker leftward, or even rightward, lateralization of visuospatial attention.

Despite these rather clear-cut results, a closer understanding of the relationship between alertness on the one hand and processing speed and the spatial distribution of attention on the other is still lacking. For example, it remains unclear exactly at which processing stage alertness exerts its speed effects. Posner (1978) originally proposed that alerting stimuli affect the processes underlying the preparation and/or execution of the motor response. Similarly, Sturm and Willmes (2001) suggested that an optimal level of alertness is evoked only under conditions in which very rapid responding is necessary, but not when simple event monitoring is required without a need for fast responses. In fact, in the vast majority of the studies (on the effects of alertness) reviewed above, the task required speeded motor responses, supporting such a “motor interpretation” of alertness effects. However, as perceptual and motor aspects of performance are confounded in these tasks, alertness-related perceptual improvements, such as enhanced stimulus extraction and encoding would appear equally likely. Consistent with this, Thiel et al. (2004), for example, observed increased activity under phasic alertness conditions mainly in extrastriate cortex—a brain region more intimately involved in perceptual, rather than motor, processes. Given this, an assessment of alertness-related effects on perceptual processing capacity in conditions without a speeded motor demand is in order to ascertain whether and to what degree phasic and intrinsic alertness influence perceptual processes proper.

A second question concerns the temporal dynamics of alertness-related effects. Heilman et al. (1993, 2003), as well as Posner and Petersen (1990), proposed a neuro-cognitive model according to which such effects result from right-hemisphere frontal brain regions that exert top-down control, via thalamic nuclei, on posterior cortical areas related to perceptual processing, by activating noradrenergic nuclei in the ponto-mesencephalic part of the brainstem (see also Mesulam, 2000, for a similar idea). This model closely coincides with the intrinsic alertness network identified by the fMRI studies reviewed above. However, although neuroimaging provides mainly a spatial picture of the core structures involved in alertness-related effects, explicit assumptions can be derived from the neurocognitive model about how these effects develop and operate in time. For example, if the effects of intrinsic alertness are generated in anterior cortical areas in a top-down manner, via a fronto-mesencephalic-thalamic route, the gradual build-up of a preparatory set should be observable as an increase of processing speed over time. Moreover, as alertness affects the spatial distribution of attention due to overlapping neural systems (e.g., in the right posterior parietal cortex), as reviewed above, it would be interesting to see whether spatial-attentional effects occur in parallel with or only after an enhancement of processing speed. The same question also does apply to phasic alertness. In this case, however, a further issue would be of interest: If phasic alertness effects are top-down mediated, as assumed by Thiel et al. (2004), for example, speed effects should follow a similar time course as those related to intrinsic alertness, reflecting the involvement of similar “high-level centers” of the alertness network as with intrinsic activation. On the other hand, warning stimuli in a phasic alertness task might also directly activate “low-level centers,” for instance, via sensory input to the ascending reticular activating system (ARAS; Jones, 2003), giving rise to a faster evolving effect on processing speed than under intrinsic alertness conditions.

These questions were addressed in the present study, to achieve a closer understanding of the nature and the temporal dynamics of the interaction between alertness and spatial or nonspatial components of attention. To this end, the present experiments investigated the effects of alertness on perceptual aspects of processing capacity and on spatial attention, while also examining the time course of these effects. In terms of the theoretical and methodological approach, the experiments were based on Bundesen’s TVA (e.g., Bundesen, 1990, 1998; Bundesen, Habekost, & Kyllingsbæk, 2005), which provides a means to assess processing capacity and spatial attention independently of each other within the same task and without involving confounding by speeded motor response.

TVA is a mathematical model with strong relations to the biased-competition account of visual attention (Desimone & Duncan, 1995; for a detailed mathematical description of TVA, see Bundesen, 1990, 1998; Duncan et al., 1999; also, Kyllingsbæk, 2006; for a neural interpretation of TVA, see Bundesen et al., 2005). On this view, visual objects are processed in parallel and compete for selection, that is, access to a limited visual short-term memory (VSTM) store (which encompasses around four objects in normal subjects). The race among objects is decided according to a speed criterion: The objects processed fastest are selected until VSTM is filled. Biases come into play if some objects receive attentional weights over others due to either automatic (bottom-up) or intentional (top-down) factors, conferring a speed advantage in

the race for selection. According to TVA, the probability with which an object is selected into VSTM is thus determined by (a) the general processing capacity available (reflected by an object's basic processing rate) and the (available) size of VSTM storage (selection terminates if VSTM is filled), and (b) the attentional weight assigned to an object. One aspect of weighting in TVA, which is especially relevant to the present study, concerns the spatial distribution of attentional weights within the visual field. Independent quantitative estimates of these three attentional components—visual perceptual processing speed, VSTM storage capacity, and spatial distribution of attention—are derived from subjects' performance in a whole report task of briefly presented letter arrays.

We compared TVA-based whole report performance under two conditions: a no-cue condition was assumed to reflect possible changes in intrinsic alertness over the course of a trial (e.g., Coull & Nobre, 1998; Posner, 1978; Sturm et al. 1999), whereas an alerting cue condition was assumed to reflect modulations of phasic alertness. In this way, it was possible to examine whether different levels of alertness would affect processing speed, VSTM capacity, and spatial attentional weighting differentially or, alternatively, in a global manner. In addition, by introducing different cue-target SOAs (stimulus onset asynchronies), it was also possible to map the time course of these effects, so as to ascertain whether alertness-related effects on processing capacity and spatial attention develop in a parallel or a sequential manner.

The present study consists of three experiments. Experiment 1 focused on processing speed and VSTM capacity, whereas Experiments 2 and 3 were concerned with spatial-attentional weighting. The cue-target SOAs were varied randomly across trials in Experiments 1 and 2, but fixed throughout a trial block in Experiment 3.

Experiment 1

Experiment 1 was designed to investigate modulations of perceptual processing capacity under conditions of phasic and intrinsic alertness, in particular: Would higher levels of alertness have a specific effect on perceptual processing speed, or a global effect on perceptual processing capacity, enhancing both visual processing speed and VSTM storage capacity? This question was examined using a whole report task in which subjects were presented with columns of five letters, displayed in either the left or the right hemifield, for varying exposure durations. This standard procedure (introduced by Duncan et al., 1999, and successfully used in further studies, e.g., Bublak et al., 2005; Bublak, Redel, & Finke, 2006; Finke, Bublak, Dose, Muller, & Schneider, 2006; Finke et al., 2005; Habekost & Bundesen, 2003), permits quantitative estimates to be derived for visual processing speed (the number of visual objects processed per second, estimated by the TVA parameter C) and VSTM storage capacity (the number of objects maintained in parallel, estimated by the parameter K).

The letter display was presented either without a preceding cue (no-cue condition) or after a warning signal that was noninformative as to the time or the side of the imminent target display (alerting-cue condition), thus realizing the experimental conditions for intrinsic and, respectively, phasic alertness. By varying the SOA between cue and display onset, it was possible to map the time course of the effects that different levels of alertness exert on processing speed and VSTM capacity, respectively. We expected

processing speed to be enhanced by the cue in the phasic alertness condition and by the increase in the expectancy of the target display over time (SOA) in the intrinsic alertness condition.

Method

Subjects. Eleven right-handed healthy volunteers ($M_{\text{age}} = 24.2$ years, $SD = 3.3$; range: 21 to 30 years; 2 men, 9 women) participated in Experiment 1. All subjects had normal or corrected-to-normal vision and none of them suffered from color blindness or any psychiatric or neurological disorder. All subjects were naïve as to the purpose of the experiment and received either course credit or monetary payment (€8 per hour) for their participation. Written informed consent according to the Declaration of Helsinki II was obtained from all participants.

Whole report task. On each trial, five equidistant red target letters (each 0.5° high \times 0.4° wide) were presented in a vertical column, 2.5° of visual angle either to the left or to the right of the fixation cross (see Figure 1). Subjects had to verbally report as many letters as possible that they had recognized with certainty. The target letters could be reported in any order, and there was no emphasis on speed of report. The experimenter entered the reported letter(s) on the computer keyboard and initiated the next trial after the subject had indicated that he/she was ready.

The letters for a given trial display were randomly chosen from the set (ABEFHJKLMNPRSTWXYZ), with a particular letter

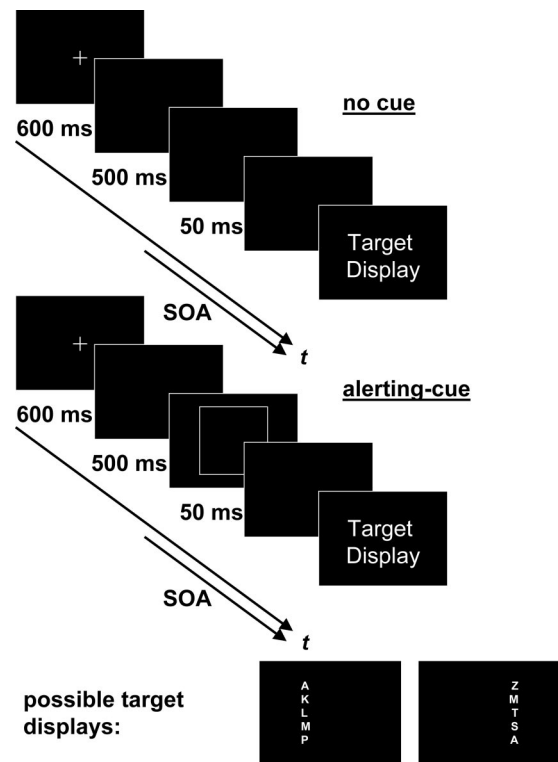


Figure 1. Sequence of frames presented on a given trial for the two cueing conditions in Experiment 1. Top panel: no-cue, bottom panel: alerting-cue. Two (unmasked) target displays with target letters in the left and the right hemifield (left- and right-hand panel), respectively, are also shown. SOA = stimulus onset asynchronies.

appearing only once. Letter arrays were presented for three different exposure durations, either masked or unmasked. Masks consisted of letter-sized squares (of 0.5°) filled with a “+” and an “×” and presented for 500 ms at each letter location. Due to iconic memory buffering, the effective exposure durations are usually prolonged by several hundred milliseconds in unmasked as compared to masked conditions (Sperling, 1960).¹ Thus, by orthogonally combining the three exposure durations with the two masking conditions, six different “effective” exposure durations resulted. These were expected to generate a broad range of performance, tracking the whole course of the function relating response accuracy to (effective) exposure duration.

The three target exposure durations were determined individually for each subject in a pretest phase (part of the first experimental session) and then introduced into the experimental phase. The pretest consisted of 48 masked trials (four trials for each SOA and hemifield) with a fixed exposure duration of 86 ms, to assess whether the subject reported, on average, one letter (20%) per trial correctly. There were six participants who achieved this criterion and for whom exposure durations of 43, 86, and 157 ms were introduced into the experimental phases. However, for five participants, pretest performance was below the 20% criterion, so exposure durations of 86, 157, and 300 ms were used instead.

Note that whole report performance was assessed in terms of the level of accuracy achieved at predefined, brief exposure durations (rather than in terms of response speed), effectively ruling out confounding of the results by stimulus material- and motor response-related factors. Moreover, the speed and VSTM measures derived from this procedure were determined using the same stimulus material (letters) and response requirements (verbal, non-speed report).

Alertness conditions. In the alerting-cue condition (assumed to involve a phasic alertness enhancement for a period of a few hundred milliseconds), a white outline square ($5^\circ \times 5^\circ$) was flashed briefly, for 50 ms, around the whole (potential) display array. In the no-cue condition (involving intrinsic alertness), the screen remained blank for the same length of time (see Figure 1).

The alerting cue (outline frame around the whole display array) was noninformative as to the side of the upcoming target letters. Thus, although alerting the observers to the imminent appearance of the target array, this warning signal was designed to induce a spatially diffuse distribution of attentional weighting across the (potential) stimulus display (i.e., it could not be used to systematically orient spatial attention to the stimulus side). The noninformativeness of the alerting-cue with regard to the target location is likely to have discouraged subjects from making eye movements. In any case, because the stimulus exposure durations were relatively short, eye movements were unlikely to affect performance systematically. However, to avoid suboptimal fixation that might occur at the beginning of a trial, the experimenter checked for central fixation by a video-based eye tracking device (EyeLink system, SR Research Ltd., Ontario, Canada) at the start of each trial and initiated the stimulus sequence (within about one second) when the subject fixated correctly. That is, a trial started only if a subject’s fixation was seen to settle on the central cross within a spatial range of one degree of visual angle. Furthermore, subjects were explicitly (and with emphasis) instructed to maintain central fixation over the entire trial period.

SOA variation. Six cue-target stimulus onset asynchronies were used: 80, 100, 200, 300, 450, or 650 ms. By using six different, randomized cue-target SOAs that ranged from less than 100 ms to over half second, the alerting cue was expected to primarily induce a more general alerting/arousing effect, rather than supporting any specific temporal expectations about the onset of the stimulus array.

Procedure. The PC-controlled experiment was conducted in a dimly lit, soundproof cubicle. Stimuli were presented on a 17” monitor ($1,024 \times 768$ pixel screen resolution, 70 Hz refresh rate). Subjects viewed the monitor from a distance of 50 cm, controlled by the aid of a head and chin rest.

Figure 1 shows the sequence of frames presented on a no-cue (top panel) and an alerting-cue (bottom panel) trial. Following initiation of a trial sequence (by the experimenter), participants first fixated a white fixation cross ($0.3^\circ \times 0.3^\circ$) displayed for 600 ms in the center of the screen on a black background. The cross was followed by a 500-ms blank screen. Then, either the alerting cue appeared for 50 ms or the screen remained blank for a 50-ms period.² After the variable cue-target SOA, the whole report display was presented for the predetermined exposure duration. Following registration of the subject’s report, the next trial started after an intertrial interval of 1,000 ms. Cue/no-cue conditions as well as the six SOAs were presented in random order within the same block.

In two previous studies using a similar paradigm (Finke et al., 2006, 2005), highly reliable estimates of the parameters C (speed) and K (VSTM capacity) were obtained on the basis of 16 trials per target condition. On this basis, in the present experiment, each subject completed eight blocks of 288 trials each (2 Cueing Conditions \times 6 SOAs \times 2 Hemifields \times 2 Masking Conditions \times 3 Exposure Durations \times 16 Trials per target condition), altogether 2304 trials per subject. Trials were randomly assigned to the eight blocks. Subjects performed three blocks each in Sessions 1 and 2 (about 1.5 hr per session), and two blocks in Session 3 (about 1 hr), with 5-min breaks between blocks. The order of the sessions was counterbalanced across the subjects. Each subject performed the three sessions at the same time of day and within (a maximum of) 2 weeks. Before each block, the subjects were given written and verbal instructions.

Estimation of TVA parameters. The whole report task provided quantitative estimates for visual processing speed and VSTM storage capacity, reflected by the TVA parameters C and K ,

¹ In TVA, this additional effective exposure duration is termed μ (Bundesen, 1990, 1998; Duncan et al., 1999).

² Given the 500-ms blank screen between fixation cross offset and cue onset (in the alerting-cue condition), the offset of the fixation marker may have invoked some kind of temporal expectancy for the critical trial events. However, the timing was the same on each trial, that is, the same in both the alerting-cue and the no-cue condition (which were presented in random order). Accordingly, the offset of the fixation marker would have helped subjects to anticipate the onset of the alerting cue and/or the stimulus display on cue and no-cue trials, respectively. Thus, although the fixation marker offset may have been confounding, to some extent, our alertness manipulations, it seems unlikely that it completely counteracted their intended effects. This may be so, in particular, because the offset of a relatively small central cross is not as potent an alerting stimulus as the onset of a white outline square in eccentric vision.

respectively. These parameters were estimated applying the algorithms described in detail by Kyllingsbæk (2006) and used in several recent studies (Bublak et al., 2005, 2006; Duncan et al., 1999; Finke et al., 2006, 2005; Habekost & Bundesen, 2003; Hung, Driver, & Walsh, 2005). In general, the probability of identifying a given object x is modeled by an exponential growth function, relating accuracy of report to effective exposure duration. Consider the function relating the mean number of reported objects to the exposure duration. The slope of this function at its origin, coordinate $(t_0, 0)$ indicates the total rate of information uptake in objects per second (denoted by C), and its asymptote the maximum number of objects that can be represented at a time in VSTM (denoted by K). Further information will be provided in the Results section.

Results

The results will be described first in terms of the qualitative pattern of performance, followed by the TVA parameter estimates for “visual perceptual processing speed” and “VSTM storage capacity.” Effects were examined by repeated-measures analyses of variances (ANOVAs); comparisons between experimental conditions were based on two-tailed (post hoc) paired t tests for VSTM capacity K , and on one-tailed paired t tests for the parameter visual perceptual processing speed C , due to the directed predictions in this case.

Response accuracy. Figure 2 illustrates the qualitative pattern of performance for a representative subject at the 80-ms SOA: the observed number of letters reported correctly (Mean[obs]) as a function of the effective exposure duration t , separately for the no-cue and the alerting-cue condition. With the results of the parameter estimation (see below) in mind, only the most relevant SOA condition, 80 ms, is illustrated. Along with the observed data points, the maximum likelihood fits (e.g., Ross, 2000) based on the TVA parameter estimates are presented for the two cueing conditions.

According to TVA, in masked conditions, the effective exposure duration of the stimulus display is the difference $t - t_0$, with t being

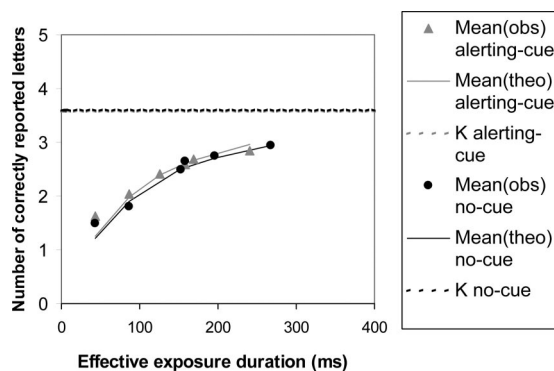


Figure 2. Whole-report performance for a representative participant at 80 ms SOA (stimulus onset asynchronies), separately for the two cueing conditions (no-cue, alerting-cue). The mean number of correctly reported letters is shown as a function of effective exposure duration. Mean(obs) = observed number of letters reported correctly; Mean(theo) = predicted number of letters reported correctly; C = visual perceptual processing speed; K = visual short-term memory storage capacity.

the display presentation time and t_0 the estimated minimal effective exposure duration below which information uptake from the display is assumed to be zero. Under nonmasked stimulus conditions, an effective exposure duration of μ ms is added to $t - t_0$. TVA assumes that, for a given subject, t_0 and μ are constant across experimental conditions (e.g., Bundesen, 1990).

A central factor in TVA is the time taken to complete identification of any display element (= processing speed C). For each element, these times are exponentially distributed (Bundesen, 1990, 1998; Duncan et al., 1999). The identification probability for an object is modeled by an exponential growth function relating the mean number of reported objects to the exposure duration t . The slope of the function at the point in which it arises from the value zero (i.e., point $[t_0, 0]$) gives the overall rate at which the presented stimuli are processed (processing speed C), and the asymptote of the function gives the maximum number of objects that can be represented in parallel in VSTM (storage capacity K).

As can be seen from Figure 2, in both cueing conditions, the theoretically predicted functions, Mean(theo), exhibit a steep initial rise, in line with previously published studies (e.g., Duncan et al., 1999; Finke et al., 2005). However, the mean scores show a somewhat more marked increase in the alerting-cue, relative to the no-cue condition, indicating a higher processing speed C . As exposure duration increases to a few hundred milliseconds, both curves approach a similar asymptotic level of 3.5 minus 4 reported letters. Accordingly, the two lines indicating the subject's predicted VSTM storage capacity K in the two conditions are at about the same height.

There is a close correspondence between the predicted and the observed mean scores in both conditions. Across subjects, the average Pearson product-moment correlation between the observed values and the best TVA data fits across all SOAs was .84 ($SD = .02$) in the no-cue condition and .85 ($SD = .03$) in the alerting-cue condition.

Parameter estimates.

Processing capacity. In TVA, the attentional capacity of visual processing is defined by two parameters: visual perceptual processing speed C and VSTM storage capacity K (Bundesen, 1990, 1998; Bundesen et al., 2005). The following section describes the time course of these parameters across SOA for the two cueing conditions. Parameter C was estimated as the average of the summed processing rate values v for objects presented to the left and the right of fixation, respectively. With reference to Figure 2, parameter C is the slope at point $(t_0, 0)$ of the function relating the number of elements reported to t , that is, C is effectively a measure of the identification rate in elements/second (Duncan et al., 1999). And parameter K reflects the maximum number of letters reported on any single trial at any exposure duration.

Visual perceptual processing speed (C). Figure 3 illustrates the time course of the parameter visual perceptual processing speed C for the no-cue and alerting-cue conditions.

The results described qualitatively above were confirmed by a repeated-measures ANOVA of processing speed C with the factors cue (no cue, alerting cue) and SOA (80, 100, 200, 300, 450, 650 ms). The analysis revealed a marginally significant main effect of cue, $F(1, 10) = 4.17$, $p = .07$, a significant main effect of SOA, $F(5, 6) = 57.12$, $p < .001$, $\eta^2 = .97$, and a significant Cue \times SOA interaction, $F(5, 6) = 7.28$, $p < .05$, $\eta^2 = .85$. Visual perceptual processing speed was significantly faster in the alerting-cue com-

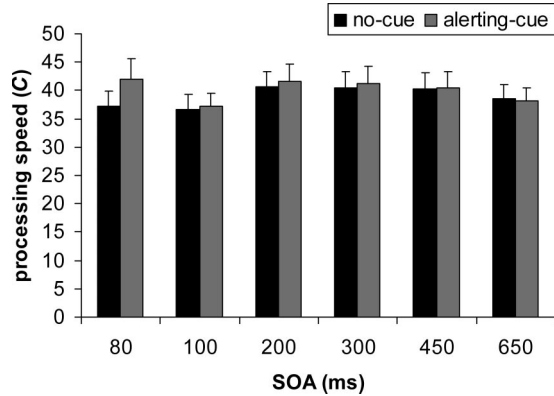


Figure 3. Parameter *C* (visual perceptual processing speed = numbers of elements processed per second) as a function of SOA (stimulus onset asynchronies), separately for the no-cue and the alerting-cue condition in Experiment 1. The error bars show the standard errors.

pared to the no-cue conditions at the 80-ms SOA, $t(10) = -2.41$, $p < .05$, but not at longer SOAs (all $ps > .25$). Moreover, in the alerting-cue condition, the processing speed decreased between the 80- and the 100-ms SOA, $t(10) = 2.26$, $p < .05$. And in both cueing conditions, processing speed significantly increased from the 100- to the 200-ms SOA, no-cue: $t(10) = -4.09$, $p < .01$, alerting-cue: $t(10) = 3.39$, $p < .01$; reaching a plateau between 200 and 450 ms following cue onset, followed by some decline towards the 650-ms SOA.

VSTM storage capacity (*K*). Figure 4 illustrates the time course of the parameter VSTM storage capacity *K* for the no-cue and alerting-cue conditions. A Cue \times SOA ANOVA with *K* as dependent variable failed to reveal any significant effects (all $ps > .16$).

Time-on-task effects. To examine whether the pattern of performance in Experiment 1 was influenced by time-on-task effects, the average accuracies for the different display conditions were computed for the left and right hemifields, separately for the trial blocks in the first and the second half of each session. Next, *t* tests were carried out to compare the accuracies (averaged across sessions) between the first versus the second half. None of these comparisons revealed a significant decrease in performance from the first to the second half of the sessions, alerting-cue: all $ts < 0.91$, all $ps > .22$, no-cue: all $ts < 0.41$, all $ps > .16$.

Discussion

One main result of Experiment 1 was a fast and short-lived enhancement of perceptual processing speed in the alerting-cue as compared to the no-cue condition at the shortest (80-ms) SOA. Apart from the initial phasic enhancement of performance in the alerting-cue condition, visual perceptual processing speed gradually increased over time, achieving its maximum at around 300 ms after cue onset, in both the alerting-cue and the no-cue conditions. This pattern presumably reflects a temporal range effect—subjects prepare optimally for target displays presented in the middle of the SOA range—which can be attributed to an intrinsic enhancement of alertness as a function of time prior to target display onset. Taken together, these results suggest that alertness operates via

both a “fast route,” in the case of phasic alertness, and a “slow route,” in the case of intrinsic alertness.

Because the present, TVA-based approach provided estimates of perceptual processing capacity that are independent of motor response speed, the findings in Experiment 1 are the first to demonstrate that alertness does not only affect the time it takes to respond to extracted and encoded target information (Posner, 1978), but also directly influences the extraction/encoding of this very information. Thus, previously reported decreases in RTs following an alerting stimulus (e.g., Fan et al., 2005; Posner & Boies, 1971; Posner & Petersen, 1990; van Zomeran & Brouwer, 1994) are not exclusively attributable to heightened readiness to respond to a target stimulus; rather, they are likely to reflect increases in visual perceptual processing speed as well.

The present findings also show that higher levels of alertness do not have a general effect on all aspects of perceptual processing capacity; rather, they produce a differential and specific enhancement of the speed aspects of processing capacity, only. The fact that the speed of processing can be distinctly affected by modulations of alertness, without consequences for the VSTM storage component, supports one of the main assumptions underlying TVA (e.g., Bundesen, 1990) that the two parameters can vary independently of each other.

In the neural theory of visual attention (NTVA; Bundesen et al., 2005), an extension as well as interpretation of TVA at the level of neurons or neuronal assemblies, perceptual categorizations of objects are assumed to be based on activations (*v* values) in the set of neurons that represent the object. The speed at which a visual object *x* is categorized is determined by the number of cortical neurons representing object *x* on the one hand, and by the level of activation of the individual neurons representing object *x* on the other. In these terms, an NTVA-based interpretation of our main finding would be that, for a transitory period of phasic alerting, a larger set of neurons was allocated to the letters in the target display and/or these neurons were activated to a higher degree.

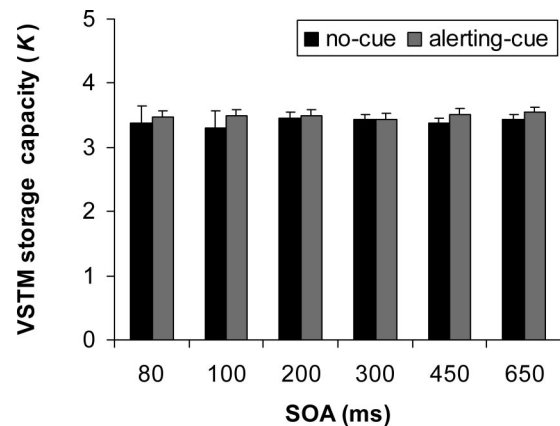


Figure 4. Parameter *K* (VSTM [visual short term memory] storage capacity = maximum number of objects that can be represented in parallel) as a function of SOA (stimulus onset asynchronies), separately for the no-cue and the alerting-cue conditions in Experiment 1. The error bars show the standard errors.

Experiment 2

Experiment 2 examined the effects of alertness on the spatial distribution of attention, in particular: What is the time course of these effects, and do spatial attentional effects occur in parallel with or only after an enhancement of processing speed?

In TVA, the spatial distribution of attention across the visual field is reflected by a spatial laterality index (parameter w_λ), relating the attentional weights for objects in the left- and the right-visual hemifield (w_{left} and w_{right}). These weights can be derived from performance in a whole report task in which subjects have to report a stimulus that is accompanied by another stimulus in either the same or the opposite visual hemifield (see Kyllingsbæk, 2006). Under the latter condition of stimulus competition across hemifields, accuracy of report is better for objects (letters) that receive a greater spatial-attentional weight (Duncan et al., 1999).

However, the probability with which an object is identified does not only depend on its relative attentional weight, but also on the sensory effectiveness, which is influenced by stimulus properties such as discriminability, luminance, contrast, retinal eccentricity, and so forth. In TVA, the parameter for sensory effectiveness, A (which is assumed to be independent of spatial attentional weighting), refers to the accuracy of reporting a single element presented alone, under conditions of no stimulus competition. Thus, A reflects the total processing rate for each hemifield, rather than how capacity is divided between the various objects of a display, providing a further TVA-based indicator of processing speed (Duncan et al., 1999). Similar to the spatial attentional weighting, a bias of sensory effectiveness towards one hemifield is expressed by a laterality index, termed A_λ .

According to TVA, then one possible explanation of a rightward spatial bias found under low-alertness conditions (e.g., Bellgrove et al., 2004; George et al., 2005; Manly et al., 2005) would be that attentional weights are reduced for the left compared to the right hemifield, unbalancing the competition between left- and right-lateralized targets. Alternatively, basic sensory effectiveness may be reduced in the left hemifield, unbalancing sensory processing between hemifields³ (see Bundesen, 1990, Equation 2).

On this background, the aim of Experiment 2 was to examine the influence of the level of intrinsic/phasic alertness on both the spatial distribution of attentional weighting and on sensory effectiveness. To that end, we applied a whole report task in which subjects had to name stimuli presented either unilaterally, on either side of the visual field, or bilaterally, in the left and the right hemifield. As in Experiment 1, the whole report task was presented in a no-cue and an alerting-cue condition. Also, the same SOA variation as in Experiment 1 was used to map the time course of the effects of alertness level on sensory effectiveness and spatial attentional weighting.

Method

Subjects. There were 14 right-handed healthy volunteers ($M_{\text{age}} = 24$ years, $SD = 3.01$, range: 23 to 30 years; 3 men, 11 women) who participated in Experiment 2.

Procedure. Figure 5 illustrates the sequence of frames presented in a trial in Experiment 2. Targets appeared with equal frequency at each of the possible stimulus locations in the corners

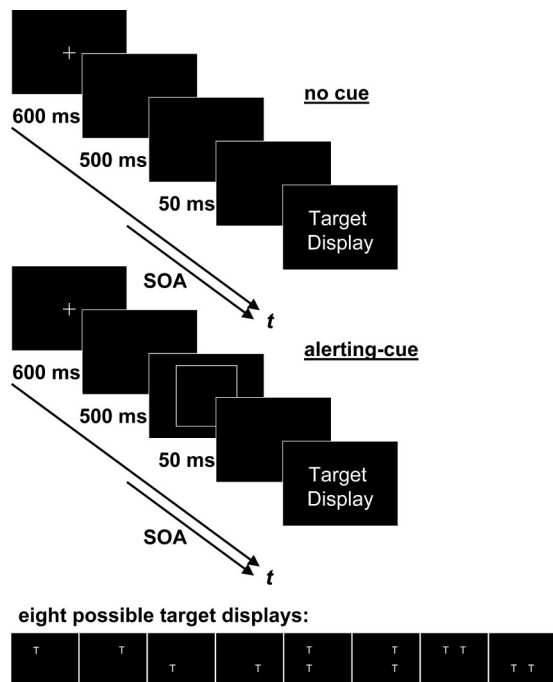


Figure 5. Sequence of frames presented on a no-cue trial (top panel) and an alerting-cue trial (middle panel) together with the eight possible target displays (bottom panel; the “T” symbols denote target locations) in Experiment 2. SOA = stimulus onset asynchronies.

of an imaginary square (with an edge length of 5°): upper left, lower left, upper right, lower right corner (see Figure 5, bottom panel). On each trial, either a single target or two targets, on the same side or on opposite sides, were presented. Dual targets were placed either vertically (column display) or horizontally (row display), but never diagonally. All target stimuli were masked.

Experimental design. The experiment was divided into two 1.5-hr sessions, each comprising four blocks that were separated by 5-min breaks. The order of the sessions was counterbalanced across subjects to control for sequence effects. Subjects completed each of the two sessions at the same time of day and within the same week. Before each block of trials, subjects were given standardized written and verbal instructions.

The experimental phase comprised eight different target conditions (four single target and four dual target conditions) for each SOA (80, 100, 200, 300, 450, 650 ms) and each of the two cueing conditions (no cue, alerting cue). In previous studies using a similar paradigm (Finke et al., 2006, 2005), highly reliable estimates for the parameter spatial distribution of attentional weighting (w_λ) were obtained on the basis of 18 trials per target condition. Therefore, in the present experiment, 18 trials were used for each target, SOA and cueing condition. In total, the experiment comprised 1,728 trials per subject.

³ In neglect patients, Duncan et al. (1999) observed in a TVA based partial report task—besides the expected rightward spatial bias—a significant impairment of relative sensory effectiveness in the left visual hemifield. Thus, target letters presented alone were identified less well in the left field. The results indicate the possibility that alertness might also affect sensory effectiveness on one hemifield.

Performance accuracy rate was recorded continuously and reported to the subject as a feedback indicator after each testing block.

Target exposure duration. At the beginning of each session, the target exposure durations were determined individually for each subject. A pretest (no-cue condition, 72 trials, with three trials for each SOA and single-target display) with a fixed exposure duration of 71 ms was used to determine whether a participant was able to reach an accuracy of 60 to 80% for single-target report ($n = 4$ participants). If the participant performed outside this range, the exposure duration in the experimental phase was adjusted accordingly (i.e., extended to 86 ms for one participant who reached only 50 to 60%, and shortened to 57 ms for nine participants who reached 80 to 90% accuracy).

Estimation of TVA parameters. Applying the algorithms described in detail by Kyllingsbæk (2006; see also Bublak et al., 2005, 2006; Duncan et al., 1999; Finke et al., 2005, 2006; Habeck & Bundesen, 2003; Hung et al., 2005), the whole report task permitted quantitative estimates to be derived for the parameters sensory effectiveness (as an indicator of visual processing speed) and attentional weighting (a spatial parameter of visual, top-down controlled selective attention), for each of the four stimulus positions used in the task (upper left, upper right, lower right, lower left): parameters A_i and w_i , respectively (where i is the stimulus position). Basically, A values are estimated from performance on single-element trials, and w values from performance losses in multi-element displays.

From these estimates, indexes of sensory effectiveness and attentional weighting were calculated for each hemifield (by averaging across the respective values for the upper and lower positions within each hemifield): A_{left} and A_{right} ; w_{left} and w_{right} . Then, the laterality indexes were computed, with parameter $A_\lambda = A_{\text{left}}/(A_{\text{left}} + A_{\text{right}})$ expressing the spatial bias of sensory effectiveness and parameter $w_\lambda = w_{\text{left}}/(w_{\text{left}} + w_{\text{right}})$, the spatial bias of attentional weighting. Accordingly, parameter values of 0.5 indicate equality between hemifields, parameter values above 0.5 reflect a left lateralization, and values below 0.5 a right lateralization.

Results

To check whether differential effects occurred for the two target types—unilateral, bilateral—that form the basis for the parameter estimations—sensory effectiveness, attentional weighting—and, thus, separate analyses for the target types are appropriate, a repeated-measures ANOVA was carried out with the factors side (left and right visual field), target type (unilateral targets, bilateral targets), SOA (80, 100, 200, 300, 450, 650 ms), and cue (no cue, alerting cue). This ANOVA revealed a plethora of significant effects (target type, Side \times Target Type, Side \times SOA, Target Type \times Cue, SOA \times Cue, Side \times SOA \times Cue, Side \times Target Type \times SOA, Side \times Target Type \times Cue, Target Type \times SOA \times Cue). Most important, the four-way interaction of Side \times Target Type \times SOA \times Cue was significant (with all $F_s > 4.18$, all $p_s < .05$). Therefore, we analyzed the two target type conditions separately in Side \times SOA \times Cue ANOVAs. An exception is the analysis of sensory effectiveness, where Cue \times SOA ANOVAs were carried out, assessing a general speed measure combined across hemifields.

In what follows, we first analyze the qualitative pattern of performance (correctly identified target letters) for each of the three aspects in question—sensory effectiveness (parameter A), spatial bias of sensory effectiveness (parameter A_λ), and spatial bias of attentional weighting (parameter w_λ)—and then report the quantitative analysis of the parameter estimates derived in TVA-based model fits to the data. The data fitting provided individual estimates of the parameters sensory effectiveness and attentional weighting, separately for each target location. The mean scores for the different experimental conditions and the values predicted (based on the best fits of the TVA model parameters) showed a satisfactory correspondence: The mean correlation between the observed and predicted scores across all SOAs was .71 ($SD = .15$) in the no-cue condition and .76 ($SD = .14$) in the alerting-cue condition.

Sensory effectiveness.

Analysis of performance accuracy. First, to verify whether the pattern of speed effects revealed in Experiment 1 was also evident in Experiment 2, a SOA \times Cue ANOVA of response accuracy in the unilateral target condition (with performance averaged across hemifields) was conducted. Performance for unilateral targets was examined to assess the overall sensory effectiveness (effectively an indicator of visual processing speed) as a function of the level of intrinsic/phasic alertness at a given point in time (SOA). The pattern of performance in unilateral target conditions for the two cueing conditions and the six SOAs is shown in Figure 6.

This ANOVA revealed the following (marginally) significant effects: SOA main effect, $F(5, 9) = 3.21, p = .06$, cue main effect, $F(1, 13) = 6.91, p < .05, \eta^2 = .35$, and SOA \times Cue interaction, $F(5, 9) = 9.59, p < .01, \eta^2 = .84$. Post hoc tests revealed significantly better performance in the alerting-cue compared to the no-cue condition at the SOAs of 80, 450 and 650 ms, $t(13) = -2.14, p < .05, t(13) = -6.03, p < .001, t(13) = -6.93, p < .001$, respectively. In contrast to the no-cue condition, a significant decrease in accuracy between the 80- and 100-ms SOAs was

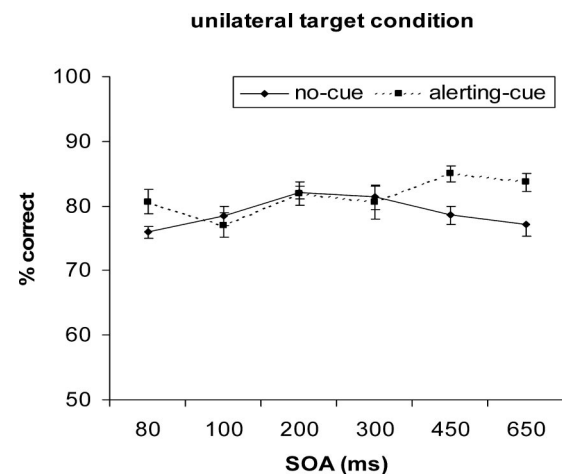


Figure 6. Mean proportions of correctly identified unilaterally presented target letters (% correct) in both cueing conditions as a function of SOA (stimulus onset asynchronies) averaged across hemifields. The error bars give the standard errors.

evident in the alerting-cue condition, $t(13) = 3.40, p < .01$, replicating the short-lasting alerting effect already seen in Experiment 1. Furthermore, although there was a significant decrease in accuracy between the SOAs of 300 and 450 ms, $t(13) = 2.18, p < .05$, in the no-cue condition, a marginally significant increase prevailed in the alerting-cue condition, $t(13) = -2.14, p = .05$. A significant increase in accuracy performance between the 100- and 200-ms SOAs was evident in both the alerting-cue, $t(13) = -3.26, p < .01$, and the no-cue condition, $t(13) = -3.46, p < .01$.

Analysis of the estimates of parameter A. Figure 7 shows the time course of the parameter sensory effectiveness A (averaged across hemifields) for the no-cue and alerting-cue conditions in Experiment 2.

The A parameter was examined in a repeated-measures ANOVA with the factors cue and SOA, which revealed the main effect of cue, $F(1, 13) = 10.16, p < .01, \eta^2 = .44$, and the Cue \times SOA interaction, $F(5, 9) = 16.82, p < .001, \eta^2 = .90$, to be significant. The main effect of SOA was nonsignificant, $F = 2.44, p > .10$. In close correspondence to the observed performance in the unilateral target condition (see Figure 6), post hoc tests revealed sensory effectiveness to be significantly higher in the alerting-cue condition compared to the no-cue condition at the SOAs of 80 (due to the initial alerting effect at the shortest SOA), 450, and 650 ms, $t(13) = -3.82, p < .01, t(13) = 2.68, p < .05, t(13) = -3.33, p < .05$, respectively. Following the initial alerting effect at the 80-ms SOA, a significant decrease of sensory processing between the 80- and 100-ms SOAs was evident in the alerting-cue condition, $t(13) = 3.59, p < .01$. In the no-cue condition, there was a significant increase of sensory effectiveness between the 100- and 200-ms SOA, $t(13) = -2.27, p < .05$, and a significant decrease between the 300- and 450-ms SOAs, $t(13) = 3.10, p < .01$, indicative of a heightened intrinsic alertness state at intermediate SOAs.

Spatial bias of sensory effectiveness.

Analysis of performance accuracy. As stated above, performance in the unilateral target condition is assumed to reflect the total processing rate for each hemifield, rather than how capacity is distributed across the different objects of a display (Duncan,

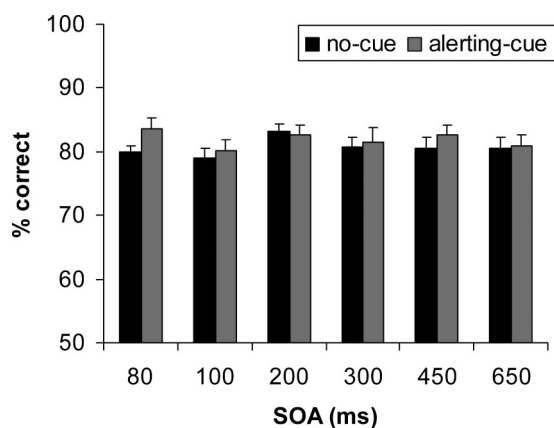


Figure 7. Values of A (sensory effectiveness averaged across hemifields) as a function of SOA (stimulus onset asynchronies) for the no-cue and the alerting-cue condition in Experiment 2. The error bars give the standard errors.

Bundesen, Olson, Humphreys, Chavda, & Shibuya, 1999). For the unilateral target conditions, the ANOVA revealed significant effects for side, cue, Side \times SOA, and SOA \times Cue; the three-way interaction Side \times SOA \times Cue was also significant (with all F s > 5.62 , all p s $< .05$). The main effect of SOA was marginally significant, $F(5, 9) = 3.09, p = .07$. The three-way interaction was analyzed further by ANOVAs carried out separately for the two different sides, with the factors SOA and cue.

Unilateral target condition, left hemifield (Figure 8). There were (marginally) significant main effects of SOA, $F(5, 9) = 12.11, p < .001, \eta^2 = .87$, and cue, $F(1, 13) = 3.90, p = .07$, and a significant SOA \times Cue interaction, $F(6, 9) = 10.55, p < .001, \eta^2 = .85$. Post hoc tests revealed reliably better performance in the alerting-cue condition compared to the no-cue condition at the SOAs of 80, $t(13) = 2.06, p < .05$, 450, $t(13) = -7.09, p < .001$, and 650 ms, $t(13) = -6.64, p < .001$. In contrast, at the 200-ms SOA, $t(13) = 3.96, p < .01$, and 300-ms SOA, $t(13) = 4.66, p < .01$, performance was significantly better in the no-cue condition compared to the alerting-cue condition. In the alerting cue condition, there was a significant decrease in performance between 80- and 100-ms SOAs, $t(13) = 2.56, p < .05$, a significant increase between the 100- and 200-ms, $t(13) = -3.09, p < .01$, as well as the 300- and 450-ms SOAs, $t(13) = -3.76, p < .01$. In the no-cue condition, a significant increase in performance was evident between 100- and 200-ms SOAs, $t(13) = -6.61, p < .001$, and a significant decrease between 300- and 450-ms SOAs, $t(13) = 8.78, p < .001$.

Unilateral target condition, right hemifield (Figure 9). The ANOVA revealed the main effect of cue, $F(1, 13) = 5.43, p < .05, \eta^2 = .29$, and the SOA \times Cue interaction, $F(5, 9) = 9.63, p < .01, \eta^2 = .84$, to be significant; the main effect of SOA was nonsignificant, $F = 2.61, p > .10$. Post hoc tests revealed significantly better performance in the alerting-cue condition compared to the no-cue condition at the SOAs of 200 ms, $t(13) = -3.51, p < .01$, 300 ms, $t(13) = -3.73, p < .01$, 450 ms, $t(13) = -2.85, p < .05$, and 650 ms, $t(13) = -3.59, p < .01$. In the alerting-cue condition, there was a marginally significant decrease in performance between the SOAs of 80 and 100 ms, $t(13) = 2.14, p = .052$, and 450 and 650 ms, $t(13) = 1.99, p = .068$. Moreover, a significant increase of accuracy was observed between 100- and 200-ms SOAs, $t(13) = -2.33, p < .05$. In the no-cue condition, there was a significant decrease in performance between 100- and 200-ms SOAs, $t(13) = 7.33, p < .001$, and a significant increase between the 300- and 450-ms SOAs, $t(13) = -3.06, p < .01$, and performance was a significant lower at the 650- relative to the 450-ms SOAs, $t(13) = 3.25, p < .01$.

Analysis of the estimates of parameter A_λ . Figure 10 shows the time course of the sensory effectiveness parameter A_λ for the no-cue and alerting-cue conditions in Experiment 2.

A_λ parameters were examined in a repeated-measures ANOVA with the factors cue and SOA, which revealed the interaction to be significant, $F(5, 9) = 21.97, p < .001, \eta^2 = .92$. This was due to a significant change in A_λ in the no-cue condition around the 200-ms SOA, $t(13) = 4.25, p < .05$. A_λ changed towards a leftward lateralization between the 100- and 200-ms SOAs, $t(13) = -5.52, p < .01$, and then reverted to a rightward lateralization by the 450-ms SOA (in contrast, A_λ stayed constant in the alerting-cue condition). This pattern is also apparent in the unilateral target conditions in Figures 8 and 9, with subjects showing

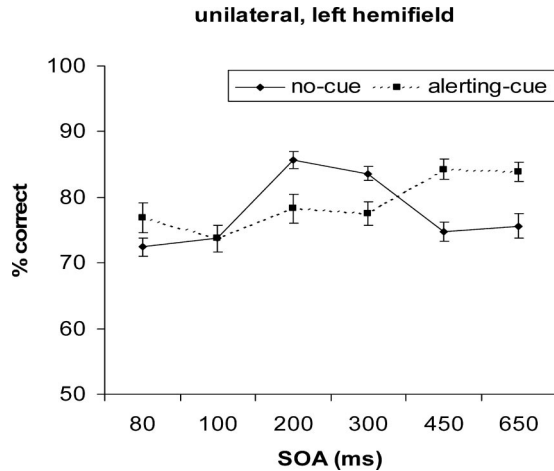


Figure 8. Mean proportions of correctly identified unilaterally, left-sided presented target letters (% correct) in both cueing conditions as a function of SOA (stimulus onset asynchronies). The error bars give the standard errors.

superior performance for the left, compared to the right, visual hemifield at the 200-ms SOA; this follows a decrease in accuracy for the right hemifield between the 80- and 200-ms SOAs and precedes a decrease for the left hemifield (with a concurrent increase for the right hemifield) between the 300- and 450-ms SOAs.

Spatial bias of attentional weighting.

Analysis of performance accuracy. As already stated, dual-target displays containing a target in each hemifield are crucial for the TVA-based estimation of the attentional weighting parameter: It is the only condition in which spatial-attentional weights have to be distributed across the left and the right hemifield, in which the weight distribution is determined by a competitive process between the two hemifields. For the bilateral target condition, the

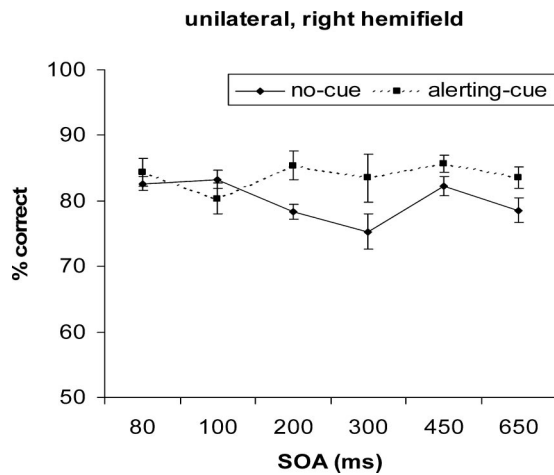


Figure 9. Mean proportions of correctly identified unilaterally, right-sided presented target letters (% correct) in both cueing conditions as a function of SOA (stimulus onset asynchronies). The error bars give the standard errors.

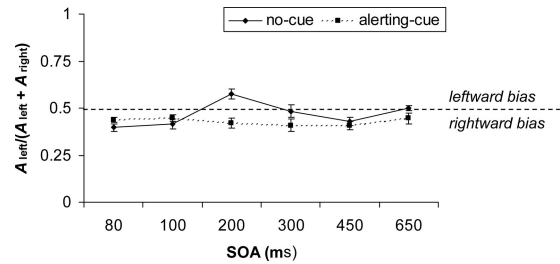


Figure 10. Values of A_λ (laterality index of sensory effectiveness) as a function of SOA (stimulus onset asynchronies) for the no-cue and the alerting-cue condition in Experiment 2. The error bars give the standard errors. Values of $w_\lambda > .50$ = leftward bias; $w_\lambda < .50$ = rightward bias; $w_\lambda = .50$ = no bias.

ANOVA revealed the Side \times SOA, the SOA \times Cue, and the Side \times SOA \times Cue interactions to be significant (all $F_s > 4.28$, all $p_s < .05$). The main effects of side, SOA, and cue, as well as the Side \times Cue interaction were nonsignificant (all $F_s < 3.13$, all $p_s > .10$). The three-way interaction was analyzed further in separate ANOVAs for the two different sides, with SOA and cue as factors.

Bilateral target condition, left hemifield (Figure 11). There was a significant main effect of SOA, $F(5, 9) = 6.89, p < .01, \eta^2 = .79$, and a significant SOA \times Cue interaction, $F(6, 9) = 40.06, p < .001, \eta^2 = .96$, the main effect of cue was nonsignificant, $F(5, 9) = .09, p > .80$. Post hoc tests revealed superior performance in the alerting-cue compared to the no-cue condition at the 80- and 100-ms SOAs, $t(13) = -5.59, p < .001, t(13) = -3.25, p < .01$, respectively, but significantly better performance in the no-cue compared to the alerting-cue condition at the 450- and 650-ms SOAs, $t(13) = 4.12, p < .01, t(13) = 4.86, p < .001$, respectively. This difference between cueing conditions at the shortest and longest SOAs was due to gradual decrease of response accuracy in the alerting-cue condition and a steady increase in the no-cue condition between the 80- and 650-ms SOAs, alerting-cue:

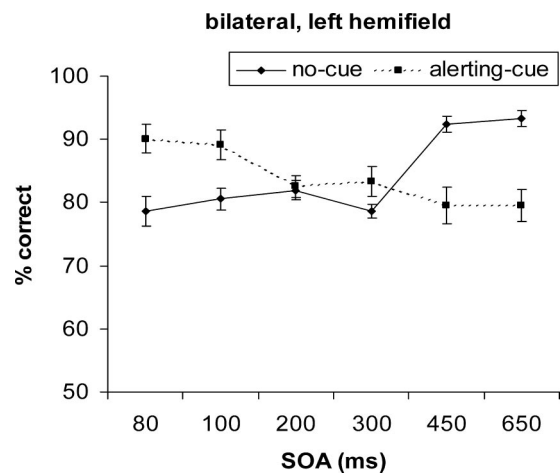


Figure 11. Mean proportions of correctly identified bilaterally presented target letters (% correct) in both cueing conditions as a function of SOA (stimulus onset asynchronies) in the left hemifield. The error bars give the standard errors.

$t(13) = 3.05, p < .01$, no-cue: $t(13) = -9.99, p < .001$. In the no-cue condition, this increase was especially pronounced between 300- and 450-ms SOAs, $t(13) = -10.67, p < .001$.

Bilateral target condition, right hemifield (Figure 12). There were significant main effects of SOA, $F(5, 9) = 4.83, p < .05, \eta^2 = .73$, and cue, $F(1, 13) = 6.87, p < .05, \eta^2 = .35$, and the SOA \times Cue interaction was significant, $F(6, 9) = 5.42, p < .05, \eta^2 = .75$.

Comparing cueing conditions, post hoc tests showed performance to be superior in the alerting-cue condition compared to the no-cue condition at the 80-ms SOA, $t(13) = -3.37, p < .01$, conversely, performance was better in the no-cue condition compared to the alerting-cue condition at the 200-, 300-, 450-, and 650-ms SOAs, $t(13) = 1.96, p = .07, t(13) = 2.22, p < .05, t(13) = 4.24, p < .01, t(13) = 5.49, p < .001$, respectively. Although both curves follow a similar course overall, the SOA \times Cue interaction was mainly due to a significant increase in performance in the no-cue condition between the 100- and 200-ms SOAs, $t(13) = -3.50, p < .01$.

Analysis of the estimates of parameter w_λ . Figure 13 illustrates the SOA-dependent time course of the spatial distribution of the attentional weighting parameter w_λ for the no-cue and alerting-cue conditions.

ANOVA revealed significant main effects for cue, $F(1, 13) = 9.89, p < .01, \eta^2 = .43$, and SOA, $F(5, 9) = 11.68, p < .001, \eta^2 = .87$, and a significant Cue \times SOA interaction, $F(5, 9) = 5.68, p < .05, \eta^2 = .76$.

Significant differences between the no-cue and the alerting-cue condition were obtained only for the 200- and 300-ms SOAs, $t(13) = -3.14, p < .05, t(13) = -3.74, p < .01$, respectively, due to a rightward spatial attentional bias in the no-cue condition and a leftward bias in the alerting-cue condition. In the latter, a slight, but relatively stable leftward lateralization of spatial attention (known as pseudoneglect) was evident across the range of cue-target SOAs (see also the pattern of performance in the bilateral target condition, Figures 11 and 12); in fact, post hoc tests revealed

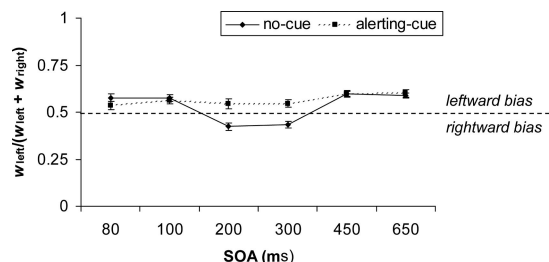


Figure 13. Parameter w_λ (spatial distribution of attentional weighting) as a function of SOA (stimulus onset asynchronies) for the no-cue and the alerting-cue condition in Experiment 2. The error bars give the standard errors. Values of $w_\lambda > .50$ = leftward attentional bias; $w_\lambda < .50$ = rightward attentional bias; $w_\lambda = .50$ = no bias.

this leftward bias to increase between the shortest and the longest SOAs, 80 versus 450 ms, $t(13) = -2.113, p < .05$, 80 versus 650 ms, $t(13) = -1.80, p < .05$. In contrast, in the no-cue condition, there was a significant decrease in the initial leftward lateralization—that is, an increase in rightward lateralization—between the SOAs of 100 and 200 ms, $t(13) = 5.91, p < .001$. This rightward bias lasted until the 300-ms SOA, after which it reversed again into leftward lateralization at the longest SOAs, 300 versus 450 ms, $t(13) = -7.81, p < .001$. The change in lateralization to the right at the intermediate, 200 and 300 ms, SOAs is in accordance with the performance pattern reported above for the bilateral target condition, which was characterized by superior accuracy for the right compared to the left hemifield at the same SOAs. This pattern resulted from a significant increase in accuracy for the right hemifield target between the 100- and 200-ms SOAs and a significant decrease for the left hemifield target between the 200- and 300-ms SOAs (see Figures 11 and 12).

Control of eye movements. Similar to Experiment 1, to avoid suboptimal fixation that might occur already at the beginning of a trial, the experimenter controlled for central fixation at the start of each trial (by means of an EyeLink video-based eye tracking device) and initiated the stimulus sequence only when the subject's gaze direction was seen to remain within a $\approx 1^\circ$ window around the fixation cross. Moreover, to rule out that the effects described above for the 200- and 300-ms SOAs depended on eye movements just before the target was presented, two further subjects were tested with eye fixation recorded and controlled for automatically. For these subjects, trials on which the fixation position deviated by more than 1° of visual angle from the central cross were rejected and repeated at the end of the respective experimental block. The results for the two (eye movement control) subjects are presented in the Appendix. More important, the time course of changes in the parameters A_λ and w_λ were comparable to those found in the group with experimenter-controlled fixation. We take this to indicate that the leftward lateralization of sensory effectiveness and the simultaneous rightward spatial lateralization at the 200- and 300-ms SOAs occurred independently of any eye movements.

Time-on-task effects. To examine for time-on-task effects in Experiment 2, the average accuracies for the different display conditions were computed for the left and right hemifields, separately for the trial blocks in the first and the second half of each session. Next, t tests were carried out to compare the accuracies (averaged across sessions) between the first versus the second half.

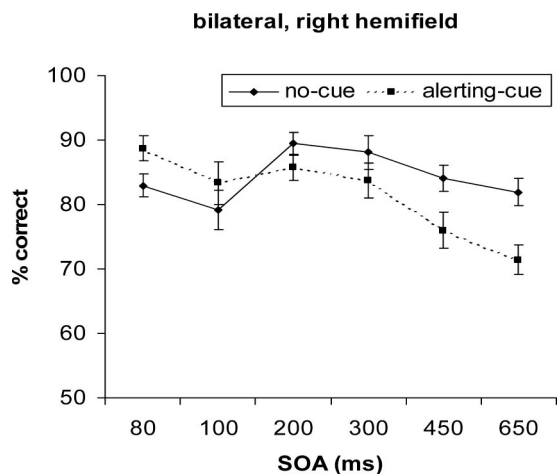


Figure 12. Mean proportions of correctly identified bilaterally presented target letters (% correct) in both cueing conditions as a function of SOA (stimulus onset asynchronies) in the right hemifield. The error bars give the standard errors.

None of these comparisons revealed a significant decrease in performance from the first to the second half of the sessions, alerting cue: all t s < 1.68, all p s > .11, no cue: all t s < 1.87, all p s > .19.

Discussion

The aim of Experiment 2 was to examine the effects of alertness on the spatial distribution of attention, in particular: Would such effects become evident as a bias in sensory effectiveness or in attentional weighting, per se, and would they occur in parallel with each other or only after the alertness-related enhancement of processing speed?

With respect to processing speed (as indicated by sensory effectiveness), we found a temporary enhancement at the shortest (80 ms) SOA in the alerting-cue condition. In both the alerting-cue and the no-cue conditions, sensory effectiveness increased at the SOA of 200 ms. Sensory effectiveness continued to increase gradually at the longer SOAs in the alerting-cue condition, although it slightly decreased at the longest SOAs in the no-cue condition. Taken together, these results are in close correspondence with Experiment 1: Again, there was a rapid and transitory speed enhancement under conditions of phasic alertness, and also a later component of a speed enhancement that became evident at the 200- and 300-ms SOAs independently of the cueing condition (i.e., the presentation of an alerting cue), indicative of a temporal range effect induced by an intrinsic change in the state of alertness.

In the no-cue condition, the increase in sensory effectiveness at the 200-ms SOA was especially pronounced for stimuli in the left hemifield, giving rise to a spatial bias of sensory effectiveness toward the left side at this point in time. In contrast, at the other SOAs, sensory effectiveness was biased toward the right hemifield in both the no-cue and the alerting-cue conditions. This “default” rightward bias may be related to the left-hemisphere advantage for processing verbal stimuli (Kimura, 1973), improving the report of letters displayed briefly and unilaterally in the right hemifield.⁴ The reverse pattern emerged at the 200-ms SOA, suggesting a right-hemisphere (left-hemifield) dominance in this case.

With respect to spatial attentional weighting, a continuous bias towards the left hemifield was found in the alerting-cue condition (in line with the pseudoneglect phenomenon that prevails in alert healthy subjects), which appeared to increase slightly over time. In contrast, in the no-cue condition, spatial weighting showed a marked change over time: The initial leftward bias changed into a rightward bias at the intermediate SOAs of 200 and 300 ms, and then returned to a leftward lateralization at the longest SOAs. Again, this change was driven mainly by left hemifield stimuli. For these, accuracy of letter report improved continuously over time in the no-cue condition, although it decreased in the alerting-cue condition (a pattern that was evident for both hemifields in the latter condition, however).

It is unlikely that these effects can be simply explained by the occurrence of eye movements in our task, for the following reasons. First, the latency of saccadic eye movements is too long to take hold of stimuli at very brief stimulus exposure durations. Second, stimuli were displayed unpredictably in either the left or the right hemifield, so that maintaining central fixation (which was also emphasized by the instruction) was the best strategy to perform optimally. Third, an eye movement account cannot explain

the differential effects found in the two cueing conditions, as the alerting cue was noninformative as to the spatial direction of the imminent stimuli. Fourth, any systematic deviation of eye movements towards one hemifield would not argue against our interpretation because such a bias would have to be interpreted as an attentional effect (“overt orienting”). Finally, in two further subjects, eye movements were explicitly controlled—with much the same pattern of effects as for the other subjects (especially at the short and intermediate SOAs where the most relevant effects occurred in Experiment 2).

In summary, Experiment 2 revealed an intricate pattern of both simultaneous and sequentially operating effects. Under conditions of phasic alertness (alerting-cue condition), an initial speed enhancement occurred in the presence of a rightward bias of sensory effectiveness and a leftward bias of spatial attention. These biases appear to represent default states that are maintained (and, in fact, strengthened) over time depending on alerting cue-induced activation. In the absence of such a cue, under conditions of intrinsic alertness (no-cue condition), a speed enhancement emerges after some delay, which operates more strongly in the left hemifield, giving rise to a lateralization of sensory effectiveness to the left side. At the same time, spatial attentional weighting shifts towards the right hemifield, and, after a delay, returns again to a leftward lateralization.

As a result, we are left with a seemingly paradoxical effect at the intermediate SOAs (200 and 300 ms) in the no-cue condition, in which there was an increase in processing speed (as indicated by sensory effectiveness). This implies an alert state that, on the evidence outlined in the Introduction, should prevent spatial attention from shifting rightward—whereas, in fact, spatial attentional weighting was biased towards the right hemifield during this same period, not returning to a leftward bias until the later SOAs. Consideration of how this paradox (which is a central issue for our results) can be explained will be deferred until the General Discussion.

For this, it is first of all necessary to examine whether the superposition of these seemingly contradictory effects—enhancement of sensory effectiveness predominantly in the left hemifield, rightward spatial bias of attentional weighting—are related to the presumed change of the intrinsic alertness state in the no-cue condition. If this assumption is correct, the effects observed at the 200- and 300-ms SOAs (in Experiment 2) should not obtain when the SOAs are kept constant during trial blocks (rather than varying randomly across trials within blocks as in Experiment 2). Experiment 3 was conducted to test this prediction.

⁴ It could be argued that the results of our study are specific to verbal material, as the tasks used required letter identification. However, the functional dominance of the left hemisphere for verbal material should not differentially influence spatial attentional weighting (or other TVA parameters) in the alerting-cue condition versus the no-cue condition, because the (nonverbal) cue imposed no demands on verbal stimulus processing. Thus, arguably, the phasic alerting effects revealed in the present experiments are nonverbal in nature. Nevertheless, this should be tested in a follow-up study using, for example, picture material that is difficult to verbalize.

Experiment 3

In Experiments 1 and 2, SOA was varied randomly within trial blocks to prevent subjects from anticipating the precise onset of the stimulus display. In both experiments, optimum processing speed was observed at intermediate SOAs, independently of the cueing condition. We took this pattern to reflect a temporal range effect, based on subjects gradually (i.e., with increasing SOA) building up an expectancy for the onset of the target display in the middle of the range of SOAs, which is coupled with an enhanced state of intrinsic alertness. In Experiment 2, this enhancement became manifest in terms of a gain in sensory effectiveness especially in the left hemifield, and was associated with a spatial bias of attentional weighting toward the right side.

These effects may be related to the dynamic configuration of the mental set, and the accompanying change in the alertness state, necessary for stimulus anticipation (under conditions of variable SOAs). If this assumption is correct, such effects should not be observed if the requirement for such a dynamic, online configuration is absent. This situation was realized in Experiment 3 by keeping the SOA constant throughout a block of trials, thus enabling subjects to readily anticipate the onset of a stimulus display and to maintain a more constant and optimal level of intrinsic alertness. Accordingly, we expected that the differences between the alerting-cue and no-cue conditions and, thus, the changes of sensory effectiveness and spatial attentional weighting in the no-cue condition would disappear—compared to the randomized SOA conditions of Experiment 2.

Method

Participants. There were 14 right-handed healthy volunteers ($M_{\text{age}} = 24.17$ years, $SD = 3.21$; range: 21 to 29 years; 4 men, 10 women) who participated in Experiment 3. There were no significant differences in terms of age, gender, or education between the subjects of Experiments 2 and 3 ($p > .65$).

Procedure. In Experiment 3, the experimental procedure and the sequence of frames presented on a given trial were identical to

Experiment 2, except that the SOAs were held constant within trials blocks (rather than being randomized as in Experiment 2).

Experimental design. Experiment 3 consisted of three blocks that were separated by 5-min breaks; it took about 2 hr to complete. The order of the blocked SOA conditions was counterbalanced across subjects. In contrast to Experiment 2, only three different SOAs (short, intermediate, and long: 80, 200, and 450 ms) were used in Experiment 3, to map performance for the most relevant periods during a trial in a less time-consuming procedure. The cueing conditions (no cue/alerting cue) occurred with equal frequency in each SOA block.

As in Experiment 2, each target condition (target location, see Figure 5), SOA, and cueing condition was repeated in 18 trials. Each block consisted of 288 trials (2 Cueing Conditions \times 1 SOA \times 8 Target Conditions \times 18 Trials). Altogether, the experiment comprised 864 trials per subject. The first 20 trials in each block were excluded from analysis to ensure the presence of a stable expectancy state in the subjects.

Results and Discussion

Sensory effectiveness (A_λ). The A_λ parameters were examined by a mixed-design ANOVA with cue (no cue, alerting cue) and SOA (80, 200, 450 ms) as within-subject factors and experiment (Experiment 2, Experiment 3) as between-subject factor. This analysis revealed significant effects for SOA, Cue \times Experiment, and SOA \times Experiment (all $F_s > 4.93$, all $p_s < .05$). The main effects of cue and experiment as well as the Cue \times SOA and the Cue \times SOA \times Experiment interactions were nonsignificant (all $p_s > .12$).

For the no-cue condition (Figure 14, left panel), post hoc tests revealed a significant difference in sensory effectiveness between the two experiments (randomized vs. blocked SOAs) at the 200-ms SOA, $t(26) = -4.71$, $p < .001$. Thus, in contrast to the variable SOA condition of Experiment 2, no significant changes to a leftward lateralization of sensory effectiveness were evident when subjects could maintain a stable expectancy in the blocked SOA condition of Experiment 3. Moreover, for the alerting-cue condi-

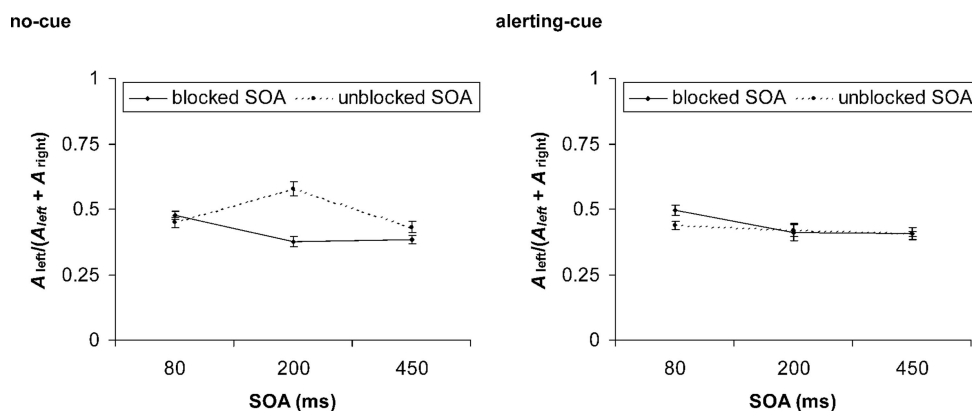


Figure 14. Parameter A_λ (latency index of sensory effectiveness) as a function of SOA (stimulus onset asynchronies), separately for Experiment 2 (unblocked SOA) and Experiment 3 (blocked SOA) in the no-cue condition (left panel) and in the alerting-cue condition (right panel). The error bars give the standard errors. Values of $A_\lambda > .50$ = leftward bias; $A_\lambda < .50$ = rightward bias; $A_\lambda = .50$ = no bias.

tion (Figure 14, right panel), no significant differences between experiments were revealed, indicative of comparable effects of alerting on sensory effectiveness in both experiments (all p s > .13). In Experiment 3, in both cueing conditions, there was a significant increase in a rightward bias of sensory effectiveness between the 80- and 200-ms SOAs, no cue: $t(13) = 4.70, p < .001$; alerting cue: $t(13) = 2.59, p < .05$, and, respectively, the 80- and 450-ms SOAs, no cue: $t(13) = 4.96, p < .001$; alerting cue: $t(13) = 2.93, p < .05$.

Spatial distribution of attentional weighting (w_λ). The w_λ parameters were examined by an analogous ANOVA (to the A_λ parameters), which revealed significant effects for SOA, Cue \times SOA, SOA \times Experiment, and Cue \times SOA \times Experiment (with all F s > 4.39, all p s < .01). The main effect of experiment was nonsignificant (p s > .40). To further analyze the three-way interaction, separate ANOVAs were carried out for the two cue types, with the within-subject factor SOA and the between-subject factor experiment.

Alerting-cue condition (Figure 15, right panel). For the alerting-cue condition, the ANOVA revealed only a significant main effect of SOA, $F(2, 25) = 12.44, p < .001, \eta^2 = .54$. This effect reflects an increasing leftward lateralization in the alerting-cue condition between the SOAs of 80 and 450 ms—in both Experiment 2 (see above) and Experiment 3, $t(14) = -3.48, p < .01$.

No-cue condition (Figure 15, left panel). For the no-cue condition, the ANOVA revealed a significant main effect of SOA, $F(2, 25) = 8.57, p < .001, \eta^2 = .45$, and a significant SOA \times Experiment interaction, $F(2, 25) = 11.32, p < .001, \eta^2 = .52$. The main effect of experiment was nonsignificant (p s > .20). Post hoc tests revealed a significant difference between the blocked (Experiment 3) and randomized (Experiment 2) SOA conditions only for the 200-ms SOA, $t(26) = 3.86, p < .001$. In contrast to the results of Experiment 2 (see above), no significant changes in the spatial distribution of attentional weighting were evident in the no-cue condition of Experiment 3 ($p > .58$).

In summary: In contrast to randomized SOA conditions of Experiment 2, under the blocked SOA conditions of Experiment 3, there was no temporary enhancement and no leftward lateraliza-

tion of sensory effectiveness at the 200-ms SOA. Instead, in both the alerting-cue and the no-cue conditions, there was a lateralization of sensory effectiveness towards the right hemifield across all SOAs, which increased over time. Similarly, a constant leftward spatial bias of attentional weighting was revealed, again across all SOAs and in both cueing conditions. Taken together, these results confirm the assumption that the changes in sensory effectiveness and spatial weighting observed in Experiment 2 were in fact related to the dynamic (online) configuration of a mental set for anticipating the onset of the stimulus display, which was not required under conditions in which a more stable expectancy could be invoked from the outset of a trial.

General Discussion

There is ample evidence that the state of alertness not only affects processing speed, a nonspatial attentional component typically assessed by simple RT tasks, but has also a significant influence on the spatial distribution of attention. The present study was designed to obtain a more clear-cut picture of both the nature and the time course of these alertness effects. To that end, we applied whole report of brief letter arrays, a task not requiring speeded motor responses, under conditions with and without an alerting cue and with varying (cue-stimulus) SOAs. Based on the theoretical framework of TVA (e.g., Bundesen, 1990, 1998), accuracy of performance in these tasks was modeled to derive estimates of perceptual processing speed and VSTM storage capacity in Experiment 1, and of sensory effectiveness, lateralization of sensory effectiveness, and lateralization of spatial attentional weighting in Experiments 2 and 3.

Experiment 1 revealed a fast evolving and short-lasting effect of the alerting cue on visual processing speed, but not on VSTM storage capacity. The speed of processing was significantly increased under conditions of phasic alertness (alerting-cue condition) at the shortest SOA of 80 ms, whereas the storage capacity remained unaffected. Another important finding was an increase in visual processing speed with longer SOAs, which was evident whether an alerting cue had been presented. This slower but longer lasting effect of a heightened readiness to process the target objects

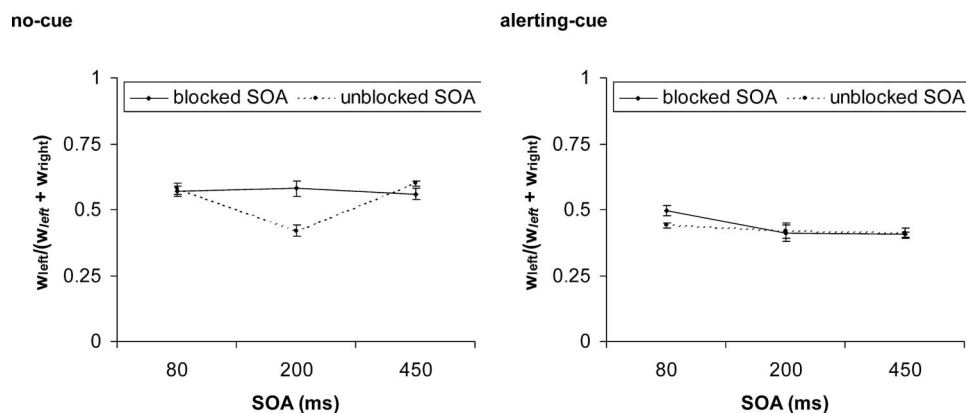


Figure 15. Parameter w_λ (spatial distribution of attentional weighting) as a function of SOA (stimulus onset asynchronies), separately for Experiment 2 (unblocked SOA) and Experiment 3 (blocked SOA) in the no-cue (left panel) and in the alerting-cue condition (right panel). The error bars give the standard errors. Values of $w_\lambda > .50$ = leftward bias; $w_\lambda < .50$ = rightward bias; $w_\lambda = .50$ = no bias.

(letters) was assumed to reflect the gradual buildup of an expectancy for the imminent presentation of the stimulus array, associated with an enhanced state of intrinsic alertness endogenously generated by the subjects (rather than exogenously induced by an alerting cue).

These results were largely replicated in Experiment 2, in which a slightly different whole report paradigm was used, providing an estimation of sensory effectiveness as a measure of processing speed. Moreover, the no-cue condition of Experiment 2 yielded a pattern of spatial effects, with a leftward lateralization of sensory effectiveness and a rightward lateralization of attentional weighting at intermediate SOAs (of 200 and 300 ms). During the same time period, processing speed showed a maximum enhancement in both Experiments 1 and 2, which was attributed to the increase in intrinsic alertness. At longer SOAs, the spatial deviations reverted to the rightward bias of sensory effectiveness and the leftward bias of attentional weighting that had been present at earlier SOAs and that characterized the lateralization evident in the alerting-cue condition.

Experiment 3 confirmed that these changes in spatial bias for both sensory effectiveness and spatial weighting were associated with the random SOA variation of Experiment 2, as no such effects were revealed when different SOAs were presented constantly during experimental blocks. As a result, the differential effects in the no-cue condition of Experiment 2 can be interpreted as resulting from the gradual buildup of a stimulus expectancy brought about by the requirement to dynamically configure the intrinsic alertness system under conditions of a randomized SOA variation. In contrast, if this system can be stably configured to a constant mental set, the same effects emerge as those induced by an external trigger, that is, an alerting cue.

These results are a first step towards clarification of the questions raised in the Introduction. First, they show that alertness effects can operate already at the perceptual level, enhancing stimulus processing speed (but not VSTM storage capacity). This selective effect on processing speed provides strong support for one of the main assumptions underlying TVA (e.g., Bundesen, 1990), namely, that the two parameters can vary independently of each other. It also demonstrates that an alertness-dependent performance enhancement can arise from accelerated visual stimulus coding for object selection, rather than just from expedited motor reactions owing to enhanced response preparation and/or execution processes.

Second, the results demonstrate that the development of the effects of processing speed over time differs between conditions of phasic and intrinsic alertness. Phasic alertness modulations are evoked rapidly, but are rather short-lived; intrinsic alertness, by contrast, is characterized by a gradual increase in processing speed that is sustained for a longer period of time. The latter pattern is in line with a neuro-cognitive model, outlined in the Introduction, according to which intrinsic alertness effects are mediated, in a top-down manner, by higher order (frontal cortical) centers that modulate (posterior) perceptual processing areas via lower level relay nodes (thalamic and noradrenergic brainstem nuclei; Heilman et al., 1993; Mesulam, 2000; Posner & Petersen, 1990). In contrast, phasic alertness effects would be related to a fast processing route that largely bypasses the top-down (cortical) stage underlying intrinsic alertness, presumably involving direct sensory

input to lower-level centers such as the thalamus or the ascending reticular activating system (Jones, 2003).

This view would also be compatible with the neural interpretation of TVA (NTVA) put forward by Bundesen et al. (2005). According to NTVA, processing of visual objects occurs in a perceptual cycle comprising two waves—the first being unselective, the second selective—involving different thalamo-cortical loops. In the first, unselective wave, visual input is matched to stored feature representations resulting in the computation of η values reflecting the strength of the evidence that objects at particular spatial scales and positions have particular (e.g., letter-like) features. (TVA assumes that the η values are multiplied by a factor reflecting the fact that letters instead of, say, numbers have to be reported; this factor is assumed to be set by top-down, task-related input and can be regarded a constant throughout our experiments.) During the second, selective wave of processing, η values are multiplied by a perceptual bias parameter β . This parameter favors the classification of objects with respect to a certain category (e.g., letters) and determines the activation level of neurons representing visual objects. It is derived from higher order cortical centers, for instance in the frontal lobe.

Based on these assumptions, a plausible explanation for the sequential effects of phasic and intrinsic alertness in Experiment 1 could be as follows: The fast and short-lasting effect of the alerting cue on processing speed may be related to the first wave of processing: The alerting cue may enhance the efficiency of cortical feature detectors, supporting the encoding of visual objects as letters. In contrast, the slower and longer lasting effect may directly affect the second wave of processing, increasing the firing rate of object-representing neurons. The fast (phasic) effect may be considered as bottom-up or cue-driven, while the slower (intrinsic) effect may be more top-down related. Thus, it is plausible that the phasic alertness route does not only operate faster and more transiently, but also less specifically compared to the intrinsic alertness route. Consistent with this view, we found a left hemifield advantage for letter report only under conditions of intrinsic, but not under conditions of phasic, alertness in Experiment 2—pointing to the right-hemispheric dominance of the intrinsic alertness system.

Finally, our results also reveal a differential time course of spatial effects between the two cueing conditions. After presentation of an alerting cue, both sensory effectiveness and attentional weighting exhibited a constant spatial bias towards one hemifield (the right hemifield in the case of sensory effectiveness, the left hemifield in the case of attentional weighting). The leftward bias of spatial attention grew significantly stronger over time. In contrast, under intrinsic alertness conditions (i.e., without an alerting cue), a cross-over pattern was observed for both sensory effectiveness and attentional weighting, with the former deviating temporarily to the left and the latter to the right hemifield. The rightward deviation occurred during the same time period in which speed effects reached a maximum, reflecting an enhanced intrinsic alertness state. This is a rather counterintuitive result, as empirical evidence suggests enhanced alertness to be associated with a leftward spatial deviation, whereas our results suggest exactly the opposite, namely that high alertness is related to a rightward spatial bias. This paradox requires an explanation.

One account could be that the relative decrease of attentional weights for items in the left hemifield serves to compensate for the

concomitant increase in perceptual bias for categorizations of objects in this hemifield, as mentioned above. This may be due to some antagonistic interaction between the systems underlying sensory processing and attentional weighting, with excitation of one system leading to inhibition of the other. This would predict that sensory effectiveness and spatial-attentional weighting are intimately correlated, which however is not always supported by empirical data (e.g., Duncan et al., 1999). Nevertheless, this account cannot be ruled out.

An alternative (or additional) explanation derives from the observation (in Experiment 2) that a similar sequence of events prevailed in both the phasic and the intrinsic alertness condition. In both conditions, an initial increase in alertness led to a boost of processing speed at first, which was followed by leftward bias of spatial attention. In the phasic alertness condition, processing speed peaked at around 80 ms, and the spatial-attentional bias towards the left hemifield was maintained and grew stronger at the longest SOAs. In the intrinsic alertness condition (i.e., without alerting cue), processing speed peaked at around 200 ms (with a bias towards the left hemifield), at which time spatial attention was deviated towards the right, and this was followed by a return to the left hemifield after a delay of some 250 ms (at the 450-ms SOA). Thus, increased alertness, whether generated phasically or intrinsically, appears to give rise to a cascade of effects: first a speed enhancement and, after some delay, a leftward orientation of spatial attention. This account would be compatible with the neuro-cognitive model described above. Assuming that spatial-attentional weighting effects are mediated by the posterior parietal cortex—in line, for instance, with data from neglect patients (Bublak et al., 2005; Duncan et al., 1999)—a delayed effect of alertness would be expected, because activation of posterior areas is implemented via a neural relay station in the thalamus and brainstem.

This interpretation of the data assumes that both phasic and intrinsic alertness rely on the same underlying neural circuit, but engage this circuit in separate time intervals. Phasic alertness (i.e., with an alerting cue) takes a fast route through the circuit, which bypasses the top-down (cortical) implementation stage. This initial stage is necessary for generating intrinsic alertness, which therefore takes a slower route. As a result, the processing speed effects associated with phasic and intrinsic alertness are temporally separated. For the same reason, the effects on spatial attention, which result from the same mechanism, are temporally separated as well. That is, the successive effects of alertness on processing speed and on spatial attention would be the same, whether they result from intrinsic or from phasic alertness. However, as intrinsic alertness acts with a delay relative to phasic alertness, the succession of phasic and intrinsic effects are not synchronized in time. The result is a pattern of overlapping effects, as was observed in Experiment 2. The key assumption that phasic and intrinsic alertness rely on a common underlying circuit is corroborated by the results of Experiment 3, in which the differences between the alertness conditions disappeared when SOA was blocked rather than randomized (as in Experiment 2).

On these premises, the parallelism of enhanced processing speed and a rightward bias of spatial attention (indicating lowered alertness) would no longer represent a paradox. Rather, if speed effects precede spatial effects, then, at a certain point in time, increased processing speed in the presence of a rightward spatial bias would

be a regular observation. Increased speed would just indicate accomplishment of the first stage of the activation process induced by alertness, whereas the rightward bias would indicate that the second stage (i.e., the spatial effect) has not yet been reached. Thus, in a snapshot of a moment in time, one would simply observe a certain state, or phase, of processing in the alertness circuit. This account presupposes that speed and spatial attention are mediated by independent systems—which is, however, a basic assumption in TVA.

In summary, the present results demonstrate that alerting cues affect spatial and nonspatial components of attention in an independent manner and in different time windows. That is, “alertness”—rather than being synonymous with a capacity parameter such as processing speed—is to be regarded as a basic attentional factor influencing various components of attention in parallel, but with differential time courses.

The present results also have implications for the relationship between alertness and spatially lateralized as well as nonlateralized components of attention in attentional dysfunctions. Consistent with our findings, in neglect patients, alertness cues can ameliorate the spatial bias for short periods of time (Robertson et al., 1998, 1995) as well as have a longer lasting effect after weeks of alertness training (Thimm et al., 2006). It is noteworthy in this context that, in the normal participants tested in the present study, two major effects of the cue manipulation could be observed in different time windows within the same subjects. This opens the door to assess in neglect patients precisely which attentional components are affected, and in which time ranges, by alertness cueing and how this would impact on alertness training (e.g., Thimm et al., 2006) in patients with pathologically biased attentional states.

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Appendix

To analyze whether the estimated A_λ and w_λ values in the two eye movement-controlled subjects deviated significantly from the group without eye movement control, binomial tests for the two parameters, the two cueing conditions, and the six SOAs were conducted separately for each of the two fixation controlled subjects. Regarding parameter A_λ (see Table A1), neither Subject 1 nor Subject 2 showed any significant deviations from the eye

movement uncontrolled group (Subject 1: all $ps > .18$, Subject 2: all $ps > .18$).

Regarding parameter w_λ , Subject 2 also showed no significant deviations compared to the uncontrolled eye movement group (Subject 2: all $ps > .18$; see Table A1). Subject 1 showed a marginally significant deviation in the no-cue condition for the 650-ms SOA ($p = .06$); all other comparisons were nonsignificant (all $ps > .42$; see Table A1).

Table A1

Individual A_λ and W Values (Left- and Right-Hand Side, Respectively) for Two Subjects With Eye Movement Control and Averaged A and W Values Over the 14 Subjects Without Eye Movement Control in Experiment 2, Separately for the Two Cueing Conditions and the Six SOAs

Variable	$A_{\lambda(80)}$	$A_{\lambda(100)}$	$A_{\lambda(200)}$	$A_{\lambda(300)}$	$A_{\lambda(450)}$	$A_{\lambda(650)}$	$W_{\lambda(80)}$	$W_{\lambda(100)}$	$W_{\lambda(200)}$	$W_{\lambda(300)}$	$W_{\lambda(450)}$	$W_{\lambda(650)}$
No cue												
Controlled												
Subject 1	.38	.45	.59	.56	.46	.48	.58	.57	.43	.43	.61	.58
Subject 2	.43	.43	.56	.50	.40	.52	.56	.58	.46	.41	.55	.59
Uncontrolled	.40	.42	.58	.48	.43	.50	.58	.58	.42	.43	.60	.59
Alerting cue												
Controlled												
Subject 1	.43	.39	.43	.41	.39	.41	.52	.57	.53	.54	.61	.60
Subject 2	.34	.45	.32	.37	.42	.52	.58	.56	.55	.57	.57	.56
Uncontrolled	.44	.45	.42	.41	.41	.45	.54	.56	.54	.55	.60	.60

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