Rapid targeting followed by sustained deployment of visual spatial attention

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We investigated preparatory attention processes when a spatial discrimination was required at a cued location, by measuring electroencephalography following a central symbolic cue to deploy spatial attention. Electroencephalography activity in response to the cue revealed three cue-related activations: an early-onset positivity following the P1 at posterior scalp sites contralateral to the cued location, followed by cue-related frontal scalp activity and later-onset sustained activity at posterior scalp sites contralateral to the cued location. The early contralateral positivity may reflect rapid targeting of the cued location. Our results also extend the findings of cue-related frontal activity followed by posterior activity contralateral to the cued location, found with nonspatial feature discriminations, to a task requiring a spatial discrimination. *NeuroReport* 00:000–000 © 2006 Lippincott Williams & Wilkins.

Keywords: attentional deployment, cued attention, event-related potential, sual spatial attention

Introduction

Growing evidence from functional neuroimaging exists that top-down deployment of visual spatial attention involves networks of frontal, parietal and occipital regions that selectively modulate representations of the to-be-attended target's location and features, before target presentation (e.g. [1]). The temporal resolution of electroencephalography (EEG) has revealed multiple processes underlying the deployment of attention. EEG studies of symbolically cued deployment of visual spatial attention have shown that, during the delay between a cue to deploy attention and the arrival of the target, there are at least three temporally distinct cue-related effects. Considered together, these studies report: (i) early-latency (relative to the cue onset) activity at posterior scalp sites contralateral to the cued direction of attention, suggesting rapid deployment processes with visual hemifield specificity [e.g. an 'early directing attention negativity' (EDAN)] [2–7]; (ii) mid-latency cue-specific activity at anterior scalp sites [e.g. an 'anterior directing attention negativity' (ADAN)] [2–10], consistent with a frontal deployment process; (iii) late-latency activity at posterior scalp sites contralateral to the cued location [a 'late directing attention positivity' (LDAP)], suggesting modulation of parietal and/or occipital representations of the cued location [3,7–11]. Most of these studies used centrally presented symbolic cues to a location to prepare participants for subsequent nonspatial feature discrimination tasks, or used simple detection tasks. In the present study, we expand upon the previous work by asking whether these attentional deployment activations are found when participants are cued to a location with 100% validity in preparation for a spatial discrimination.

Methods

Eight (four women) right-handed, paid volunteers, aged 24–30 years, gave written informed consent in accordance with the policies of the Committee on Clinical Investigations at Albert Einstein College of Medicine and the University of California, San Francisco. All participants were neurologically normal and had normal or corrected-to-normal vision.

Design

Cueing experiment

Each trial consisted of a sequential pair of stimuli (S1, S2) presented on a black background. The cue (S1, 60 ms) was a grey directional symbol presented at fixation ('<' or '>', 1.5° high and 1.1° wide, varied randomly from trial to trial), and served to direct the participant's attention to the left or right visual field. The cue was followed 800 ms later by the S2 (60 ms), a white, vertically oriented rectangle (1.4° high, 0.3° wide) presented with equal probability to the left or right of fixation. Left and right locations were marked throughout the trial by a white horizontal bar (0.1° high by 0.3° wide) located at 1.5° above the horizontal meridian and 5.0° from fixation on the left and right. If the S2 occurred on the cued side, participants made a go/no-go spatial discrimination. Participants ignored any S2s that occurred on the noncued side. Thus, the cues were not predictive of S2 location, but were 100% informative with respect to deployment of attention. On 80% of trials, the S2 was a nontarget that occurred just above the location marker (5.0° to the left or right of fixation, 2.0° above the horizontal meridian). On the remaining 20% of trials, the S2 was a target that occurred adjacent to the location marker (5.5° to the left or right of fixation). Participants were instructed to covertly deploy attention to the peripheral marker at the cued location and to use the spatial relationship between the S2 and the marker to discriminate the target and nontarget S2 at the cued location, responding to targets with a button release. Trials with eye movements were detected with DC electrooculogram recordings and removed from further analysis. The intertrial interval was 4.5 s. Participants received 24 blocks of 25 cue-S2 trials within a single session (600 trials).

Control experiment

A control experiment examined whether direction-specific differences in the response to cues could be due to physical differences in the cue symbols ('<' and '>'). Although cues had equal luminance and number of line segments (two) on either side of fixation, they had a small asymmetry in line segment position. An additional group of participants (n=7, four men; age 24–30 years), naive to the attention experiment, passively viewed seven different symbols (<, >, ^, +, [,], ⊥), randomly presented one at a time at fixation with a rate of one per second. Symbols were located 0.3° higher than in the attention experiment owing to equipment changes. No location markers were present in the periphery and no spatial connotation was given to the <, > symbols.

Electroencephalogram recording

EEG was recorded from 12 bilateral scalp locations over frontal, central, parietal, inferior parietal, temporal and occipital regions: F_L, F_R, C_L, C_R, P_L, P_R, IP_L, IP_R, T_L, T_R, O_L, O_R (10–20 nomenclature: F3, F4, C3, C4, P3, P4, T5, T6, O1, O2), referenced to the nose, with a band-pass of 0.1–40 Hz. The inferior parietal sites (IP_L, IP_R, not 10–20 locations) were located half the distance from P3 and P4 to the left and right mastoids, respectively. In the control experiment, temporal electrodes were closer to T3 and T4 than T5 and T6 owing to electrode-cap changes. EEG epochs with electrooculogram artifacts were rejected offline. Event-related potentials (ERPs) were obtained by averaging EEG epochs binned according to the two types of cue (left or right), using a 100 ms precue baseline.

Cueing experiment analyses

To determine whether early effects occurred in this study, we measured the peak amplitude of the P1 (between 100 and 125 ms postcue), the mean amplitude over a short window (25 ms) immediately following the P1 peak (125–150 ms), and the N1 peak amplitude (between 160 and 210 ms postcue). The most prominent activity after the N1 consisted of two long duration positive components. These were evaluated by measuring the mean amplitude in windows around the peaks: 240–340 (POS1: peak at 290) and 340–500 (POS2: peak at 420). Following these components, there was a clear sustained negativity until the S2 (LATENEG: 600–800 ms postcue), and the mean amplitude over the duration of this sustained activity was measured. Amplitude values were computed for each electrode site and entered into a repeated-measures analysis of variance (factors: cue direction; electrode site; hemisphere) with Greenhouse–Geisser correction. If the full model specified a significant three-way interaction (Cue × Hemisphere × Electrode), then post-hoc analyses were conducted to examine significant two-way interactions (Cue × Hemisphere) at each pair of electrodes (see Table 1 for results). If warranted, additional post-hoc analyses were conducted to determine whether a cue-related effect was present within a hemisphere at a particular electrode site.

Control experiment analyses

The amplitude during the P_{ce} time window (125–150 ms) was measured for the '<' and '>' symbols, and paired t-tests were conducted for stimulus type (< vs. >) at every electrode.

Results

Behavioral results indicated that participants were able to use the cue information, performing the task with approximately 85% accuracy. The ERPs to the cue contained a P1, an N1 and two longer duration positivities followed by a slow process lasting until the S2 (see Figs 1 and 3). There was also a positive shoulder following the P1, extending to the N1, at posterior electrode sites contralateral to the cued location that we call the P_{ce} (Postivitiy, contralateral, early). A direction-specific cue effect has been reported as early as 140 ms [2], consequently, to be certain not to miss early effects we analyzed the P1 (100–125 ms), the N1 (160–210 ms) and an intervening window (P_{ce}, 125–150 ms) to determine whether there was significant direction-specific activity between the classic P1 and N1 components. Statistical tests revealed no significant difference in the P1 peak amplitude between cue conditions. The activity immediately following the P1 however, the P_{ce} (Figs 1 and 2), revealed a positivity over posterior scalp contralateral to the to-be-attended location [Cue × Electrode × Hemisphere: $F(5,35)=9.522$, $P<0.007$; significant Cue × Hemisphere post-hoc tests at O, T, P, IP, C sites; see Table 1]. This was a crossover interaction, in which the contralateral vs. ipsilateral positivity, P_{ce}, was seen over left and right scalp sites. Post-hoc tests for left and right hemispheres separately revealed that this cue effect reached significance for right hemisphere sites (at O, T, P, IP, C sites). Figure 2 shows the P_{ce} as a difference wave at each electrode derived by subtracting the cue ERPs for conditions in which the to-be-attended location is ipsilateral to the electrode from the condition in which it is contralateral to the electrode (Contra-Ipsi). This subtracts out activity common to both conditions and reveals lateralized activity specific to the direction of attention. The difference waves in Fig. 2 illustrate the short duration of the P_{ce}, approximately 50 ms. The N1 was also more positive contralateral to the cued location [Cue × Hemisphere × Electrode: $F(5,35)]=4.213$, $P<0.03$; significant Cue × Hemisphere at O, T, P, IP sites], consistent with the P_{ce} extending into the

Table 1 Statistical results for ERP components (columns) for the full model (first row) indicating the F values for the three-way interaction (Cue × Hemisphere × Electrode) with degrees of freedom F(5,35), and for post-hoc tests of the two-way interaction (Cue × Hemisphere) for each electrode pair (labeled by scalp region) with F(1,7) degrees of freedom

Electrode	P1	P_{CE}	N1	POS1	POS2	LATENEG
Cue × Hemisphere × Location						
All	NS	9.52**	4.21*	NS	4.72*	9.46**
Cue × Hemisphere post-hoc comparisons						
Frontal		NS	NS		7.56*	NS
Central		11.62*	NS		NS	11.37*
Parietal		20.66**	19.14**		NS	NS
Inferior parietal		18.70**	5.74*		NS	16.06**
Temporal		23.25**	13.96**		NS	9.43*
Occipital		11.23*	14.77**		NS	24.81**

$^*P<0.05$, $^{**}P<0.01$.

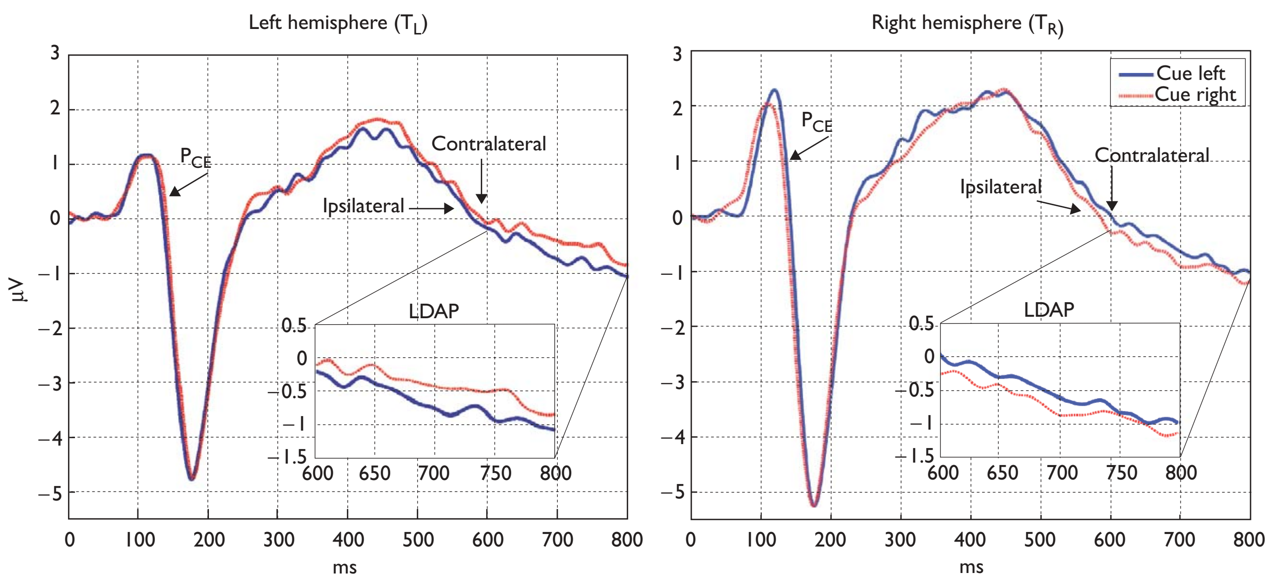

Fig. 1 Early-onset postivitiy, contralateral, early (P_{ce}) and late-onset late directing attention positivity (LDAP) direction-specific activity. Grand-averaged event-related potential (ERPs) to cues (left and right cues in blue and red, respectively) recorded at T_L and T_R (posterior temporal scalp). Cue ERPs for each hemisphere are also labeled according to whether the cued location was contralateral or ipsilateral to the recording hemisphere. The early-onset effect (P_{ce}) occurs just after the P1 peak and continues into the N1. The inset highlights the late-onset effect (600–800 ms), an increased positivity contralateral to the cued direction (LDAP). Time zero is the onset of the cue stimulus, the S2 is presented at 800 ms after cue.

N1 window. This was a crossover interaction; however, post-hoc analyses for cue effects in each hemisphere separately did not reach significance. Results of the control experiment revealed no significant difference in ERPs to the '< vs. '>' symbols during the P_{ce} period (125–150 ms), at any electrode sites, when the symbols were passively viewed among other symbols. This suggests, along with the lack of a directionally specific P1 effect in the attention experiment, that the P_{ce} effect is not due to left/right asymmetries in the physical properties of the cue symbols.

The N1 was followed by a broadly distributed positivity (POS1: peaking at 290 ms) that was larger at right hemisphere IP and T sites [effect of Hemisphere; POS1: F(1,7)=9.81, $P<0.017$; Hemisphere × Electrode: F(5,35)=3.745, $P<0.025$; post-hoc Hemisphere at IP: F(1,7)=15409, $P<0.006$ and T: F(1,7)=20.22, $P<0.003$ sites]. This positivity was followed by a larger and longer duration positive component (POS2: peaking at 420 ms) that was significantly larger over the right hemisphere than the left hemisphere at all sites [POS2: F(1,7)=18.92, $P<0.003$]. This second positive component (peak at 420 ms) was more negative over frontal scalp contralateral to the direction of attention [Cue × Hemisphere × Electrode: F(5,35)=4.716, $P<0.03$; post-hoc Cue × Hemisphere at frontal sites: F(1,7)=7.56, $P<0.03$], consistent with the ADAN reported in the literature (see Fig. 3). Post-hoc analyses revealed that this is not a crossover interaction, and that the cue-related effect occurs only at the right frontal scalp site [F(1,7)=15.203, $P<0.006$].

Later cue-related effects were observed in a sustained and broadly distributed negativity from 600 to 800 ms Similar to the LDAP, the ERP during this period was significantly more positive contralateral to the to-be-attended location [Cue × Hemisphere × Electrode: F(5,35)=9.464, $P<0.001$], see Fig. 1. This modulation was most prominent at sites over extrastriate and inferior parietal areas, although it was

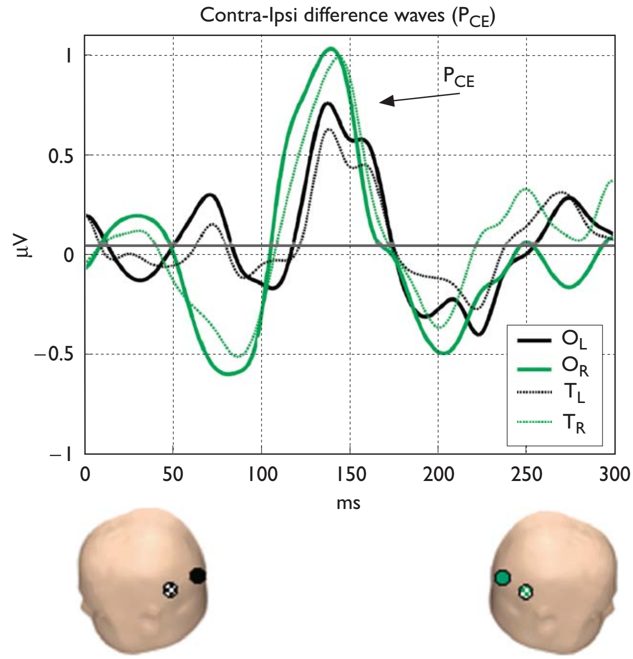

Fig. 2 Postivitiy, contralateral, early (P_{ce}) difference waves. The P_{ce} component is illustrated as a difference wave generated by subtracting the event-related potential to cues that direct attention ipsilateral to the electrode from those directing attention contralateral to the electrode (i.e. Cue right – Cue left at left electrodes; Cue left – Cue right at right electrodes). The P_{ce} is shown for electrodes over extrastriate regions (O_L, O_R, T_L, T_R).

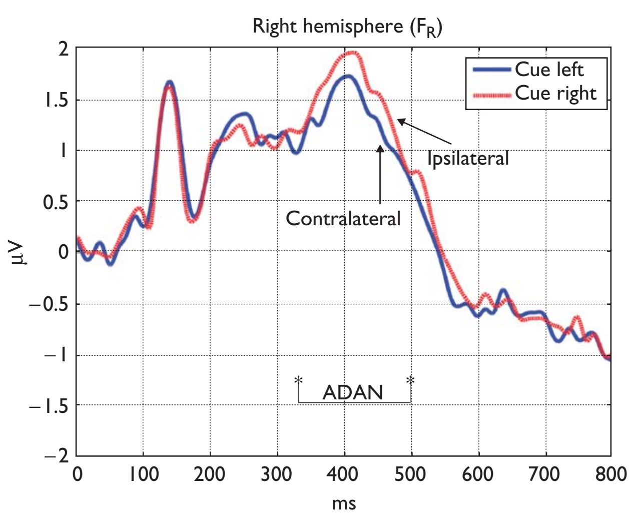

Fig. 3 Frontal cue-related activity anterior directing attention negativity (ADAN): event-related potental (ERPs) to cue left and cue right at the right frontal electrode illustrate the two late positivities (PosI, 240–340 ms and Pos2, 340–500 ms) and the cue-related negative difference occurring at 340–500 ms (or ADAN). Cue ERPs are labeled according to whether the cued location was contralateral or ipsilateral to the right hemisphere.

also significant at the central scalp (post-hoc Cue × Hemisphere at O, T, IP, C, sites, see Table 1). This was a crossover interaction and post-hoc analyses for each hemisphere revealed a trend for a cue effect in both left and right hemispheres for the T sites [T_L: $F(1,7)=5.5$, $P<0.051$; T_R: $F(1,7)=5.283$, $P<0.055$] and a trend for the left hemisphere at the IP site [$F(1,7)=5.308$, $P<0.055$]. One-tailed *t*-tests, for greater positivity to the contralateral cue (as predicted by the LDAP reported in the literature), revealed significant effects at both left and right T sites and the left IP site (T_L, $t=-2.345$; T_R, $t=2.298$; IP_L, $t=-2.304$; all $P<0.03$).

Discussion

In the present study, we cued participants to deploy attention to a specific location in preparation for a spatial discrimination there. We find cue-related activity over three different time periods: an early-onset transient positivity (~150 ms) following the P1 at posterior scalp locations contralateral to the direction of attention (P_{ce}); a mid-onset negativity at the right frontal site (~340–500 ms); and a late-onset sustained positivity (600 ms until S2 occurrence at 800 ms) at posterior electrodes contralateral to the cued direction of attention.

Harter *et al.* [3] and Nobre and colleagues [2,5] have reported an early-onset, direction-specific modulation of activity over posterior cortex contralateral to the direction of attention, occurring around the time of the N1. Although they see an increased negativity contralateral to the attended location (e.g. EDAN), we find an early-onset positivity (P_{ce}). Other studies find a posterior contralateral negativity that occurs roughly 100 ms later than the N1 [4,6]. Although some studies have reported an EDAN, others have not. Hopf and Mangun [8] found early negative-going activity over left parietal regions, rather than over contralateral sensory regions, regardless of cue direction. Velzen and Eimer [9] have claimed that the early contralateral negativity, found with cues comprised of multiple elements, is an N2pc-type component that reflects the selection of relevant elements of the cue stimulus for further processing, rather than brain activity underlying preparatory orienting of attention. Our P_{ce} component is a contralateral positivity, it occurs earlier than a typical N2pc component, and our symbolic cue is not comprised of multiple elements. The control study demonstrated that this early contralateral component was not present when the same symbols ('>', '<') were passively viewed, and thus is unlikely to reflect visual processing of a portion of the symbol itself or physical asymmetries in the symbols. Considering all the above findings together, there appears to be multiple types of early cue-related activities reflecting different brain processes, and the occurrence, timing and polarity of these early activities depends upon the nature of the cue and the task. In the present study, the use of a very simple cue and a peripheral marker may have facilitated the mapping of cue meaning to the cued location making it possible to capture the marker rapidly with respect to the cue onset. In addition, the cued marker serves as the spatial referent for the upcoming spatial discrimination task and this may have encouraged a rapid covert spatial targeting of the marker in response to the cue, producing an early latency modulation of posterior brain regions representing the cued location (the P_{ce}). The P_{ce} may not have been found in other ERP studies that contain spatial markers because the markers were not incorporated into the S2 task.

A cue-related negativity occurred from approximately 340 to 500 ms at the right frontal site, suggesting a frontal control process for covertly shifting spatial attention, consistent with ADAN in the literature (e.g. [5,8,9]), although such lateralized activity can also be interpreted as an effect of opposite polarity at the ipsilateral side (e.g. [10]). This ADAN effect was present only at the right frontal scalp site, similar to the predominance at right frontal sites noted by Nobre *et al*. [5]. The frontal scalp location is consistent with recent source localization reports that the ADAN may originate in frontal cortices [7,10]. The ADAN was followed by a late-onset sustained positivity over contralateral posterior cortex lasting until the S2 (600–800 ms), supporting top-down controlled modulation of parietal and/or sensory representations in advance of the target's occurrence, perhaps to maintain a target template [12,13] or bias one representation over another [14]. The LDAP is found in tasks using simple spatial detection [3] and nonspatial feature discrimination at the cued location [7–10]. The current study extends the LDAP effect to a task requiring a spatial discrimination at the cued location.

Conclusion

The present findings provide further support for multiple attentional deployment processes, reflected in ERP activity differentiated in time and scalp region over the course of the interval between the cue and the target. The design uses a simple cue that enables rapid deployment to the peripheral marker that is relevant to the subsequent target spatial discrimination. We find an early positive component consistent with rapid targeting of the cued spatial location. Our results also extend the findings of cue-related frontal activity followed by posterior activity contralateral to the cued location, found with nonspatial feature discriminations, to a task requiring a spatial discrimination.

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References

1. Corbetta M, Schulman GL. Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 2002; **3**:201–215.
2. Griffin IC, Nobre AC. Orienting attention to locations in internal representations. *J Cogn Neurosci* 2003; **15**:1176–1194.
3. Harter MR, Miller SL, Price NJ, LaLonde ME, Keyes AL. Neural processes involved in directing attention. *J Cogn Neurosci* 1989; **1**:223–237.
4. Mangun GR. Orienting attention in the visual fields: an electrophysiological analysis. In: Heinze HJ, Munte TF, Mangun GR, editors. *Cognitive electrophysiology*. Boston: Birkhauser; 1994. pp. 81–101.
5. Nobre AC, Sebestyen GN, Miniussi C. The dynamics of shifting visuospatial attention revealed by event-related potentials. *Neuropsychologia* 2000; **38**:964–974.
6. Yamaguchi S, Tsuchiya H, Kobayashi S. Electroencephalographic activity associated with shifts of visuospatial attention. *Brain* 1994; **117**:553–562.
7. van der Lubbe RHJ, Neggers SFW, Verleger R, Kenemans JL. Spatiotemporal overlap between brain activation related to saccade preparation and attentional orienting. *Brain Res* 2006; **1072**:133–152.
8. Hopf JM, Mangun GR. Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. *Clin Neurophysiol* 2000; **111**:1241–1257.
9. Van Velzen J, Eimer M. Early posterior ERP components do not reflect the control of attentional shifts toward expected peripheral events. *Psychophysiology* 2003; **40**:827–831.
10. Praamstra P, Boutsen L, Humphreys GW. Frontoparietal control of spatial attention and motor intention in human EEG. *J Neurophysiol* 2005; **94**:764–774.
11. Eimer M, van Velzen J, Driver J. Cross-modal interactions between audition, touch, and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *J Cogn Neurosci* 2002; **14**:254–271.
12. Duncan J, Humphreys GW. Visual search and stimulus similarity. *Psychol Rev* 1989; **96**:433–458.
13. Naatanen R. *Attention and brain function*. Hillsdale, New Jersey: Lawrence Erlbaum; 1992.
14. Desimone R, Duncan J. Neural mechanisms of selective visual attention. *Annu Rev Neurosci* 1995; **18**:193–222.

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