

Event-related potential studies of attention

Steven J. Luck, Geoffrey F. Woodman and Edward K. Vogel

Over the past 30 years, recordings of event-related potentials (ERPs) from normal individuals have played an increasingly important role in our understanding of the mechanisms of attention. This article reviews some of the recent ERP studies of attention, focusing on studies that isolate the operation of attention in specific cognitive subsystems such as perception, working memory, and response selection. Several conclusions are drawn. First, under some conditions attention modulates the initial feedforward volley of neural activity in intermediate visual processing areas. Second, these early effects can be observed for both the voluntary allocation of attention and for the automatic capture of attention following a peripheral visual transient. Third, these effects are present not only when attention is directed to a location in 2-dimensional space, but also when attention is directed to one of two spatially overlapping surfaces. Fourth, attention does not modulate sensory activity unless sensory systems are overloaded; when sensory systems are not taxed, attention may instead operate to influence memory or response processes. That is, attention operates to mitigate information overload in whichever cognitive subsystems are overloaded by a particular combination of stimuli and task.

There has been a great deal of excitement over the past decade about the possibility of using the techniques of neuroscience to answer fundamental questions about cognition, and one of the great success stories has been the use of event-related potential (ERP) recordings to study attention. ERPs have been used to study attention since the 1960s (Ref. 1), but conceptual and methodological advancements have led to a recent surge in ERP studies that provide answers to mainstream cognitive questions. The purpose of this article is to review several of these studies, making them accessible to a broader audience. Towards this end, the basics of the ERP technique and its advantages for studying cognition are described in Box 1. In this review, we will focus on studies that have sought to isolate the operation of attention within specific cognitive subsystems, but recent ERP studies have also addressed other important issues, such as the time course of attentional orienting (as described in Box 2).

Evidence for early selection

Perhaps the most fundamental question about attention is whether attention modulates information processing at a sensory stage or at a later stage. There are obvious cases in which attention operates after a stimulus has been perceived; for example, we may see a stimulus and simply choose not to make an overt response to it. It is much more difficult to determine whether attention can sometimes suppress the sensory processing of a stimulus. In fact, it is not clear that traditional behavioral methods have ever yielded unambiguous evidence for early selection^{2,3}. However, ERPs are well suited for addressing this 'locus-of-

selection' issue; indeed, this was the first mainstream question about attention that ERPs were used to answer^{1,4}.

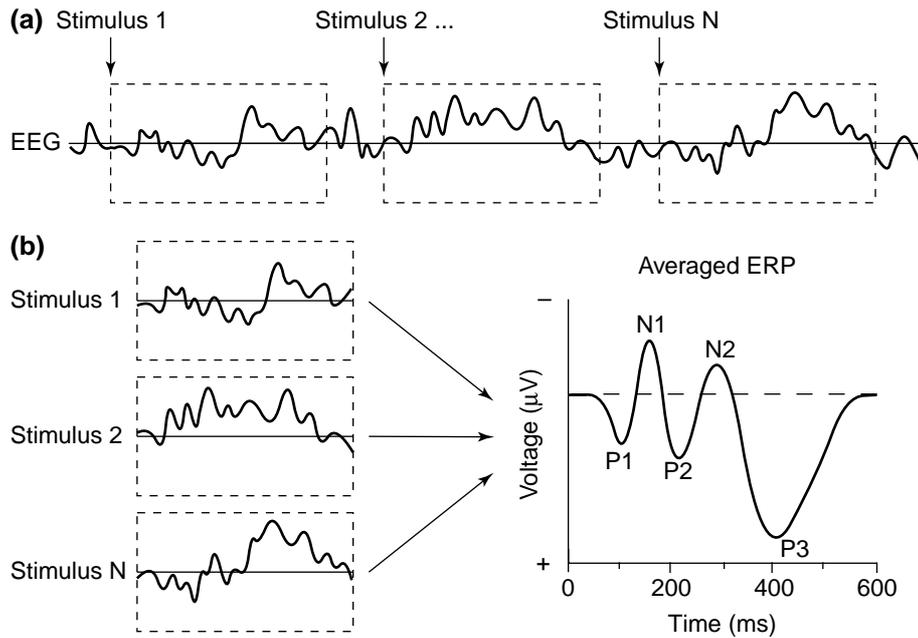
To assess the locus of selection, one simply compares the ERP waveform elicited by an attended stimulus to the ERP waveform elicited by a physically identical stimulus when it is ignored. The earliest time point at which the two waveforms differ provides an upper bound on the initial effect of attention on the processing of the stimulus (it is an upper bound because there might be earlier effects that are not evident in the ERP waveforms). For example, Fig. 1 compares two ERP waveforms, both elicited by a rectangle presented in the left visual field; one waveform was elicited by this stimulus when attention directed to the left visual field, and the other was elicited by this same stimulus when attention was directed to the right visual field. These waveforms begin to differ in the latency range of the P1 wave – between 60 and 100 ms poststimulus – which indicates that attention modulates the processing of the stimulus at or before this time. Many studies have shown this general pattern of results^{5–9}. Because visual information has just begun to reach the extrastriate visual areas during this time range¹⁰, these results provide strong evidence that attention influences sensory coding, at least under some conditions¹¹.

These ERP results have been interpreted as a sensory 'gain control' mechanism that simply causes larger P1 responses for attended-location stimuli relative to ignored-location stimuli¹². However, this interpretation leads to a quandary: if attention simply increases the gain of the sensory input, it seems that attention would increase the noise as well as the signal, leading to no improvement in the signal-to-noise ratio. As a solution to this problem, Hawkins and his colleagues proposed a

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Box 1. Reaction time for the 21st century



trends in Cognitive Sciences

Fig. 1. Extraction of the ERP waveform from the ongoing EEG. (a) Stimuli (1... N) are presented while the EEG is being recorded, but the specific response to each stimulus is too small to be seen in the much larger EEG. (b) To isolate the ERP from the ongoing EEG, the EEG segments following each stimulus are extracted and averaged together to create the averaged ERP waveform.

In the early years of cognitive psychology, reaction-time measurements were incredibly useful for understanding a broad range of cognitive processes, ranging from perception to memory, language, and motor programming. As we enter the 21st century, the techniques of cognitive neuroscience – especially ERPs and functional neuroimaging techniques – are beginning to serve as high-tech substitutes for reaction-time measurements. There are three main reasons for this. First, and most obviously, they provide a link to the exploding field of neuroscience. Second, and less obviously, they are intrinsically multidimensional measures of processing and are therefore well suited to separately measuring the subcomponents of cognition. For example, a single trial of a typical reaction-time experiment consists of a stimulus followed by a response, with no direct means of observing the processing that occurs between them. In an ERP experiment, in contrast, the stimulus elicits a continuous ERP waveform that can be used to directly observe neural activity that is interposed between the stimulus and the response. Moreover, the distribution of voltage over the scalp can be used to further isolate specific cognitive processes. Functional neuroimaging techniques do not provide a high-resolution measure of processing between a stimulus and a response, but they instead provide a very detailed 3-D map of brain activity in which processes can be isolated spatially. A third valuable aspect of these techniques is that they allow processing to be measured in the absence of overt responses; in attention research, this is particularly important because it is useful to compare the processing of attended and unattended stimuli without requiring subjects to respond to the unattended stimuli (for evidence that requiring subjects to respond to nominally unattended stimuli changes the nature of attentional processing, see Ref. a).

The ERP technique is relatively straightforward. ERPs begin as postsynaptic potentials generated during neurotransmission. These electrical potentials passively travel through the brain and skull to the scalp, where they contribute to the overall electroencephalogram (EEG). The EEG is recorded from a set of electrodes on the surface of the scalp, and time-locked signal-averaging is used to extract the very small ERPs from the much larger EEG. As shown in Fig. 1, the segment of EEG following each stimulus (or each response) is extracted from the EEG, and these segments are then lined up in time and averaged. Any brain activity that is unrelated to the stimulus will average to zero (assuming a large number of trials), and any brain activity that is consistently time-locked to the stimulus will remain in the average. The resulting averaged ERP waveform consists of several positive and negative deflections that are called 'peaks,' 'waves,' or 'components,' and these peaks are typically named with a P or N to indicate positive or negative and a number to indicate the timing of the peak (e.g. 'P1' for the first positive peak or 'P110' to indicate a precise latency of 100 ms). The sequence of components following a stimulus reflects the sequence of neural processes triggered by the stimulus, beginning with early sensory processes and proceeding through decision- and response-related processes. The amplitude and latency of the successive peaks can be used to measure the time course of cognitive processing, and the distribution of voltage over the scalp can be used to estimate the neuroanatomical loci of these processes.

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model in which there are two sources of noise, external stimulus noise and internal neural noise; an attention-related

increase in sensory gain amplifies the stimulus noise but not the neural noise, leading to improved perception¹³.

Box 2. The time course of attention shifting

It is generally accepted that attention can shift from location to location or from object to object, but there is significant controversy over the time course of these shifts, with some investigators arguing that attention can shift approximately every 50 ms (Ref. a) and others arguing that shifts of attention require about 500 ms (Ref. b). These arguments are based on inferences from behavioral data, but it is difficult to directly observe shifts of attention from such data. ERPs, in contrast, can provide an on-line, millisecond-by-millisecond measure of the focus of attention, making it possible to measure the timing of attention shifts somewhat more directly.

One recent ERP study measured the speed of attentional switching between objects during a difficult visual search task (Ref. c). To assess the direction of attention at any given moment, this study examined the N2pc ERP component, which is distinguished by being more negative over the cerebral hemisphere contralateral to the attended object (Ref. d). As attention shifts from the left visual field to the right visual field, this ERP component shifts from the right hemisphere to the left hemisphere, providing a millisecond-by-millisecond measure of the shifting of attention. This study found that, even in a very difficult visual search task, attention can shift serially from object to object approximately every 100 ms.

Another study used ERPs to measure the time course of the shifting of attention following a symbolic attention-directing cue (Ref. e). To measure the direction of attention, a steady-state visual evoked potential (SSVEP) paradigm was used in which task-irrelevant stimuli flickered rapidly at two possible target locations,

with slightly different flicker frequencies at the two locations. Each trial contained a cue stimulus that directed the subjects to attend to one of these two locations in anticipation of a target at the cued location. The task-irrelevant flickering was present in the period between the cue and the target, and the ERP activity elicited by the flickering was used to measure sensory responsiveness at the two locations during this period. The ERP responses corresponding to the two locations were isolated by taking advantage of their slightly different flicker rates. These responses became enhanced 600–800 ms after the onset of the cue, indicating that several hundred milliseconds were required to shift attention and increase sensory responsiveness. This is in marked contrast with the rate of attention switching obtained in the visual search study described above, indicating that the time course of attention may differ greatly depending on the experimental paradigm.

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Lu and Doshier have recently proposed a more detailed version of this model and have provided a novel psychophysical approach to distinguishing between gain control mechanisms and other potential mechanisms of attention¹⁴. In their psychophysical experiments, subjects are presented with stimuli at attended and ignored locations, and the stimuli are embedded in varying levels of visual noise. When the stimulus contains a large amount of noise, accuracy is limited primarily by this stimulus noise, and increasing the sensory gain at the attended location should amplify both the signal and the noise, leading to minimal improvements in perceptual accuracy. In contrast, when the stimulus contains very little noise, accuracy is limited by neural noise rather than by stimulus noise, and increasing the sensory gain at the attended location should amplify the

signal without amplifying the neural noise, leading to substantial improvements in perceptual accuracy. This is the pattern of results that was obtained, which provides psychophysical support for the gain-control interpretation of the ERP findings. However, this does not imply that attention always operates in this manner – as discussed below, attention may operate rather differently in other experimental paradigms.

Neural substrates of early selection

As described in Box 3, it is extremely difficult to localize the neural generator sources of an ERP component. However, significant progress has recently been made in identifying the neural origins of the ERP attention effects, particularly the P1 modulation. First, it has been possible to demonstrate that an earlier ERP component called the C1 wave is generated in striate cortex (area V1; see Box 3)^{15,16} but is not influenced by attention^{17–19}. This finding indicates that attention operates after information has passed through striate cortex. Second, dipole modeling studies of the P1 wave have shown that its distribution over the scalp is consistent with a neural generator source in lateral extrastriate cortex¹⁷. Third, Wijers and his colleagues have shown that both the P1 wave itself and the effect of spatial attention on the P1 are present, although slightly delayed, for stimuli that are presented on an isoluminant background²⁰. Because isoluminant stimuli primarily activate ventral-stream areas, this finding suggests that the P1 attention effect is generated within the ventral pathway. Fourth, studies that have combined ERP recordings with positron emission tomography (PET) have indicated that the P1 wave is associated with activation in the posterior fusiform gyrus^{21,22} and/or dorsal occipital areas²³. Together, these converging

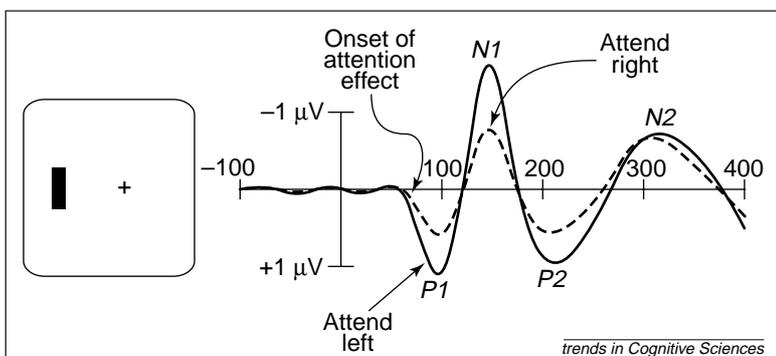


Fig. 1. Paradigm for using ERPs to study attention. Stimulus display (left) and idealized results (right). Subjects fixate a central cross and attend either to the left or right visual field. Stimuli are then presented to the left and right visual fields in a rapid sequence. In this example, the ERP elicited by a left visual field stimulus contains larger P1 and N1 components when the stimulus is attended ('Attend left') than when it is ignored ('Attend right').

Box 3. Localizing ERPs

In most cases, the cortical activation underlying an ERP component can be well approximated by a current dipole (a tiny positive–negative pair of electrical charges). Computing the distribution of voltage that would be observed on the surface for a known dipole location and orientation is called the ‘forward problem’, and it is easy to solve with relatively straightforward mathematics. To localize an ERP generator on the basis of the observed scalp distribution is called the ‘inverse problem,’ and this is much more of a problem. It can be solved if there are only 1–2 dipoles, but it becomes extremely difficult if the number of dipoles is unknown and potentially large (i.e. more than about 4). The reason for this is that the inverse problem is ‘ill-posed,’ meaning that there is no single solution; in fact, there are infinitely many patterns of dipoles that could explain any given distribution of voltage on the scalp.

There are two general ways in which investigators have attempted to circumvent the underdetermined nature of the inverse problem. The first is to use mathematical constraints to reduce the number of possible solutions. For example, on the basis of biophysical principles, it is reasonable to assume that ERPs are generated only in the cortical gray matter and always have an orientation that is perpendicular to the cortical surface. By taking this constraint into account, it is possible to reduce (but not eliminate) the problem of multiple solutions for a given scalp distribution.

A second approach has been to forego mathematical procedures for localization and to instead make specific, testable predictions about the anatomical source of an ERP component on the basis of the known anatomy and physiology of specific brain regions. For example, many previous studies have shown that the topographic mapping of area V1 is organized such that the upper and lower visual fields are mapped onto regions of V1 that are

oriented 180° from each other in the calcarine sulcus; this leads to the prediction that ERP activity generated in area V1 should be opposite in polarity for upper- versus lower-field stimuli. Consistent with this prediction, the C1 wave is negative for upper-field stimuli and positive for lower-field stimuli; combined with its timing (~60–80 ms), this finding provides good evidence that the C1 wave is generated in area V1 (Refs a,b). Other studies have also used previous anatomical and physiological results as the basis for predictions about ERP components (Refs c,d). This approach can also be combined with mathematical modeling and with parallel functional neuroimaging experiments to provide converging evidence about the neural sources of an ERP component (Ref. e). However, there is no approach that is currently guaranteed to correctly localize an ERP generator, and it is necessary to retain a healthy degree of skepticism.

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results indicate that spatial attention modulates sensory processing in extrastriate areas of the ventral visual pathway.

The experimental paradigm shown in Fig. 1 has also been modified for use with single-cell recordings in macaque monkeys²⁴. When both the attended and ignored locations are inside the receptive field of a given neuron in extrastriate area V4, that neuron will fire at a faster rate for attended-location stimuli than for unattended stimuli. Moreover, this attention effect begins at 60 ms poststimulus, which is the onset of stimulus-evoked activity in V4. This provides even stronger and more specific evidence that attention modulates the feedforward transmission of information through the visual system. However, although the single-cell attention effects are somewhat similar to the P1 ERP attention effects, it is not yet clear that the P1 effect arises in area V4. Specifically, the single-cell V4 effects were observed only when both the attended and ignored locations were inside the receptive field of the cell being recorded, whereas P1 effects are typically observed with attended and ignored locations that are too far apart to fall within a single V4 receptive field. In addition, V4 neurons rarely respond to stimuli that fall more than 1° into the ipsilateral visual field, whereas the P1 wave can be observed for ipsilateral stimuli that are very far away from the midline. Thus, it is likely that the P1 effect arises in a somewhat more anterior visual area with larger receptive fields, such as area TE.

Recordings were also obtained from striate cortex in this study, and as in the classic study of Moran and Desimone²⁵,

attention did not reliably influence neural activity in striate cortex. This result is also consistent with the ERP studies described above that found no effect of attention on the striate-cortex C1 wave^{17–19}. In contrast, recent functional magnetic resonance imaging (fMRI) studies have demonstrated increased striate-cortex activity in the hemisphere contralateral to the attended location^{26,27}. There are two likely explanations for this discrepant result. First, it is possible that the tasks used in the fMRI experiments caused attention to operate differently than in the ERP and single-cell experiments. Second, it is possible that the fMRI results do not reflect a modulation of the initial feedforward sensory response, but instead reflect a tonic activation or a feedback signal.

To explore these possibilities, Martinez and her colleagues conducted both ERP and fMRI recordings from a set of subjects who performed the same spatial attention task for both recordings²⁸. Even though the task was held constant across recording techniques, discrepant striate-cortex results were again obtained. That is, the C1 component was not influenced by attention in the ERP recordings, but increased striate activity was observed contralateral to the attended location in the fMRI recordings. Thus, the fMRI effects probably do not reflect a modulation of the initial feedforward sensory response, as indexed by the C1 wave, but rather reflect a tonic increase in neural activity that would not influence the stimulus-triggered ERP waveform or some sort of feedback signal that would influence ERP activity at a later

time. In support of a feedback effect in V1, a recent single-unit study found that attention did not modulate the initial V1 response, but instead influenced the V1 firing rate beginning approximately 200 ms after the initial response²⁹. Thus, an fMRI effect in area V1 does not imply a modulation of the initial sensory response, and the lack of a C1 ERP effect does not imply that V1 activity is not affected by attention; to obtain a complete picture, both types of evidence are needed.

Early selection in other paradigms

The ERP studies described so far have primarily used variants of the experimental paradigm shown in Fig. 1, but this is not a paradigm that has been widely used in traditional cognitive studies of attention. However, similar results have been observed with more common tasks such as spatial cuing^{3,8,30} and visual search^{31,32}.

In spatial cuing studies, a cue stimulus directs the subject to attend to a particular location on each trial, and a target is then presented either at the attended location or at an unattended location. Subjects are required to respond to the target no matter where it appears, and many studies have found that responses are faster and more accurate when the target appears at the cued location (valid trials) than when the target appears at an uncued location (invalid trials)^{33,34}. Similarly, larger sensory-evoked ERP responses are observed for the targets on valid trials than on invalid trials^{3,8,30}, indicating that the enhanced behavioral speed and accuracy are caused, at least in part, by enhanced sensory processing.

When the attention-directing cue is presented at the to-be-attended location (a peripheral cue) rather than at fixation (a central cue), attention may be summoned automatically to the cued location. For example, even if the cue is nonpredictive such that the target is equally likely to appear at the cued location or at an uncued location, peripheral cues will still cause an orienting of attention to the cued location³⁵. If the delay between a nonpredictive peripheral cue and a target is short, responses are faster on valid trials than on invalid trials. However, if the delay between the cue and the target is long, then responses are found to be slower on valid trials than on invalid trials. This phenomenon is called inhibition of return, because it is thought to reflect a bias against revisiting a location that has recently been attended³⁶.

Until recently, it was not known whether the excitatory effect at short delays or the inhibitory effect at long delays are entirely due to changes in motor response thresholds or to changes in sensory responsiveness. However, recent psychophysical studies have shown that both the excitatory and inhibitory effects are at least partially due to changes in perceptual quality, with improved perception on valid trials at short delays and impaired perception on valid trials at long delays^{37,38}. Similarly, ERP studies have shown that the sensory-evoked P1 wave is enhanced on valid trials at short delays and suppressed on valid trials at long delays^{39–41}. Thus, both the excitatory and the inhibitory effects of peripheral cues reflect, at least in part, modulations of sensory processing.

Many recent cognitive studies of attention have also focused on the issue of whether attention is directed to spatial locations *per se* or to the objects at those locations. These studies have indicated that, depending on the conditions, attention can be directed to locations, to objects, or to

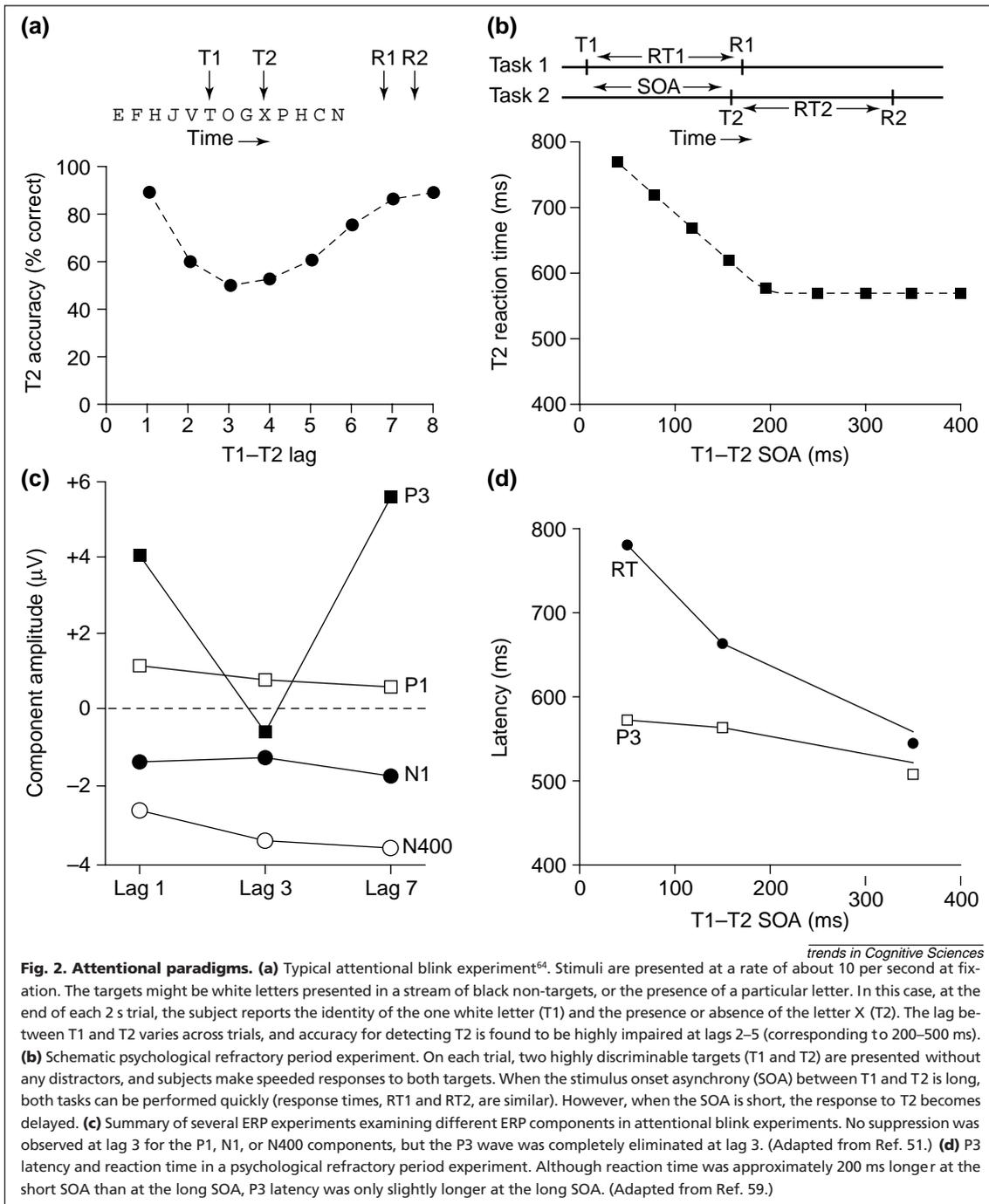
surfaces^{42–45}. Location is represented at the very earliest stages of the visual system, followed at later stages by surfaces and then objects, and it therefore seems plausible that surface- and object-based attention effects might arise at a later stage than spatial attention effects. However, a recent ERP study has unambiguously demonstrated that attending to one of two superimposed surfaces yields the same pattern of enhanced sensory processing that has been observed in studies of spatial attention⁴⁶. The surfaces were defined by patterns of red and green dots that moved in such a manner that they yielded the perception of two transparent surfaces, one red and one green, sliding across each other. Even though the two perceived surfaces were completely overlapping in space, larger P1 waves were observed for a given surface when it was attended than when the other surface was attended. Moreover, when the perception of two separate surfaces was eliminated by using stationary colored dots, the ERP modulations were eliminated; this indicates that ERP modulations observed for the moving stimuli reflected the allocation of attention to the motion-and-color-defined surface rather than to the color alone. Thus, directing attention to a surface (or to a surface-defining motion pattern) appears to influence processing just as early as directing attention to a region of 2D space.

Late selection in dual-task paradigms

Selection occurs at early stages of processing under some conditions, but there are many conditions under which both attended and unattended stimuli are fully identified and attention operates at a post-perceptual stage. Lavie^{47,48} has proposed that selection operates at an early stage only under conditions of high perceptual load. This makes sense: why should attention suppress the perception of an unattended stimulus unless the perceptual system is overloaded? Luck and Hillyard¹¹ have extended this logic beyond the simple early-late dichotomy, proposing that attention can operate in a variety of cognitive subsystems (e.g. early sensory analysis, object recognition, working memory, response selection, etc.) depending on the nature of the stimuli and the task, such that selective processing will occur in a given subsystem when that subsystem suffers from interference due to the competing demands of multiple stimuli or tasks. For example, if the task requires subjects to discriminate the identity of a target embedded in a dense array of similar distractors, then attention will be used to eliminate distractor interference during the perception of the target. In contrast, if subjects are presented with a stream of 30 colored letters at a rate of one letter per 500 ms and are required to report all of the red letters at the end of the trial, then there will be no need to suppress the non-red letters before they are perceived, but it will be necessary to store only the red letters in working memory to avoid exceeding the limited capacity of working memory.

Isolating different cognitive subsystems

Recent ERP studies have supported this conceptualization of attention by showing that attention operates in different cognitive subsystems for different tasks. In particular, the early-selection studies described in the preceding sections have been complemented by ERP studies of two paradigms in which attention would be expected to operate at later stages, namely the



attentional blink paradigm and the psychological refractory period paradigm. These paradigms are very different from those used to demonstrate early selection, but this is sensible given that different paradigms will stress different cognitive subsystems. Ultimately, it would be useful to show that the locus of attention shifts systematically from stage to stage as a result of parametric manipulations in a single experimental paradigm, but such an experiment has not yet been published. However, the existing studies are sufficient to demonstrate that attention operates at different stages under different conditions.

The attentional blink and psychological refractory period paradigms are illustrated in Fig. 2a,b. Both paradigms involve the presentation of two targets – labeled T1 and T2 – on each trial. In the attentional blink paradigm, these targets are embedded in a rapid stream of non-targets, all presented visually at fixation. Each trial typically consists of

about 20 stimuli presented at a rate of about 10 stimuli per second, and the subject is required to report the two targets at the end of the trial. The psychological refractory period is similar, but has two main differences. First, the targets are presented in isolation, without any distractors. Second, subjects are asked to respond to each target as quickly as possible rather than waiting until the end of the trial to respond.

In both paradigms, it is reasonable to suppose that it is difficult to process T2 while T1 is being processed, and this is borne out by the typical results: When the amount of time between T1 and T2 is relatively short, responses to T2 are less accurate (in the attentional blink paradigm) or slower (in the psychological refractory period paradigm). When the amount of time between T1 and T2 is sufficiently long, however, the processing of T1 is largely complete before T2 is presented, leading to a return to baseline

Box 4. Isolating overlapping ERP waveforms

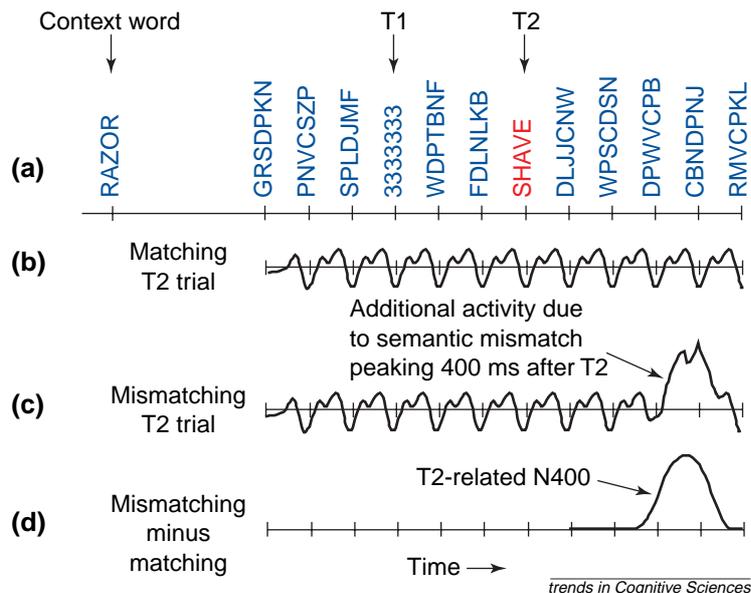


Fig. 1. Overlapping ERP components during presentation of a rapid stream of stimuli. (a) The stimuli on a typical trial, beginning with a 1 s presentation of a context word followed by a stream of stimuli presented at a rate of 10 per second (all stimuli were presented in normal upright orientation at fixation). The targets were a number (T1) followed by a word (T2). At the end of each trial, subjects reported whether T1 was odd or even and whether T2 was semantically related or semantically unrelated to the context word. (b) The overlapping ERP components for a trial in which the T2 word matches the semantic context for that trial. (c) The activity for a semantic mismatch trial, which is equivalent to the matching trials plus the addition of mismatch-related ERP activity following T2. (d) The result of subtracting the matching trials from the mismatching trials, which isolates mismatch-related activity triggered by T2 (primarily the N400 component).

The use of ERP recordings in tasks with rapid streams of stimuli leads to significant technical challenges. Specifically, each item presented in a rapid stream produces an ERP response that lasts for several hundred milliseconds, long past the onset of the next stimulus. Consequently, the ERP elicited by a given item will be overlapped by the ERPs elicited by previous and subsequent items, making it difficult to isolate the ERP for each individual stimulus. Under certain conditions, this overlap can be eliminated mathematically (Ref. a), but in many cases a simple subtraction procedure can be used both to eliminate overlap and to isolate specific ERP components.

The essence of this approach is to manipulate an experimental variable that is known to influence the amplitude of a particular ERP component and to subtract the ERP waveform from trials on which this ERP component is small from the ERP waveform from trials on which it is large. This manipulation is then factorially crossed with the experimental manipulation of interest. For example, we have used this approach in an attentional blink experiment to isolate the N400 elicited by the second target (T2) (Ref. b). As illustrated in Fig. 1, we isolated the T2-related N400 component by subtracting trials on

which T2 was expected to elicit a small N400 from trials on which T2 was expected to elicit a large N400. N400 amplitude was modulated by a manipulation of semantic mismatch: previous studies have shown that words that mismatch the current semantic context generate a large N400 (e.g. the last word in the sentence, 'The monkey eagerly bit into the ripe, yellow telephone'), and words that match the semantic context produce little or no N400 (e.g. the last word in the sentence, 'The monkey eagerly bit into the ripe, yellow banana'). In our experiment, we established a semantic context at the beginning of each trial by presenting a 'context word' that subjects were required to remember. The first target (T1) was a number, and the second (T2) was a word, either semantically related or semantically unrelated to the context word.

As shown in Fig. 1, match and mismatch trials will have largely identical patterns of ERP overlap from the preceding and subse-

quent items in the stream. The only difference between these trials will be that the semantic mismatch trials should elicit a larger N400 than the semantic match trials. The mismatch-minus-match subtraction therefore isolates the T2-related N400 response. The manipulation of semantic mismatch was factorially crossed with a manipulation of T1–T2 lag so that the N400 could be measured before, during, and after the attentional blink period. Similar approaches have been used to isolate the P3 wave (Ref. c) and the lateralized readiness potential (Ref. d) in studies of the psychological refractory period.

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for both reaction time and accuracy. There is one notable exception to the similarity in the results across these paradigms, namely that accuracy in the attentional blink paradigm is not usually impaired when T2 immediately follows T1, whereas reaction times increase monotonically as the T1–T2 delay decreases in the psychological refractory period paradigm (the reasons for this are complex – for a detailed discussion, see Ref. 49).

Although these paradigms are conceptually similar and lead to largely parallel results, they stress different cognitive subsystems. Specifically, the use of speeded responses in the psychological refractory period creates the potential for interference between T1 processing and T2 processing at the stages of response selection and execution, but the stimuli are so simple that there should be little or no interference at earlier stages. In contrast, responses are unspeeded in the attentional

blink paradigm, minimizing response-related interference. Moreover, the stimuli are still fairly simple, and it should be simple to identify every stimulus in the stream even at a rate of 10 stimuli per second⁵⁰. The likely source of interference in this paradigm, then, is the possibility that the representation of one stimulus might be overwritten by the representation of the next stimulus unless the relevant stimuli are stored in a durable form. That is, previous research has indicated that it may take several hundred milliseconds to store a visual stimulus in working memory such that it cannot be overwritten by subsequent stimuli, and attention may be necessary to prevent the stimuli following T1 from interfering with the process of storing T1 in working memory. Consequently, if T2 is presented shortly after T1, it will fail to be stored in working memory and will be unavailable for report at the end of the trial.

ERP support for a multiple subsystems view

This theoretical analysis of the attentional blink and psychological refractory period paradigms has been supported by recent ERP experiments (see Box 4 for a discussion of the methods necessary for isolating ERPs under conditions of rapid stimulation). In the attentional blink paradigm, a variety of ERP components have been compared to determine the first stage at which processing is suppressed during the attentional blink^{51,52}. As illustrated in Fig. 2c, no change in amplitude or latency was observed for the P1, N1, or N400 components, which respectively reflect early sensory analysis⁵³, visual discrimination processes⁵⁴, and semantic analysis⁵⁵. However, the P3 wave – which is thought to reflect the updating of working memory⁵⁶ – was completely suppressed during the attentional blink. This is consistent with the proposal that the attentional blink occurs after perception is complete and reflects a failure to store T2 in working memory while T1 is being analyzed^{57,58}.

A very different pattern of results has been obtained in psychological refractory period experiments. In these experiments⁵⁹, the P3 wave is slightly reduced in amplitude and slightly delayed in latency when the interval between T1 and T2 is shortened, but these effects are not nearly large enough to account for the large delays in reaction time (see Fig. 2d). However, the lateralized readiness potential – which reflects motor preparation⁶⁰ – is significantly delayed when the interval between T1 and T2 is shortened⁶¹. Thus, attention-related modulations appear to occur primarily in response-related processes in the psychological refractory period paradigm, whereas the modulation occurs in working memory in the attentional blink paradigm. That is, response-related processing is modulated by attention in a task that stresses response systems by requiring rapid responses, whereas working memory is modulated by attention in a paradigm that stresses working memory by requiring multiple items to be stored in a short period of time.

Conclusions

Together with the experiments on early selection described at the beginning of this article, these experiments illustrate how ERPs have been used to show that attention can operate in different cognitive subsystems under different conditions. Most existing ERP studies have explored coarsely defined cognitive subsystems (e.g. early versus late), but the excellent temporal

Outstanding questions

- It is now clear that attention can operate in different cognitive subsystems under different conditions, but it is not yet clear whether there are completely different attention mechanisms operating in these different subsystems. Do these different attention effects reflect (a) completely independent attention mechanisms? (b) a collection of loosely interconnected but somewhat independent attention mechanisms? (c) a set of separable attention mechanisms that are centrally controlled? or (d) a unitary attention mechanism that can operate in a variety of subsystems?
- Studies that have combined PET and ERP measures have found an area in the posterior fusiform gyrus that may be the generator source of the P1 spatial attention effect^{21,22}, but another study indicated that the generator might instead be in the dorsal occipital cortex²³. What is the actual generator site, and how can we be sure?
- Both ERP and psychophysical studies have been used to estimate the speed with which attention can shift from one location to the next, but these estimates range from less than 50 ms per shift to over 500 ms per shift (see Box 2). What is responsible for these radically different estimates of the time course of attentional orienting?
- ERP studies suggest that the impairment in T2 processing arises from different stages of processing in the attentional blink and psychological refractory period paradigms^{51,52,59}. However, recent behavioral studies indicate that these impairments reflect a single attentional bottleneck^{62,63}. How can this discrepancy be resolved?

resolution of the ERP technique should make finer distinctions possible, especially when appropriate experimental designs are used to highlight specific cognitive subsystems. In the future, the ability to isolate attentional processes to specific cognitive subsystems should make it possible to replace blanket statements about attention (e.g. 'Attention is not needed for the detection of simple features' or 'Attention is distributed like a gradient') with much more specific statements about how attention operates within a particular subsystem (e.g. 'Attention binds features together to facilitate visual form recognition').

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