



## BIROn - Birkbeck Institutional Research Online

Eimer, Martin (2014) The neural basis of attentional control in visual search. Trends in Cognitive Sciences 18 (10), pp. 526-535. ISSN 1364-6613.

Downloaded from: <https://eprints.bbk.ac.uk/id/eprint/9940/>

*Usage Guidelines:*

Please refer to usage guidelines at <https://eprints.bbk.ac.uk/policies.html> or alternatively contact [lib-eprints@bbk.ac.uk](mailto:lib-eprints@bbk.ac.uk).

1  
2  
3  
4  
5  
6 **The neural basis of attentional control in visual search**  
7  
8  
9

10  
11  
12  
13  
14  
15  
16  
17  
18 **Martin Eimer**  
19  
20  
21  
22  
23  
24  
25  
26

27  
28 Department of Psychological Sciences, Birkbeck College, University of London,  
29  
30 Malet Street, London WC1E 7HX, UK  
31  
32 Email: [m.eimer@bbk.ac.uk](mailto:m.eimer@bbk.ac.uk)  
33  
34  
35  
36  
37  
38  
39  
40  
41

42 **Words in main text: 2974**  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

## Abstract

How do we localize and identify target objects among distractors in visual scenes? The role of selective attention in visual search has been studied for decades, and the outlines of a general processing model are now beginning to emerge. Attentional processes unfold in real time, and this review describes four temporally and functionally dissociable stages of attention in visual search (preparation, guidance, selection, and identification). Insights from neuroscientific studies of visual attention suggest that our ability to find target objects in visual search is based on processes that operate at each of these four stages in close association with working memory and recurrent feedback mechanisms.

**Keywords:** visual search, selective attention, top-down control, visual cortex, working memory, recurrent feedback

## Introduction

1  
2  
3  
4 In visual environments where multiple objects compete for attention, the challenge  
5 is to find relevant information and to ignore objects and events that are unrelated to  
6 current task goals (Figure 1). Many studies of visual spatial attention have investigated how  
7 prior knowledge about the position of target objects in the visual field facilitates behavioural  
8 performance and neural processing [1,2]. However, the fundamental problem for visual  
9 search is the absence of precise advance information about target locations. In many  
10 laboratory-based visual search tasks, target locations are determined randomly on each trial  
11 and are therefore completely unpredictable. In real-world search, attention may benefit  
12 from contextual spatial information (e.g., kitchen knives are typically found on kitchen  
13 counters), but the exact locations of target objects are still unknown. To understand our  
14 ability to find known target objects at uncertain locations, it is useful to consider how  
15 attentional processes in visual search operate in real time. Based primarily on  
16 neuroscientific studies of attention in the human and monkey brain, this review describes  
17 four successive stages of attentional selectivity in visual search (Figure 2). Each of these  
18 stages performs a specific function, and each is characterized by a particular neural  
19 signature. Within this framework, ‘attention’ is not seen as a single functionally and  
20 anatomically distinct control system, but as emerging from the coordinated operation of a  
21 set of neurocognitive mechanisms in real time.  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41

## Preparation

42  
43  
44  
45  
46 Search starts by deciding which object or feature to look for, and representing this  
47 search goal in memory. William James [3] believed that such preparatory “images in the  
48 mind” are the single most important aspect of selective attention. Representations of  
49 search goals in working memory (attentional templates [4]) can be activated before the  
50 relevant visual scene is physically present, and are assumed to control subsequent stages of  
51 the search process in a goal-directed fashion [5,6].  
52  
53  
54  
55  
56  
57

58 How are James’ “images in the mind” implemented at the neural level? The sensory  
59 recruitment model of working memory (see Box 1) suggests that visual target objects for a  
60  
61  
62  
63  
64  
65

1 search task are represented in posterior visual-perceptual brain regions. There is indeed  
2 evidence that visual cortical areas are activated in a goal-selective fashion during the  
3 preparation phase of visual search. The activity of neurons in inferior temporal cortex (IT)  
4 that selectively respond to a particular object is enhanced in a sustained fashion while  
5 monkeys prepare to find this object in an upcoming search display (Figure 3a), and such  
6 preparatory “baseline shifts” of neural activity level may reflect an activated attentional  
7 template [7]. Similar target-selective preparatory activation patterns have been found in  
8 human event-related brain potential (ERP) and fMRI experiments [8-14]. Some fMRI studies  
9 have demonstrated increased activity in colour- or motion-selective visual areas when  
10 observers prepare for targets defined in these dimensions [9-11]. Others have found more  
11 globally distributed goal-sensitive activation patterns in visual cortex during the preparation  
12 of search for specific target shapes [12], or for target object categories in real-world visual  
13 scenes (e.g., people, cars, houses, faces [13,14]). The exact locus of preparatory activity  
14 patterns within the visual processing hierarchy may depend on the nature of the current  
15 search goal [12], with lower-level visual areas responsible for representing simple target  
16 features [15], and higher-level regions involved in the preparation for more abstractly  
17 defined targets [13].

18 While the existence of goal-selective activity modulations in visual cortex during the  
19 preparation phase is well documented, it remains unclear whether these modulations  
20 causally affect subsequent stages of visual search. The existence of correlations between  
21 the target-selectivity of preparatory pre-stimulus activation patterns in visual cortex and the  
22 quality of subsequent target detection performance [10,12-14,16] suggests that preparatory  
23 modulations of visual activity might indeed act as attentional templates that are causally  
24 involved in the control of visual search. However, this conclusion is by no means universally  
25 accepted [17-19]. When the location of targets is uncertain, target-selective visual activation  
26 patterns elicited during the preparation for visual search should represent search goals in a  
27 position-independent fashion (Box 1). Although spatially global working memory  
28 representations do exist in visual cortex [15], the question whether preparatory goal-  
29 selective patterns of visual activity are generally position-invariant, and whether this is a  
30 necessary requirement for their role as attentional templates still needs to be systematically  
31 addressed.

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

In line with the involvement of prefrontal cortex in visual working memory (Box 1), preparatory activation patterns that are sensitive to current task goals have also been observed in prefrontal areas [13,20,21]. These effects may be linked to top-down aspects of attentional preparation, with prefrontal cortex controlling target-selective preparatory modulations of visual activity, but could also reflect explicit representations of search goals. Because many object representations in prefrontal cortex are position-invariant, they could act as location-independent preparatory attentional templates that control subsequent stages of visual search when no precise spatial information about target locations is available.

## Guidance

While preparation takes place prior to the arrival of visual input, guidance and selection operate once a search display has been encountered. Models of visual search [22-24] assume that information about the presence of task-relevant features is accumulated in parallel (guidance) and is then used to control the allocation of spatial attention to possible target objects (selection). When target locations are uncertain, guidance processes may operate globally across the entire visual field.

A plausible neural basis of spatially global attentional guidance in visual search has been identified in studies of feature-based attention. When monkeys search for target events defined by a particular feature (such as orientation or motion direction), neurons in visual areas V4 or middle temporal (MT) cortex that are selective for this task-relevant feature increase their activity, while neurons with opposite feature preferences are inhibited [25,26]. Critically, these activity modulations are also elicited in response to stimuli at task-irrelevant unattended locations (Figure 3b), suggesting that feature-based attention is a spatially global phenomenon. During search for colour- or shape-defined target objects, V4 neurons that prefer target-defining features increase their activity when a target object is present in their receptive field, even when monkeys fixate elsewhere, fail to detect the target, and shift gaze to another object [27]. Such observations underline the fact that feature-based attention operates in parallel across the visual field, independent of the current focus of spatial attention. Analogous spatially global feature-based attentional

1 modulations of visual activity have been found in human electrophysiological and fMRI  
2 experiments [28-30]. When observers attend to target features in one visual hemifield,  
3 objects in the other irrelevant hemifield elicit enhanced visual responses when their  
4 features match the features that are currently task-relevant.  
5  
6

7  
8 Because feature-based attentional modulations of visual processing operate in a  
9 spatially global fashion, they can provide guidance signals for the subsequent allocation of  
10 spatial attention to candidate target objects. Models of visual attention [18,24] postulate  
11 that during the parallel analysis of visual input, processing is selectively weighted in favor of  
12 target-defining features. The neural mechanisms of feature-based attention can implement  
13 such task-dependent attentional biases in a spatially global fashion across the visual field.  
14 Feature-based attentional guidance is not necessarily limited to simple visual attributes such  
15 as orientation, color, or movement direction, but can also operate in a spatially global  
16 fashion when search goals are more abstractly defined, such as during search for target  
17 objects from a particular target category in real-world visual scenes [31]. If guidance  
18 depends on the mechanisms of feature-based attention, the fact that visual features differ  
19 considerably in their ability to guide spatial attention [32] could be related to systematic  
20 differences in the ability of these features to produce task-dependent spatially global  
21 modulations of visual activity during the guidance phase of visual search.  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34

35 Feature-based attentional guidance mechanisms are likely to be closely linked to the  
36 processes that operate during the preceding preparation stage. If preparatory goal-selective  
37 baseline shifts of visual activity operate in a position-independent fashion, they could be  
38 directly responsible for the emergence of spatially global feature-based attention effects  
39 during the parallel processing of visual input. For example, spatially global working memory  
40 representations of target features [15] may remain active after search display onset,  
41 resulting in feature-selective modulations of sensory responses across the visual field. The  
42 observation that feature-based attention effects can spread to currently empty regions of  
43 visual space [30] suggests that preparation and guidance might interact in this way. In  
44 addition, top-down signals from position-invariant representations of search targets in  
45 prefrontal cortex to visual areas may also play a role in the control of feature-based  
46 attention [33]. Despite such close functional links between preparation and guidance, these  
47 two stages are not only temporally distinct (i.e., one operates before and the other after the  
48 onset of visual stimulation), but are also functionally dissociable. For example, preparation is  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1 not followed by feature-selective attentional guidance processes when search displays  
2 without any target-matching features are encountered. The reverse scenario (guidance  
3 without corresponding preparation) is realized when attention is guided towards salient  
4 visual events irrespective of or even contrary to current selection intentions [34].  
5  
6  
7  
8  
9

## 10 11 **Selection**

12  
13  
14  
15 Feature-based attentional guidance highlights the presence of target-defining  
16 features, and this information can then be employed to select candidate target objects.  
17 Because representations in visual cortex are position-dependent [35], objects compete for  
18 representational space in cortical maps [36]. In this context, 'selection' can be defined as the  
19 emergence of spatially specific biases in favor of one or more objects at particular locations  
20 within these maps. The transition from guidance to selection is therefore marked by the  
21 transition from feature-selective activation patterns that are triggered in a spatially global  
22 fashion across the visual field to spatially specific modulations of neural responses to  
23 potentially task-relevant objects. In contrast to the common assumption that spatial  
24 attention is generally faster than attention for features [37,38], feature-based attention  
25 should precede spatial attention during visual search when the location of target objects is  
26 not known in advance [39].  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38

39 How does information accumulated during the parallel guidance phase control the  
40 subsequent spatial selection of target objects? The biased competition model of visual  
41 attention [5] assumes that feature-selective attentional biases generated at particular levels  
42 of the visual processing hierarchy during the guidance phase trigger competitive advantages  
43 for possible target objects, and these are then propagated in a spatially selective fashion to  
44 lower and higher levels. Other models [18,40] postulate dedicated 'source' areas of  
45 attentional control where task-relevant locations are represented, 'sites' of spatially  
46 selective processing in visual areas, and recurrent pathways (see Box 2) from source to site  
47 regions. In these models, the allocation of spatial attention is controlled by priority maps  
48 [40,41] in posterior parietal cortex [42], the frontal eye fields (FEF) [43], or the thalamus  
49 [18]. Priority maps send recurrent top-down control signals to visual cortex, where they  
50 elicit spatially specific enhancements of visual responses to possible target objects. The  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65



1 observation that electrical stimulation of the FEF triggers activity in spatially corresponding  
2 regions of visual area V4 [44] suggests that these two areas are indeed causally linked. An  
3 important and controversial question is whether recurrent signals from priority maps to  
4 visual areas always address one particular location at a time or whether multiple locations  
5 can be addressed simultaneously. Does object selection in visual search operate serially or  
6 in a parallel fashion (see Box 3)?  
7  
8  
9  
10

11 The spatial selection of candidate target objects is reflected by enhanced neural  
12 responses in ventral visual cortex that start around 150-200 ms post-stimulus [7,45]. In ERP  
13 studies of visual search, target selection is marked by the emergence of the N2pc  
14 component at around 180 ms after search display onset. The N2pc is an enhanced negativity  
15 at posterior electrodes contralateral to candidate target objects in visual search displays  
16 [46,47]. This component is generated during the spatially selective enhancement of target  
17 processing in ventral visual cortex [39], which is controlled by recurrent signals from higher-  
18 level attentional control areas such as FEF [48]. Because it tracks the operation of selective  
19 attention on a millisecond-by-millisecond basis, the N2pc can provide unique insights into  
20 the time course of attentional object selection in visual search (Box 3 and Figure 4).  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34

### 35 **Identification**

36  
37  
38 The emergence of spatially specific modulations of target processing in visual cortex  
39 does not imply that selected objects are instantly recognized. When spatial attention is  
40 employed to track multiple moving objects, access to the features and identity of these  
41 objects is remarkably poor [49], indicating that selection and identification are independent  
42 processes [50]. Many models of visual attention distinguish between a selection stage  
43 where task-relevant objects are individuated in a spatially specific fashion, and a subsequent  
44 identification stage where the features of these objects are integrated and object identity  
45 becomes accessible to awareness and action control [24,51,52]. The independence of  
46 selection and identification is underlined by their sensitivity to different factors. Selection  
47 efficiency is determined by the similarity between targets and competing distractors [4]. In  
48 contrast, the efficiency of identification depends on the complexity of target objects [36,51].  
49 Performance impairments observed in tasks where spatial selection demands are minimal  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1 and several target objects are presented simultaneously or in rapid succession [53-55] also  
2 point towards capacity limitations at an identification stage that follows object selection.  
3

4 Selection and identification are associated with distinct ERP markers in visual search  
5 (Figure 5). The N2pc component reflects target selection, and a later sustained posterior  
6 contralateral negativity is elicited during the subsequent object identification stage [56,57].  
7 This sustained negativity is equivalent to the CDA component observed during the delay  
8 period of working memory tasks [58], and its presence during the identification of target  
9 objects in visual search demonstrates the involvement visual working memory [18,59].  
10 Working memory is required for object identification because spatially specific  
11 enhancements of target processing that emerge during the preceding selection stage  
12 remain transient unless they are sustained by recurrent input from higher-order control  
13 areas to visual cortex [18]. Such sustained feedback loops could represent the neural basis  
14 of working memory maintenance [60]. They may be critical for integrating features into  
15 object files [61], and for matching perceptual representations of selected objects with  
16 stored representations of search targets during the identification stage. Visual areas such as  
17 superior intraparietal sulcus and the lateral occipital complex that are sensitive to the  
18 number of memorized objects and their complexity [62,63] are likely to be involved in the  
19 maintenance of possible target objects in visual search.  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38

### 39 **Concluding comments**

40  
41  
42 Our ability to find task-relevant objects in visual scenes depends on attentional  
43 processes that unfold in real time. In this review, preparation, guidance, selection, and  
44 identification are described as temporally and functionally distinct stages of visual search.  
45 This four-stage model can be useful to interpret psychological and neuroscientific findings  
46 within a general processing framework of visual search, and to clarify the roles of working  
47 memory and recurrent feedback mechanisms at different stages of the search process.  
48  
49  
50  
51  
52  
53

54 This model can only provide a basic outline of the attentional control processes that  
55 are active during visual search in complex real-world scenes, and needs to be qualified in  
56 several important respects. Although Figure 2 may suggest that the four stages are  
57 organized in a strictly sequential fashion, it is possible that at least some of these stages  
58  
59  
60  
61  
62  
63  
64  
65

1 overlap in time. For example, the identification of selected objects may be a relatively slow  
2 process that could operate in parallel with the attentional selection of other candidate  
3 target objects [24]. Identification involves the comparison of visual object representations  
4 with representations of current search goals (see Box 1), which implies that attentional  
5 templates in working memory that are set up during the preparation stage remain active  
6 throughout the search process. Furthermore, when targets are not detected on the basis of  
7 a single guidance/selection/identification cycle, search will become iterative, with each new  
8 iteration of this cycle initiated by a mismatch between selected object representations and  
9 current search goals at the identification stage. Search is likely to be based on complex  
10 interactions between serial and parallel mechanisms, and the simple serial architecture  
11 illustrated in Figure 2 is not intended to be a fully realistic representation of these  
12 mechanisms. However, because visual search unfolds in real time, and because each of the  
13 stages described here depends on the output of operations that take place at preceding  
14 stages, the attentional control processes that contribute to successful search performance  
15 retain important serial characteristics, which were highlighted in this review.

16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29 Another important aspect of visual search that was not discussed here concerns the  
30 role of eye movements. Spatial attention and saccade programming are known to be closely  
31 linked [41,64]. Selection does not only control the access of task-relevant objects to working  
32 memory, but also provides spatial coordinates for upcoming eye movements. Research on  
33 saccades and microsaccades [65-67] has provided important insights into the control of  
34 selective attention during search in real-world visual scenes. For example, semantic and  
35 spatial expectations linked to particular scene contexts strongly constrain which parts of a  
36 scene will be visually examined [65,68], which demonstrates that high-level world  
37 knowledge plays an important role for attentional guidance and selection. The implicit  
38 acquisition of contextual information can guide spatial attention even in simple search  
39 displays [69]. Such observations show that visual search does not always operate in the  
40 complete absence of prior information about likely target locations, and raise important  
41 questions for the control of attentional guidance and selection processes. Instead of  
42 operating in a spatially unconstrained global fashion across the entire visual field, these  
43 processes may sometimes be confined to spatially restricted attentional windows [34] that  
44 are linked to context-dependent expectations about target locations. Furthermore, the  
45 concept of preparatory attentional templates may have to be extended to include not only  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1 representations of target features or objects, but also of scene contexts and likely target  
2 positions.  
3

4           Visual search performance varies greatly across task contexts [70]. It is unlikely that  
5 such differences can all be attributed to one particular stage (such as serial selection [71]).  
6 In this review, search is described as a process that unfolds in real time, and involves  
7 successive attentional mechanisms at multiple stages of processing. The efficiency of visual  
8 search for known targets at uncertain locations is determined by the complex interplay of all  
9 of these mechanisms.  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

**Box 1: The functions of working memory during visual search**

1  
2  
3  
4 Working memory is responsible for the active retention of task-relevant information  
5 that is not currently available to sensory perception. Classic accounts of working memory  
6 [72] postulate specialized stores for different types of information, and a central role of  
7 prefrontal cortex during working memory storage. The sustained activation of prefrontal  
8 neurons during memory maintenance [73,74] is in line with this hypothesis. However, it has  
9 recently become evident that posterior visual areas are also activated when visual  
10 information is memorized [63,75]. In ERP studies, a sustained posterior contralateral delay  
11 activity (CDA) is observed during visual working memory maintenance, and this component  
12 is sensitive to memory load and individual differences in working memory capacity [58,76].  
13 The emerging “sensory recruitment” model of visual working memory claims that brain  
14 areas involved in visual perception are also the primary locus for the short-term storage of  
15 visual information, while prefrontal cortex performs more generic top-down control  
16 functions [77,78].  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28

29 Working memory plays different roles in the preparation and object identification  
30 phases of visual search. During preparation, working memory holds a representation of the  
31 current search goal (attentional template). During the identification stage, representations  
32 of selected objects are maintained in working memory and compared to search goals. These  
33 two functions differ markedly in terms of their capacity. While approximately 3-4 items can  
34 be simultaneously maintained in working memory [79], there is evidence that only a single  
35 attentional template can be active at any given moment [6,80,81]. This discrepancy suggests  
36 qualitative differences between the attentional template and object maintenance functions  
37 of visual working memory. Maintenance is based on spatially selective enhancements of  
38 object representations in visual cortex (“attention directed at internal representations” [82])  
39 that are sustained by recurrent feedback mechanisms [60]. Individual differences in working  
40 memory capacity are therefore closely linked to differences in the ability to select and  
41 maintain multiple spatially specific object representations [83]. In contrast, preparatory  
42 attentional templates should be position-independent, because target locations are  
43 uncertain in visual search, and subsequent feature-based attentional guidance mechanisms  
44 operate in parallel across the visual field. Many object representations in prefrontal cortex  
45 areas are position-invariant, and spatially global representations of memorized visual  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

1 features also exist in visual cortex [15]. If attentional templates are based on position-  
2 invariant or spatially global representations of search targets, the observation that these  
3 templates are strongly capacity-limited suggests that only one position-invariant  
4 representation can be active during the preparation stage of visual search.  
5  
6  
7  
8  
9

## 10 **Box 2: The role of recurrent feedback processes in visual search**

11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

Visual processing does not operate in a strictly hierarchical bottom-up fashion, with lower-level visual areas representing simple features at specific locations projecting to neurons at higher levels that progressively code more complex properties of visual objects in a position-invariant fashion. Such feedforward connections are accompanied by parallel feedback projections from higher to lower levels of the visual processing hierarchy [35]. This recurrent architecture allows top-down control signals to modulate visual processing in a flexible task-dependent fashion [84]. According to the Reverse Hierarchy Theory [85], visual input is transmitted in parallel to a high level of processing where complex visual properties and object categories are represented. Information about the presence of potentially task-relevant objects is then fed back to lower visual areas where a detailed analysis of these objects takes place.

Recurrent feedback plays a central role in the object selection and identification stages of visual search [86,87]. During identification, recurrent feedback loops between higher-level control regions and visual cortex are responsible for the maintenance of spatially selective representations of possible target objects in visual working memory [59,60]. During the preceding selection stage, the initial transient activation of these representations is triggered by recurrent signals from control regions such as the frontal eye fields [43,48] where the locations of task-relevant features are represented in priority maps [41]. The importance of recurrent feedback connections is illustrated by the phenomenon of object substitution masking [88]. Target detection is strongly impaired when targets are immediately replaced by another visual stimulus, and therefore can no longer be addressed by recurrent feedback signals. The existence of fast recurrent pathways from category-selective areas to visual cortex [85] can also explain why category-guided object selection is often remarkably rapid [89].

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

If high-level control regions (such as prefrontal cortex) represent task-relevant information in a position-invariant fashion, how can recurrent signals originating from these regions produce spatially selective enhancements of position-dependent object representations in visual cortex? The existence of parallel and reciprocal feedforward and feedback visual pathways [35,84,85] offers a possible solution to this problem. If only those pathways that were active during the feedforward transmission of task-relevant information to higher areas mediate the flow of recurrent signals to lower areas, information about candidate target objects at particular locations in the visual field can be effectively routed back to spatially corresponding regions of visual cortex [18].

### **Box 3: Serial and parallel object selection in visual search**

The transition from spatially global guidance to spatially focal selection could coincide with the transition from parallel to serial attentional processing in visual search. In line with this assumption, several models of visual search claim that candidate target objects are selected in a strictly serial fashion. According to Feature Integration Theory [22,71], spatial attention is allocated serially to one object at a time, such that the attentional selection of a new object is always preceded by a de-allocation of attention from its previous location. In Guided Search [24], guidance and object identification are modelled as parallel processes, but object selection is described as a serial attentional bottleneck. In contrast to such serial selection accounts, other models of visual attention assume that object selection can operate in parallel at multiple locations in the visual field [5,18]. Along similar lines, the ability to track multiple moving objects has been explained by assuming that spatial attention can be allocated independently and in parallel to different objects in the visual field [90], which has been supported by ERP studies of multiple object tracking [91,92].

Although serial and parallel selection scenarios are often regarded as mutually exclusive accounts of visual search, it is possible that these two types of attentional selection are employed in different task contexts. This is illustrated by two ERP studies [93,94] that both used the N2pc component to distinguish serial and parallel selection mechanisms in visual search (Figure 4). Woodman and Luck [93] obtained evidence that

1 targets are selected in a serial fashion when observers search for difficult-to-discriminate  
2 target objects in crowded visual search displays. In contrast, Eimer and Grubert [94] found  
3 that multiple targets are selected in a parallel and independent fashion when the target  
4 identification task (letter/digit discrimination) is highly practiced and search displays contain  
5 few competing distractor items. The fact that these two N2pc studies draw opposite  
6 conclusions about the serial versus parallel nature of visual search suggests a more  
7 ecumenical view of attentional object selection. Parallel and serial selection could both be  
8 available options in visual search, with the choice between these selection strategies  
9 determined by the nature of a particular search task. Serial selection may be the preferred  
10 option when a task imposes high demands on object selection and identification  
11 mechanisms, while a parallel strategy is chosen under conditions where selection and  
12 identification requirements are less challenging.  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65



## Outstanding Questions

- How do goal-selective modulations of neural activity during the preparation stage affect attentional processes at subsequent stages of visual search? Do preparatory 'baseline shifts' play a causal role for the selection and identification of search targets?
- How are spatially global feature-based attention effects that emerge during the guidance stage of visual search set up and controlled?
- Are both serial and parallel selection strategies available for the control of visual search? Which factors determine whether the spatial selection of candidate target objects operates in a serial or parallel fashion?
- Do preparation, guidance, selection, and identification operate in a sequential fashion during visual search, or can some of these stages be activated in parallel?
- Can other processing bottlenecks identified in the attention literature be linked to the current four-stage model of selective attention? For example, are dual-task interference effects in psychological refractory period (PRP) experiments which have been attributed to capacity limitations at a central response selection stage [95] generated during the object identification stage described here?

## Glossary

1  
2  
3  
4 **Attentional template:** Working memory representation of a current search goal that is  
5 activated prior to search, and is assumed to control subsequent attentional guidance and  
6 selection processes.  
7  
8

9  
10  
11 **Baseline shift:** Sustained increase in the baseline activity of neurons that are selective for a  
12 task-relevant feature or object during the preparation phase of visual search.  
13  
14

15  
16  
17 **Feature-based attention:** Allocation of selective attention to specific task-relevant visual  
18 features. During the guidance phase of visual search, feature-based attention is reflected by  
19 a task-dependent modulation of feature-selective activity in visual cortex that operates in a  
20 spatially global fashion across the visual field.  
21  
22  
23

24  
25  
26  
27 **Position-dependent representation:** Representation of visual information within a spatial  
28 coordinate frame that is defined by the position of a visual stimulus on the retina  
29 (retinotopic representation) or in the external world (spatiotopic representation).  
30  
31

32  
33  
34  
35 **Position-invariant representation:** Visual representation that is not sensitive to the position  
36 of the represented stimulus on the retina or in the external world.  
37  
38

39  
40  
41 **Spatial attention:** Allocation of selective attention to specific locations within the visual  
42 field. During the selection phase of visual search, spatial attention is reflected by spatially  
43 specific processing enhancements for candidate target objects at particular locations.  
44  
45  
46

## Acknowledgements

47  
48  
49  
50  
51  
52  
53  
54  
55  
56 This work was supported by the Economic and Social Research Council (ESRC), UK. Thanks to Anna  
57 Grubert and John Towler for comments, and to Joanna Parketny for creating Figure 1.  
58  
59  
60  
61  
62  
63  
64  
65

## References

1. Posner, M. I. et al. (1980). Attention and the detection of signals. *J Exp Psychol Gen*, 109, 160-174.
2. Moran, J. and Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, 229, 782-784.
3. James, W. (1890). *The Principles of Psychology*. Harvard University Press.
4. Duncan, J. and Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychol Rev*, 96, 433.
5. Desimone, R. and Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annu Rev Neurosci*, 18, 193-222.
6. Olivers, C. N. L. et al. (2011). Different states in visual working memory: when it guides attention and when it does not. *Trends Cogn Sci*, 15, 327-334.
7. Chelazzi, L. et al. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *J Neurophysiol*, 80, 2918–2940.
8. Carlisle, N. B. et al. (2011). Attentional templates in visual working memory *J Neurosci*, 31, 9315-9322.
9. Chawla, D. et al. (1999). The physiological basis of attentional modulation in extrastriate visual areas. *Nat Neurosci*, 2, 671–676.
10. Giesbrecht, B. et al. (2006). Pre-target activity in visual cortex predicts behavioral performance on spatial and feature attention tasks. *Brain Res*, 1080, 63–72.
11. Shibata, K. et al. (2008) The effects of feature attention on prestimulus cortical activity in the human visual system. *Cereb Cortex*, 18, 1664–1675.
12. Stokes, M. et al. (2009). Shape-specific preparatory activity mediates attention to targets in human visual cortex. *Proc Natl Acad Sci U S A*, 106, 19569–19574.
13. Peelen, M.V. and Kastner, S. (2011). A neural basis for real-world visual search in human occipitotemporal cortex. *Proc Natl Acad Sci U S A*, 108, 12125–12130.
14. Soon, C. S. et al. (2013). Preparatory patterns of neural activity predict visual category search speed. *NeuroImage*, 66, 215-222.
15. Ester, E. F. et al. (2009). Spatially global representations in human primary visual cortex during working memory maintenance. *J Neurosci*, 29, 15258-15265.
16. Puri, A.M. et al. (2009). Category expectation modulates baseline and stimulus-evoked activity in human inferotemporal cortex. *Brain Res*, 1301, 89–99.
17. Fannon, S. P. et al. (2007). Baseline shifts do not predict attentional modulation of target processing during feature-based visual attention. *Front Hum Neurosci*, 2, 7.
18. Bundesen, C. et al. (2005). A neural theory of visual attention: bridging cognition and neurophysiology. *Psychol Rev*, 112, 291.
19. McMains, S. A. et al. (2007). Mechanisms of feature- and space-based attention: response modulation and baseline increases. *J Neurophysiol*, 98, 2110.
20. Warden, M. R. and Miller, E. K. (2010). Task-dependent changes in short-term memory in the prefrontal cortex. *J Neurosci*, 30, 15801-15810.
21. Stokes, M. G. et al. (2013). Dynamic coding for cognitive control in prefrontal cortex. *Neuron*, 78, 364-375.
22. Treisman, A. and Sato, S. (1990). Conjunction search revisited. *J Exp Psychol Hum Percept Perform*, 16, 459.
23. Wolfe, J.M. (1994). Guided Search 2.0: A revised model of visual search. *Psychon B Rev*, 1, 202–238.

- 1 24. Wolfe, J.M. (2007). Guided Search 4.0: Current Progress with a model of visual  
2 search. In W. Gray (Ed.), *Integrated Models of Cognitive Systems* (pp. 99-119). New  
3 York: Oxford.
- 4 25. Martinez-Trujillo, J. C. and Treue, S. (2004). Feature-based attention increases the  
5 selectivity of population responses in primate visual cortex. *Curr Biol*, *14*, 744–751.
- 6 26. Cohen, M. R. and Maunsell, J. H. (2011). Using neuronal populations to study the  
7 mechanisms underlying spatial and feature attention. *Neuron*, *70*, 1192-1204.
- 8 27. Bichot, N. P. (2005). Parallel and serial neural mechanisms for visual search in  
9 macaque area V4. *Science*, *308*, 529–534.
- 10 28. Zhang, W. and Luck, S. J. (2009). Feature-based attention modulates feedforward  
11 visual processing. *Nat Neurosci*, *12*, 24-25.
- 12 29. Saenz, M. et al. (2002). Global effects of feature-based attention in human visual  
13 cortex. *Nat Neurosci*, *5*, 631–632.
- 14 30. Serences, J. T. and Boynton, G. M. (2007). Feature-based attentional modulations in  
15 the absence of direct visual stimulation. *Neuron*, *55*, 301–312.
- 16 31. Peelen, M. V. et al. (2009). Neural mechanisms of rapid natural scene categorization  
17 in human visual cortex. *Nature*, *460*, 94-97.
- 18 32. Wolfe, J. M. and Horowitz, T. S. (2004). What attributes guide the deployment of  
19 visual attention and how do they do it? *Nat Rev Neurosci*, *5*, 495-501.
- 20 33. Maunsell, J. H. and Treue, S. (2006). Feature-based attention in visual cortex. *Trends*  
21 *Neurosci*, *29*, 317-322.
- 22 34. Theeuwes, J. (2010). Top–down and bottom–up control of visual selection. *Acta*  
23 *Psychol*, *135*, 77-99.
- 24 35. Kravitz, D. J. et al. (2013). The ventral visual pathway: an expanded neural  
25 framework for the processing of object quality. *Trends Cogn Sci*, *17*, 26-49.
- 26 36. Franconeri, S. L. et al. (2013). Flexible cognitive resources: competitive content maps  
27 for attention and memory. *Trends Cogn Sci*, *17*, 134-141.
- 28 37. Anllo-Vento, L. and Hillyard, S. A. (1996). Selective attention to the color and  
29 direction of moving stimuli: electrophysiological correlates of hierarchical feature  
30 selection. *Perc Psychophys*, *58*, 191-206.
- 31 38. Liu, T. et al. (2007). Comparing the time course and efficacy of spatial and feature-  
32 based attention. *Vision Res*, *47*, 108-113.
- 33 39. Hopf, J. M. et al. (2004). Attention to features precedes attention to locations in  
34 visual search: Evidence from electromagnetic brain responses in humans. *J Neurosci*,  
35 *24*, 1822–1832.
- 36 40. Itti, L. and Koch, C. (2001). Computational modelling of visual attention. *Nature Rev*  
37 *Neurosci*, *2*, 194-203.
- 38 41. Fecteau, J. H. and Munoz, D. P. (2006). Saliency, relevance, and firing: a priority map  
39 for target selection. *Trends Cogn Sci*, *10*, 382-390.
- 40 42. Gottlieb, J. P. et al. (1998). The representation of visual saliency in monkey parietal  
41 cortex. *Nature*, *391*, 481-484.
- 42 43. Schall, J. D. (2004). On the role of frontal eye field in guiding attention and saccades.  
43 *Vision Res*, *44*, 1453-1467.
- 44 44. Moore, T. and Armstrong, K. M. (2003). Selective gating of visual signals by  
45 microstimulation of frontal cortex. *Nature*, *421*, 370-373.
- 46 45. Chelazzi, L. et al. (2001). Responses of neurons in macaque area V4 during memory-  
47 guided visual search. *Cereb Cortex*, *11*, 761-772.

- 1 46. Luck, S. J. and Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence  
2 from human electrophysiology. *J Exp Psychol Hum Percept Perform*, 20, 1000–1014.
- 3 47. Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity.  
4 *Electroen Clin Neuro*, 99, 225–234.
- 5 48. Cohen, J. Y. et al. (2009). On the origin of event-related potentials indexing covert  
6 attentional selection during visual search. *J Neurophysiol*, 102, 2375.
- 7 49. Horowitz, T. S. et al. (2007). Tracking unique objects. *Percept Psychophys*, 69, 172-  
8 184.
- 9 50. Ghorashi, S. et al. (2010). Spatial selection and target identification are separable  
10 processes in visual search. *J Vis*, 10, 7.
- 11 51. Xu, Y. and Chun, M. M. (2009). Selecting and perceiving multiple visual objects.  
12 *Trends Cogn Sci*, 13, 167-174.
- 13 52. Huang, L. and Pashler, H. (2007). A Boolean map theory of visual attention. *Psychol*  
14 *Rev*, 114, 599.
- 15 53. Duncan, J. (1980). The locus of interference in the perception of simultaneous  
16 stimuli. *Psychol Rev*, 87, 272.
- 17 54. Raymond, J. E. et al. (1992). Temporary suppression of visual processing in an RSVP  
18 task: An attentional blink? *J Exp Psychol Hum Percept Perform*, 18, 849.
- 19 55. Duncan, J. et al. (1994). Direct measurement of attentional dwell time in human  
20 vision. *Nature*, 369, 313-315.
- 21 56. Mazza, V. et al. (2007). Attentional selection and identification of visual objects are  
22 reflected by distinct electrophysiological responses. *Exp Brain Res*, 181, 531–536.
- 23 57. Jolicœur, P. et al. (2008). Dissociation of the N2pc and sustained posterior  
24 contralateral negativity in a choice response task. *Brain Res*, 1215, 160-172.
- 25 58. Vogel, E. K. and Machizawa, M. G. (2004). Neural activity predicts individual  
26 differences in visual working memory capacity. *Nature*, 428, 748-751.
- 27 59. Chun, M. M. and Johnson, M. K. (2011). Memory: Enduring traces of perceptual and  
28 reflective attention. *Neuron*, 72, 520-535.
- 29 60. Luck, S. J. and Vogel, E. K. (2013). Visual working memory capacity: from  
30 psychophysics and neurobiology to individual differences. *Trends Cogn Sci*, 17, 391-  
31 400.
- 32 61. Kahneman, D. et al. (1992). The reviewing of object files: Object-specific integration  
33 of information. *Cogn Psychol*, 24, 175-219.
- 34 62. Todd, J. J. and Marois, R. (2004). Capacity limit of visual short-term memory in  
35 human posterior parietal cortex. *Nature*, 428, 751-754.
- 36 63. Xu, Y. and Chun, M. M. (2006). Dissociable neural mechanisms supporting visual  
37 short-term memory for objects. *Nature*, 440, 91-95.
- 38 64. Krauzlis, R. J. et al. (2013). Superior colliculus and visual spatial attention. *Ann Rev*  
39 *Neurosci*, 36
- 40 65. Henderson, J. M. (2003). Human gaze control during real-world scene perception.  
41 *Trends Cogn Sci*, 7, 498-504.
- 42 66. Rayner, K. (2009). Eye movements and attention in reading, scene perception, and  
43 visual search. *Q J Exp Psychol*, 62, 1457-1506.
- 44 67. Martinez-Conde, S. et al. (2013). The impact of microsaccades on vision: towards a  
45 unified theory of saccadic function. *Nat Rev Neurosci*, 14, 83-96.
- 46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1 68. Hollingworth, A. (2009). Two forms of scene memory guide visual search: Memory  
2 for scene context and memory for the binding of target object to scene location. *Vis*  
3 *Cogn*, 17, 273-291.
- 4 69. Chun, M. M. (2000). Contextual cueing of visual attention. *Trends Cogn Sci*, 4, 170-  
5 178.
- 6 70. Wolfe, J. M. (1998). What can 1 million trials tell us about visual search? *Psychol Sci*,  
7 9, 33-39.
- 8 71. Treisman, A. and Gelade, G. (1980). A feature-integration theory of attention.  
9 *Cognitive Psychol*, 12, 97-136.
- 10 72. Baddeley, A. (2012). Working memory: theories, models, and controversies. *Ann Rev*  
11 *Psychol*, 63, 1-29.
- 12 73. Fuster, J. M. and Alexander, G. E. (1971). Neuron activity related to short-term  
13 memory. *Science*, 173, 652-654.
- 14 74. Curtis, C. E. and D'Esposito, M. (2003). Persistent activity in the prefrontal cortex  
15 during working memory. *Trends Cogn Sci*, 7, 415-423.
- 16 75. Harrison, S. A. and Tong, F. (2009). Decoding reveals the contents of visual working  
17 memory in early visual areas. *Nature*, 458, 632-635.
- 18 76. Ikkai, A. et al. (2010). Contralateral delay activity provides a neural measure of the  
19 number of representations in visual working memory. *J Neurophysiol*, 103, 1963.
- 20 77. Postle, B. R. (2006). Working memory as an emergent property of the mind and  
21 brain. *Neuroscience*, 139, 23-38.
- 22 78. D'Esposito, M. (2007). From cognitive to neural models of working memory. *Philos T*  
23 *Roy Soc B*, 362, 761-772.
- 24 79. Cowan, N. (2001). The magical number four in short-term memory: A  
25 reconsideration of mental storage capacity. *Behav Brain Sci*, 24, 87-114.
- 26 80. Houtkamp, R. and Roelfsema, P. R. (2009). Matching of visual input to only one item  
27 at any one time. *Psychol Res*, 73, 317-326.
- 28 81. Lewis-Peacock, J. A. et al. (2012). Neural evidence for a distinction between short-  
29 term memory and the focus of attention. *J Cogn Neurosci*, 24, 61-79.
- 30 82. Chun, M. M. et al. (2011). A taxonomy of external and internal attention. *Ann Rev*  
31 *Psychol*, 62, 73-101.
- 32 83. Anderson, D. E. et al. (2013). A common discrete resource for visual working memory  
33 and visual search. *Psychol Sci*, 24, 929-938.
- 34 84. Gilbert, C. D. and Li, W. (2013). Top-down influences on visual processing. *Nat Rev*  
35 *Neurosci*, 14, 350-363.
- 36 85. Hochstein, S. and Ahissar, M. (2002). View from the top: Hierarchies and reverse  
37 hierarchies in the visual system. *Neuron*, 36, 791-804.
- 38 86. Di Lollo, V. et al. (2001). The preattentive emperor has no clothes: a dynamic  
39 redressing. *J Exp Psychol Gen*, 130, 479.
- 40 87. Hamker, F. H. (2005). The reentry hypothesis: the putative interaction of the frontal  
41 eye field, ventrolateral prefrontal cortex, and areas V4, IT for attention and eye  
42 movement. *Cereb Cortex*, 15, 431-447.
- 43 88. Enns, J. T. and Di Lollo, V. (2000). What's new in visual masking? *Trends Cogn Sci*, 4,  
44 345-352.
- 45 89. Nako, R. et al. (2014). Rapid guidance of visual search by object categories. *J Exp*  
46 *Psychol Hum Percept Perform*, 40, 50-60.
- 47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

- 1 90. Cavanagh, P. and Alvarez, G. A. (2005). Tracking multiple targets with multifocal  
2 attention. *Trends Cogn Sci*, 9, 349-354.
- 3 91. Drew, T. and Vogel, E. K. (2008). Neural measures of individual differences in  
4 selecting and tracking multiple moving objects. *J Neurosci*, 28, 4183-4191.
- 5 92. Drew, T. et al. (2009). Attentional enhancement during multiple-object tracking.  
6 *Psychon B Rev*, 16, 411-417.
- 7 93. Woodman, G. F. and Luck, S. J. (2003). Serial deployment of attention during visual  
8 search. *J Exp Psychol Hum Percept Perform*, 29, 121-138.
- 9 94. Eimer, M. and Grubert, A. (2014). Spatial attention can be allocated rapidly and in  
10 parallel to new visual objects. *Curr Biol*, 24, 193-198.
- 11 95. Pashler, H. (1994). Dual-task interference in simple tasks: Data and theory. *Psychol*  
12 *Bull*, 16, 220-244.
- 13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

## Figure Legends

**Figure 1.** Finding target objects in crowded visual environments is a complex achievement. When looking for directions to the Central Line in a busy London Underground station, attention has to be allocated to goal-relevant stimuli (such as the distinctive red color code of the Central line, or the letter string “Central”), while other visual signals have to be ignored.

**Figure 2.** A four-stage model of selective attention in visual search. Preparation, guidance, selection, and identification represent four successive stages of attentional processing. Each of these stages performs a specific cognitive function (red boxes), and each stage is characterized by a particular set of processes at the neural level (blue boxes).

**Figure 3.** Neural correlates of preparation (a) and guidance (b) during visual search. **(a):** Stimulus setup used by Chelazzi et al. [7] during a memory-guided visual search task (top panel), and neural responses recorded in monkey IT cortex during the preparation phase (bottom panel). Monkeys remembered a target object presented at the start of each trial during a delay period, and moved their eyes to the location of this target in the subsequent search display. When the target object was an effective stimulus for a particular IT neuron, an initial transient sensory response was followed by a sustained increase (baseline shift) of neuronal activity throughout the preparation period. Reproduced with permission from [7]. **(b):** Top panel: Stimulus setup used by Martinez-Trujillo and Treue [25]. Monkeys attended to the direction of moving dots in one visual hemifield and ignored another set of dots in the opposite hemifield that moved in the same direction (“attend to direction”). In a baseline condition, they attended to the central fixation spot and ignored both dot arrays (“attend to fix spot”). Bottom panel: Response of a MT neuron with a receptive field on the unattended dot array. Attention to a specific movement direction in the opposite visual field increased the neural response to the unattended movement when it matched the preferred



1  
2 movement of this neuron, while attention to the opposite (“null”) direction produced  
3 inhibition. Reproduced from [25], as printed in [33].  
4  
5  
6

7 **Figure 4.** Electrophysiological evidence for serial and parallel object selection in visual  
8 search. **(a):** Top panel: Woodman and Luck [93] instructed participants to search for targets  
9 defined by a particular colour (e.g., red) and shape (gap at the top). Each search array  
10 contained two target-colour objects. One of these possible targets appeared on the vertical  
11 meridian and the other on the horizontal meridian, either near or far from fixation. Because  
12 the N2pc is a contralateral ERP component, it is not triggered by possible targets on the  
13 vertical midline, and therefore provides a pure measure of the attentional selection of the  
14 other (horizontal) target. Bottom panel: The N2pc measured at lateral posterior electrodes  
15 to near possible targets on the horizontal midline emerged 200 ms after stimulus onset, and  
16 preceded the N2pc to far possible targets by 150 ms. There was no temporal overlap  
17 between these two N2pc components, indicating that spatial attention was allocated serially  
18 first the near and then to the far target-colour object. Reproduced with permission from  
19 [93]. **(b):** Top panel: In the Eimer and Grubert study [94], two search displays that contained  
20 a colour-defined (red) target and a distractor on opposite sides were presented in rapid  
21 succession with a stimulus onset asynchrony (SOA) of 100 ms or 10 ms. One display  
22 contained a horizontal target, and the other a target on the vertical midline. Bottom panel:  
23 ERPs at lateral posterior electrodes contralateral and ipsilateral to the horizontal target, and  
24 N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs.  
25 When the SOA between the two targets was 100 ms, the N2pc to a horizontal target in the  
26 second array (H2) emerged 100 ms after the N2pc to a horizontal target in the first array  
27 (H1). When the SOA was reduced to 10 ms, these two N2pc components were triggered  
28 within 10 ms of each other, and overlapped in time. These results show that two target  
29 objects can be selected in parallel, with each selection process following its own  
30 independent time course. Reproduced with permission from [94].  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56

57 **Figure 5.** Electrophysiological correlates of successive selection and identification  
58 stages in visual search. In the study by Mazza et al. [56], search displays containing a colour  
59  
60  
61  
62  
63  
64  
65

1 singleton diamond among uniformly coloured distractors were presented for 150 ms (top  
2 panel). Participants either had to report the location of this singleton (localisation task) or its  
3 detailed shape (cut on the left or right side; discrimination task). ERP waveforms measured  
4 at posterior electrodes contralateral and ipsilateral to the target and corresponding  
5 contralateral-ipsilateral N2pc difference waveforms (bottom panels) demonstrate that N2pc  
6 components (reflecting target selection) were identical in both tasks. In contrast, the  
7 subsequent sustained posterior contralateral negativity (SPCN) that is generated during the  
8 identification stage when selected objects are maintained in working memory [58] was  
9 reliably triggered only in the shape discrimination task, demonstrating that selection and  
10 identification are separable stages of visual search. Data from [56], reproduced in a different  
11 format.  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60  
61  
62  
63  
64  
65

Figure 1



Figure 2

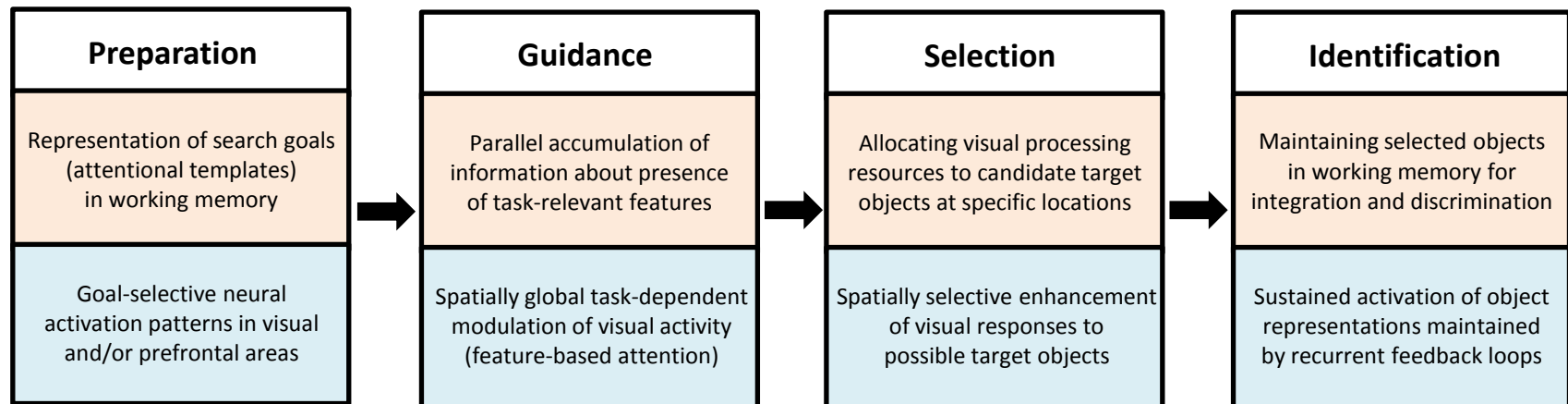
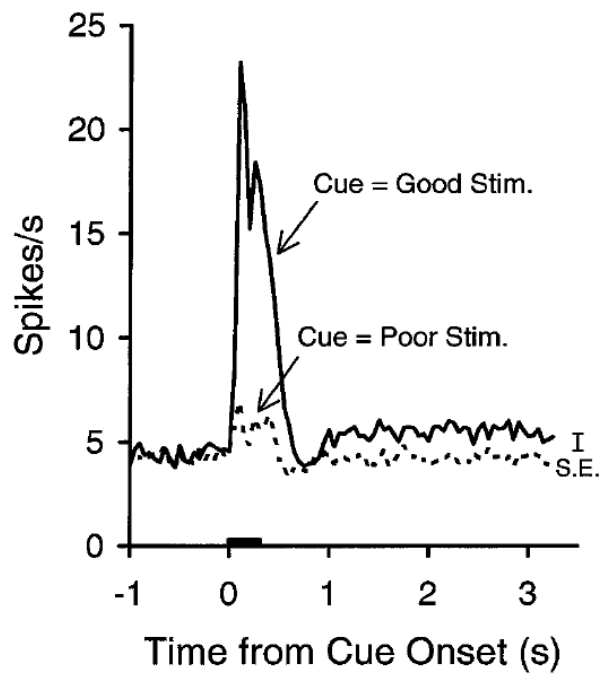
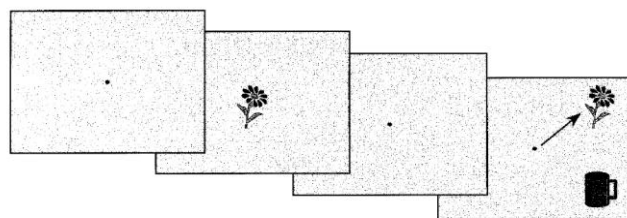


Figure 3

(a)



(b)

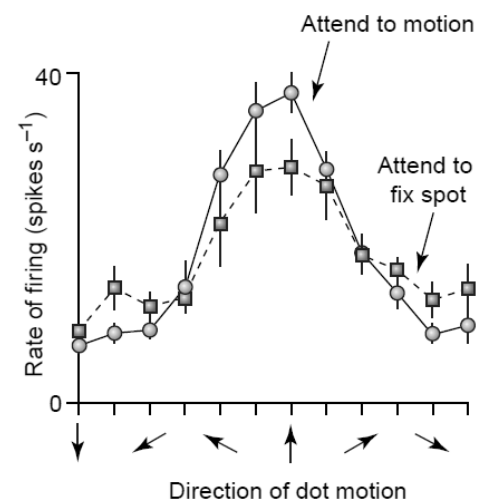
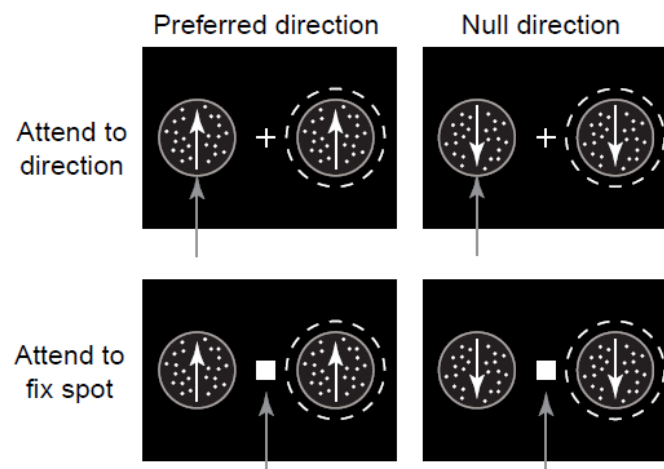
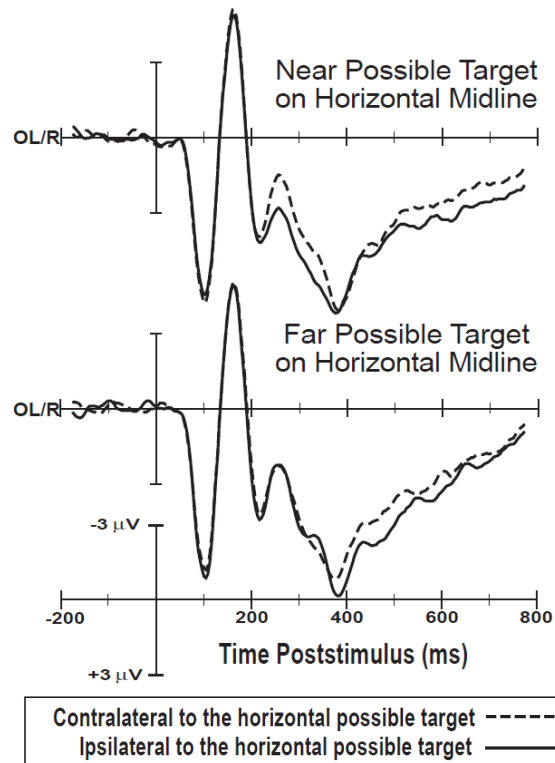
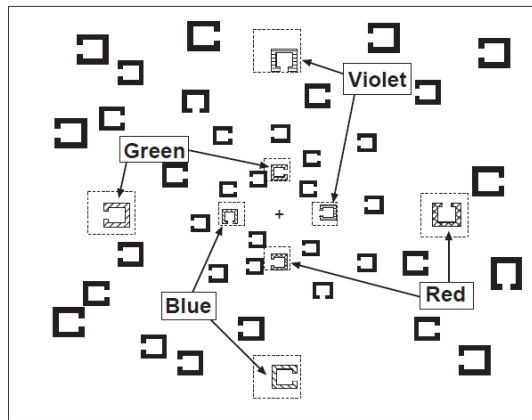


Figure 4

(a)



(b)

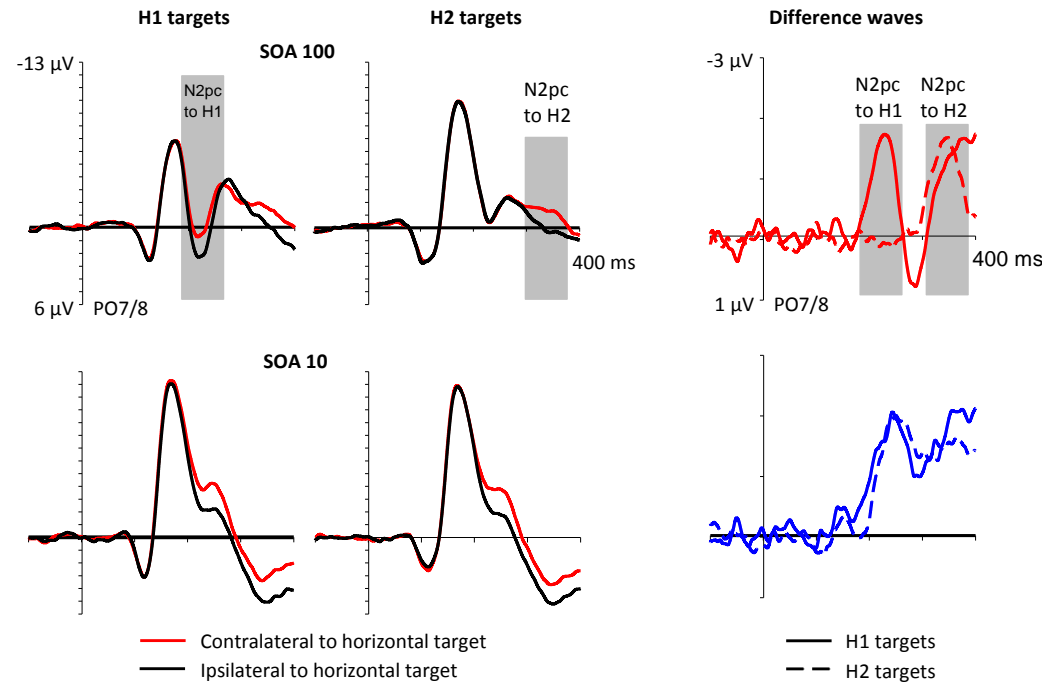
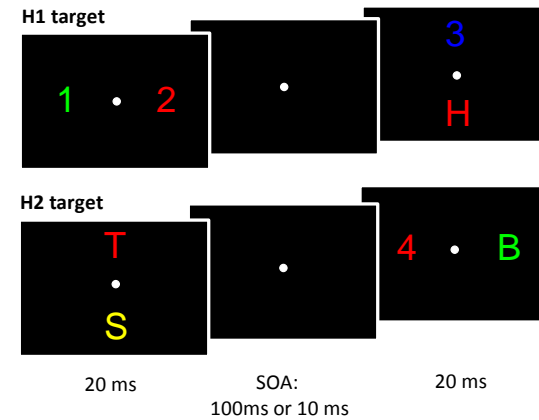


Figure 5

