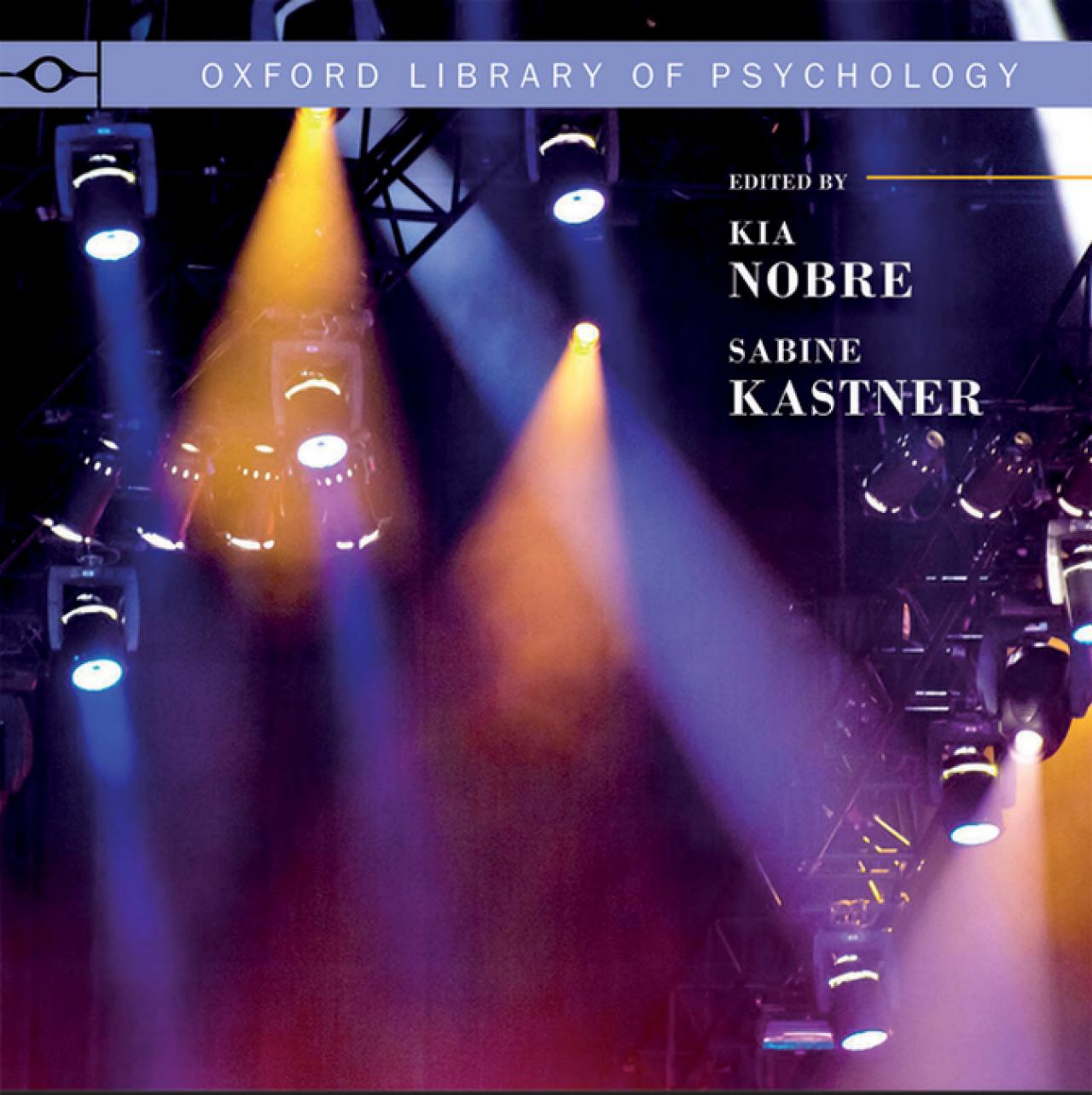

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The Oxford Handbook *of*
ATTENTION

THE OXFORD HANDBOOK OF

ATTENTION

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PART A

INTRODUCTION

CHAPTER 1

GUIDES TO THE STUDY OF ATTENTION

MICHAEL I. POSNER

This volume presents a modern look at the field of attention. The identities of the editors of this volume suggest why it and they can serve as guides to current and future research. Kia Nobre is a leader in the use of neuroimaging to study attention largely in humans, while Sabine Kastner bridges neuroimaging approaches in both humans and monkeys to the cellular approach of neurophysiology. These two methods are increasingly integrated in empirical research and theory in the field. They have selected a very strong set of authors to provide guidance on theory and empirical research on attention. In this foreword I try to trace the background of these methods within the field of attention, look briefly at the current state of integration as represented by the chapters of this Handbook, and speculate on future developments.

Historical Background

In the mid-twentieth century Moruzzi and Magoun (1949) began using animal models to explore aspects of attention. They studied the midbrain reticular system as the mechanism of arousal. In their work attention involved a state in which the animal was aroused from coma or sleep and then demonstrated both spontaneous integrated activity and processing of sensory stimuli.

Hubel and Wiesel (1968) used microelectrodes to probe the structure of the visual system. Before this method could be applied to attention, however, it was necessary to adapt the microelectrode technique to alert animals. This was accomplished in the early 1970s and applied by Mountcastle (1978) and Wurtz, Goldberg, and Robinson (1980) to examine mechanisms of orienting to visual objects in the superior colliculus and parietal lobe. Their findings suggested the importance of both of these areas to a shift of visual attention. It had been known for many years that patients with lesions of the right parietal lobe could suffer from a profound neglect of space opposite the lesion. The findings of 'attention-related cells' in the posterior parietal lobe of alert monkeys suggested that these cells might be responsible for the clinical syndrome of neglect.

An impressive result from the microelectrode work was that the time course of parietal cell activity seemed to follow a visual stimulus by 80–100 ms. Beginning in the 1970s, Hillyard (van Voorhis and Hillyard 1977) and other investigators explored the use of scalp electrodes to examine time differences in neural activity between attended and unattended visual locations. They found that early parts of the visual event-related potential (ERP) showed changes due to attention starting at about 100 ms after input. These findings showed likely convergence of the latency of psychological processes as measured by ERPs in human subjects and cellular processes measured in alert monkeys. These results were an important development for mental chronometry (i.e. the study of the time course of information processing in the human brain) because they suggested that scalp recordings could accurately reflect the underlying temporal structure of brain activity.

In the late 1980s, the Washington University School of Medicine was developing a centre for neuroimaging using positron emission tomography (PET). The centre was led by Marc Raichle. These studies helped establish neuroimaging as a means of exploring brain activity during cognitive functions in general and attention in particular (Corbetta and Shulman 2002; Posner and Raichle 1994, 1998). In general, these studies showed that most cognitive tasks, including those that are designed to explore mechanisms of attention, have activated a small number of widely scattered neural areas.

The findings from neuroimaging that cognitive tasks involve a number of different anatomical areas led to an emphasis on tracing the time dynamics of these areas during tasks involving attention. Because shifts of attention can be so rapid, it is difficult to follow them with hemodynamic imaging. To fill this role, algorithms were developed (Scherg and Berg 1993) to relate the scalp distribution recorded from high density electrical or magnetic sensors on or near the skull to brain areas active during hemodynamic imaging (see Dale et al. 2000, for a review). In some areas of attention there has been extensive validation of these algorithms (Heinze et al. 1994), and they allow precise data on the sequence of activations during the selection of visual stimuli (see Hillyard, Di Russo, and Martinez 2004, for a review). The combination of spatial localization with hemodynamic imaging and temporal precisions from electrical or magnetic recording has provided an approach to revealing the dynamic operations of the networks underlying attention in humans that fit very well with the use of cellular recording in monkeys. In current research these methods have become increasingly integrated as made clear by this Handbook.

CURRENT STATE OF RESEARCH

Theory

This volume presents nine chapters on theory related to attention. The chapters include world leaders in the field. The first six chapters (section B; Chs. 2–7) are mainly in verbal form while the remaining three (section F; Chs. 38–40) are computational. Taken together these chapters develop theoretical methods that summarize empirical findings and data concerning the localization, connectivity, and time course of a wide variety of attentional tasks. The chapters present a comprehensive view of the current state of theory in this field.

Empirical studies

This volume makes a distinction between orienting towards locations in empty space (section B; Chs. 8–19) and orienting to objects that occupy that space (section C; Chs. 21–25). Sections B and C summarize major results in this field. While it is unusual for people to operate in a space without objects, the empty fields discussed in section B allow one to concentrate on the mechanisms of top-down influence without having to consider at the same time the structure of the perceptual field. Section C provides the important constraints that a context of multiple distractors and multiple targets provide.

Section D deals with how attention relates to voluntary control of motor activity (Ch. 26), working memory (Ch. 30), executive functions (Chs. 28–29), emotion (Ch. 27), and consciousness (Ch. 31). These are all important functions of cognition in which attention is involved along with other brain systems. It is not always easy to disentangle these multiple processes within complex task, but these chapters provide a summary of current efforts to do so.

Development and disorders

Although our chapter on development of attention networks is in section B (Ch. 20) and section E has chapters on ageing (Ch. 36) and developmental disorders (Ch. 37), the three can be put together as a summary of lifespan typical and atypical development. While very early development depends heavily on spatial orienting, it is clear that what develop in childhood are more general control networks that allow for self-regulation. The developmental process continues throughout life so that it is probably not completely appropriate to consider ageing as a disorder, although declines in function are clearly involved.

Disorders ought to be viewed in relation to typical development. Three chapters in section D deal mainly with neurological disorders (Chs. 32–34). Disorders involving clear cases of brain injury from stroke, tumour, or closed head injury provide important clues to critical brain areas important for attention.

FUTURE OF RESEARCH

Although the job of predicting the future of the field is mainly left to Ch. 41 in section H, here I provide some speculations on developments towards the integration between cellular and systems approaches.

Networks

New methods have greatly reduced the gap between cellular and synaptic mechanisms and systems approaches to the field of attention. On the one hand, imaging reveals the brain areas and connections important at rest and during cognitive activity, while on the other hand multiple electrodes allow simultaneous recording from many neurons and brain areas. This has allowed modern theories to concentrate on a detailed account of how networks control the flow of information.

It is altogether likely that new methods will be developed. For example, within the last few years magnetic resonance imaging has been expanded to view white matter connections (Behrens and Sporns 2012) and to reveal networks active during the resting state (Raichle 2009).

The development of optogenetic methods provides the opportunity to view and manipulate cells at the millisecond level in appropriate organisms (Deisseroth 2011). This invasive technology is not appropriate for humans, but starting with algae it has progressed to primates. Further ingenious application of genomics to imaging may eventually allow the complete integration of cellular with systems level analysis even within the human brain.

A fascinating new method with interesting links to the study of attention involves the use of video games to open the critical period usually involved in vision (Li, Ngo, Nguen, and Levi 2011). For many years it was believed that there is an early period in which visual input is needed in order to avoid loss of function. The video games may have increased cholinergic activity associated with visual orienting thus allowing better plasticity beyond the critical period. This has led to speculations that cholinergic agonists might help improve plasticity of visual function (Rokem and Silver 2010).

Evolution

Currently the cellular versus systems approach overlaps somewhat with human versus animal studies. While there is convincing evidence that some forms of attention are present in fruit flies (Miller, Ngo, and van Swinderen 2012) and thus likely throughout the animal kingdom, many forms (e.g. control of language) are unique or are nearly unique to humans. In areas such as orienting to visual objects monkeys and even rodents have been important for understanding the anatomy and neurochemistry of attention.

Even when human control is less similar to animal models the studies may provide an important perspective on where human abilities come from. An important current case is the role of Von Economo cells present in the human insula and anterior cingulate in top-down control of emotion and cognition (Seeley et al. 2012). The evolution of these cells in social animals and non-human primates may provide an important perspective on the development of self-regulation in humans. With new knowledge of genetics the evolutional approach will doubtless advance in the future.

Individuality

Most work on attention and most of the chapters of this volume deal with the forms of attention common to all people. However, the network approach does provide a natural link between universal properties of attention and individual differences.

The efficiency of the neural network underlying attention may be the reason that individuals differ in attention. In part, these differences in efficiency are due to genetic polymorphisms (see chapter 20 for a current discussion). The interaction of these polymorphisms with training and other environmental influences may provide new insight into how various forms of training may change gene expression and thus the efficiency of attention networks. Already it is possible to change connectivity with some forms of training (Tang and Posner 2009) and thus the interaction of training with genetics is likely to provide important future perspectives on child rearing and education (van Ijzendoorn et al. 2011).

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PART B

THEORETICAL MODELS OF ATTENTION

CHAPTER 2

APPROACHES TO VISUAL SEARCH: FEATURE INTEGRATION THEORY AND GUIDED SEARCH

JEREMY M. WOLFE

INTRODUCTION

THE visual world is full of objects and it is an interesting fact that we can see more of that world than we can understand at any given moment. Thus, looking at this picture of a park just off Market St in San Francisco (Fig.2.1), you immediately see a rectangle filled with visual stuff but you do not immediately know the answer to fairly basic questions that one might ask about the objects in the scene. What colour is the bus? (white). Are there any people present? (no). This chapter will be devoted to the investigation of these limits on our perception through the theoretical lenses of Feature Integration Theory (Treisman 1988; Treisman and Gelade 1980) and Guided Search Theory (Wolfe 1994, 2007; Wolfe, Cave, and Franzel 1989). The chapter will be organized around the four terms that make up the names of the theories. **Features:** What are the basic features that are seen immediately in that rectangle of an image? **Integration:** How are those features combined into object representations? In particular, we will focus on the need for attention-demanding feature 'binding' in object recognition. **Guidance:** How can unbound features be used to guide **Search** for those objects or properties of a scene that are not immediately available to us when we look at a scene?

VISUAL SEARCH

Most of the work discussed in this chapter will involve the visual search paradigm in which an observer looks for one or more targets in a display containing some distractor

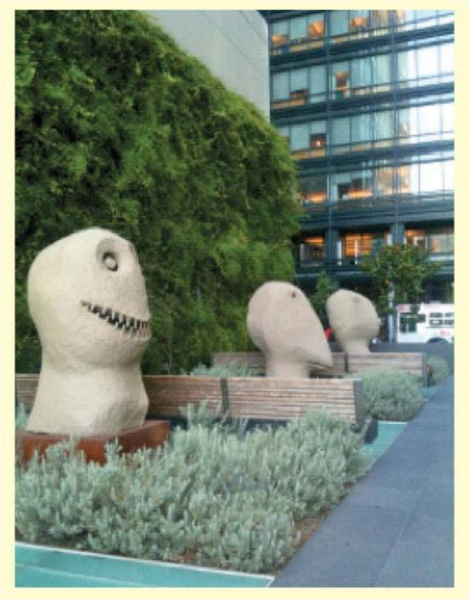

FIGURE 2.1 A park in San Francisco.

items. Search tasks are ubiquitous in daily life. Where is my coffee cup, the cellphone, the keyboard, the mouse, etc.? Such searches are typically concluded so quickly that we do not even register them as searches. We notice when the search is more prolonged. Where on stage is my child amidst the rest of the school choir? Moreover, our civilization has created socially important search tasks from airport baggage security (Gale, Mugglestone, Purdy, and McClumpha 2000; Rubenstein 2001) to medical image perception (Berbaum et al. 1998; Krupinski, Berger, Dallas, and Roehrig 2003; Kundel and Nodine 2004; Nodine, Krupinski, and Kundel 1993). These typically require trained expert searchers.

Beyond its face validity as a task that we perform all the time, visual search is a useful paradigm in the lab because it gives us a way to quantify the capacity limitations described in our initial example. With the San Francisco image, we can assert that you were not immediately aware of the presence of the bus or the absence of humans. With stimuli like those in Fig. 2.2, we can measure that.

Suppose that we showed observers a succession of displays like this and asked them to press one key if a red square was present and another if no red square was present. We could measure reaction time (or 'response time'—in either case, abbreviated 'RT') and/or accuracy as a function of 'set size', the number of items in the display. We would find, to a first approximation, that the set size did not matter. Observers would be as fast and accurate with the 33-item display on the right as they are with the 9-item display on the left. The slope of the RT x set size function will be near zero. We can call such searches 'efficient' searches. In contrast, if observers were asked to find the item of medium size amidst the large and small items of Fig.2.2, we would obtain a very different pattern of results. RTs would increase roughly linearly with set size. The slope of the RT x set size function would probably be in the range of 20–40 msec/item for trials having

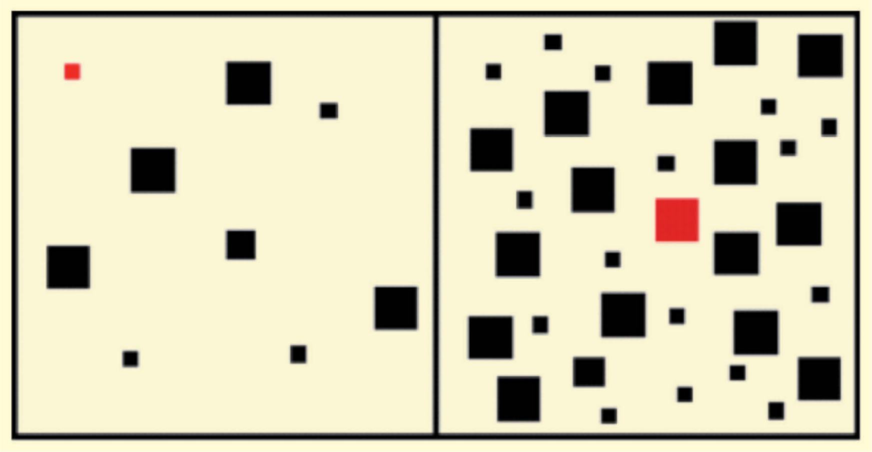

FIGURE 2.2 Search tasks: in each display, there are two targets; one, rather obviously, is red. The other is the square of medium size.

a medium-sized target. For target-absent trials, the slope would be roughly twice the target-present slope. (In fact, the ratio of absent to present slopes in an experiment with targets on 50% of trials appears to be reliably a bit more than 2:1—a fact that has theoretical importance, to be discussed below (Wolfe 1998).) If the display was presented only briefly or the observer was forced to respond by some very short deadline, we would find that the error rate for the 33-item display would be higher than the error rate for the 9-item display in the medium-target task but not in the red-target task. These speed–accuracy trade-off methods can be powerful tools in theoretical analysis of search tasks (Dukewich and Klein 2009; Guest and Lamberts 2011; McElree and Carrasco 1999). We can call tasks producing these sorts of results 'inefficient'.

FEATURE INTEGRATION THEORY

The distinction between what we are calling 'efficient' (Neisser 1963) and 'inefficient' (Atkinson, Holmgren, and Juola 1969) was central to the development of Treisman's Feature Integration Theory (Treisman and Gelade 1980). She argued that there was a limited set of basic features that could be processed 'preattentively', in parallel. In Fig. 2.2, colour is the example of such a feature. A target, defined by a unique basic feature would 'pop out' of a display. It would be available to awareness and for action without apparent capacity limitations. In contrast, many other search tasks, even if they involved quite simple perceptual discriminations (e.g. the distinction between big, medium, and small) showed a pattern of search results that Treisman argued was consistent with a serial self-terminating search; a search that proceeded one item after another until the target was discovered or the search was terminated—in the simplest case, after examining every item and determining that each was not the target. In a serial, self-terminating search,

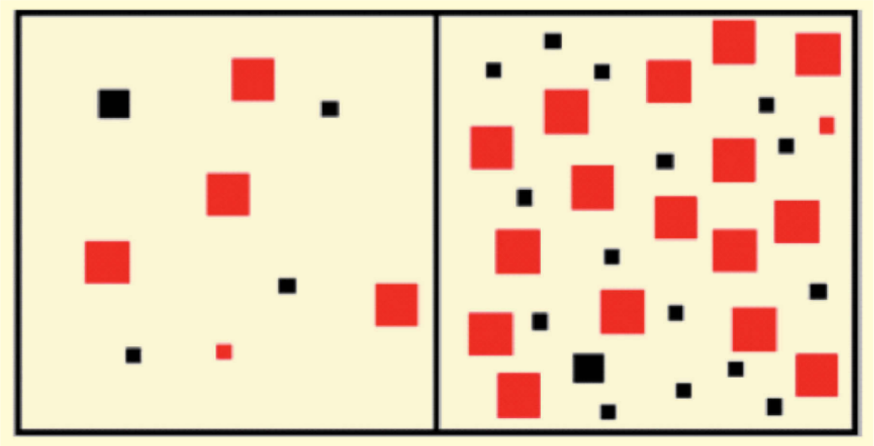

FIGURE 2.3 Conjunction search: look for the small red items.

observers would need to examine half of the items, on average, when the target was present and all of the items when it was absent. This predicted a 2:1 slope ratio between target-absent and target-present RT x set size functions; hence, the theoretical significance of the finding that those slope ratios may be reliably greater than 2:1.

The description of search tasks as 'parallel' and 'serial' has proven enduringly popular—to the distress of theoreticians who note that the patterns of results can be explained in many ways (Townsend 1971, 1990; Townsend and Wenger 2004; J. Palmer 1995; J. Palmer and McLean 1995). It is to avoid those theoretical commitments that we use the theory-neutral terms 'efficient' and 'inefficient'.

Conjunction searches like the one illustrated in Fig. 2.3 were critical to Treisman's originally dichotomous view of search. In Fig. 2.3, the target is defined by the conjunction of two features. It is the small red item. A sole small item in a field of large items or a sole red item in a field of black items would pop out. However, the small red item did not. The phenomenal experience of conjunction search was not a pop-out experience, and in a large body of Treisman's data, the RT x set size functions had slopes in the inefficient range. Treisman's conclusion was that while basic features were processed in parallel across the field, serial deployment of attention was required to integrate two or more features together. To change the language a little, serial attention was needed to 'bind' features to object representations. This was Treisman's solution to the 'binding problem'. There are multiple definitions of the problem (Treisman 1996). A useful way to think about it is in neural terms. If we stay with Fig. 2.3, there would be neurons that respond to an item's size and others that respond to its colour. How would one know which colours went with which size? Having higher-order cells for all possible combinations of all features at all locations seems implausible. Thus, there was a problem, and a limited-capacity, attention-directed binding process was the solution in Feature Integration Theory.

Here we are talking about the binding of two properties of one object, colour and size. However, as Treisman (2006) explains, binding is a more general issue. She identifies no fewer than seven types of binding. Some of these are conceptually quite similar to 'property binding' (her name in this paper for the binding of basic features like colour and size). For instance, knowing that two parts belong to one object is also a binding problem. Other forms could be similar at an abstract or computational level while being rather different phenomenologically. For instance, she notes that the fine discrimination of specific orientations (e.g. 22 deg. from 26 deg.) is thought to rely on ratios of two or more broadly tuned orientation channels (Olzak and Thomas 1986). So, in some sense, the outputs of those two coarse channels must be bound to produce the fine resolution. Unlike the binding of colour and size, the unbound components are not introspectively available in this case of what Treisman calls 'range binding'.

For those forms of binding, where the unbound properties are available, illusory conjunctions have been an important phenomenon, marshalled in support of Feature Integration Theory. The phenomenon is not easily demonstrated on the static page, but take a quick glance at Fig. 2.4 and then cover it up so that you cannot see it before returning to this text.

If you followed instructions, you are probably in a good position to list many of the colours and shapes that are present in the figure. You are probably quite sure that there was a diamond and, if asked, you are quite sure that there was no circle present. You are in a less confident position to report the conjunctions of colour and shape. What colour was the diamond? Odds are that you would not say 'blue' since nothing in the image was blue. However, Treisman found that there was quite a good chance that you would report seeing the diamond in the colour of one of the other shapes (Treisman and Schmidt 1982), perhaps yellow. It was as if the colours and shapes were floating free at some level in your visual system and, especially once the image was no longer present to provide a clear answer, those features could bind to form illusory conjunctions.

The original idea was that features were completely free-floating, but even in the first glimpse, the world doesn't look like a soup of loose features, and subsequent work reveals a role for location (Prinzmetal and Keysar 1989; Hazeltine, Prinzmetal, and Elliot 1997). The illusory conjunction phenomenon went well beyond simple shapes and colours to include, for example, letters and words (Prinzmetal 1991; Treisman and Souther 1986; Virzi and Egeth 1984) and clock times (Goolkasian 1988). Thus, basic features were not

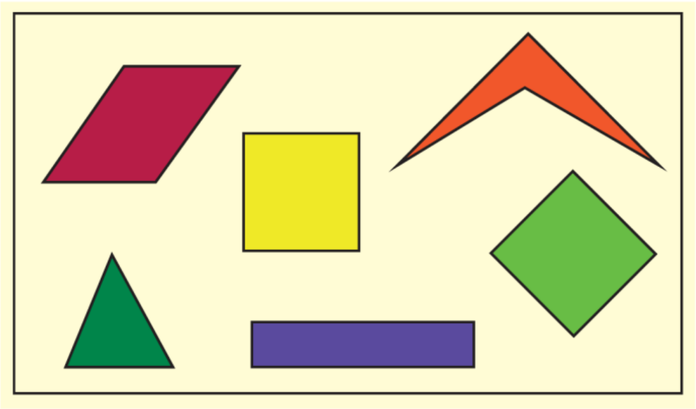

FIGURE 2.4 Stimuli for an illusory conjunction demonstration. Take a quick glance at the figure, cover it up, and return to the text.

the only units involved. It has been argued that illusory conjunctions are basically a phenomenon of memory (Briand and Klein 1989; Tsal 1989a, 1989b) and, indeed, memory for basic features can be quite terrible. In one experiment, Wolfe et al. showed observers an array of 20+ red and green dots. At one moment, signalled by a tone, one of the dots brightened and either did or did not change colour from red to green or green to red. Observers were close to chance performance when asked if the new colour was the same as the old one (Wolfe, Reinecke, and Brawn 2006). Observers knew that they had been looking at red and green dots, but the binding of colour to dot was clearly very fragile.

Still, binding errors need not be entirely in the remembered past tense. When items are relatively close to each other, especially in the periphery, observers experience 'crowding' phenomena (Levi 2008; Pelli and Tillman 2008) in which it may be possible to see features but not know how those features are bound together or even how they are bound to a location. That is, you might know there is a line at a location but you may be unable to determine its orientation. As Treisman would predict, attention allows illusory conjunctions to be resolved (Scolari, Kohnen, Barton, and Awh 2007) but the spatial grain of attention in the periphery is coarse (S. He, Cavanagh, and Intriligator 1996; Intriligator and Cavanagh 2001). So, away from fixation, illusory conjunctions may be a fact of life, even when the image remains continuously visible. Rosenholtz et al. talk about 'mongrels' that are created in the periphery by a system with weak spatial localization abilities and in which image statistics (e.g. average orientation) are calculated over multiple items. Portilla and Simoncelli (2000) developed a method for generating natural-looking textures from a set of image statistics. That is, if you took a picture of a forest, extracted the Portilla and Simoncelli statistics, and then synthesized a new image from those statistics, it would not be the original image but it would look forest-like. Rosenholtz et al. note that if this process is run over a standard search display like a search for a T among Ls, it creates new images in which some of the Ls have come to look like Ts. Arguing that this is the situation for vision away from the point of fixation, they have used the phenomenon to develop a theory of search performance (Rosenholtz, Chan, and Balas 2009). Even if crowding and mongrels are not quite the same things as illusory conjunctions, the problem of jumbled, possibly misbound features is similar. Attention-demanding binding is the Feature Integration solution to that problem (or, in more recent formulations, a leading solution among several—Treisman 2006).

INTEGRATION: IS ATTENTIVE BINDING REALLY NECESSARY?

Various challenges have been presented to the idea that binding requires attention and that binding is required for object identification. Quite early, Houck and Hoffman did an experiment with the McCollough Effect (Houck and Hoffman 1986). The McCollough effect is an orientation-contingent, colour after-effect based on adapting to, say, red vertical and green horizontal gratings. After adaptation, black and white vertical gratings would look greenish while black and white horizontal gratings would look pink (McCollough 1965). Houck and Hoffman found that the effect could be produced without attention to the adapting stimuli even though the effect clearly requires some sort of association of orientation and colour. If attention is required to bind colour to orientation, how could orientation-contingent colour adaptation occur without attention? One could attack the notion of 'without attention'. It is remarkably difficult to guarantee that a stimulus is unattended and it is virtually impossible to convince reviewers of this claim. As a consequence, more recent papers often refer to the 'near-absence' of attention (Reddy and Koch 2006; Reddy, Wilken, and Koch 2004).

Putting aside that methodological issue, there are situations where simple spatial co-occurrence of two features is all that is needed for the task at hand. Houck and Hoffman show one such case. A similar account could be invoked to explain other situations where conjunctive properties influence behaviour, apparently without attentive binding (Mordkoff, Yantis, and Egeth 1990). A particularly interesting case has to do with our remarkable ability to determine if humans or animals are present in scenes apparently without directing attention to the target object (VanRullen and Thorpe 2001; Kirchner and Thorpe 2006; Evans and Treisman 2005).

It may be that loose collections of unbound features are adequate to discriminate animal from non-animal (Treisman 2006), as is cartooned in Fig. 2.5.

Figure 2.5 is a cartoon because we cannot easily list or portray unbound 'animal' or 'oven' features but the point is that some discriminations in laboratory tasks will not require binding. Co-occurrence may be enough, though it must be confessed that other results such as the ability to identify a face in the 'near-absence' of attention are harder to explain with this unbound bundle of features idea (Reddy and Koch 2006).

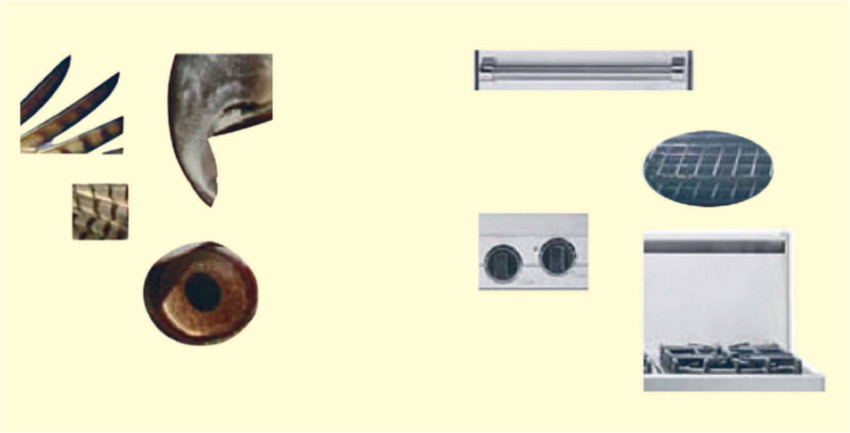

FIGURE 2.5 An unbound collection of features might be all that is required to determine if the 'animal' is on the left or right. This is only a cartoon as we do not know exactly what those 'unbound features' would look like.

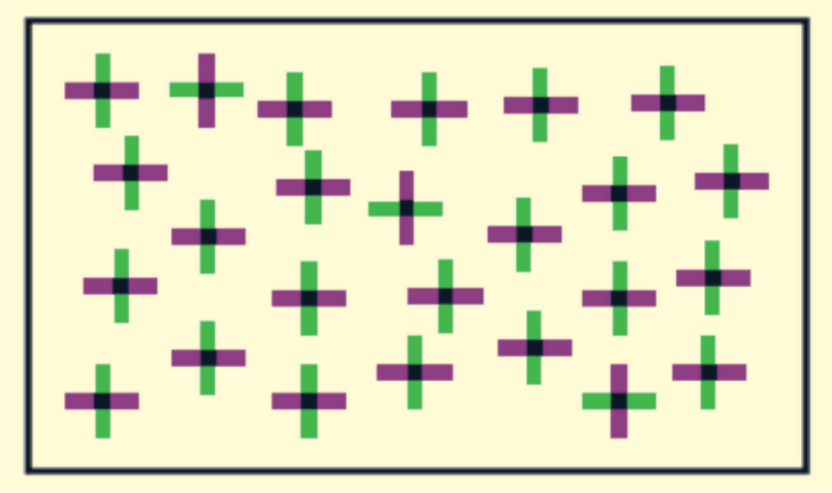

FIGURE 2.6 Search for the pluses with purple vertical and green horizontal components. Before attention arrives, all of these items are unbound collections of the same green, purple, vertical, and horizontal features.

Perhaps the best way to demonstrate the critical role of attentive binding is to create simple stimuli that eliminate the effectiveness of spatial co-occurrence of features. Figure 2.6 shows an example. You are a looking for 'pluses' with purple vertical and green horizontal components. You will find that this is an inefficient search. (There are three targets. Did you find them all?) Wolfe and Bennett (1997) argued that this was hard because before the arrival of attention, each one of these items was an unbound collection of purple, green, vertical, and horizontal features. As all the features of one item are in more or less the same location, associated with the same object, attention and binding are required before it can be determined if purple goes with vertical or horizontal.

One could object that, in fact, a purple-vertical-green-horizontal plus is just a green-vertical-purple-horizontal plus, rotated 90 degrees and, as a consequence, it is not surprising that one is hard to find amidst the other. Figure 2.7 shows stimuli intended to counter that argument. Here the targets and distractors are clearly very different objects. The targets look like puzzle pieces and the distractors look like some unusually rectangular, single-celled organism with a flagellum. These are designed to have very similar preattentive, unbound features. Each has a closed region and some straight and curved lines. The result, in the upper of the two search displays of Fig. 2.7, is a relatively inefficient search (Wolfe and Bennett 1997). Very similar stimuli produce an easier search in the second example because the targets are now the only items with the preattentively available attribute of 'closure' (Chen 1982; Elder and Zucker 1993, 1998).

Treisman's fundamental point about binding seems to be valid. If you eliminate the usefulness of spatial co-occurrence and if no basic feature distinguishes targets from distractors, an inefficient search is going to be required as the observer binds one item after another in the effort to identify a target.

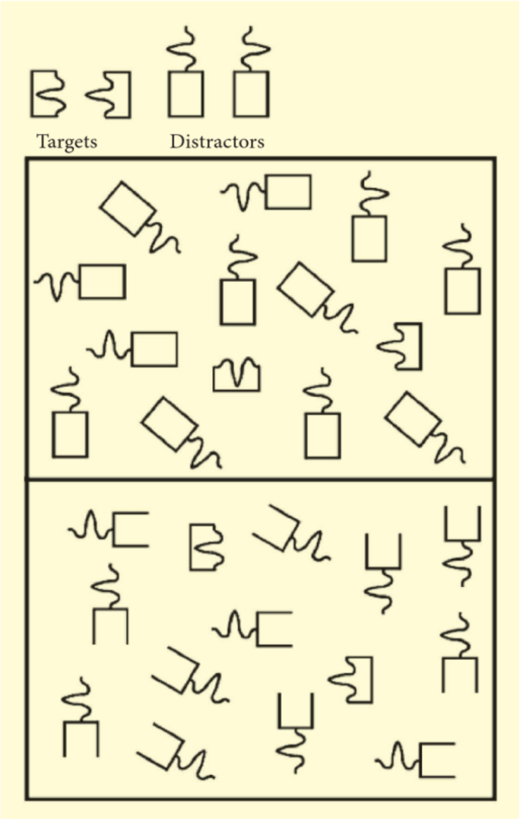

FIGURE 2.7 A search for something like puzzle pieces among distractors with tails. This is easier in the lower panel because there the targets are the only items exhibiting 'closure'.

Guidance: Efficient Conjunction Search and the Role of Guidance

While it may be true that binding requires attention, it turns out not to be true that search tasks fall into two neat categories; efficient feature, 'pop-out' searches that do not require binding and can be done in parallel and all other searches that do require binding and are thus inefficient. While Treisman's original data were broadly consistent with this view, it rapidly became clear that conjunction searches, in particular, did not need to be inefficient. In the 1980s, exceptions started to appear (Alkhateeb, Morland, Ruddock, and Savage 1990; Dehaene 1989; McLeod, Driver, and Crisp, 1988; Nakayama and Silverman 1986; Sagi 1988; Zohary and Hochstein 1989). At first, it seemed like there might be a set of exceptions to the general rule, rather like irregular verb forms. Maybe stereopsis (Nakayama and Silverman 1986) or motion (McLeod et al. 1988) were special

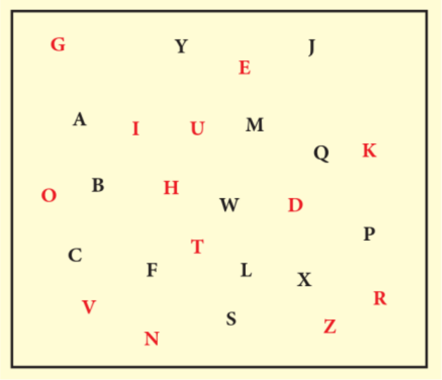

FIGURE 2.8 If you search for the red 'K', you will guide attention to red items and away from black. Reproduced from Egeth, H. E., Virzi, R. A. & Garbart, H. Searching for conjunctively defined targets. *Journal of Experimental Psychology: Human Perception and Performance*, 10, 32–39 © 1984, American Psychological Association.

features that operated under different rules of binding. However, by 1989, Wolfe et al. had data showing quite efficient search for colour x orientation searches and enough other examples had surfaced that it was time for a modification of the basic Feature Integration story (Wolfe, Cave, and Franzel 1989).

In retrospect, the key idea was made obvious by Egeth et al. (1984) and illustrated in Fig. 2.8. If you are asked to search for the letter 'V', you will perform some sort of relatively inefficient search. (It is complicated because letters are complicated bundles of features.) If you are asked to look for a red 'T', you will, again, perform some sort of relatively inefficient search, but this time only through the red items. A black item is simply never going to be a red T and you can use that knowledge about the basic features of the target to *guide* attention to items that have the features that make them more likely to be the target. If half of the items were red in this example, then the slope of the RT x set size function would be half that of an unguided letter search because half of the letters could be eliminated without ever being attended. The key observation of Guided Search (Wolfe et al. 1989) was that this could be a general property of search tasks. If observers were asked to search for a red vertical item among red horizontals and green verticals, preattentive, basic feature information could be used to guide attention toward red items and toward vertical items. The intersection of the sets of red and vertical items would be an excellent place to look for a red vertical target. Indeed, were guidance perfect, search for a basic conjunction of two features like colour and orientation should have been perfectly efficient. Such searches are more efficient than original Feature Integration Theory predicted but the slopes are greater than zero. We will return to the apparent imperfection of guidance later. For the present, where Feature Integration Theory saw two types of search—parallel and serial—Guided Search saw two ends of a continuum of guidance. Efficient 'parallel' search tasks were those where guidance was adequate to allow the deployment of attention to the target item first time, every time. Inefficient searches were those where no guidance was possible beyond guidance to the presence of an object in a location. Each of these items needed to be attended to, one after the other, until the target was found or the search was abandoned. In between were guided searches, where some basic feature information could be used to prioritize some items as more worthy of attention than others. The slope of the RT x set size function, in this view, becomes an estimate of the percentage of items that remain candidate targets even after guidance has done its work. If unguided, inefficient search has a standard slope of, say, 40 msec/item, then a search task producing a slope of 10 msec/item would imply that guidance could eliminate 3/4 of the items from consideration.

Working out the details of this straightforward idea is not entirely straightforward. The remainder of this chapter will discuss the nature of guiding features and the mechanics of Guided Search. While this chapter will focus on Guided Search, it is worth noting that there is a family of models that share aspects of Feature Integration and/or Guided Search architecture to greater or lesser extent (Cave 1999; Tsotsos 2011; E. Cohen and Ruppin 1999; Vidyasagar 1999; Hubner 2001; Lee, Buxton, and Feng 2005; Mozer and Baldwin 2008).

FEATURES

The nature of guiding features

In Treisman's original formulation, 'the visual scene is initially coded along a number of separable dimensions, such as color, orientation, spatial frequency, brightness, direction of movement' (Treisman and Gelade 1980). In her terminology, 'colour' would be a 'dimension' and 'red' a feature within that dimension. We often use the term 'attribute' for 'dimension' since dimension also gets used to talk about depth—which is a preattentive attribute. The cognitive architecture for early Feature Integration and early Guided Search was something like what is shown in Fig. 2.9. (It might or might not map directly onto neural structures.)

The stimulus was decomposed into a set of basic features. With the deployment of selective attention, the features of a particular object could be bound into a recognizable object with bound features in a particular location. In early Guided Search, the main addition to the standard Feature Integration story would be the idea that information about the decomposed features could be used to guide the deployment of attention. Thus, in Fig. 2.9, an intention to look for something horizontal would make use of the orientation map to deploy attention toward items showing some horizontal-ness in that map.

The architecture of the current version of Guided Search is somewhat different. The important change is that the representation that guides attention has been pulled out of the path from early vision to bound, recognized objects. This change was made when it became clear that the properties of the guiding representation were not the same as the building blocks of perception. Guidance is based on representations that do not 'see' the world as we experience it. This point is discussed more extensively elsewhere

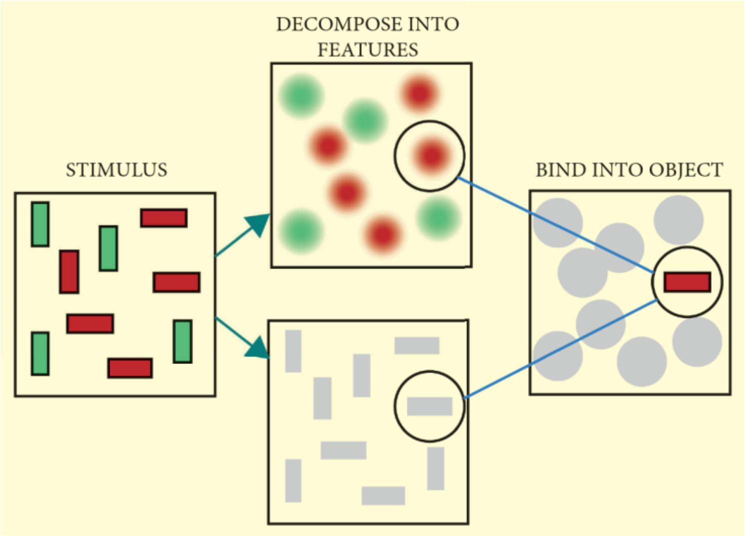

FIGURE 2.9 Cartoon of the cognitive architecture for early Feature Integration Theory and early Guided Search.

(Wolfe 2005, 2007, 2012; Wolfe and Horowitz 2004; Wolfe, Reijnen, Van Wert, and Kuzmova 2009). A single example will suffice here (Lindsey et al. 2010).

Suppose that your task is to search for desaturated targets. In the example in Fig. 2.10, the distractors would be fully saturated reds or blues and unsaturated whites. The targets would be pinkish on the left and pale blue on the right. This electronic or printed figure will not be colourmetrically precise, but the stimuli in the experiment were designed so that the targets lay perceptually exactly halfway between the distractors (details in Lindsey et al. 2010). This was done for a wide range of colours. Interestingly, searches for

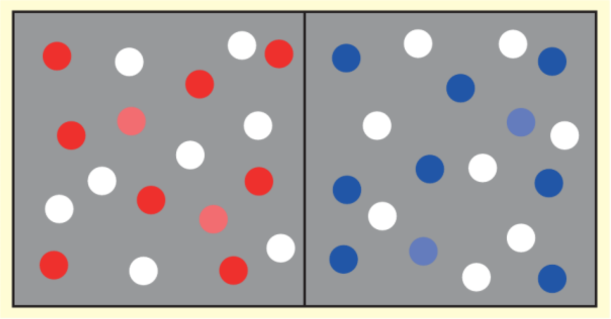

FIGURE 2.10 Search for the desaturated targets among saturated and achromatic distractors. Adapted from Lindsey, D. T., Brown, A. M., Reijnen, E., Rich, A. N., Kuzmova, Y., and Wolfe, J. M. , Color Channels, not Color Appearance or Color Categories, Guide Visual Search for Desaturated Color Targets, *Psychological Science*, 21 (9) pp. 225–31, copyright © 2010 by SAGE Publications. Reprinted by Permission of SAGE Publications.

the pinkish (maybe 'skin-coloured') targets were hundreds of msec faster than searches for other desaturated colours. In perceptual space, the distance from blue to pale blue might be the same as the distance from red to pale red. However, in the guiding representation, the red–pale red difference is, apparently, much more significant.

Consequently, the current version of Guided Search adopts an architecture like that cartooned in Fig. 2.11. Between early visual processes and bound representations of objects, there is a tight bottleneck. Access to that bottleneck is gated by a guiding representation that is itself an abstraction from early vision and, as noted, does not 'see' the world exactly as we see it. Once an object is selected, re-entrant processes (Di Lollo, Enns, and Rensink 2000; Hochstein and Ahissar 2002) reach back to make contact with the perceptual properties of the object. Treisman's current thinking also holds that re-entry is required for binding (Bouvier and Treisman 2010).

What are the features? (Wolfe and Horowitz 2004—revised)

A great deal of work has gone into defining the set of stimulus attributes that guide attention. Not all of this work is done by people who have adopted a Guided Search viewpoint, so in different papers, these attributes might be described as preattentive dimensions, pop-out features, etc. The goal is to determine the set of attributes that support efficient search and the guidance of attention.

Wolfe and Horowitz (2004) created a list of guiding attributes. Here that list is updated in a set of five annotated tables. Tables 1–3 1.1–1.3 rank candidates into categories of the 'undoubted', the 'probable and possible', and the 'doubtful' attributes. In addition, Table 2.4 is reserved for 'complicated' attributes and Table 2.5 introduces the idea of

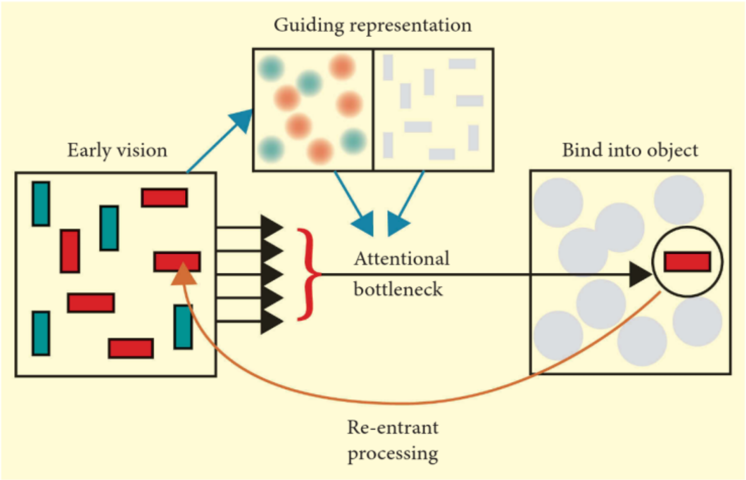

FIGURE 2.11 Guided Search architecture with the 'guiding representation' pulled out of the main path from early vision to perception.

Table 2.1 The Undoubted Feature Dimensions: 'Undoubted' means that the status of these properties is attested by a large body of work with converging methods

	The Undoubted Feature Dimensions	Notes
Colour	Bauer, Jolicoeur, & Cowan 1998; Bauer, Jolicoeur, & Cowan 1996; Brawn & Snowden 1999; Carter 1982; D'Zmura 1991; Daoutis, Pilling, & Davies 2006; Duncan 1988; Farmer & Taylor 1980; Green & Anderson 1956; Lindsey et al. 2010; Monnier & Nagy 2001; Nagy & Sanchez 1990; Nagy, Young, & Neriani 2004; Smith 1962; Treisman & Gormican 1988; Treisman & Souther 1985	1
Motion	Braddick & Holliday 1991; Burr, Baldassi, Morrone, & Verghese 2009; Dick, Ullman, & Sagi 1987; Horowitz, Wolfe, DiMase, and Klieger 2007; Kawahara 1993; McLeod et al. 1988; Muhlenen & Muller 1999; Nakayama & Silverman 1986; Nothdurft 1993b; Rosenholtz 2001a; Takeuchi 1997	2
Orientation	Bergen & Julesz 1983; Cavanagh, Arguin, & Treisman 1990; Foster & Ward 1991a, 1991b; Moraglia 1989a; Sagi 1990; Wolfe & Friedman-Hill 1992; Wolfe, Friedman-Hill, Stewart, & O'Connell 1992; Wolfe, Klempen, & Shulman 1999	
Size (incl. length & spatial freq.)	Cavanagh et al. 1990; Found & Muller 2001; Moraglia 1989b; D. Sagi 1988; Stuart 1993; Treisman & Gormican 1988; Verghese & Nakayama 1994; Verghese & Pelli 1994; L. G. Williams 1966	3

Notes:

1. Colour is certainly a feature. The currently interesting questions have to do with what aspects of colour signals guide attention as noted in the example in Fig. 2.10.
2. It is possible that motion could be decomposed into separate attributes of speed and direction (Driver, McLeod, & Dienes 1992).
3. We are calling this dimension 'size' but it covers a number of properties that, again, might be treated separately. It is possible that spatial frequency should be treated as its own dimension (Bilsky & Wolfe 1995), especially considering its possible role in guidance in scenes (Oliva, Torralba, Castelhano, & Henderson 2003). See also Alvarez & Cavanagh 2008.

Table 2.2 Probable and possible feature dimensions: The items can make a reasonable case for their status as guiding attributes. However, more data would be needed to address dissenting opinions or the possibility of alternative explanations

	Probable and Possible Feature Dimensions	**Notes**
Luminance onset (flicker)	Spalek, Kawahara, & Di Lollo 2009; Theeuwes 1995; Yantis & Jonides 1990	
Luminance polarity	Gilchrist, Humphreys, & Riddoch 1996; Theeuwes & Kooi 1994	4
Vernier offset	Fahle 1991a, 1991b	5
Stereoscopic depth & tilt	Z. J. He & Nakayama 1992; Holliday & Braddick 1991; McSorley & Findlay 2001; Moore, Elsinger, & Lleras 2001; Nakayama & Silverman 1986; O'Toole & Walker 1997; Sousa, Brenner, & Smeets 2009	6,7
Pictorial depth cues	Aks & Enns 1993; Enns & Rensink 1990, 1993; Enns, Rensink, & Douglas 1990; Epstein, Babler, & Bownds 1992; Sun & Perona 1996a; Von Grünau & Dubé 1994	6,7
Shape	Bergen & Julesz 1983; Cheal & Lyon 1992; Chen 1982, 1990; Kristjánsson & Tse 2001; Pilon & Friedman 1998; Pomerantz & Pristach 1989; Treisman & Gormican 1988; Tsal, Meiran, & Lamy 1995; Wolfe & Bennett 1997	8

Table 2.2 (continued)

	Probable and Possible Feature Dimensions	Notes
Line termination	Donnelly, Humphreys, & Riddoch 1991; Julesz & Bergen 1983; Taylor & Badcock 1988	8
Closure	Chen 1982; Elder & Zucker 1994, 1998; Enns 1986; Kanbe 2009; Kovacs & Julesz 1993; Treisman & Souther 1985; D. Williams & Julesz 1992	8
Topological status	Chen 1982, 1990, 2005; Rubin & Kanwisher 1985	8
Curvature	Fahle 1991b; Foster & Savage 2002; Gurnsey, Humphrey, & Kapitan 1992; Sakai, Morishita, & Matsumoto 2007; Treisman & Gormican 1988; Wolfe, Yee, & Friedman-Hill 1992	8
Lighting direction (shading)	Adams 2008; Aks & Enns 1992; Braun 1993; Kleffner & Ramachandran 1992; Ostrovsky, Cavanagh, & Sinha 2004; Ramachandran 1988; Sun & Perona 1996a, 1996b; Symons, Cuddy, & Humphrey 2000	9
Glossiness (lustre)	Wolfe & Franzel 1988	10
Expansion/looming	Braddick & Holliday 1991; Franconeri & Simons 2003; Skarratt, Cole, & Gellatly 2009; Takeuchi 1997	11
Number	Reijnen, Krummenacher, & Wolfe 2011; Taylor & Badcock 1988; Treisman & Gormican 1988	12
Aspect ratio	Treisman & Gormican 1988	

Notes:

4. Luminance polarity clearly supports efficient search but it might be nothing more than the black-white or luminance axis of a 3D colour space. Thus it could be grouped with colour.
5. The difficulty with Vernier as a guiding property in its own right is that it might be reducible to an orientation cue (Findlay 1973; Fahle & Harris 1998).
6. The taxonomy of depth cues as guiding attributes is not clear. Maybe it is a single, broad dimension of something like 3D layout (cf. Oliva & Torralba 2001) combining a variety of depth cues including stereopsis, the various pictorial depth cues, and shading into a representation of the 3D world. The relevant experiments would combine different guiding depth cues in a single display in order to see if they could act independently.
7. Depth guides attention in the sense that a 'near' item will pop out among far, for example. However, it also acts to modulate features like size. An item that is little in the image may be big in the world if it is far away. See 'modulators' in Table 5.
8. Rather like depth, it is not clear if 'shape' is one guiding dimension or many. Here we hedge our bets, listing shape and a collection of other properties that might be part of a family of shape attributes. To see the problem, consider line termination, closure, and curvature. Each supports efficient search, but are they actually independent attributes? Do an 'O' and a 'C' differ in closure or line termination or both? The issue has been complicated by the failure to settle on a generally accepted set of shape features (Kourtzi & Connor 2011; Logothetis, Pauls, & Poggio 1995; Yamane, Carlson, Bowman, Wang, & Connor 2008; Zhang et al. 2011).
9. The earlier evidence for guidance by shading (e.g. Ramachandran's 'eggs': Ramachandran 1988) has been undermined somewhat by later work (Cavanagh 1999; Ostrovsky et al. 2004). It is possible that shading information should be grouped with other cues like stereopsis, as part of one, omnibus 3D depth property.
10. The evidence for shininess or gloss comes from a single experiment on binocular lustre (Wolfe & Franzel 1988). Unpublished work in our lab casts doubt on the generality of the finding.
11. 'Expansion' and/or 'looming' cues are somewhat problematic because they might be decomposed into a depth cue, a size cue, a motion cue, or some combination of these, though an ability to deploy attention to something that might hit you in the head seems like a good idea.
12. Recent evidence shows that numerosity (does this cluster contain more dots than the other clusters?) is, at best, a rather weak feature, requiring large (>3:1) ratios between target and distractor numerosities (Reijnen et al. 2011).

Table 2.3 Doubtful cases and probable non-features: These are the proposed preattentive features where the preponderance of data seems to argue against their role as guiding features. It must be acknowledged that other authors would come to different conclusions about some of these attributes. Moreover, some attributes have their status on the basis of single experiments and would benefit from further study

	Doubtful cases & probable non-features	Notes
Novelty	Flowers & Lohr 1985; Frith 1974; Johnston, Hawley, & Farnham 1993; Q. Wang, Cavanagh, & Green 1994; Wolfe 2001; Zhaoping & Frith 2011	13
Learned features (e.g. letters)	Atkinson et al. 1969; Golcu & Gilbert 2009; Grice & Canham 1990; Kinchla 1974; Kinchla & Collyer 1974; Shiffrin & Gardner 1972	14
Alphanumeric category	Brand 1971; Duncan 1983; Jonides & Gleitman 1972; Krueger 1984	15
Intersection	Bergen & Adelson 1988; Bergen & Julesz 1983; Julesz 1981, 1984; Julesz & Bergen 1983; Julesz & Krose 1988; Nothdurft 1991; Wolfe & DiMase 2003	16
Optic flow	Braddick & Holliday 1991; Bravo 1998; Royden, Wolfe, & Klempen 2001, but see Rushton, Bradshaw, & Warren 2007	
Colour change	Theeuwes 1995	
3D volumes (e.g. geons)	J. M. Brown, Weisstein, & May 1992; Pilon & Friedman 1998	
Luminosity	Correani, Scot-Samuel, & Leonards 2006	17
Material type	Wolfe & Myers 2010	
Scene category	Greene & Wolfe 2011	
Duration	Morgan, Giora, & Solomon 2008	
Stare-in-crowd	Doi & Ueda 2007; Palanica & Itier 2011; M. A. Williams, Moss, & Bradshaw 2002; Von Grünau & Anston 1995	18
Eye of origin/ binocular rivalry	Paffen, Hooge, Benjamins, & Hogendoorn 2011; Shneor & Hochstein 2006; Wolfe & Franzel 1988; Zhaoping 2008	19
Your name	Bundesen, Kyllingsbaek, Houmann, & Jensen 1997	
Threat	Batty, Cave, & Pauli 2005; Lipp 2006; Notebaert, Crombez, Van Damme, De Houwer, & Theeuwes 2011; Öhman, Flykt, & Esteves 2001; Soares, Esteves, Lundqvist, & Ohman 2009; Tipples, Young, Quinlan, Broks, & Ellis 2002	20
Biological motion	Pratt, Radulescu, Guo, & Abrams 2010; L. Wang, Zhang, He, & Jiang 2010	21

Notes:

13. There are various claims for a guiding role for novelty and/or familiarity. The phenomena seem to be rather weak. For instance, as a general rule, a basic feature will continue to guide attention in the presence of some distractor heterogeneity in an irrelevant attribute. Thus, vertical will pop out among horizontal even if all the items are of different colour. However, while a novel mirror-reversed N might pop out among Ns (Wang et al. 1994), it is not clear that it would pop out among a heterogeneous set of normal letters.
14. Is it possible to learn a new preattentive feature? This is a long-standing question in visual search. Much of the work involves alphanumeric characters as over-learned sets of stimuli (Caerwinski, Lightfoot, & Shiffrin 1992; Malinowski & Hübner 2001; Sigman & Gilbert 2000; Sireteanu & Rettenbach 1995). The problem is that it is very hard to tell the difference between learning a new feature and learning to better exploit existing signals (e.g. line terminations, closure, etc.). This is a case where reasonable researchers could and do disagree (Shiffrin & Schneider 1977).

Table 2.3 (continued)

15. It was thought that a letter might pop out among numbers and vice versa but these results (e.g. the 'zero-oh' effect) have been hard to replicate.
16. Intersection once seemed to be a good candidate for feature status but more recent results have demoted it to 'unlikely' status (Wolfe & DiMase 2003).
17. People have a strong belief that they can detect when someone is staring at them. They even believe that they can detect someone staring at them from behind them (Simons & Chabris 2010). However, while we are very good at assessing someone else's gaze direction, especially if it is toward us (Watt, Craven, & Quinn 2007), we are probably not able to do so in a search setting and/or without attending to that person—but see Stein, Senju, Peelen, & Sterzer 2011.
18. Correani et al. (2006) found that luminosity did support efficient search. However, a series of control experiments showed this to be attributable to local luminance effects and not to luminosity itself.
19. Wolfe and Franzel (1988) had argued that eye-of-origin information and binocular rivalry signals were not available to guide search. However, more recent results suggest some sensitivity to those signals.
20. There is little question that threatening stimuli elicit threat-specific responses as seen, for example, in the responses of phobics to snakes or spiders (LoBue & DeLoache 2008; Rakison & Derringer 2008; Reinecke, Rinck, & Becker 2006). However, there does not appear to be a specific role for 'threat' in guiding search once other features are controlled (e.g. snakes have thin, curvy, and pointed attributes as well as possibly frightening ones).
21. Biological motion is a special stimulus (Blake 1993; Blake & Shiffrar 2007; Johansson 1973), but to date there is not a convincing demonstration that it is capable of supporting efficient visual search. It is possible that motion that implies animacy will have feature status (Gao, McCarthy, & Scholl 2010; Gao, Newman, & Scholl 2009; Gao & Scholl 2011).

Table 2.4 Complicated cases

Complicated		Notes
Faces (familiar, upright, angry, real, schematic, etc.)	D. V. Becker, Anderson, Mortensen, Neufield, & Neel 2011; S. I. Becker, Horstmann, & Remington 2011; Devue, Van der Stigchel, Brèdart, & Theeuwes 2009; Doi & Ueda 2007; Eastwood, Smilek, & Merikle 2001; Frischen, Eastwood, & Smilek 2008; Von Grünau & Anston 1995; Hansen & Hansen 1988; Hershler & Hochstein 2005, 2006; Horstmann, Bergmann, Burghaus, & Becker 2010; Langton, Law, Burton, & Schweinberger 2008; Nothdurft 1993c; D. G. Purcell, Stewart, & Skov 1996; Suzuki & Cavanagh 1995; Tong & Nakayama 1999; VanRullen 2006; M. A. Williams et al. 2002)	22
Other semantic categories (e.g. 'animal')	Levin, Takarae, Miner, & Keil 2001	

Notes:

22. No candidate features have generated more controversy than the family of face features. There are many demonstrations of apparently efficient search for real faces, schematic faces, angry faces, happy faces, and so forth. There are also many papers pointing to feature confounds in these stimuli. There are good reviews in some recent articles on the topic (S. I. Becker et al. 2011; Frischen et al. 2008). In previous versions of this list, faces were placed in the unlikely category (Wolfe and Horowitz 2004) but the literature is so large and so persistent that it seems best to describe the case as 'complicated' and leave its resolution to the future.

Table 2.5 Modulators

Modulators	23
Cast shadows	Rensink & Cavanagh 2004
Amodal completion	Rensink & Enns 1998; Wolfe et al. 2011
Apparent depth	Aks & Enns 1996; Champion & Warren 2008; Wheatley, Cook, & Vidyasagar 2004

Notes:

23. The entries under this category do not appear to be preattentive features in their own right. However, they are properties that seem to be computed prior to the deployment of attention and that have an influence on other basic features. Thus, apparent depth can change the apparent size of an item and it is the apparent size, rather than the retinal or image size, that is critical in search (Aks & Enns 1996). The amodal completion of contours behind occluders can disrupt a feature. Rensink and Enns (1998) showed that the size of an element in the image could be lost when that element was tied to another element by amodal completion. On the other hand, it is possible to create oriented items that are only oriented if unoriented elements are tied together by amodal completion. Though these oriented bars are visually compelling, this orientation feature does not guide attention (Wolfe et al. 2011).

preattentive properties that modulate other guiding attributes without guiding attention in their own right. The referencing is extensive but not exhaustive.

To summarize, there appear to be one to two dozen guiding attributes. Some of these are more powerful directors of attention than others. It seems clear that attributes like colour and motion guide easily and effectively while an attribute like numerosity may guide but only rather weakly. It would be wonderful if we could rank order attributes in terms of their effectiveness. However, while some direct comparison between features has been done (Nothdurft 1993a), a comprehensive hierarchy does not exist. There are hierarchies within dimensions as well. Red really does seem to be a particularly powerful guiding colour, but again, there is a vast amount we do not know, including why a feature like red should be more effective than some other colour. There is plenty of interesting speculation (Changizi, Zhang, and Shimojo 2006).

Guidance by scene-based features: The next frontier

For all the detail and complexity of the feature list already presented, it has become increasingly clear that these features are not the whole story when it comes to describing sources of guidance. This can be illustrated if you look for people in Fig. 2.12. You will not search randomly and you will rapidly find the man on the sidewalk, halfway down the street. Eye movement data indicate that you will search first in locations where people are likely to be (Ehinger, Hidalgo-Sotelo, Torralba, and Oliva 2009; Torralba, Oliva, Castelhano, and Henderson 2006). People are on horizontal surfaces. They do not generally float. In addition, you know something about the size of people. Because you can very rapidly extract the spatial layout of a scene (Greene and Oliva 2009), you should

FIGURE 2.12 Find the two people in this scene. Which one did you find first, and why?

be able to determine if an object is a candidate human on the basis of the interaction of the size of an object in the image and its apparent depth (Sherman, Greene, and Wolfe 2011). Both of these factors may have kept you from noticing the other man, apparently very small and perched on the ledge of the first window on the right. The pixels and the rough local contrast are the same for each man (courtesy of Photoshop) but one target is far more plausible. If you found the plausible target first, it was probably scene guidance that directed your attention. While the classical features can be useful, the apparent efficiency of search in real-world scenes cannot be based on those features alone (Vickery, King, and Jiang 2005; Wolfe, Alvarez, Rosenholtz, Kuzmova, and Sherman 2011).

Our understanding of scene guidance is relatively young but it seems clear that observers make use of what can be called scene semantic guidance (forks are likely to be next to plates) and scene syntactic guidance (paintings hang on walls) (Castelhano and Heaven 2010; Henderson, Brockmole, Castelhano, and Mack 2007; Henderson and Ferreira 2004; Neider and Zelinsky 2006; Vo and Henderson 2009). Some of this guidance is probably relatively slow. After all, you cannot look for forks next to plates until you have identified the plates. However, the guidance that is based on scene structure and category can be based on information that is available very quickly from the global processing of the 'gist' of a scene (Fei-Fei, Iyer, Koch, and Perona 2007; Kirchner and Thorpe 2006; Oliva 2005; Sanocki and Epstein 1997). It is possible to know that you are viewing a man-made, navigable, urban scene before you have selectively attended to the various objects that make up that scene (Greene and Oliva 2009).

Two paths to awareness

The ability to extract some information from scenes without selective attention to objects reflects the working of a non-selective pathway from the stimulus to visual awareness (Wolfe, Vo, Evans, and Greene 2011). The capabilities of this pathway should not be overstated. You will not recognize specific objects without selective attention and binding. However, a non-selective pathway is a useful addition to the diagram in Fig. 2.11. This elaboration is shown in Fig. 2.13. Early visual processing of a scene feeds a non-selective pathway that can provide some information about spatial layout and the gist of the scene. It also feeds the Guiding Representation, here represented by colour, shape, and now gist—a scene guidance component. Finally, early vision provides the input to the selective pathway that supports object recognition. It has a selective attentional bottleneck whose selections are modulated by the Guiding Representation.

At any given moment, the contents of visual awareness include visual 'stuff' at all locations, provided by the non-selective pathway and one (or perhaps a few) bound objects, provided by the selective pathway. A more detailed account of this two-pathway architecture can be found in Wolfe et al. (2011).

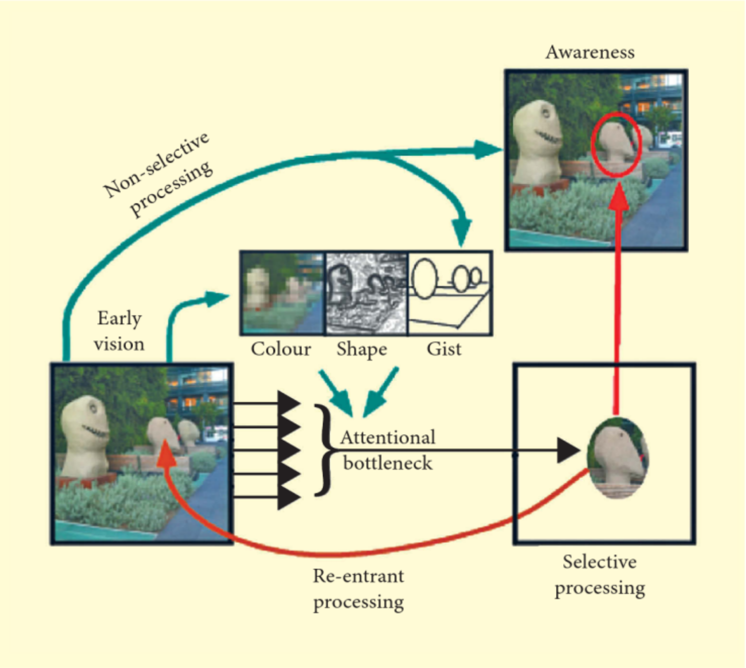

FIGURE 2.13 Guided Search architecture with the addition of a non-selective pathway. The non-selective pathway supports awareness of visual 'stuff' across the entire visual field in parallel. It is capable of limited semantic processing (e.g. of scene 'gist'). It is not subject to the attentional bottleneck and it is not capable of most acts of recognition.

GUIDANCE: THE RULES

The ability of a preattentive feature to guide attention is highly rule-governed. There are general rules that appear to operate over all dimensions and rules specific to a single dimension.

1. The greater the difference, along a preattentive dimension, between the target and the distractors, the more efficient the search (Duncan and Humphreys 1989). Thus, it will be easier to find vertical among 30 deg. tilted items than among 15 deg. tilted items.
2. The greater the differences between the distractors (distractor heterogeneity), the less efficient the search (Duncan and Humphreys 1989). Thus, it may be harder to find vertical among a mix of 15 and 30 deg. tilted distractors than among homogeneous 15 deg. distractors, even though the average difference between target and distractors is greater for the heterogeneous example (Rosenholtz 2001b).
3. The minimum target–distractor difference required to produce efficient search will be much greater than the just noticeable difference for those stimuli. Thus, with attentional scrutiny, it is possible to tell the difference between a vertical line and one tilted 1–2 deg. from vertical. It is not possible to search efficiently for vertical among 2 deg. distractors. Efficient search will require something more like 10 to 15 deg. differences (Foster and Ward 1991b; Foster and Westland 1998).
4. For purposes of guidance, differences are greater across categorical boundaries. It will be easier to find a steep item among shallow items than to find the steepest item among other steep items even if the angular differences are the same in the two conditions (Wolfe, Friedman-Hill, et al. 1992).
5. The detailed properties of guiding attributes need to be worked out separately for each attribute and are not necessarily predicted from conscious perception of the attribute. As noted earlier, for purposes of guidance, pink/peach/skin(?) colours seem to have special status (Lindsey et al. 2010). As another example, in orientation, one might wonder if guidance is represented in a 90 deg. or 180 deg. framework. Obviously, a simple line has the same orientation after a 180 deg. rotation but a polar object (e.g. a Christmas tree or sailboat) does not have the same appearance after a 180 deg. rotation. Visual search ignores object polarity. The biggest orientation difference is 90 deg., not 180 deg. (Wolfe et al. 1999).
6. Guidance will be stronger if the observer sees the actual guiding feature (e.g. the colour ‘red’) rather than merely the name of the feature (e.g. the word ‘red’) just prior to the appearance of the search display. This priming can be produced by a deliberate cue before the onset of the trial (Wolfe, Horowitz, Kenner, Hyle, and Vasan 2004). Similarly, finding the target on one trial effectively

primes that feature for the next (Kristjánsson and Driver 2008; Maljkovic and Nakayama 1994).

7. It is easier to find the presence of a feature than to find its absence. This is the root of many search asymmetries (Treisman and Gormican 1988; Treisman and Souther 1985) in which the search for A among B is notably more efficient than the search for B among A. Thus, it is easier to find the presence of a moving target among stationary distractors than to find a stationary target among moving distractors (Dick et al. 1987; Royden et al. 2001; Horowitz et al. 2007). There is a great deal more to be said about asymmetries (Wolfe 2001), much of it first said by Treisman, as noted above. Rosenholtz has noted that the designs of asymmetry experiments are sometimes themselves asymmetrical (Rosenholtz 2001a) and this is worth keeping in mind when evaluating search asymmetry results.
8. Not all search asymmetries are evidence for the preattentive processing of the stimulus property under study. Sometimes it is easier to find A among B than B among A, not because A pops out, but because it is easier to reject a succession of Bs as distractors. In these cases, both A vs B and B vs A tend to produce inefficient slopes. Thus, for example, if there is a real 'anger superiority effect' (Hansen and Hansen 1988), it may not be that 'angry' pops out, but rather that angry faces hold attention, making it harder to move through them when they are the distractors. As a result, search for an angry target among easily dismissed, happy distractors is more efficient than search for a happy target among hard-to-dismiss, angry distractors, but neither of these searches will be efficient.
9. It is possible to guide by more than one feature at a time. In Guided Search, this is how relatively efficient conjunction search is accomplished. If there are several target features, you can guide your attention to all of them. Indeed, higher-order conjunctions with three or even six defining features can be easier than the classic two-feature conjunction search (Wolfe et al. 1989; Wolfe 2010). There is a debate about how this is accomplished. We have argued that it is possible to simultaneously guide to multiple features (Friedman-Hill and Wolfe 1995). Huang and Pashler argue that guidance to multiple features must be done in a series of nested steps. For example, one might select all red items and then select the vertical items within the red set (Huang and Pashler 2007, 2012).
10. It is not possible to guide to two features from the same dimension/attribute at the same time. Conjunctions of two colours or two orientations are inefficient (Wolfe et al. 1990). Even though it is easy to identify an item that is red and yellow, it is not efficient to search for that item among red/blue and blue/yellow distractors.
11. It is relatively efficient to search for a conjunction of an item of one colour with a part of another colour. (Find the red thing with a yellow part among red things with blue parts and blue things with yellow parts.) This suggests that the

preattentive representations of objects have some part–whole structure to them (Wolfe, Friedman-Hill, and Bilsky 1994). Interestingly, search for orientation x orientation conjunctions of items with part–whole structure is not efficient. The vertical item with an oblique part is relatively hard to find amidst vertical items with horizontal parts and horizontal items with oblique parts (Bilsky and Wolfe 1995). The difference between colour and orientation could be due to different susceptibility to rotation. If you tilt your head, a red thing with a yellow part is still a red thing with a yellow part. A vertical thing with a horizontal part might not be rotationally invariant in the same way.

GUIDED SEARCH 2013: HOW DO WE SEARCH?

Figure 2.14 elaborates on Fig. 2.13 to provide a roadmap of the steps in visual search as imagined by the 2013 incarnation of the Guided Search model. Sections below refer to the letters on the figure:

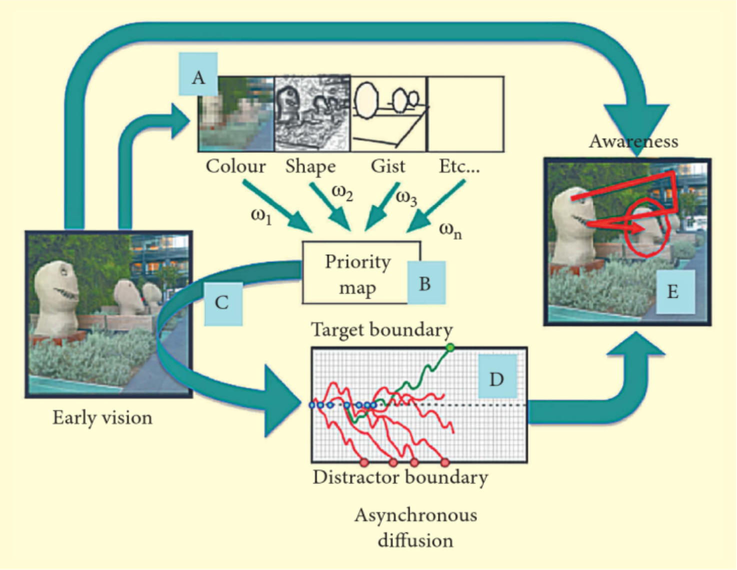

FIGURE 2.14 Guided Search 2013: A. A set of attributes, including scene-based attributes like gist, is derived from early visual processing. B. A priority map is created from a weighted average of those sources of guidance. C. The priority map controls selection of items, one after another, for binding and recognition. D. Binding and recognition are modelled as a diffusion process. Since the diffusion takes longer than the time between attentional selections, the result is an asynchronous diffusion with multiple items in process at the same time. See text for further details.

A. As described in the figure, a set of basic attributes is extracted from the early stages of visual processing. For each attribute, two forms of guidance are possible. *Bottom-up guidance* is stimulus-driven, based on local differences. Bottom-up guidance is essentially the same as 'salience' (Nothdurft 2000; Donk and van Zoest 2008; Lamy and Zoaris 2009). *Top-down guidance* is user-driven, based on what the observer's current understanding of the task demands. Thus, returning to Fig. 2.8, if you are looking for a red T, colour guidance will be directed to red. If you are looking for a black T, guidance will be directed to black. Nothing has changed in the stimulus or in the bottom-up salience of items. It is the top-down guidance that changes in this case. When neurophysiological studies refer to attention to multiple items in parallel (e.g. enhancing neural responses of all red items), they are generally describing what we refer to as top-down guidance (Bichot, Rossi, and Desimone 2005; Treue and Trujillo 1999; Carrasco, Eckstein, Verghese, Boynton, and Treue 2009).

The top-down/bottom-up terminology is not entirely unambiguous. Consider priming effects. Exposure to red will speed subsequent search for red. We have described this as a form of implicit top-down guidance (Wolfe et al. 2004) because something about the observer—in this case, their history—has changed the guidance of attention. Response to the same stimulus would be different if the observer's history was different. Others see priming as an automatic process that should be considered to be 'bottom-up' (Kristjánsson and Campana 2010).

B. Guidance by different attributes is combined into a 'priority map'. In the first versions of Guided Search this was called an 'activation map'. 'Priority map' (Serences and Yantis 2006) better captures the role of this representation, which is to prioritize items in the visual input for selective attention, binding, and recognition. In the absence of top-down guidance, a priority map built from pure bottom-up signals would be a 'salience map' (Koch and Ullman 1985; Itti and Koch 2000; Parkhurst, Law, and Niebur 2002). Each attribute makes a weighted contribution to the priority map. Thus, if you are looking for red vertical items, the weights on colour and orientation will be set high and other attributes will be de-emphasized. In order to guide to 'red', one can imagine either setting a high weight for a separate feature, 'red', or enhancing red within the colour module and setting a high weight for guidance by colour. See the work on 'dimension weighting' for more detail on this issue (Found and Muller 1996; Muller, Reimann, and Krummenacher 2003; Zehetleitner, Krummenacher, Geyer, Hegenloh, and Müller 2011).

Weights can be adjusted but not to the full extent that the user might wish. Notably, it does not seem possible to set the weight on bottom-up salience signals to zero. There has been a long-standing debate about what sorts of salient signals capture attention. Claims have been made for luminance onsets (Jonides and Yantis 1988; Yantis and Jonides 1990), new objects (Yantis 1993), and for many specific attributes (Franconeri and Simons 2003; Rauschenberger 2003; Turatto and Glafano 2000; Pratt, Radulescu, Guo, and Abrams 2010). There are generally counterclaims (Gibson and Kelsey 1998), but on balance, it seems that a highly salient signal from an irrelevant attribute will have some influence on the course of search, regardless of the desires of the searcher.

Some researchers are not fond of the idea of a priority map (Chan and Hayward 2009; Huang and Pashler 2012). However, while the details vary, some version of such a map is a part of many models of search and has been the subject of much neurophysiological investigation (Bisley and Goldberg 2010; Fecteau and Munoz 2006; Gottlieb, Balan, Oristaglio, and Schneider 2009; Li 2002; Thompson and Bichot 2004).

C. The priority map is so named because its role is to prioritize the selection of items. Since Koch and Ullman (1985), it has been proposed that something like a winner-take-all operation selects the next item for attention. This is straightforward for the first selection in an image but what about subsequent selections? The critical question is whether attention ever revisits the same location/item during the course of a search. The original assumption was that items were not revisited. This was the assumption of Feature Integration and the first versions of Guided Search. The phenomenon of 'Inhibition of Return' (IOR) seemed to provide a mechanism to prevent resampling from the display (Klein 1988; Posner 1980) since IOR showed that it was harder to get attention back to a previously attended item than to direct attention to a previously unattended item. However, subsequent results suggested that IOR probably only marked the most recently attended items (Abrams and Pratt 1996; Pratt and Abrams 1995; Tipper, Weaver, and Watson 1996) making it hard to see how this mechanism could prevent revisitations once the set size becomes large.

Horowitz and Wolfe did a series of experiments designed to directly test if items were being sampled with or without replacement during visual search and came to the conclusion that 'visual search has no memory' (Horowitz and Wolfe 1998, 2003)—at least, no memory for the deployments of covert attention. Their data were consistent with sampling with replacement, giving no role to IOR or other means of preventing revisitation. Other evidence suggested that this claim might be too strong (Peterson, Kramer, Wang, Irwin, and McCarley 2001; Shore and Klein 2000; Takeda 2004). Over the short timescale required for many standard laboratory search tasks, it seems most likely that neither extreme position is correct. Items are not sampled entirely without regard to the prior history of search but neither are they inhibited in a manner that can prevent some resampling. In Klein's words, inhibition of return appears to be a 'foraging facilitator' (Klein and MacInnes 1999), one of several mechanisms that bias attention toward new items during search (Klein 2009).

When search is more prolonged, as it is in many real-world tasks, strategic plans can play a role in preventing revisiting. Reading is a simple example. If you search this page of text for the word 'covert', you will most likely start at the top left and read the page in a manner that eliminates most resampling from the display without requiring specific inhibition of or memory for rejected items. Your prospective plan of search serves the role that memory would serve (McDaniel, Robinson-Riegler, and Einstein 1998). Similar factors are probably at work in many real-world searches (Hollingworth 2009; Hollingworth and Henderson 2002).

D. In the 2013 version of Guided Search, the recognition/classification of an object is modelled as a diffusion process (Ratcliff 1978). While we have used a Ratcliff-style diffuser, there is, at present, no reason to choose between any particular member of the class of models in which information accumulates toward a threshold over time (Brown and Heathcote 2008; Donkin, Brown, Heathcote, and Wagenmakers 2011; Purcell et al. 2010). The unique aspect of the Guided Search version is that it proposes an *asynchronous* diffusion process. That is, items are selected one at a time and begin diffusing toward a target or distractor boundary once they are selected. Since the rate of selection (say, 20–40 Hz) is faster than the time required to identify an item (say, 150–300 msec), multiple items are diffusing at the same time. Metaphorically, this can be seen as a 'pipeline' or a 'carwash' (Moore and Wolfe 2001; Wolfe 2003), albeit a carwash in which one car could enter second and leave first.

This architecture is a hybrid of serial and parallel processing (E. Cohen and Ruppin 1999; Herd and O'Reilly 2005; Thornton and Gilden 2007; Townsend and Wenger 2004; Verghese 2001). Selection is imagined to be strictly serial though nothing very dramatic would change if a small number of items could be selected at one time. Diffusion is parallel in the sense that multiple items are undergoing the process of binding and recognition at the same time.

Diffusion models produce the positively skewed reaction time distributions that are characteristic of visual search (E. M. Palmer, Horowitz, Torralba, and Wolfe 2011; Wolfe, Palmer, and Horowitz 2010). Errors are produced when a distractor reaches the target boundary or a target reaches the distractor boundary. An error could also be generated if the search was terminated with a guess (see next section). Changes in the parameters of the diffuser can be used to model various effects seen in the data. Thus, if the boundaries are brought closer together, the error rate will rise and the RTs will decline; a speed-accuracy trade-off. False alarms and miss errors can be traded off against each other by changing the starting point of the diffuser.

When do we stop?

The architecture of Fig. 2.14 makes the process of finding a target reasonably clear. With some preattentive guidance, items are selected into the diffuser and search ends when one of those items goes over the target boundary. But what happens if there is no target or if no item reaches the target boundary or if there are an unknown number of targets in the display? At some point, search must end. When is it time to quit? Feature Integration assumed that observers would quit when all items had been examined on target absent trials (or almost all, with miss errors produced when observers quit without checking the target). Early versions of Guided Search argued that observers searched through all items that received guiding activation above some threshold. Neither of these accounts works well if distractors are not perfectly tracked during search. Moreover, in real scenes, it is completely unclear what the 'set size' might be or what it would mean to attend to all items (Wolfe, Alvarez, et al. 2011).

A different approach adds another diffuser to the model. In this diffuser, a signal accumulates over time and the trial is terminated when that signal crosses a quitting threshold. The threshold is set dynamically, based on the observer's experience. After quitting correctly, the quitting threshold moves down, causing the observer to quit more quickly. After an error, it rises and the observer becomes more cautious about quitting. This adjustment can be observed in the pattern of RTs in search experiments (Chun and Wolfe 1996; Ishibashi, Kita, and Wolfe 2012).

Experiments that manipulate target prevalence are useful in constraining models of quitting behaviour in search (Colquhoun and Baddeley 1967; Fleck and Mitroff 2007; Wolfe, Horowitz, and Kenner 2005; Wolfe et al. 2007; Wolfe and VanWert 2010). When targets are rare, miss errors rise, false alarms fall, and RTs become shorter. If targets are common, miss errors fall, false alarms rise, and RTs become longer. To see this full pattern of behaviour, it is important to use stimuli that are ambiguous enough to produce false-alarm errors. Classic search experiments (find the T among Ls, etc.) tend not to produce false alarms. In contrast, real-world tasks like breast cancer screening (Wolfe, Birdwell, and Evans 2011) or airport baggage screening are characterized by ambiguous stimuli and very low prevalence. Wolfe and VanWert (2010) found that the effects of prevalence could be modelled as a change in criterion (which would be represented by a change in the starting point of the diffuser in Fig. 2.14) and a concurrent change in a quitting threshold. At low prevalence, the starting point moves toward the distractor bound, making miss errors more common, and the quitting threshold drops, making RTs shorter (and also increasing miss errors, if one assumes an 'absent' response when the quitting threshold is reached). Models that adjust only the starting point or only the quitting threshold, fail to capture the pattern of the data. It should be noted that search termination remains a complex and underinvestigated topic.

WHAT WE DIDN'T DISCUSS

Having discussed search termination, it is time to consider chapter termination. Before ending, it is worth noting that there are a number of important topics that have been largely omitted here. Some of these will be discussed elsewhere in this volume. Any complete account of search would include some treatment of:

Eye movements: What is the relationship between covert deployments of attention and overt deployments of the eyes (Hwang, Wang, and Pomplun 2011; Kowler 2011; Malcolm and Henderson 2010; Neider, Boot, and Kramer 2010).

The psychophysics of simple searches: There is an important body of work on the fine-grained details of simple searches. The tasks used in these studies permit a degree of control that is not common in standard search tasks and not possible in real-world search tasks (Najemnik and Geisler 2005; J. Palmer, Verghese, and Pavel, 2000; Cameron, Tai, Eckstein, and Carrasco 2004; Dosher, Han, and Lu 2010; Baldassi and Verghese 2002).

Memory in repeated search: What happens when the same scene is searched more than once? Contextual cueing shows learning (Brockmole and Henderson 2006; Chun and

Jiang 1998; Kunar, Flusberg, Horowitz, and Wolfe 2007). Repeated searches through simple, laboratory-style search displays do not produce an improvement in search efficiency (Wolfe, Klempen, and Dahlen 2000) but there is learning in repeated search through real scenes (Hollingworth 2009; Hollingworth and Henderson 2002; Vo and Wolfe 2012).

The neural basis of search: What might be the neural locus and operation of a priority map (Serences and Yantis 2006; Shipp 2004; Bisley and Goldberg 2010) or a diffuser (Ratcliff, Philiastides, and Sajda 2009) or a serial selection process (Buschman and Miller 2009; Chelazzi 1999) or set size effects (J. Y. Cohen, Heitz, Woodman, and Schall 2009)?

Of course, this is merely a sampling of the topics that have been studied from a neural perspective and a sampling of the topics, important to search, that have been omitted from this chapter.

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CHAPTER 3

LOAD THEORY OF ATTENTION AND COGNITIVE CONTROL

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INTRODUCTION

In order to achieve our goals successfully in today's busy world, we need to attend selectively to relevant information and avoid distraction by irrelevant information. To get a sense of the importance of this selective attention process, you only need to imagine trying to read this chapter in a busy city street, such as Oxford Street in central London. Without the ability to focus on the book, you would be faced with the challenge of understanding black letters on white paper amid a colourful clutter of sights and sounds (including jostling crowds, tempting shop windows, blaring sirens, and even a range of smells!) The ability to control your processing of the background information is essential if you are ever to get to the end of the chapter.

However, our everyday experience portrays a complex and somewhat puzzling picture of this ability. At times, we notice every little distraction, from the humming of the computer fan to the distant sound of people talking outside. At other times, we become so absorbed in a task that we may even miss someone talking directly to us. This everyday experience was reflected in the mixed pattern of empirical findings which emerged over decades of research starting in the 1950s: some experiments suggested that people could be highly selective, other experiments found high levels of distraction. Load theory set out to resolve this puzzle. What governs our ability to focus? Why are we sometimes highly distracted by information we wish to ignore when at other times we regrettably fail to notice important information? In this chapter we describe load theory and the evidence to support it, as well as reviewing the mechanisms that are proposed to underlie the observed load effects. We also highlight some of the theory's wider influences in areas as diverse as emotion processing, developmental psychology, and the understanding of psychological disorders. Although there is some interesting current work examining the effects of processing load as they might occur between and within sensory modalities other than vision, the current review focuses only on evidence from the visual domain.

BACKGROUND

Attention research began with Broadbent's (1958) seminal 'filter model' which proposed that the perceptual system has limited capacity and must therefore be protected from overload by an attentional filter that excludes unattended information at an early stage of processing, as soon as rudimentary analysis of the simple perceptual features of the input is complete. This was termed an 'early selection' model, because of the central claim that the filter acted relatively early in the processing stream. The model provided a good account for observations that people were often unable to report the contents of unattended information channels (for example, information presented to one ear while people attended to the other ear, e.g. Cherry 1953). However, it could not accommodate subsequent findings indicating that unattended information could in fact be perceived beyond the level of simple physical features. For example, messages to the participants that were inserted in the unattended channel (e.g. 'you may stop now') were sometimes perceived if they were preceded by the mention of the participant's own name (Moray 1959). This suggests that people were in fact able to process the semantic meaning of some of the ignored information (otherwise they would not have been able to recognize their name). These findings drove the development of a rival filter model, which proposed that attention acts at a much later stage of processing, filtering out irrelevant information from post-perceptual processes such as memory and overt responses, but allowing full perception of all information before unattended information is filtered out (Deutsch and Deutsch 1963). This was therefore termed a 'late-selection' model.

The stage was now set for a debate between the early and late selection positions which generated around forty years of research and discussion (see Driver 2001; Lavie 2006; Lavie and Tsal 1994, for more detailed overviews of this debate and its research). Load theory set out to provide a resolution between the two positions.

The central tenet of load theory (e.g. Lavie 1995, 2005, 2010) is that perceptual processing can only become selective when the limits of perceptual capacity are reached. If a task imposes sufficient demands to exceed capacity, task-irrelevant items are not processed and can therefore be successfully ignored (in other words, early selection can occur). By contrast, if a task imposes only low perceptual demands, the remaining capacity is automatically allocated to the processing of task-irrelevant items, which may then cause distraction (reflecting late selection). Load theory thus proposes a resolution for the early/late selection debate in suggesting that both types of selection can occur, depending on the perceptual demands of the task at hand. The theory also highlights the importance of higher-level cognitive mechanisms (such as working memory) that provide a form of 'executive' control in determining whether or not distraction can be avoided. These will be discussed later in the chapter.

PERCEPTUAL LOAD

Studies of perceptual load have used a range of load manipulations and a wide variety of measures of the extent to which irrelevant information is processed. Perceptual load can be manipulated through varying either the number of items in the display, or the perceptual similarity between the display items, or the processing requirements of the task. Irrelevant information processing can be measured either through behavioural indices of distractor interference (including response competition, negative priming, attentional capture, and so forth) or through reports about awareness of task-irrelevant items (or lack of it—a phenomenon known as inattentional blindness) or through neural measures of the brain response to the irrelevant stimuli. The studies reviewed below will provide examples of all these manipulations and measures.

The role of perceptual load in distractor interference

The first tests of the theory's predictions concerning perceptual load used the response competition paradigm: a well-established measure of distractor interference. In a typical task, participants make speeded responses according to which of two target letters (e.g. X or N) is present in a search array. An irrelevant distractor letter is also presented, typically in the periphery and well separated from the target. Distractor interference is assessed by measuring reaction times to the target as a function of the distractor's congruency with the target response. The distractor can either be congruent (e.g. X when the target is X), incongruent (e.g. X when the target is N), or neutral (e.g. the letter L which has no response associations in this example). Distractor interference is inferred from the slowing of reaction times in the presence of incongruent distractors as compared with congruent or neutral distractors. Distractor interference as measured in this way is typically reduced under high (vs low) perceptual load. For example, Lavie (1995) modified this response competition task to manipulate the level of perceptual load in the target processing. In some experiments, the target letter was presented in one of six central positions, either alone (low load) or among five other letters that were similar to the target (high load; see also Lavie and Cox 1997). In other experiments, load was manipulated by varying the processing requirements within the same target displays, requiring feature detection (e.g. blue or red) under low load or a complex feature conjunction discrimination (e.g. of colour, shape, and position) under high load. Regardless of the load manipulation used, distractor interference was reliably reduced under high (vs low) perceptual load, in support of the predictions of load theory.

One might ask, however, whether the reduced response competition effects seen under high load could in fact reflect an increase in active suppression of responses to the distractor under high load (i.e. a late-selection effect, whereby the distractor is perceived but the response towards it is inhibited), rather than the reduction in perceptual processing of the distractor (i.e. an early-selection effect) that load theory predicts. Lavie and Fox (2000) investigated this issue directly. They presented participants with pairs of letter search displays (a 'prime' display followed by a 'probe' display). On some trials, the letter that had served as the distractor in the prime display became the target in the subsequent probe display—a manipulation which would normally be expected to lead to negative priming (whereby people are slower to respond to a target if they have just ignored it on the previous trial). Since negative priming effects clearly indicate distractor perception, load theory predicts that they should only occur in conditions of low perceptual load. Indeed, these negative priming effects were observed as predicted under low perceptual load. However, across several experiments, negative priming was eliminated under high-load conditions. This rules out an account for perceptual load effects in terms of response inhibition, because an increase in inhibition of the distractor responses would lead to increased (rather than decreased) negative priming effects. Instead, the observed decrease in negative priming under high load provides additional support for perceptual load theory, in suggesting that perceptual processing of distractors is reduced under high perceptual load.

Interestingly, there is now evidence to suggest that the processing of potentially high-priority distractors can also be modulated by the perceptual load of the relevant task. For example, Beck and Lavie (2005) modified the response competition task described above in order to allow a comparison between processing of distractors presented in the periphery of the display and those presented at fixation (i.e. right where the participants were looking). Distractors at fixation caused twice the interference effects, reflecting their relative processing priority compared with distractors in the periphery. However, perceptual load modulated the interference from both types of distractor to similar extents, demonstrating that even high-priority distractors are subject to the influence of perceptual load. This claim is strengthened by a study of distraction by colourful and highly attention-capturing famous cartoon characters (e.g. Spiderman). Forster and Lavie (2008) presented the task-irrelevant characters alongside a letter search display and measured the extent to which they captured participants' attention (by comparing search reaction times when the characters were present vs absent). Despite being completely irrelevant to the task, the cartoon characters caused significant distraction, indicating that they were highly attention-capturing. However, even this interference by highly salient stimuli could be modulated by the perceptual load of the relevant task, indicating, in line with Beck and Lavie (2005), that even high-priority distractors can be rejected from processing under high perceptual load.

Whereas all the measures discussed above tested processing of externally generated stimuli, there is also evidence to suggest that perceptual load can modulate distraction by internally generated information, as measured in terms of task-unrelated thoughts (or 'mind wandering'). Forster and Lavie (2009) presented participants with a letter search task of either high or low perceptual load. Following each trial, participants were also asked to report whether their thoughts during performance had been related to the task (e.g. 'oops, I've pressed the wrong button') or unrelated to the task (e.g. 'I must stop by the supermarket on the way home'). Participants consistently reported lower levels of mind wandering under high (vs low) perceptual load, suggesting that even the processing of internally generated information may be dependent on the perceptual load of an ongoing task. Thus people's ability to avoid distraction from numerous sources depends on the level of demand imposed by the relevant task.

This conclusion has important applied implications. Perceptual load could improve performance in a range of everyday tasks, including, for example, learning and education, both in non-clinical populations and in people who may be more vulnerable to distraction (e.g. children with ADHD). Indeed, recent evidence suggests that people's performance is influenced by the effects of perceptual load regardless of their individual level of distractibility in everyday life. Forster and Lavie (2007) divided participants according to their responses on the Cognitive Failures Questionnaire (CFQ; Broadbent, Cooper, FitzGerald, and Parkes 1982), which is designed to measure individual differences in the extent to which people tend to become distracted during daily life. Under low perceptual load, the low-CFQ group experienced significantly more distractor interference in a standard response competition task than the high-CFQ group, but distractor processing was eliminated under high load for both CFQ groups. Thus even highly distractible people experience reduced distraction under high perceptual load. This finding highlights the important potential applications of this type of behavioural research to daily-life situations.

Overall, there is now broad agreement from a range of different behavioural studies that distractors interfere more under low perceptual load than under high load, supporting the central claim of load theory that successful selective attention can only be achieved if the demands of the relevant task are sufficient to exhaust perceptual capacity. It is particularly important to note that these behavioural findings have generalized across a number of different experimental designs when evaluating potential alternative claims. For example, the 'dilution account' (e.g. Tsal and Benoni 2010; Wilson, Muroi, and MacLeod 2011) suggests that distractor interference may be reduced in displays of larger (vs smaller) set size, not due to higher perceptual demands under the larger set size but due to 'dilution' of the distractor by the increased number of non-target items. Dayan and colleagues have made similar arguments in support of their Bayesian model of load effects within the response competition task, claiming that the additional noise from the non-targets under high load reduces the informative value of the large receptive fields containing the distractor and thus reduces their influence on inferences about the target identity (e.g. Dayan 2008). However, as described above, the effects of perceptual load have generalized across a range of different distractors, many of which do not share features with the targets and non-targets, meaning that their interference cannot be explained by either of these suggestions. For example, the large and colourful cartoon characters that were used as distractors by Forster and Lavie (2008) shared few features with the letters used in the relevant search task and were also far more salient than those letters. Thus the reduced influence of the distractors under high load in that study cannot be explained in terms of dilution of the large, colourful distractors by the extra letters present in the high-load display (see Lavie and Torralbo 2010, for a more detailed discussion). The lack of feature overlap also means that distractors such as these do not have any informative value with respect to the target and so cannot influence any inference regarding the target identity even in the low-load conditions in which target decisions are influenced by information processed within large receptive fields (as proposed by the Bayesian account). In addition, perceptual load has often been manipulated without any increase in the number of display items, giving rise to effects that cannot be explained by either of these alternative accounts. We describe such examples in more detail in the next section.

The role of perceptual load in visual perception

The distractor-interference measures described so far provide only an indirect test of the theory's claims concerning perceptual processing. This is because distractor-interference effects on reaction times may also be influenced by the additional processes occurring between perception and the eventual response (e.g. semantic processing and response-related decisions). A more straightforward test of the theory's predictions is provided by studies using direct measures of visual perception. This research has demonstrated that load plays a critical role in visual perception from the very early stages of visual processing (including those that are not yet conscious) to the higher-level processing that dictates our subjective visual awareness.

A clear example of the importance of load in determining whether stimuli are perceived comes from the phenomenon of inattentional blindness. The original findings were reported by Neisser and Becklen (1975) who superimposed two videos, one of a hand-shaking game and one of a ball game. Participants were asked to monitor one of the two videos (pressing a button in response to certain target events) while ignoring the other video. Most participants failed to notice unexpected events in the unattended episode (for example, only five of the twenty-four people attending to the hand game noticed that the original male players were replaced with female players!). These results provide indirect support for perceptual load theory, because the continuous video monitoring task is likely to have imposed high perceptual demands. This suggestion is supported more directly by a finding from the well-known recent demonstration of inattentional blindness, in which the attended event (a basketball game) and the unexpected event (the appearance of a person dressed as a gorilla) are presented within the same video (Simons and Chabris 1999). Participants in this study were more likely to notice the gorilla when performing an 'easy' task (counting the number of passes made) than when performing a more demanding task (maintaining two separate counts for the number of bounce passes and aerial passes). However, in both these studies, the task of monitoring the videos will have required eye movements pursuing the attended events, which is likely to have led to blurring of the unattended events on the retina. In other words, participants may have failed to report the ignored events not due to inattention but because they were in fact less visible due to a blurred image on the retina. This account could also be applied to the difficulty manipulation used in Simons and Chabris's (1999) study if one assumes that the hard task is likely to have required more eye movements than the easy task. In this case, the gorilla may have simply been less visible during performance of the hard task due to a greater rate of eye movements leading to increased retinal blurring under those conditions.

Cartwright-Finch and Lavie (2007) aimed to provide a clearer test of the prediction of load theory that awareness of task-irrelevant items should be reduced under high (vs low) load in a relevant task. They manipulated load within an inattentional blindness paradigm (originally developed by Mack and Rock 1998) in which display presentation is so brief that eye movements cannot occur during its duration. Participants carried out a visual discrimination task, determining either which line of a cross shape was blue (the horizontal or the vertical) or which of the cross lines was longer. Because the colour discrimination was very clear (one line was blue and the other was green) while the length difference was very subtle, the colour task involved low perceptual load and the length task involved high perceptual load for the very same stimulus. Participants were subsequently asked whether they noticed a small extra stimulus presented without warning in the periphery of the display on the last trial. Cartwright-Finch and Lavie found that participants in the high-load condition were much less likely to detect the unexpected peripheral stimulus than participants who were carrying out the low-load task. Since eye movements could not occur during the brief displays used, the inattentional blindness results are not open to alternative explanations in terms of blurring on the retina during eye movements. The findings thus provide strong support for the claim that perceptual load modulates people's susceptibility to inattentional blindness. Macdonald and Lavie (2011) have recently extended these findings to show that inattentional deafness (the failure to notice the appearance of an auditory stimulus while attending to an unrelated task) also depends on the level of visual perceptual load.

However, in all these studies awareness was measured retrospectively, by presenting participants with a surprise question about their noticing of an unexpected stimulus after the event. It is therefore possible that the failure to report this stimulus could reflect memory-related rather than perceptual processes (e.g. Wolfe 1999). This issue was addressed by Macdonald and Lavie (2008) in a modified inattentional blindness paradigm in which an expected task-irrelevant stimulus was presented on multiple trials. Participants were asked to make button-press responses whenever they noticed the stimulus, allowing Macdonald and Lavie to measure participants' sensitivity in detecting it. As predicted by load theory, detection sensitivity was reduced under high (vs low) perceptual load in a central letter search task, strengthening the claim that the effects of perceptual load on conscious awareness reflect perceptual rather than memory-related processes.

Studies that have established effects of perceptual load on early vision further support this interpretation. For example, Carmel et al. (2007) demonstrated that the fundamental ability to detect whether a point of light is flickering or continuous was significantly reduced under conditions of high (vs low) perceptual load in an unrelated visual task. Another study investigated the process whereby a peripheral visual stimulus presented against a background of dynamic visual noise tends to disappear from awareness after a few seconds' viewing. This process (referred to as 'filling in') was more likely to occur, and tended to occur more quickly, under low (vs high) perceptual load, indicating clear effects

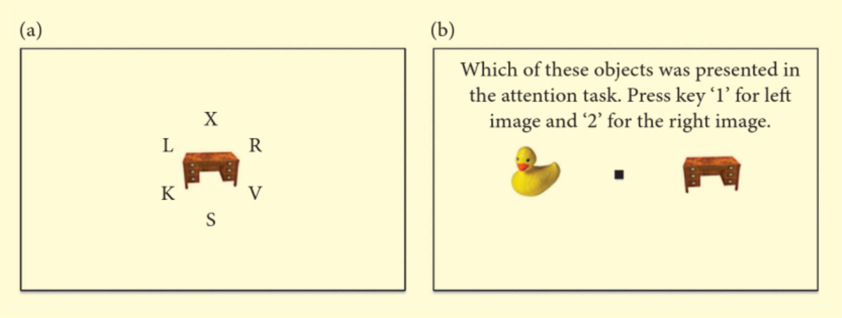

FIGURE 3.1 Examples of the stimuli used by Lavie et al. (2009, Experiment 5). Panel (a) shows a stimulus display from the high perceptual load condition. Participants were asked to report the identity (X or N) of the target letter (contained in the letter circle) while attempting to ignore the central distractor object. In the low perceptual load condition, the non-target letters were all Os. Panel (b) shows the surprise recognition test, presented after the selective attention task. Participants were asked to indicate which of the two objects had been presented as an irrelevant distractor during the attention task they had just performed. Recognition rates in the memory test were significantly higher under low perceptual load (M = 65%, *SE* = 3) than under high load (M = 50%, *SE* = 3.6), *t(11)* = 3.170, *p* ⟩.01. Reproduced from Lavie, N., Lin, Z., Zokaei, N., Thoma, V., The role of perceptual load in object recognition, *Journal of Experimental Psychology: Human Perception and Performance*, 21, 42–57, experiment 5 © 2009, The American Psychological Association.

of attention on what might otherwise have appeared to be a low-level visual phenomenon (Weil et al. 2012). Using a similar logic, Lavie et al. (2009; see Fig. 3.1) demonstrated that recognition of distractor objects was reduced under high (vs low) perceptual load, casting doubt on earlier claims that view-dependent object representations are formed automatically and do not require attentional capacity (e.g. Hummel and Stankiewicz 1996).

Whereas all the studies described so far have measured processing of visible distractors, there is also evidence that perceptual load can even influence the processing of distractors that do not reach conscious awareness. For example, Bahrami et al. (2008) tested participants' adaptation to 'invisible' oriented gratings in the periphery (which were presented monocularly and masked by a simultaneous stimulus presented to the other eye at the same retinal location, so that the gratings did not reach conscious awareness). Successful adaptation was observed when a concurrent visual task at fixation was of low perceptual load, but adaptation was eliminated under high perceptual load, suggesting that even the unconscious processing of distractors that do not reach awareness can be modulated by the perceptual load of a relevant task.

Effects of perceptual load on neural processing

The load effects on perception described so far are underpinned by load modulations of sensory neural processing in visual cortex. These have been established in numerous fMRI studies where neural activity is measured in the precise sensory brain area that mediates perception of the particular distractor stimulus presented. Load theory predicts that high perceptual load will reduce the neural response to the distractor as measured in this way.

Rees, Frith, and Lavie (1997) tested this prediction using irrelevant motion distractors in order to take advantage of the fact that the neural markers of motion perception are very well delineated (for example, area V5/MT is known to respond selectively to moving (vs static) stimuli). Rees et al. asked participants to focus attention on written words presented one at a time at the centre of the screen. In the low-load condition they responded according to whether the words were presented in upper- or lower-case letters, whereas under high-load they discriminated bisyllabic words from mono- or trisyllabic words. The screen surround was filled in with dots which were either static or moving in a radially expanding pattern. As predicted, increased load in the word perception task reduced motion-related activity in V5/MT (as well as in the other motion-responsive areas, e.g. the superior colliculus).

Since then, a large number of studies of this type have identified clear modulation by perceptual load of neural responses to distractors throughout visual cortex and even in some subcortical areas. For example, it is well known that inferotemporal cortex mediates perception of meaningful visual objects. Pinsk, Doniger, and Kastner (2004) found that responses in this area to a wide variety of distractor images were drastically reduced under high (vs low) perceptual load in an attended task. Similarly, Yi et al. (2004) found that a brain area that is known to respond to places (known as the parahippocampal place area; Epstein and Kanwisher 1998) no longer responded to pictures of places under conditions of high (vs low) load in an attended task. Moreover, they found that the neural signature of adaptation to repeated stimuli (known as 'fMR adaptation', Grill-Spector and Malach 2001; or 'repetition suppression', Henson and Rugg 2003) was no longer seen under high load.

These demonstrations have now been extended to areas as early in the visual processing stream as V1 (e.g. Bahrami, Lavie, and Rees 2007; Schwartz et al. 2005; see Fig. 3.2) and even the subcortical lateral geniculate nucleus—the gateway to visual cortex (O'Connor et al. 2002). Sensory processing in these early visual areas is highly likely to reflect early perceptual processing that has not yet reached conscious awareness. Indeed, Bahrami, Lavie, and Rees (2007) directly addressed the effects of load on early unconscious processing. They used the continuous flash suppression method whereby a strong flashing mask presented to one eye suppresses awareness of stimuli presented to the other eye (rendering them literally invisible for periods as long as 20 seconds) and manipulated perceptual load for an attended stimulus that was presented centrally to both eyes. High perceptual load reduced V1 activity related to the invisible stimuli. This strongly suggests that perceptual load can affect neural processing even at these very early stages. Consistent with this conclusion, ERP studies have demonstrated modulations by perceptual load of relatively early components including the N1 (e.g. Fu et al. 2008) and, under some circumstances, the P1 (e.g. Handy and Mangun 2000).

Accounts of the neural mechanisms underpinning these load effects include the suggestion that perceptual load might modulate the neural excitability in visual cortex, such that increasing the demands on the neurons responding to the task stimuli reduces excitability in other populations of neurons that might compete for control of perception. For example, Muggleton et al. (2008) used transcranial magnetic stimulation (TMS) to measure

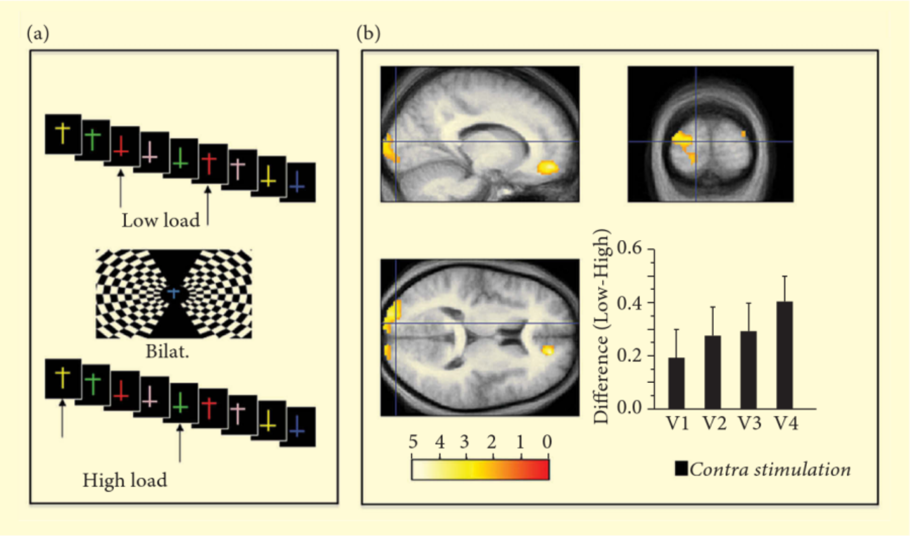

FIGURE 3.2 Stimuli and results from the perceptual load imaging experiment by Schwartz et al. (2005). Panel (a) shows the stimuli and procedure. A rapid stream of upright or inverted cross shapes of different colours was presented at fixation, accompanied by flickering checkerboards presented either on the left side, on the right side, on both sides (shown), or on neither side. Under low perceptual load, participants detected any red shape. Under high load, they detected specific conjunctions of colour and shape (e.g. yellow upright or green inverted). Panel (b) depicts the results. Visual cortex activity related to the checkerboards (pooled across unilateral and bilateral conditions) was greater under low (vs high) perceptual load, as shown in mid-saggital, coronal, and transverse sections. This difference increased across visual areas V1–V4, as shown in the bar graph. Reproduced from Schwartz, S., Vuilleumier, P., Hutton, C., Maravita, A., Dolan, R.J., and Driver, J., Attentional Load and Sensory Competition in Human Vision: Modulation of fMRI Responses by Load at Fixation during Task-irrelevant Stimulation in the Peripheral Visual Field, *Cerebral Cortex*, 15 (06), pp. 770–786 (c) 2005, Oxford University Press.

cortical excitability in area V5/MT as a function of the level of load in a static letter search task. When V5/MT is stimulated this can lead to the illusory percept of a moving flash of light (a moving phosphene). The intensity of stimulation required to elicit this percept can serve as an index of cortical excitability, such that a greater intensity is needed to elicit phosphene perception under reduced excitability. They found that high perceptual load in the letter search task increased the TMS intensity needed to elicit moving phosphenes, suggesting that the high-load task had indeed reduced excitability in V5/MT. This claim has received additional support from a recent demonstration of reduced sensory detection during the period of reduced cortical excitability under high load (Carmel et al. 2011).

Overall then, measures of neural processing have provided strong support for perceptual load theory in pinpointing the effects of load to the brain areas mediating sensory perception. Moreover, the extent of the modulations observed in these studies has important implications for real-world function. For example, the finding that the brain could not detect motion or novelty under high-load conditions has clear functional consequences due to the evolutionary importance of the detection of movement and change in the environment. Indeed, research in other species has demonstrated that birds can fail to detect even images that depict predators when pecking within a high-load seed array (Dukas and Kamil 2000).

Investigating automaticity

The manipulations that have been established through the study of perceptual load theory can also provide a method for examining the automaticity of particular cognitive processes. If processing of a certain type of stimulus remains unaffected by the level of perceptual load in an ongoing task, this might suggest that the stimulus can be processed 'automatically', regardless of the amount of capacity available. By contrast, if a particular process is shown to be eliminated under high (vs low) perceptual load, this can indicate that the process does in fact depend on limited-capacity resources.

The studies of the effects of perceptual load on early visual processing (described above) provide an example of this approach. Many aspects of early vision are considered to be automatic, in the sense that they are not under voluntary control and not subject to capacity limits. The findings described above suggest that while these processes are indeed not under voluntary control (and so proceed on all stimuli within capacity, including irrelevant stimuli that people wish to ignore), they do in fact have limited capacity and can therefore be reduced (or even eliminated) under high perceptual load.

The approach has also been applied to the study of emotion processing, which had often been argued to occur automatically (e.g. Dolan and Vuilleumier 2003)—an idea that is also intuitively appealing based on the high level of sociobiological significance that emotional stimuli are likely to possess. However, studies adopting perceptual load manipulations have challenged this viewpoint, demonstrating that the processing of emotional stimuli can be modulated by the perceptual load of the task at hand. For example, Yates, Ashwin, and Fox (2010) measured the interference caused by distractor pictures of angry faces that either had or had not been conditioned with an aversive noise under conditions of high and low load in a central letter search task. Under low load, they found more interference from fear-conditioned angry faces than from unconditioned angry faces or neutral faces. However, these effects were eliminated under high perceptual load, suggesting that attentional capture by fear-inducing stimuli is not fully automatic as may be assumed, but instead depends to some extent on attentional allocation (see also Mitchell et al. 2007).

Interestingly, famous faces are so far the only stimuli that have been shown to remain unaffected by the perceptual demands of an ongoing task, suggesting that some aspects of face processing may occur automatically. For example, Lavie, Ro, and Russell (2003) asked participants to search for names within displays of either high or low perceptual load, while ignoring peripheral distractor pictures of either famous faces or non-face objects. As predicted by load theory, congruency effects from non-face distractors were reduced under high (vs low) load. However, in a change from this normal pattern of findings, interference from distractor faces was unaffected by perceptual load. In contrast, perception of anonymous faces is significantly reduced under high perceptual load (He and Chen 2010; Jenkins, Lavie, and Driver 2005) suggesting that the automatic processing of famous faces relates to their high level of familiarity, rather than reflecting prioritized processing of faces in general.

Investigating people's perceptual capacity

The framework of load theory has also been used to study capacity differences between different groups of people. According to perceptual load theory, someone with a larger (vs smaller) perceptual processing capacity will require a more demanding perceptual task in order to exhaust their capacity and eliminate distractor processing. This approach has been useful both in developmental, ageing, and clinical contexts.

Many cognitive functions are known to develop through childhood and deteriorate in older age. What about perceptual capacity? Research using the load theory framework has shown that both children and older adults have reduced perceptual capacities compared with people in young to middle adulthood. For example, Maylor and Lavie (1998) asked groups of young and older adults to perform a version of the standard perceptual load flanker task. Under low load, the older participants demonstrated greater distractor interference than the younger participants. At the same time, the older group required a smaller increase in the search set size to prevent distractor processing compared to the younger group, suggesting that ageing reduces perceptual capacity. Similar effects have been found from studies of children's development, such that distractor–interference effects are eliminated at lower levels of perceptual load for children than for young adults, in line with the claim that perceptual capacity develops through childhood (Huang-Pollock, Carr, and Nigg 2002). Note that this research has in fact highlighted one positive consequence of reduced capacity: both the children and the older adults were less distracted by task-irrelevant stimuli compared to the young adults under intermediate levels of perceptual load. Studies using this approach have observed similar potentially beneficial effects of reduced capacity leading to reduced distraction under certain conditions (all involving lower levels of load than those needed to reduce distraction in healthy controls) in patients after parietal, frontal, and temporal brain lesions (Kumada and Humphreys 2002; Lavie and Robertson 2001) as well as in people with schizophrenia or high schizotypy (Ducato et al. 2008).

In contrast to this pattern of findings, research into autism spectrum disorder (ASD) suggests that adults with ASD might have larger perceptual capacity than typical adults. Remington et al. (2009) found that the level of perceptual load required to eliminate distractor processing in typical adults was not sufficient to prevent distractor processing in adults with ASD, and Remington, Swettenham, and Lavie (2012) showed that this pattern extends to visual detection abilities, such that adults with ASD exhibit superior detection to typical adults under higher levels of load. This confirms that ASD appears to involve enhanced perceptual capacity rather than increased vulnerability to irrelevant distraction. A recent study has made similar claims about people with high social anxiety, who also exhibited significant distractor processing under levels of perceptual load that were sufficient to extinguish distractor processing in people with low social anxiety (Moriya and Tanno 2010). Finally, similar findings from regular video game players have been used to underpin claims that they might have enhanced perceptual capacities compared with non-gamers (Green and Bavelier 2003).

Executive Control Load

Although load theory began with a focus on perceptual load, it was soon extended to address the role of load in another important determinant of selective attention, namely executive control (e.g. Lavie 2000; Lavie et al. 2004). Load theory stipulates that executive control functions such as working memory serve to maintain current stimulus processing and response priorities throughout task performance. The importance of these functions becomes particularly clear in task situations involving low perceptual load. While high perceptual load in a relevant task allows people to ignore irrelevant distractors simply by not perceiving them (early selection), low perceptual load allows the distractors to compete more effectively against the relevant stimuli (late selection). Nevertheless, people are still able to perform the task under low perceptual load, albeit less efficiently. This ability critically depends on the availability of executive control functions to actively maintain the current processing priorities. When executive control functions are loaded (for example, by asking participants to maintain additional information in working memory) they are no longer available to exert attentional control, resulting in greater processing of competing distractors. Thus the theory predicts that executive control load has the opposite effect to that of perceptual load, increasing distractor processing (rather than reducing it).

One happy side effect of these opposite predictions is that they provide a natural control for the effects of general task difficulty. Increased load, whether on perceptual or executive control processes, leads to increased task difficulty. Thus, if task difficulty were the critical determinant of distractor processing, the same effects should be seen under high executive control load as under high perceptual load. The fact that the two types of load are predicted to have opposite effects on distractor processing means that neither one can be explained in terms of task difficulty. Instead, the effects of load on distractor processing depend on the specific mental function that is loaded.

The role of executive control load in distractor interference

Behavioural studies of the impacts of executive control load have typically used a dual task design in which participants are asked to keep information in mind while also carrying out a selective attention task. For example, Lavie et al. (2004) used a standard flanker task (of low perceptual load) in which participants were asked to identify a target letter while ignoring a concurrently presented distractor letter (either congruent or incongruent with the target). Participants carried out this task under conditions of either high working memory load (where they were asked to remember six randomly chosen digits) or low working memory load (where they only had to remember one digit). Distractor congruency effects were greater under high (vs low) working memory load, supporting the claim that the availability of executive control functions is important for minimizing distractor interference.

This claim is supported by a study showing that people are more likely to experience attentional capture by salient (yet task-irrelevant) singleton distractors (e.g. a single red shape within a display of green shapes) under a high (vs low) concurrent working memory load (Lavie and de Fockert 2005; see Fig. 3.3). Notice that distractor interference in

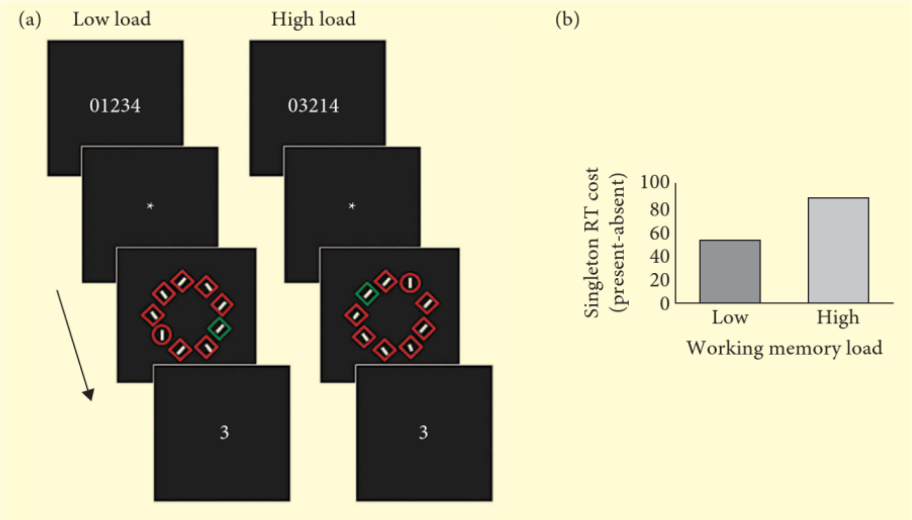

FIGURE 3.3 Examples of the stimuli and results from Lavie and de Fockert (2005, Experiment 2). Panel (a) shows the interleaving of the search task with the working memory task. Each trial began with presentation of a memory set. Under low working memory load, this consisted of the digits 0–4 in numerical order. Under high load, the sequence started with 0 but the remaining digits (1–4) were presented in random order. Participants were asked to hold the set in mind while they completed a search task. They searched for a red circle amid red diamonds, responding according to the orientation of the line contained within the circle. On some trials, one of the non-target diamonds was presented in green. Attentional capture by this unique and salient (yet task-irrelevant) 'singleton' item was measured in terms of the RT costs associated with its presence (vs absence). The trial ended with a memory probe task, in which participants named the digit from the original memory set that had followed the digit shown on screen, allowing confirmation that the set had been successfully maintained. As shown in panel (b), attentional capture by the task-irrelevant singleton in the search task was significantly larger under high (vs low) working memory load. Reproduced from *Psychonomic Bulletin and Review*, 12 (4), 2005 pp. 669–674, The role of working memory in attentional capture, Nilli Lavie and Jan De Fockert, experiment 2 © Springer Science and Business Media. With kind permission from Springer Science and Business Media.

this task was measured in terms of a general slowing in the presence (vs absence) of the singletons, which were not themselves associated with any response. Thus, the effects of working memory load are not confined to increased response competition but also appear to affect perceptual processing of distractors, as discussed further in the following section.

The role of executive control load in visual perception

Effects on reaction times cannot inform about the level of processing that was affected by load (as discussed earlier in this chapter). However, executive control load has also been shown to influence distractor processing in studies using more direct measures of visual perception and awareness. In line with this claim, people have been shown to be less susceptible to inattentional blindness (i.e. more likely to notice the task-irrelevant critical stimulus) under high (vs low) working memory load (e.g. de Fockert and Bremner 2011). A more direct test of visual perception including meaningful recognition (as opposed to detection of whether a stimulus was there or not, as measured in the typical inattentional blindness task) was offered by Carmel, Fairnie, and Lavie (2012). They asked participants to categorize written words while ignoring unfamiliar task-irrelevant faces presented in the periphery of the display. This task was carried out under high or low working memory load. After the final trial, participants were given a surprise recognition test measuring their identification of the irrelevant face that had been presented on that trial. Identification performance was better under high (vs low) working memory load, again suggesting that working memory plays an important role in determining distractor perception. There is also evidence that working memory load can influence people's susceptibility to the Ebbinghaus illusion (in which judgements about the size of a central circle are influenced by the sizes of the surrounding circles). De Fockert and Wu (2009) found that people experienced this illusion more strongly under high (vs low) concurrent working memory load, suggesting that a reduction in the availability of executive control functions for the illusion task led to increased processing of the task-irrelevant circles. Taken together, these studies confirm earlier findings from the distractor interference paradigm that people's ability to avoid distraction depends critically on the availability of executive control functions such as working memory. However, these studies go beyond those initial findings in demonstrating that executive control functions can affect distractor perception and awareness even in the absence of response competition.

Effects of executive control load on neural processing

The claim that executive control load can influence even sensory perceptual processing of distractors has also been supported by studies using neural measures. For example, de Fockert et al. (2001) varied working memory load while participants completed a selective attention task that required them to classify written names (as belonging to pop stars or politicians) while ignoring irrelevant distractor faces (which were also of pop stars or politicians). As predicted by load theory, cortical activity associated with the processing of distractor faces (e.g. in the fusiform face area; Kanwisher, McDermott, and Chun 1997) was significantly greater under conditions of high (vs low) working memory load, as was the behavioural interference caused by the face distractors. A more recent study has suggested that these high working memory load effects reflect a specific failure in the attenuation of distractor processing (rather than, for example, also including a reduction in the processing of relevant stimuli). Rissman, Gazzaley, and D'Esposito (2009) presented participants with sequences of four images (consisting of a mixture of scenes and faces) under both high and low working memory load. When the scenes were relevant to the task, the load manipulation had no effect on neural activity associated with scene processing. However, when the scenes were made irrelevant to the task, and people were asked to ignore them, activity in this area was greater under high (vs low) working memory load. This supports the findings of de Fockert et al. (2001) in demonstrating increased distractor processing under high working memory load. However, Rissman et al.'s work also extends those findings to suggest that working memory load does not appear to influence the processing of task-relevant items, thus linking the working memory effects specifically to distractor processing. A further study has demonstrated effects of working memory in areas as early in the visual processing stream as primary visual cortex (V1 and V2), suggesting that the availability of working memory during a selective attention task can affect even very early sensory processing of distractor stimuli (Kelley and Lavie 2010). Thus executive control functions appear to be important in minimizing the influence of competing distractors throughout the entire processing stream.

Summary

A substantial body of evidence now agrees that the extent to which visual distractors are processed depends on the perceptual load of the task at hand. If a task imposes high perceptual demands, task-irrelevant distractors can often be ignored successfully. By contrast, if a task imposes only low perceptual demands, the distractors receive substantially more processing and are thus more likely to interfere with behaviour. These effects of perceptual load provide a resolution to the early- versus late-selection debate in demonstrating that selection can occur either earlier or later in processing, depending on the perceptual demands of the task at hand. Research has also converged to demonstrate that the effective prioritization of task-relevant stimuli in the face of competition from irrelevant distractors depends on the availability of executive control functions for active maintenance of the processing priorities. When these functions are highly loaded, the prioritization process is impaired and distractors compete more effectively for processing resources. The consistent convergence of the findings in support of these principles across a broad range of manipulations and measures rules out any specific task factors as alternative explanations for the load effects.

We began the chapter by considering the problem of how to read this book in the middle of Oxford Street. According to load theory, your ability to focus on the page while ignoring the many distractions of the bustling city scene will depend both on the perceptual demands of the reading task and on the level of executive control that you are able to summon. If the perceptual load of the reading task is high enough to exhaust your processing capacity, you are unlikely to process the surrounding scene very thoroughly and should therefore be able to avoid distraction. However, if the task imposes only a low perceptual load (for example, if you decide to check the formatting, rather than actually reading) your excess perceptual capacity will automatically be allocated to processing the background scene and you are more likely to become distracted. Under these circumstances, it is particularly important for you to be able to draw on executive control functions, to maintain your priority of focusing on the book. If you are able to dedicate your full executive capacity to this task (i.e. if your executive capacity is not highly loaded) then you should still be able to deprioritize the distractors and avoid too much interference. However, if you are unable to summon your full executive powers (for example, because you are also trying to remember a complicated to-do list for the day), you may lose your ability to control your attention, leaving you more susceptible to distraction.

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CHAPTER 4

A MULTI-LEVEL ACCOUNT OF SELECTIVE ATTENTION

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INTRODUCTION

NEURAL information processing systems must overcome a series of bottlenecks that interrupt the sequence of events between sensory input and motor output. First, the sensory neurons that encode external stimuli are noisy. As a result, an identical stimulus will evoke a slightly different response pattern each time it is presented, and this instability can place limits on the amount of information that neurons can relay about stimulus features (Pouget, Dayan, and Zemel 2003; Seung and Sompolinsky 1993). Second, multiple items in the visual field compete for representation, and this competition must be resolved so that the most behaviourally relevant sensory stimuli are represented and allowed to guide goal-directed behaviour. Third, there are limits on the number of responses that can be selected simultaneously (Pashler 1994), and obvious limits on the number of simultaneous motor plans that can be executed. All of these factors restrict the speed and accuracy of sensory–response mappings, and at each stage, relevant stimuli must be prioritized over irrelevant distractors to ensure the successful completion of behavioural goals. The ability to prioritize relevant stimuli is generally referred to as *selective attention*, where the prefix *selective* is intentionally used to distinguish the term from changes in general arousal or states of consciousness.

There are three general mechanisms that support selection attention: signal enhancement, external and internal noise suppression, and selective read-out. The first two mechanisms influence selection by directly mediating the information content of neural representations as sensory signals are relayed and transformed across the processing hierarchy. Selective read-out is conceptually different, as it does not directly modify the quality of sensory representations. Instead, selective read-out influences the efficiency with which sensory information is used to inform decisions about the contents of the sensory array, either in the absence of or in combination with signal enhancement and noise suppression.

In this chapter, we focus on two general questions that have emerged over the last 50 years: *where* and *when* do these mechanisms of selective attention operate to enable efficient information processing? Such questions about the locus of selection are rooted in the classic debate between theories of early and late selection that have been actively pursued in the fields of cognitive psychology and cognitive neuroscience for decades. Early selection theories hold that attention filters sensory inputs based on simple low-level features (e.g. pitch of a sound, orientation of a line), whereas late selection theories hold that filtering occurs only after all basic features have been analysed and stimuli are semantically labelled. More recently, this early/late dichotomy has been subjected to increasingly sophisticated neuroscientific techniques that reveal signatures of selection in large-scale neural networks including the thalamus, sensory, and higher-order cortex. At different points in time and at different levels of the cortical hierarchy, selection can be implemented via signal enhancement, internal and external noise suppression, and the selective read-out of sensory signals. Moreover, these mechanisms operate in a complementary manner to facilitate information processing, with the relative contribution of each determined by behavioural demands and by the nature of the stimulus array.

We begin with a brief history of the early versus late selection debate, and then review current knowledge about *where* and *when* signal enhancement, noise suppression, and selective read-out exert their influence on information processing.

A HISTORICAL PERSPECTIVE ON EARLY VERSUS LATE SELECTION THEORIES

One of the first clearly articulated theories concerning the locus of attentional selection was the filter model of Broadbent (Broadbent 1958). He posited that incoming stimuli were analysed to the level of basic features (e.g. pitch, location). Based on this information, one item at a time was then selected and brought into awareness. Critically, given the breakdown of information into basic components assumed in this model, selection must happen very early in the processing stream, before the level of semantic analysis. Thus, models of this type are termed *early selection* theories. Broadbent was primarily influenced by data from dichotic listening tasks, where subjects were presented with separate auditory input in each ear. In these classical studies, subjects were typically asked to shadow the input from one ear by repeating out loud. While this task is quite attentionally engaging, subjects have little problem selecting one of the two auditory streams to shadow based on low-level features such as the pitch of the speaker's voice or the ear of origin (location). Moreover, subjects typically report having little subjective awareness of the information presented in the unattended auditory channel, as reflected quantitatively in poor recognition memory performance (Cherry 1953; Moray 1959; Neisser and Becklen 1975). Nevertheless, subjects were still able to discriminate low-level stimulus attributes such as pitch in the unattended channel, supporting

Broadbent's notion that selection must be early, as these basic attributes appeared to be all that was retained from the unattended auditory stream.

Not long after Broadbent's seminal book, Moray (1959) demonstrated that selection was not always implemented by an early filtering mechanism, as he noted that about one-third of subjects detected their own name when it was inserted in the unattended stream, despite a general lack of awareness of the overall content of the message. In a related finding, Treisman (Treisman 1960) presented subjects with two coherent sentences, one in each ear, and subjects were instructed to shadow the input from one of the channels. When the flow of the prose from the shadowed channel changed to the other ear, subjects would often continue to shadow the same sentence, even though the words were now being presented in the to-be-ignored channel. This tendency to track a sentence from the attended to the unattended channel based on syntactic structure and semantic content suggests that the message in the unattended ear was processed to a far more advanced level of analysis than predicted by the original inception of Broadbent's early selection theory.

To account for the semantic processing of the unattended channel, Anthony and Diane Deutsch (Deutsch and Deutsch 1963) formalized a *late selection* theory of attentional selection. In stark contrast to Broadbent's early filter theory, the late selection account holds that all stimuli are analysed to the level of semantic description. Moreover, the mechanism that supports semantic analysis is not capacity limited and can thus process all perceptual inputs in parallel. After this analysis is complete, attention operates by selecting a subset of the items for further processing, such as encoding into working memory (Duncan 1980). Importantly, Deutsch and Deutsch did not imply that subjects necessarily had conscious access to these early semantic descriptions. Rather, awareness only occurred after the capacity-limited process of attentional selection, accounting for the commonly held notion that observers are only aware of a small subset of potential stimuli at any given moment in time.

After these two opposite views on the locus of selection had been established, a good deal of research over the next 30 years focused on attempting to critically discriminate between the competing models. While studies on dichotic listening remained prominent (e.g. Corteen and Wook 1972), many researchers turned to investigating early and late selection in the visual domain. The prototypical approach was to infer the locus of selection based on behavioural measures such as priming that reflect the extent to which unattended stimuli impacted performance. Instances in which unattended stimuli did not influence performance were taken as support for early selection. Conversely, the influence of unattended stimuli on performance was interpreted as evidence in favour of late selection. For instance, Eriksen and Eriksen (Eriksen and Eriksen 1974) had subjects report the identity of a target letter briefly presented in an attended location indicated by a pre-cue presented at the start of each trial. One of the two possible target letters was mapped to a button press with the index finger, and the other target letter was mapped to a button press with the middle finger. The target letter was flanked on either side by additional letters that were either mapped to the same response required by the target (termed *compatible flankers*) or to the opposite response (termed *incompatible flankers*). The main observation was that response times (RT) to the targets were slower when the target was accompanied by incompatible flankers as opposed to compatible flankers. The effect of flanker identity on RT supports the late selection tenet that items outside the locus of attention are processed at least to the level of semantic description despite the fact that subjects had perfect foreknowledge of the target's location and could presumably focus attention well in advance.

However, evidence of this sort is not undisputed. First, proponents of early selection can always assert that the behavioural tasks did not adequately engage the subject's attention, thus 'leakage' through an early perceptual filter might occur. Indeed, if attentional cues are made salient enough, then irrelevant flankers do not have a measurable effect on performance, as shown by Egeth and colleagues (Francolini and Egeth 1980; Yantis and Johnston 1990). Such observations undermine the strong form of the late selection account because late selection models clearly predict an effect of incompatible distractors, regardless of the attentional focus. However, it appears that these claims against late selection rest on the assumption that the dependent measure is sensitive to a subtle influence of distractors. Indeed, using a different behavioural measure, Tipper and Driver (Tipper and Driver 1988) found evidence that the distractors used by Egeth and colleagues were in fact processed to the level of semantic content, supporting a late selection account. Moreover, the view that a semantic description was formed and then suppressed prior to the response stage can always be asserted by supporters of late selection to countermand data consistent with early selection. The main conclusion of these behavioural studies, and many others like them, is that behavioural evidence in support of either early or late selection can be obtained using very similar experimental paradigms. Therefore, in this particular area of cognitive psychology, physiological metrics have had a great deal of influence, as they can provide more direct insight into the temporal dynamics of signal enhancement, noise suppression, and the level to which sensory information gets processed.

As with the behavioural studies reviewed above, the majority of neuroimaging and electrophysiology studies investigating the neural correlates underlying attentional selection have focused on the visual rather than the auditory domain. Thus, we will limit our discussion to studies on the visual system, first discussing issues pertaining to early and late selection in terms of 'where' within the visual processing hierarchy selection plays out and then asking 'when' these modulations occur.

THE 'WHERE' OF SELECTION VIA SIGNAL ENHANCEMENT: NEURAL EVIDENCE FROM MONKEY PHYSIOLOGY AND HUMAN NEUROIMAGING

The first important question that emerges from the 'early' vs. 'late' selection debate that we will consider at the neural level is: where in the visual pathway does selective attention *first* affect neural processing? Early and late selection accounts appear to make straightforward predictions with respect to this question. An early selection theory would posit that selective attention should influence early stages of processing including primary visual cortex (striate cortex, or V1), where visual information is filtered based on basic features such as colour, motion, and orientation. In contrast, a late selection theory would predict no modulation at early processing stages, as information should be faithfully represented regardless of task demands (at least) up to stages where the visual information interfaces with other cognitive domains such as memory or action context.

The modulation of neural responses by spatially selective attention was originally demonstrated in the extrastriate cortex. In a seminal study, Moran and Desimone (Moran and Desimone 1985) recorded the activity of neurons in area V4 from monkeys trained to direct attention to a spatial location within a neuron's receptive field (RF). The target stimulus was either shown alone in the neuron's RF or in the presence of a nearby distractor. Attending to the target enhanced neural responses, but only when a competing stimulus was presented in the same RF as the target. These findings demonstrate that selective attention can gate the processing of behaviourally relevant information by effectively constricting the RF around the selected stimulus such that the distractor has little or no impact on the firing rate of the cell. Similar effects of attentional enhancement in area V4 have been demonstrated by several other groups (e.g. Connor, Preddie, Gallant, and Van Essen 1997; Haenny and Schiller 1988; McAdams and Maunsell 1999; Motter 1993), and have been found in several other extrastriate and parietal areas including V2 (Luck, Chelazzi, Hillyard, and Desimone 1997; Motter 1993), MT (e.g. Treue and Maunsell 1996) and LIP (e.g. Gottlieb, Kusunoki, and Goldberg 1998).

Despite the widespread and robust observation of attentional modulation in many areas of visual cortex, it was initially unclear if attention modulated activity in primary visual cortex. Several studies were unable to demonstrate such modulation (e.g. Luck et al. 1997), while others found relatively weak, but reliable effects (e.g. Motter 1993). While it was not clear what factors best accounted for these discrepant findings, there was an overall impression that attentional modulation at the earliest cortical processing stages may be highly dependent on task-related factors or the need to integrate information from beyond the classic RF (e.g. Ito and Gilbert 1999; Roelfsema, Lamme, and Spekreijse 1998). In either case, the few studies that recorded attention effects from different areas in the same animals (Cook and Maunsell 2002a, 2002b; Luck et al. 1997) showed that the magnitude of attentional modulation was stronger in more anterior extrastriate areas (e.g. V4) compared to more posterior areas such as V2. This graded effect was taken to suggest that attentional effects at earlier stages were caused by reactivation from higher-order extrastriate areas through cortico–cortical feedback connections, although a direct demonstration of this link has not been reported.

Thus, evidence from these initial physiology studies does not unequivocally support either early or late selection models. The finding of attentional modulation in relatively early cortical areas such as V2 and possibly even V1 is consistent with early selection accounts. However, the inconsistent observation of attention effects in V1, coupled with the possibility that these effects primarily reflect reactivation from higher-order areas, renders the evidence inconclusive. Thus, single unit recording data that emerged by the late 1990s did not clearly support either alternative, leaving the question far from being settled.

In the mid and late 1990s, the advent of functional magnetic resonance imaging (fMRI) enabled detailed studies of the human visual system and offered several advantages over previous approaches. In particular, human subjects can perform a wider range of tasks compared to non-human primates and activation changes tied to task manipulations can be examined across the entire brain (as opposed to monitoring single-unit activity in a single area). Soon, investigators had settled lingering questions about whether attention could modulate responses at the earliest anatomical levels of processing by showing response modulation in V1 with moving (Gandhi, Heeger, and Boynton 1999; Somers, Dale, Seiffert, and Tootell 1999) and stationary stimuli (Martinez et al. 1999). Even stronger evidence in support of early selection came from the subsequent demonstration of attention effects in the thalamus, i.e. the lateral geniculate nucleus (LGN) (O'Connor, Fukui, Pinsk, and Kastner 2002). The LGN is the thalamic component in the retinocortical projection and it is the first neural structure within the visual processing hierarchy that can be modulated by feedback input (via afferent input from the thalamic reticular nucleus, striate cortex, and the brainstem). Interestingly, attention effects in the LGN were found to be stronger than in area V1, more on the order of extrastriate areas such as V4 (O'Connor et al. 2002). Thus, these findings not only challenge the notion that cognitive processing primarily involves cortical networks, but also the notion that attentional modulation in early sensory areas can be explained solely by cortico–cortical re-entrant signals from later stages of the hierarchy, as such an account would have predicted smaller effects of attention in the LGN than in V1. Instead, fMRI signals may reflect the summed modulatory feedback that a given area receives from cortical, thalamic, and brainstem sources, as opposed to just local spiking activity. If this is indeed the case, then larger attentional modulation in LGN might be related to the larger number of afferent inputs that this region receives compared to primary visual cortex. Thus, fMRI evidence gathered over the last 15 years provides compelling support for anatomically early attention effects by demonstrating modulation in V1 and the LGN, the earliest stages of visual processing that receive feedback influences from other sources (see also chapters by Beck and Kastner, and Saalmann and Kastner).

The ability of fMRI measurements to index attentional modulation across the entire brain also provides key insights into how each area is driven by 'sensory-driven' or 'bottom-up' versus 'cognitively driven' or 'top-down' influences. For instance, sensory-driven population responses during passive viewing follow a characteristic pattern when measured with fMRI: the strongest responses are typically observed in early visual areas such as V1 and progressively weaker responses are observed at successively later stages of the hierarchy (see Fig. 4.1a). For example, 90% of the maximum response can be evoked in V1 by a simple visual stimulus, whereas the same input might evoke a modulation of only 10% in higher-order areas of parietal and frontal cortex (e.g. Treue 2003). On the other hand, the response modulation associated with deploying

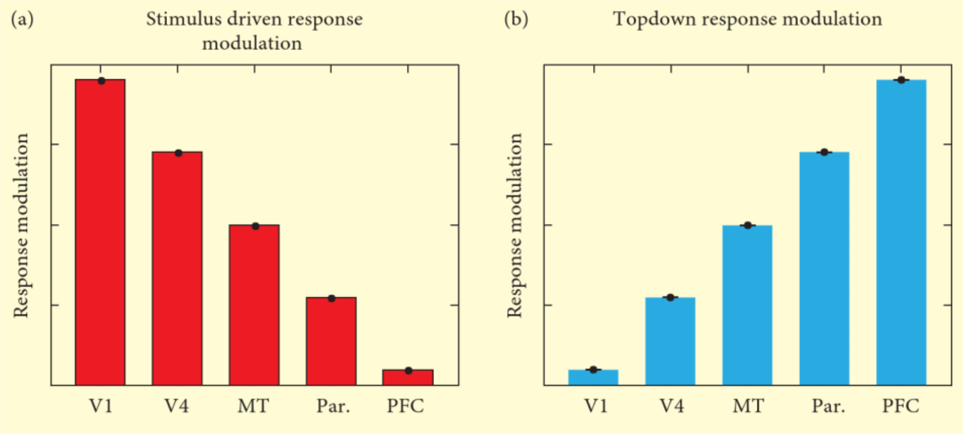

FIGURE 4.1 Schematic showing the relative magnitude of stimulus-driven and top-down modulation across the cortical hierarchy from occipital to parietal (Par.) to pre-frontal cortex (PFC). (a) The magnitude of sensory modulation gradually decreases. (b) In contrast, the magnitude of top-down modulations is largest in PFC and gradually decreases in earlier visual areas.

top-down attention to a fixed sensory stimulus exhibits the opposite pattern: a 90% increase in activation might be expected in areas of parietal and frontal cortex, whereas a modulation of 10% is expected in early visual cortex (see Fig. 4.1b).

Based on the neural evidence of attentional modulation at early processing stages, the preponderance of evidence seems to favour early selection as opposed to late selection accounts. However, several caveats should be noted. First, none of the studies reviewed thus far addressed the question of *what* was selected or what type of information was modulated at each processing stage. This is a critical issue, as the observation of an attentional modulation at a specific stage of the visual hierarchy does not speak to the issue of what kind of information is targeted by attention. For example, an increase in activation levels within a neural population that is thought to encode a certain feature—such as motion in area MT—does not necessarily mean that selective attention operates on the feature 'motion'. This is particularly true when neural effects are inferred based on fMRI measurements, as the blood oxygen level dependent (BOLD) signal reflects the aggregate activity across all neurons in a region and is generally insensitive to feature selective changes in population response profiles (see Serences and Saproo 2012). Thus, any attentional modulation that is measured within a given region may be targeted on any type of information processed in the area, or may simply reflect a general increase in the activity of all neurons within a region in a non-selective manner (i.e. analogous to a change in general arousal). Such effects may thus translate into a scaling of responses in a region without actually influencing the selectivity of the population response or the amount of stimulus-specific information that is encoded about relevant sensory stimuli. In addition, even though neuroimaging methods excel at pinpointing the anatomical locus of selection, fMRI does not have the temporal resolution to conclusively distinguish between modulations of afferent signals and modulations related to later re-entrant feedback. In contrast, electrophysiology studies that examine the temporal dynamics of the selection process have been able to shed more light on these issues by exploiting temporally precise markers that are thought to index the depth of information processing.

THE 'WHEN' OF SELECTION VIA SIGNAL ENHANCEMENT: THE TEMPORAL DYNAMICS OF SELECTIVE ATTENTION

As noted in the last section, the evidence is now compelling that attention can modulate neural activity very early in the visual processing stream (e.g. in LGN), consistent with early selection accounts. However, this is a necessary but not sufficient condition to support the early filtering of sensory information, as early selection also requires that the modulations occur early in *time*, before extensive processing has taken place at later stages. While still a matter of debate, studies that use human subjects and event-related potentials (ERPs) provide some of the most diagnostic information regarding the timing of attention effects.

The ERPs elicited by visual stimuli are generally decomposed into several components, the C1 (starting about 50–90 ms post-stimulus), the P1 (80–130 ms), and the N1 (140–200 ms). In a typical experimental paradigm, subjects are told to attend to a specific location in the visual field and a stimulus is either flashed at the attended location or at another, unattended, location. The classic finding is that the P1 and N1 components evoked by an attended stimulus are larger than the same components evoked by an unattended stimulus (see Mangun, Hillyard, and Luck 1993). Moreover, recent studies suggest that the earliest ERP component—the C1—can also be modulated by attentional factors, despite its onset as early as 50 ms after the presentation of a stimulus. Similarly early modulations have been shown in studies examining spatial attention (Kelly, Gomez-Ramirez, and Foxe 2008; Slotnick, Hopfinger, Klein, and Sutter 2002; Zhang, Zhaoping, Zhou, and Fang 2012—although see Martinez et al. 1999; Noesselt et al. 2002), auditory–visual coupling (Van der Burg, Talsma, Olivers, Hickey, and Theeuwes 2011), and in studies that examined the exogenous (or stimulus-driven) capture of attention to one of two superimposed visual surfaces (Khoe, Mitchell, Reynolds, and Hillyard 2005). Moreover, the C1 can be reasonably localized to V1 because the polarity of the response reverses when stimuli are presented in the upper and lower visual fields, consistent with the known anatomical layout and retinotopy of V1. Thus, the early onset of attention-related increases in response amplitude has led many researchers to conclude that attention modulates the afferent volley of sensory responses as they ascend the cortical hierarchy (Hillyard and Anllo-Vento 1998; Hillyard, Vogel, and Luck 1998). This evidence provides solid support for early selection, because strong forms of late selection cannot accommodate the differential processing of attended stimulus features during the initial feedforward sweep of sensory activity.

Taken together, the observation of enhanced early ERP responses suggests that attention mimics the effect of a physical increase in the salience of the sensory input (Hillyard and Anllo-Vento 1998; Hillyard et al. 1998). Importantly, early gain signals have also been associated with attention to basic features such as colour (Zhang and Luck 2009), which is consistent with Broadbent's original notion that early selection operates on basic stimulus features, not just on spatial locations. Importantly, these early amplitude modulations of ERP waveforms clearly violate assumptions made by pure late selection theories of attention that posit equivalent sensory analysis of all items present in the visual (or auditory) scene up to a relatively advanced levels of analysis. In addition, these early modulations are consistent with a recent line of work by Carrasco and co-workers, who have shown that attention actually increases the perceived salience of basic feature properties so that contrast becomes brighter, motion more salient, and so on (Carrasco 2009; Carrasco, Ling, and Read 2004; Carrasco and McElree 2001; Fuller, Park, and Carrasco 2009; Liu, Abrams, and Carrasco 2009; Liu, Fuller, and Carrasco 2006; see chapter by Carrasco; see also: Anton-Erxleben, Abrams, and Carrasco 2011; Carrasco, Fuller, and Ling 2008; Prinzmetal, Long, and Leonhardt 2008; Schneider 2006, 2011; Schneider and Komlos 2008). Collectively, these results support the intuitive notion that modulating the gain of responses in early visual areas should have a corresponding impact on the perceptual experience of attended features, contributing not only to increases in behavioural performance, but also to qualitative shifts in phenomenal experience.

Even though these results provide strong support for the feasibility of early selection accounts, there are several caveats. First, in order to directly compare responses evoked by attended and unattended stimuli, one must assume that the stimuli are processed in an identical manner except for the presence/absence of attentional gain. Presumably, if fundamentally different neural mechanisms were responsible for the observed differences in the response to attended and unattended stimuli, then the voltage distribution across the scalp would differ across these conditions. However, the voltage distribution across the scalp is nearly identical for attended and unattended stimuli (e.g. Mangun et al. 1993), suggesting that attention-related differences in ERP amplitude are indeed driven by changes in sensory gain and not by changes in the nature of the processing that is being carried out. Second, early sensory gain models predict that any amplitude and/or phase shifts due to attention should mirror those produced by actual changes in the physical attributes of the stimulus. In line with the predictions of early selection models, increasing stimulus brightness produces an increase in P1 and N1 amplitude that mirrors increases due to attention (particularly in the case of the P1; Johannes, Munte, Heinze, and Mangun 1995; Wijers, Lange, Mulder, and Mulder 1997).

Another key piece of evidence on the timing of attentional modulation comes from monkey single cell recording studies, which have demonstrated two patterns of neural activity that are consistent with early selection: an increase in spontaneous activity due to allocation of spatial attention and before the onset of a stimulus, and the rapid onset of a modulatory attention effect on visually evoked activity, presumably before recurrent feedback can influence the magnitude of spiking. Luck et al. (1997) were able to show both of these effects in single neurons recorded from the same animals (see also Kastner, Pinsk, De Weerd, Desimone, and Ungerleider 1999). In their paradigm, a monkey was trained to covertly attend to one of two spatial locations and to detect a pre-specified target at that location. In one condition, a single stimulus was presented within the RF of a V4 neuron and another stimulus was presented in the mirror symmetrical position across the vertical meridian (outside of the neuron's RF). When attention was directed inside the neuron's RF before the stimulus display was presented, there was an increase in the spiking rate of the neuron relative to when attention was directed to the other location outside of the RF. This divergence in activity, or *baseline shift*, was found during the 500 ms epochs before the onset of the stimulus display (see also Kastner et al. 1999; Ress, Backus, and Heeger 2000; Serences, Yantis, Culberson, and Awh 2004). Therefore, the observed modulation in spiking rate was not due to exogenous sensory stimulation. A second condition in the paradigm of Luck et al. (1997) evaluated the effects of attention on the post-stimulus activity of neurons in V4. To achieve maximum post-stimulus attention effects, both the target and the distractor were presented within the RF of a single V4 neuron (as in Moran and Desimone 1985). The monkey attended to one of the two possible stimulus locations, and spiking activity to the onset of a stimulus was recorded as a function of the locus of attention. Post-stimulus histograms revealed a clear separation of activity approximately 60 ms after stimulus onset such that attended stimuli evoked a larger response compared to unattended stimuli (see also Buffalo, Fries, Landman, Liang, and Desimone 2010). Similar results were also observed for single neurons in area V2, and are consistent with the similarly early modulation of the C1 ERP component measured from human subjects. Interestingly, however, no baseline shifts were observed in V1, perhaps because the RFs were too small to accommodate both attended and unattended stimuli.

Functional brain imaging studies in humans have extended these results by demonstrating increases in baseline activity not only at attended locations, but also in neural populations that respond preferentially to basic stimulus features such as motion (Chawla, Rees, and Friston 1999; Serences and Boynton 2007) and to more complex stimuli such as shapes (Stokes, Thompson, Nobre, and Duncan 2009) and objects (Peelen, Fei-Fei, and Kastner 2009). In these studies, baseline increases have been found at all stages of visual processing including the visual thalamus and striate cortex, which is somewhat inconsistent with reports from monkey physiology (which reported no baseline shifts in V1). One way to reconcile the apparent discrepancies between fMRI and physiology data is to consider the neural basis of the BOLD signal measured with fMRI. BOLD responses have been shown to more strongly correlate with local field potentials (LFPs) than with the action potentials that are typically recorded in physiology studies (Logothetis, Pauls, Augath, Trinath, and Oeltermann 2001; Logothetis and Wandell 2004). Critically, LFPs reflect multiple types of neuro-modulation including subthreshold changes in membrane potential, synaptic events, oscillatory activity, and after-potentials that follow action potentials. In addition, hemodynamic signals likely reflect the combined influence of small modulatory effects across large populations of neurons that may not be reliable at the level of single neuron recordings. Thus, BOLD fMRI might be more sensitive with respect to detecting the presence of an attentional modulation, at the expense of precise information about the origin of the modulatory signal.

The baseline shift and the early attentional modulation of stimulus-evoked responses represent complementary aspects of an early selection mechanism in monkey visual cortex. First, the baseline shift is consistent with a mechanism that increases the gain of the afferent volley of neural activity that is evoked by the presentation of a stimulus (Sylvester, Shulman, Jack, and Corbetta 2009). Thus, cells whose RFs correspond to an attended region of space already have a competitive advantage over cells whose RFs correspond to unattended regions of space, and they will tend to dominate the winner-take-all circuits posited by models such as biased competition (Desimone and Duncan 1995; Reynolds and Desimone 1999). Moreover, heightened spiking rates can be observed shortly after the presentation of an attended target, further amplifying the competitive advantage of relevant over irrelevant stimuli (e.g. Fig. 4.3a in Luck et al. 1997). Together, these findings are consistent with Broadbent's original conception that attention can use rudimentary qualities of the impinging sensory input such as location to influence attentional selection.

Taken at face value, the ERP, single cell, and fMRI studies reviewed in this section provide clear evidence for early signal gain in visual processing. Of course, these findings depend on linking propositions between observed neural activity and the ultimate behaviour of the organism that are often vague (Teller 1984). However, there is at least some evidence to support a correlation between enhanced sensory ERP components and decreased RTs in spatial cueing paradigms (e.g. Mangun et al. 1993; Zhang et al. 2012). While correlations cannot establish causal relationships, they substantially advance the argument that early modulation of neural activity directly contributes to behaviour. Moreover, caution must be exercised when interpreting the timing of the modulation effects. While it is widely accepted that the P1 and early modulations such as those documented by Luck et al. (1997) reflect feedforward processing, areas of parietal cortex (LIP) and frontal cortex can exert stimulus-driven responses with a latency on the order of 40–50 ms, raising the possibility that attentional feedback to early visual cortex could occur on an extremely short time scale (Bar et al. 2006; Bisley, Krishna, and Goldberg 2004). Nevertheless, it now seems clear that attentional modulation can occur well before the onset of neural markers that indicate more advanced neural processing, such as semantic analysis and the updating of information in working memory, processes that are typically thought to occur 300–400 ms post-stimulus (Kutas and Federmeier 2011; Kutas, Neville, and Holcomb 1987; Polich 2007).

Finally, it is important to point out that even though these studies are consistent with early selection accounts, they do not establish that early selection is the *only* mechanism of selective attention. Indeed, other ERP and single cell studies indicate that late selection can influence information processing as well. For example, early ERP components such as the P1 and N1 are similar for seen and unseen items in an attentional blink paradigm; however, large attenuations in later ERP components thought to index the updating of working memory are observed in the same context (Vogel, Luck, and Shapiro 1998). Thus, the emerging consensus from the cognitive neuroscience literature clarifies and solidifies earlier notions that both early and late selection can occur depending on task demands and are not mutually exclusive (Lavie and Tsal 1994; Vogel, Woodman, and Luck 2005; Yantis and Johnston 1990). However, the physiological evidence makes an especially compelling case indicating that pure inceptions of late selection theories can probably be entirely discarded.

Where and When of Noise Suppression via External Distractor Exclusion

Consider a classical visual search task, where subjects are presented with a display composed of green and red letters, e.g. T's and L's. The subject's task is to identify a target item composed of a conjunction of the two features present in the display, i.e. colour and shape (e.g. a red T) among the distractors (Treisman and Gelade 1980; see chapter by Wolfe). This type of task is designed to resemble real-world search situations, in which the visual system is constantly faced with an enormous amount of clutter from which behaviourally relevant information needs to be selected. Visual search entails at least two conceptually different processes: (i) the selection of the task-relevant stimulus and (ii) the filtering of multiple distractor stimuli that form the vast majority of information in the display. Thus far, we have focused almost exclusively on the anatomical and temporal properties of the target selection process. However, understanding the process of suppressing distractors is at least—if not more—important. Ultimately, these two processes are intimately linked, and there is now strong evidence that the neural mechanisms that support target selection and distractor exclusion interact to a high degree in visual cortex (e.g. Pinsk, Doniger, and Kastner 2004; Seidl, Peelen, and Kastner 2012). However, for reasons of clarity we will discuss the neural basis of distractor exclusion separately and without consideration of these interactions as they are not well understood at present.

The neural fate of unattended (distractor) information presents a second important question that arises from the early vs. late debate that we discussed above. Early selection accounts hold that unattended information should be mainly represented at early stages of processing, where the visual information is represented at a featural level, but not at later stages, where features are combined in complex ways to form objects and other semantically meaningful stimuli. In contrast, a late selection account would assume a neural representation at both early and advanced visual processing stages. Unfortunately, much less is known about the neural basis of distractor exclusion compared to the neural basis of target selection. This asymmetry is mainly due to the fact that most studies evaluate the effects of attention on a visual stimulus relative to a condition when the same stimulus is unattended. In this type of scenario, the effects of selective attention on unattended stimuli cannot be determined. Thus, some of the evidence discussed below will be indirect, but still important and telling about the mechanisms of distractor exclusion.

One example of such indirect evidence is the seminal work by Desimone and colleagues that led to the development of the biased competition model (Desimone and Duncan 1995; Kastner, De Weerd, Desimone, and Ungerleider 1998; Moran and Desimone 1985; Reynolds, Chelazzi, and Desimone 1999). As discussed above, the basic findings were two-fold. First, multiple stimuli appearing in a neuron's RF will interact in a mutually suppressive way suggesting that they are not processed independently. Instead, multiple stimuli engage in a competitive process that occurs automatically at the level of the RF. Second, when attention is allocated to one of two competing stimuli, the neural response to the attended stimulus is nearly as large as when the stimulus is presented in isolation (i.e. without the competing distractor). Thus, attention appears to restore the response of the attended stimulus and operates by counteracting the competing (suppressive) influence of the second stimulus. This finding suggests that attention not only boosts the response evoked by attended stimuli, but also acts to attenuate distractor interference by resolving competitive interactions between stimuli. Importantly, this mechanism of distractor exclusion has been shown to be tied to the RF and its immediate surround and scales with increasing RF size across the visual processing hierarchy (Kastner et al. 2001; Sundberg, Mitchell, and Reynolds 2009). However, as mentioned above, these studies did not directly measure the effects of attention on distractor stimuli, since only responses evoked by attended stimuli were considered. Thus, the conclusions drawn about the neural fate of distractor stimuli were based solely on changes in target-evoked responses as a function of different target–distractor configurations.

Recent studies using neuroimaging methods in human subjects have provided more direct evidence regarding the fate of unattended distractor stimuli. Some of the first evidence was obtained from studies in which the perceptual or cognitive load associated with a target stimulus was systematically and parametrically varied while responses evoked by the target and by distractors were separately assessed. In one study, the subject's attentional resources were parametrically modulated by manipulating the difficulty of a task at fixation while neural responses associated with an irrelevant and unattended peripheral motion stimulus were probed (Rees, Frith, and Lavie 1997) (see also chapter by Lavie). The response evoked by the unattended stimulus was significantly attenuated in motion-selective area MT when the task at fixation was difficult (high perceptual load) compared to when the task at fixation was easy (low perceptual load). O'Connor et al. (2002) extended these results by showing that responses evoked by an unattended visual stimulus also decreased in the thalamus, primary visual cortex, and extrastriate cortex depending on the load of a concurrent attentional task (see also Pinsk, et al. 2004; Schwartz et al. 2005). Interestingly, the load-dependent attenuation of distractor-related activity was strongest in the thalamus and extrastriate cortex and weaker in primary visual cortex, mirroring the pattern of effects observed for target-related attentional modulation (see section above, *The 'where' of selection via signal enhancement*). Thus, in addition to a gain control mechanism that modulates target-related neural signals throughout the visual processing hierarchy, active distractor suppression also appears to operate at multiple levels including the earliest stages of visual processing.

Corroborating evidence supporting an anatomically early locus of distractor suppression has also been found in studies of feature-based attention. One of the hallmarks of feature-based selection is that it operates by increasing neural responses to the selected feature (e.g. a particular direction of motion) regardless of spatial location, thus operating in a global manner across the visual field (Martinez-Trujillo and Treue 2004; Saenz, Buracas, and Boynton 2002; Serences and Boynton 2007; Treue and Martinez Trujillo 1999; see chapter by Scolari). In line with studies that examine the consequences of spatial selection on distractor processing, the response of neurons that are tuned to an attended feature (e.g. a direction of motion) are enhanced whereas the response of neurons tuned far from the attended feature are suppressed (Cohen and Maunsell 2011; Martinez-Trujillo and Treue 2004; Scolari, Byers, and Serences 2012; Serences, Saproo, Scolari, Ho, and Muftuler 2009). This joint enhancement and suppression occurs for all neurons that are sensitive to attended feature dimension, irrespective of whether the attended stimulus directly falls within their spatial receptive field. These results thus suggest that the exclusion of distractor information can happen at relatively early stages of sensory processing and that distractor suppression is not strictly tied to acts of selection based on spatial location.

In general, the spatial and feature-based suppression of distractor-related activity is more compatible with early selection accounts as it occurs at early stages of the visual hierarchy (although the timing of these effects is largely an open question). However, these studies all dealt with basic visual features as opposed to more complex objects and experimental settings that more closely resemble real-world search scenarios. Interestingly, and in line with studies that use basic visual features, most studies that examine the influence of attention on the processing of more complex objects reveal little representation of unattended distractor categories. In one classic study, a house and a face stimulus were presented simultaneously in separate hemifields and subjects were cued to attend either to the location of the face or to the location of the house (Serences, Schwarzbach, Courtney, Golay, and Yantis 2004; Wojciulik, Kanwisher, and Driver 1998). When subjects attended to the face stimuli, face-selective regions of ventral visual cortex were more responsive than house-selective regions of ventral visual cortex. The opposite was true when subjects attended to houses. More recent studies have extended these findings to more naturalistic and thus complex scenarios by showing that neural activity in object-selective cortex is entirely dominated by task-related demands when subjects extract categorical information from natural scenes. In one study, subjects attended to briefly presented street scenes and detected the presence of people or cars in the scenes. In object-selective ventral visual cortex, only task-relevant information was processed to the categorical level even when the relevant information was not spatially attended. In contrast, task-irrelevant information was not processed to the categorical level even when it was spatially attended (Peelen et al. 2009). Subsequent studies demonstrated that task-irrelevant objects can sometimes be processed up to the categorical level; however, their representation is weaker than that of task-relevant objects (Seidl et al. 2012). In addition, distractors that were task-relevant in an immediately preceding trial that become task-irrelevant in the present trial are also actively suppressed (Fig. 4.2). Together, these and other related findings strongly suggest that distractor information is largely filtered out at the level of object-selective cortex, thereby further supporting early selection accounts of attentional modulation.

While the pattern of results regarding the fate of distractors is largely consistent across single-unit and neuroimaging studies, results from patient literature are more mixed with respect to early and late selection accounts. For example, the BOLD response evoked by faces and by common objects in patients suffering from visuo-spatial hemineglect was similar when the stimuli were presented to the neglected hemifield and when the stimuli were presented to the intact hemifield (Rees et al. 2000; Vuilleumier et al. 2001). The similarity in magnitude of the response suggests that even unattended

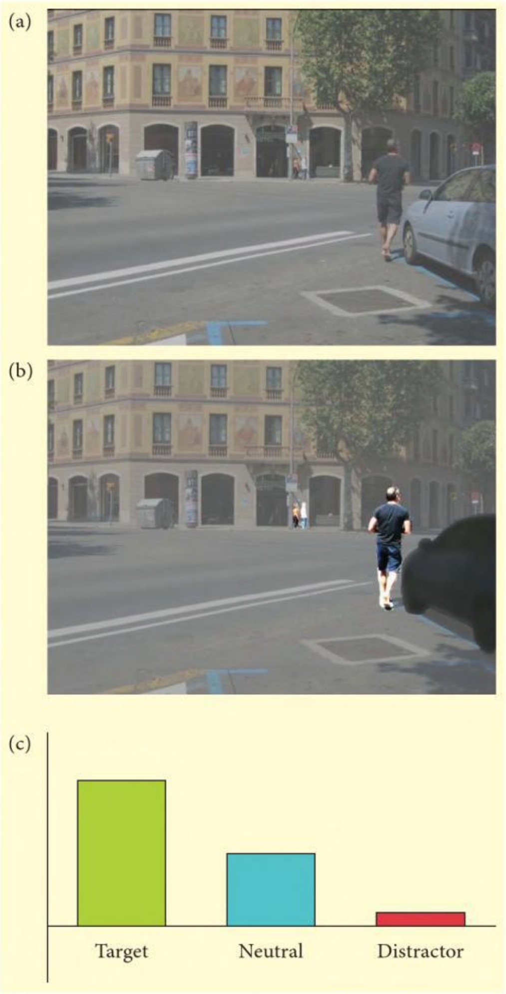

FIGURE 4.2 Object category-based selection from natural scenes. In the scene (a), people are the category that is relevant to ongoing behaviour (i.e. target category), and cars are the object category that was previously relevant but is presently not relevant (i.e. distractor category), whereas all other object categories present in the scene are never task-relevant (i.e. neutral category, such as trees or houses). Visual search in natural scenes is accomplished through a combination of enhancing task-relevant information and suppressing a previous attentional set relative to processing of neutral categories. The resulting representation of object categories in object-selective cortex is schematically shown in the modified scene (b) relative to the original scene (a). (A) Adapted from Seidl, K. N., Peelen, M. V., and Kastner, S., Neural evidence for distractor suppression during visual search in real-world scenes, *Journal of Neuroscience*, 32, pp. 11812–11819 © 2012, The Society for Neuroscience.

stimuli undergo processing to a relatively advanced stage of processing, perhaps even to the level of category-specific object representations. However, in light of previous findings suggesting that object-based selection operates in a spatially global manner (similar to feature-based attention, e.g. Peelen et al. 2009), it is possible that objects presented in the intact hemifield heavily influenced the representation in the lesioned hemisphere. On this account, object identity was never represented in the lesioned hemisphere. Instead, activation observed in the lesioned hemisphere may have been related to the global processing of the attended target. Other lesion work suggests that neglected—and thus unattended—stimuli undergo significant processing, at least to the point at which they can influence behaviour (Marshall and Halligan 1988). For instance, neglect patients show behavioural interference effects tied to the presentation of incompatible distractors in their neglected hemifield, even though they report little awareness of the competing distractors (Shomstein, Kimchi, Hammer, and Behrmann 2010). Thus, it appears that at least some information about stimuli from the neglected hemifield can be processed; however, the depth of processing is not entirely clear, nor is the influence of parametric manipulations of task difficulty. Future studies will be required to determine the extent to which these late selection effects are still observed when sufficient attentional resources are allocated to the non-neglected side of space.

While relatively little is known about the fate of unattended distractor stimuli, even less is known about the temporal dynamics of distractor exclusion (or the 'when' of distractor exclusion). One possibility is that the processing of target-related information is simply sped up relative to the processing of distractor information. Such changes in the efficiency of processing may be reflected in the latency at which the target and distractor-evoked responses are registered in the visual system. To evaluate this possibility, several single-unit recording studies examined the response latency associated with identical stimuli when they were attended or unattended. With the exception of one study, the results suggest that attention does not significantly alter the response latency of single neurons (Bisley et al. 2004; Cook and Maunsell 2004; Lee, Williford, and Maunsell 2007; Reynolds, Pasternak, and Desimone 2000). In the one study that did find a positive effect, the latency shift was found both at the level of single neurons and at the level of local populations (Sundberg, Mitchell, Gawne, and Reynolds 2012), and was on the order of 1–2 msec. Despite this relatively modest shift, the decreased response latency may still have a significant impact on the computations performed by a network or neurons given that much of the information in a neural code likely depends on spike timing. Furthermore, small differences measured at the single cell or local population level can easily translate into more robust differences when averaged across larger neuronal populations, such as those observed using scalp EEG or electrocorticography (ECoG). Interestingly, a recent ERP study demonstrated that the enhancement of target-related activity measured over visual cortex started 220 msec after the onset of an attentional cue, whereas the suppression of distractor-evoked responses lagged by an additional 130 msec (Andersen and Muller 2010). Thus, while the temporal dynamics of distractor suppression are still not well understood, both of these studies highlight the importance of addressing the interaction between the facilitatory and suppressive effects of selective attention.

WHERE AND WHEN OF ATTENTION-RELATED INTERNAL NOISE REDUCTION

Signal enhancement can be used to efficiently encode relevant stimuli and to attenuate the influence of external distractors on information processing. In addition, recent research—primarily using single-unit physiology—also demonstrates that selective attention can reduce the intrinsic internal noise observed in spiking activity as quantified by a reduction in the ratio of the mean response to the variance of the response (termed the *Fano Factor*; Mitchell, Sundberg, and Reynolds 2007). Such internal noise reduction likely plays a complementary role to signal enhancement, as the signal-to-noise ratio (SNR) of neurons increases with gain and also with a reduction in noise (Fig. 4.3). This may be particularly important in light of neurobiologically observed

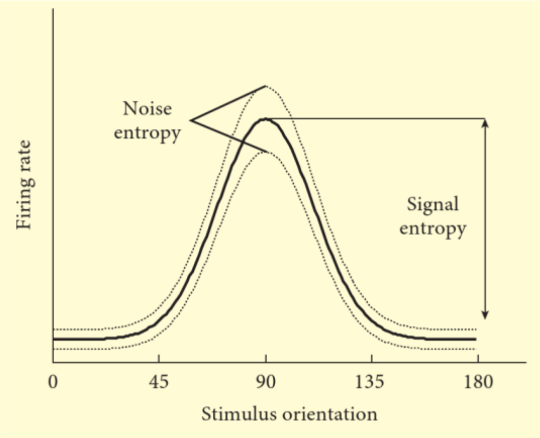

FIGURE 4.3 The amount of information that a sensory neuron encodes about sensory features depends on both response gain and response variance. Depicted here is a cartoon schematic of the tuning function of a simple cell in primary visual cortex that responds maximally to a 90° oriented bar of light. Mutual Information (or MI; Shannon 1949) is a useful metric for quantifying how much information about a sensory stimulus can be gained by measuring the response of this neuron to a visual stimulus. MI is, intuitively speaking, the difference between the signal entropy—or the amount of variance in the neural response that is systematically related to changes in the stimulus—and the noise entropy—or the amount of variance in the neural response that is unrelated to changes in the stimulus (i.e. 'noise'). Increasing the gain of sensory neurons will increase the signal entropy by increasing the range over which responses vary as a function of the stimulus. All else being equal, this will increase the MI between neural responses and the stimulus features being encoded. Alternatively, decreasing the variability of a neuron (i.e. decreasing the Fano Factor) will reduce the amount of variability in neural responses that is unrelated to changes in the stimulus. All else being equal, this will also increase the MI between neural responses and the stimulus features being encoded.

neuronal noise, which often far exceeds the typical assumption of a Poisson distribution (where the variance is equivalent to the mean; Anderson, Mitchell, and Reynolds 2011). In extreme cases where the Poisson expectation is far exceeded, increasing gain will have little effect on the information conveyed by a single unit about an attended stimulus feature because the noise will increase at a fast enough rate to offset any gain-related improvements in SNR. In these situations, reducing the variability of single unit responses may be a critical component to ensuring that relevant sensory stimuli get processed more efficiently than irrelevant distractors.

Even though attention can attenuate trial-by-trial variability in single-unit responses, a considerable amount of noise remains in the system. Thus, some pooling or averaging of responses is required to form stable representations of relevant sensory features. However, averaging cannot remove noise that is correlated between similarly tuned neurons, thus placing a limit on the precision of sensory representations that are based on population codes (Abbott and Dayan 1999; Averbeck, Latham, and Pouget 2006; Averbeck and Lee 2006; Bair, Zohary, and Newsome 2001; Johnson 1980; Kohn and Smith 2005; Mitchell et al. 2007; Shadlen, Britten, Newsome, and Movshon 1996; Shadlen and Newsome 1994). Given the potential limits imposed by correlated noise, several recent studies have focused on uncovering the role of attention in decreasing shared noise between similarly tuned neurons to improve the efficacy of pooling sensory signals. For example, Mitchell and co-workers (Mitchell, Sundberg, and Reynolds 2009) demonstrated that spatial attention can attenuate correlated noise, particularly low-frequency noise, in mid-level area V4. Assuming a simple population read-out rule that is based on averaging responses across all neurons tuned to the attended stimulus, the observed decorrelations can lead to an estimated 40% improvement in the SNR of the neuronal population, as compared to an estimated 10% improvement in SNR due solely to increases in gain (Mitchell et al. 2009). While the exact benefit in terms of SNR needs further exploration under different task conditions and assumptions about how population codes are used to information perceptual decisions, this asymmetry highlights the powerful role that changes in variability and covariance can play in influencing the quality of sensory representations. Further underscoring the importance of noise correlations, Cohen and Maunsell (Cohen and Maunsell 2009, 2010, 2011) demonstrated decorrelations related to both space- and feature-based attention in areas V4 and MT. Importantly, the degree of decorrelation predicted trial-by-trial fluctuations in behavioural performance.

While this field of inquiry is nascent, and attention-mediated changes in variability and covariance have only been documented in a few mid-level structures, even less is known about the time course of these modulations. In one relevant experiment, Mitchell et al. (2007, 2009) used a stimulus that moved into the receptive field of a V4 neuron for 1000 ms before leaving the receptive field. Thus, the authors could examine changes in the Fano Factor and in covariance across counting windows that varied in size from approximately 10 msec to 400 msec. They observed that both the attention-related reduction in the Fano Factor and the attention-related reduction in covariance onset quite rapidly. In fact, spatial attention seemed to anticipate the trajectory of the moving stimulus, and significant decreases in internal noise were already evident at the point that the stimulus entered a neuron's RF. This onset latency is early enough in time to influence decision-making in speeded perceptual tasks, consistent with the documented relationship between covariability and accuracy on a cueing task (Cohen and Maunsell 2009, 2011). In addition, the magnitude of attention-related reductions in variance and covariance increased as the size of the counting window increased, suggesting that attention had the largest modulatory impact on low-frequency noise.

Collectively, these studies thus suggest that attention improves the efficiency of information processing in large part via changes in the variance and covariance of neurons in mid-level visual areas. Moreover, the temporally early onset of these effects suggests that changes in the noise characteristics of sensory neurons might operate relatively early in information processing during the extraction of basic low-level features. However, given that only a handful of studies have been done in this area there is still much to learn about the anatomical extent of these noise modulations as well as their onset time and the temporal window over which they operate.

Late Selection via the Efficient Read-Out of Sensory Signals

Although most of the discussion surrounding early versus late selection has centred on the anatomical locus, timing, and nature of sensory gain modulations, a parallel line of reasoning proposes that many of the effects attributed to selective attention can be explained without invoking either early or late modulations in early sensory regions. Instead, these *selective read-out* models posit that decision mechanisms can pool responses selectively from neurons that are optimally tuned to discriminate the attended stimulus, and that this selective pooling is sufficient to improve information processing even in the complete absence of sensory gain modulations (Dosher, Liu, Blair, and Lu 2004; Eckstein, Peterson, Pham, and Droll 2009; Eckstein, Thomas, Palmer, and Shimozaki 2000; Palmer, Verghese, and Pavel 2000; Shaw 1984). While it is clear that sensory gain modulations do occur as the result of attention, these models nevertheless make a critical, and often overlooked, point about the importance of maximizing the efficiency of how populations of sensory neurons are read out during decision-making (Fig. 4.4).

The power of selective read-out is perhaps most evident when considering how attention can greatly attenuate—or sometimes even eliminate—the influence of irrelevant distracting items that compete with relevant stimuli (Palmer and Moore 2009; Yigit-Elliott, Palmer, and Moore 2011). Since these models posit that decision mechanisms only read out responses from sensory neurons that are optimally tuned to make the relevant discrimination, the influence of irrelevant distracting items is automatically attenuated as responses associated with these stimuli have no impact whatsoever on the decision process. In this manner, selective read-out mechanisms can efficiently shunt

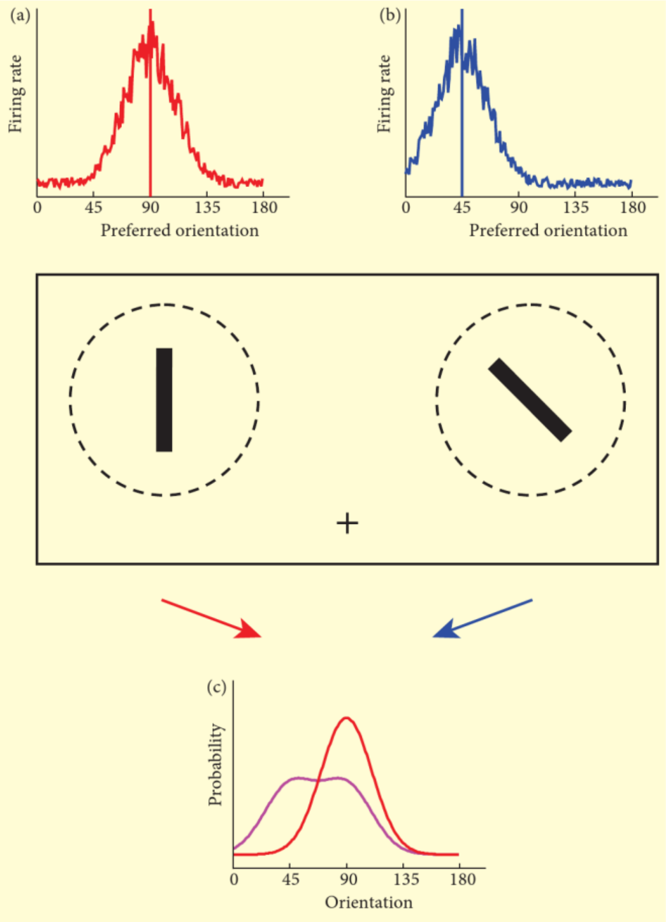

FIGURE 4.4 Selectively basing perceptual decisions on neural populations that are most sensitive to the relevant stimulus can improve the speed and accuracy of behavioural responses. (bottom panel) Schematic of a stimulus display presented briefly to a subject. The subject's task is to report, as quickly and accurately as possible, whether or not a vertical line is present in the display. (a) The response profile evoked by the vertical 90° stimulus across a population of sensory neurons that are maximally responsive (i.e. 'tuned to') different orientations and that have a spatial receptive field in the left hemifield. (b) The response profile evoked by a 45° stimulus across a different population of sensory neurons that have a spatial receptive field in the right hemifield. (c—Magenta line) If the subject has no advance knowledge about where the vertical line might appear, then they might reasonably pool responses across both neural populations before assessing the likelihood that a vertical line was present. This will lead to a relatively blurred and imprecise estimate of the stimulus features that gave rise to the sensory responses profiles show in panels a and b. (c—Red line) In contrast, if the subject knows in advance that the vertical line, if present, will appear in the left hemifield, then they need only base their likelihood estimate on the output of the neurons that have a spatial receptive field in the left hemifield (the neural response profile depicted in panel (a)). A comparison of the magenta and red lines suggests that inferences in this case will be more precise because irrelevant information provided by the neurons shown in panel b is not allowed to influence decision-making. Thus, selectively basing decisions on the most sensitive neurons can improve the efficiency of information processing, even in the absence of any direct modulation of sensory responses (e.g. gain or variance modulation).

interference from sensory neurons that encode irrelevant features, thereby increasing the discriminability of neural signals associated with attended stimuli.

While the selective read-out framework is appealing because complex modulations of sensory responses are not required, most of the work in this field is based on pure theory and mathematical models. Thus, even though selective read-out models can account for a variety of observed attentional modulations without recourse to sensory gain, this usually amounts to a proof of concept as opposed to a proof of existence. However, one recent neuroimaging study provides direct evidence that selective read-out plays an important role in implementing efficient information processing. Pestilli and co-workers (Pestilli, Carrasco, Heeger, and Gardner 2011) had observers search for a target embedded in a set of distractors, and demonstrated that sensory gain alone was not sufficient to account for the observed improvement in behaviour with attention. Instead, the data suggest that decision mechanisms over-weighted sensory responses associated with the attended stimulus and under-weighted responses associated with unattended distractors. This biased read-out process thereby ensured that signals associated with the attended stimulus dominated the decision process whereas signals associated with distractors had little or no impact. Again, the key element of this account is that selection occurs when sensory signals are integrated and evaluated by late-stage decision mechanisms, long after basic stimulus features are fully analyzed.

Related work has been done in the context of perceptual learning, where improvements in behaviour with practice are often thought to involve changes in the optimality of sensory read-out (Law and Gold 2008, 2009; Petrov, Dosher, and Lu 2005). For instance, Law and Gold (2008) found that firing rates in MT neurons did not significantly change after extensive training on a motion discrimination task. However, there were concurrent changes in the firing rates of the neurons in the lateral intraparietal area (LIP), an area implicated in accumulating sensory evidence during decision-making (Law and Gold 2008; see also Gold and Shadlen 2007). These data suggest that read-out from informative sensory neurons plays a more important role—at least in their task—than changes in sensory gain. In addition, even though the study ostensibly examined perceptual learning, Law and Gold (2008) used a motion stimulus that moved in a direction that was tailored to the tuning preference of the MT cells that they isolated each day. Thus, their task deviates from classic studies of learning that use a fixed stimulus feature, and may more closely resemble a more general perceptual task used in many attention studies (e.g. Treue and Maunsell 1996). The results are also consistent with some models of selective attention (Palmer and Moore 2009; Palmer et al. 2000), in which the most sensitive MT responses are pooled with linear weights and uninformative neurons are filtered out, leading to lower discrimination thresholds (Gold, Law, Connolly, and Bennur 2010; Law and Gold 2009).

While these empirical studies and the associated theories provide evidence for the importance of biased read-out as a mechanism of late selection, many important questions remain. For example, it seems likely that the importance of selective read-out depends critically on the number of competing items in the display. If only one item is present, then there is no need to selectively read out signals from only the attended item, so increasing the gain of sensory responses should be adequate to achieve whatever signal-to-noise ratio is required to perform the required perceptual task. However, the benefits of sensory gain will likely decrease as the number of competing distractors increases, at least under the reasonable assumption that gain cannot be increased indefinitely. In this situation, shunting the influence of distractors by discounting their impact on a late decision mechanism is a computationally and metabolically efficient way to implement selection and to ensure that only the most relevant sensory stimuli influence working memory and subsequent behavioural responses. Selective read-out therefore provides an example of a robust late-selection mechanism that, especially when combined with early sensory gain, highlights the increasingly accepted idea that selection is achieved through a combination of mechanisms that simultaneously operate at nearly all stages of information processing.

Conclusions

Over the last several decades, data from neuroimaging and electrophysiology studies have shown that the neural mechanisms of selective attention operate at almost all stages of the visual system, as well as in many areas outside of classically defined visual cortex. When viewed together, these studies firmly establish that selection is neither early nor late. Instead, the locus of selection, both in terms of anatomy and time, flexibly depends on the demands placed on sensory processing machinery by the behavioural goals of an observer. Tasks that require highly focused attention on a specific location or feature will encourage early selection, whereas less demanding tasks that can be performed with a more diffuse attentional focus will accommodate late selection. Finally, a complete understanding of selective information processing is not all about understanding where and when the gain of sensory neurons is modulated: emerging evidence suggests equally important roles for modulating the variance and covariance of sensory neurons, and for selectively reading out information from only the most informative sensory neurons.

Moving ahead, the major challenge for future investigators is to meld the multiple mechanisms that support selective attention into a unified framework. For instance, it is well accepted that each stage of the visual processing hierarchy contributes differently to visual perception. Therefore, it also seems likely that selective attention implements different functions in different visual areas, and that each function is determined by the specific processing capabilities of a region. For example, at the thalamic level, attention may serve to control neural response gain. At early cortical processing stages, attention may influence feature and context selective responses, which may facilitate the basic mechanisms of scene segmentation and grouping (e.g. Ito and Gilbert 1999). At intermediate cortical processing stages where multiple stimuli often fall within a single RF, attention may mediate the filtering of unwanted information through internal and external noise reduction (i.e. distractor exclusion). These diverse modulatory processes appear to be controlled by a higher-order fronto-parietal network of brain areas that may coordinate large-scale attentional modulation via subcortical structures such as the superior colliculus (Zenon and Krauzlis 2012; see chapter by Krauzlis) and the pulvinar nucleus of the thalamus (Saalmann, Pinsk, Wang, Li, and Kastner 2012; see chapter by Saalmann). Ultimately, however, these brain systems cooperate to select relevant visual information for further processing in memory and other cognitive systems in order to guide actions. In this respect, attention can be described as a multi-level selection process that operates by integrating information across multiple anatomical and temporal scales to achieve behavioural goals in a flexible and adaptive manner.

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CHAPTER 5

LARGE-SCALE NETWORKS FOR ATTENTIONAL BIASES

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The core concept of 'attention' is a fundamental principle of cognition—the adaptive and proactive selectivity of our interface with the surrounding environment. Contrary to our intuition, we do not apprehend the complete and continuous stream of events unfolding around us. Instead, at any given moment we sample a handful of details that happen to be relevant or interesting within our current context and motivational state. Attention refers to the set of mechanisms that tune psychological and neural processing in order to identify and select the relevant events against all the competing distractions. This type of definition casts attention as function rather than as representation or as state. It is about orienting, focusing, and selecting.

Some History

Some of the earliest known empirical studies of selective attention were by Herman von Helmholtz (1867). He built an apparatus akin to a tachistoscope, which could illuminate a display containing several letters for a fraction of a second (Fig. 5.1). Using it, he confronted the severe limitations in our perceptual abilities, noting that it was impossible to view all the letters simultaneously in a single glance. He then demonstrated our ability to orient attention to specific spatial locations at will, while still maintaining visual fixation on a single point. By orienting attention covertly to different locations of the array in turn, over multiple iterations, he could reconstitute the entire array. Summarizing early seminal experimental work and using introspective methods, William James (1890) provided insightful and lucid descriptions of varieties, effects, and mechanisms of attention, which remain rich and contemporary. According to James, attention is a pervasive faculty that shapes conscious experience: 'My experience is what I agree to attend to' (James 1890/1950: 403). At any given moment, the span of consciousness is limited to a single object or thought, attended to reflexively or voluntarily, due to immediate (intrinsic) or derived (associated) relevance. Focusing attention by anticipatory preparation

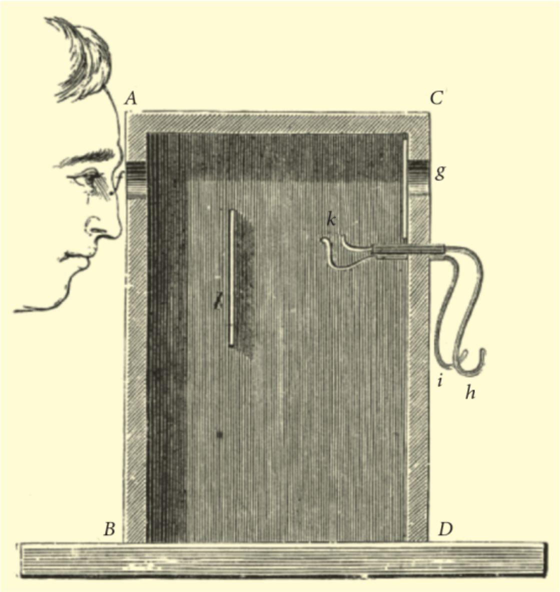


FIGURE 5.1 Apparatus built by Helmholtz to investigate the scope of perception while avoiding ocular movements. A drawing was fastened (at position g) to the back of a hollow box painted black inside. The observer maintained fixation on a small hole pierced in the drawing that was visible at all times. The image was illuminated by making contact between two electrical wires (I and h), triggering a spark illuminating the drawing. A white piece of cardboard (l) protected the observer's eye while also reflecting the light from the spark onto the drawing. 'The sparks were produced by a large Ruhmkorff induction coil connected with the terminals of a Leyden jar. The contact in the primary coil was made or broken by hand' Reproduced from von Helmholtz, *Treatise on Physiological Optics, Volume III*, figure 32 © 2005, Dover Publications.

using ideational centres concerned with the object to which the attention is paid results in adjustments in sense organs so that objects (or ideas of objects) are better perceived, conceived, distinguished, remembered, or more readily reacted to (James 1890/1950).

The early twentieth century witnessed a polarization of psychology between the psychoanalysts, who overemphasized the power of mental phenomena, and the behaviourists, who discredited it. The empirical study of attention regained a more balanced approach in the 1950s, when it became incorporated in the emerging 'information-processing' paradigm. Starting from the premise that our information-processing abilities are severely limited, the initial major experimental questions addressed the locus of the bottleneck. Experimental tasks were developed to test the consequences of focusing versus dividing attention in the presence of two or more competing streams (Cherry 1953). Opposing categorical views were put forward, which placed the information-processing limits at extremes of the information-processing stream: at very early, perceptual stages (Broadbent 1958) versus at late post-perceptual stages following semantic evaluation of stimuli (Deutsch and Deutsch 1963). The evidence was inconclusive in arbitrating between 'early selection' and 'late selection' theories, showing that it was possible to focus effectively on one stream of information based on physical characteristics of stimuli so that competing distractors generally did not reach awareness (compatible with early selection), but that high-level semantic or associative features of the unattended stream could nevertheless influence behaviour and occasionally break through into awareness (compatible with late selection; Treisman 1960) (for further discussion of this debate see Serences and Kastner (in chapter 4), this volume). A cogent theoretical model incorporating elements of both early and late selection was proposed by Anne Treisman (1960, 1969), in which modulatory mechanisms operating at perceptual levels attenuate processing of irrelevant material rather than blocking it completely, and in which stimulus representations have different thresholds of activation depending on their personal significance, conditional probability, or other contextual constraints (Treisman 1960). Nilli Lavie's 'perceptual-load theory' is another, contemporary hybrid model, which holds that a perceptual bottleneck only occurs when the perceptual demands of a task are high (Lavie 1995), see Lavie and Dalton (in chapter 3), this volume).

The present-day scene of attention research opens around the 1970s and 1980s as spectacular technological advances enabled increasingly sophisticated anatomical and functional brain studies in humans and non-human primates. The classical questions about the locus of capacity limitations quickly became obsolete, replaced by the clear realization that modulatory mechanisms operate at multiple levels of analysis in a distributed fashion in the brain (Nobre 2004; Nobre et al. 2011). Current research is directed toward characterizing the control and modulatory mechanisms of attention at the levels of individual neurons, neural systems, and large-scale networks. Orienting visual spatial attention according to task goals is the most widely investigated and, therefore, the most well understood paradigm.

Scope of the Chapter

The main focus of this chapter is to consider the mechanisms of attentional control, with particular emphasis on the process of top-down signals biasing information processing. Starting from the paradigmatic case of visual spatial attention, we will present a theoretical account suggesting that attention is controlled by a large-scale 'frontoparietal' network of brain areas that combines representational mapping of physically salient and relevant events, motor programs for intended actions, and motivational factors. We will summarize some principles emerging from a network approach to the control of attention. We will review evidence refining the characterization of the functional anatomy of the network, and supporting its critical role in modulating information processing.

Stepping outside the well-trodden terrain of visual spatial attention, we reflect on the scope of attentional control mechanisms more broadly. We examine the various possible '*sources*' of biases that can prepare perceptual mechanisms to improve interactions with the environment. In addition to the recognized effects of task goals, we entertain other possible potent modulators of ongoing information processing, such as long-term memories and motivational factors associated with anticipated events. We move on to consider the different '*types*' of biases that can operate upon information processing. Whereas studies in the literature have probed how biases can facilitate neural processing according to receptive-field properties of neurons, it is clear that it is possible to anticipate stimulus properties that may not be easily mapped onto receptive fields, such as the timing of events or the meaning of words. Finally, we show that attention can act upon multiple '*slates*' of information processing. We thus return to an old conception put forward by William James (1890) that attention is not restricted to operate upon objects from the sensory stream, but can also prioritize and select objects of thought. We describe a new body of work showing how attentional biases can act within representations maintained in visual short-term memory. To conclude, we discuss how this plurality of sources, types, and slates for attentional biases invites a reconsideration of the conceptualization of attention.

MODULATORY BIASES

One of the more influential theoretical models for modulatory mechanisms of attention is the 'biased competition model' (Desimone and Duncan 1995). According to this model, the limits of perception arise because of the inherently competitive organization of perceptual systems. Through the visual hierarchy, convergence of inputs from afferent areas leads to increasingly complex receptive-field properties with increasingly lower spatial and temporal resolution. At downstream areas, such as in inferior temporal (IT) cortex, multiple objects or attributes can fall within the receptive field of the same neuron. Averaging the response across all the stimuli impinging on the receptive field would conflate the coding of the various stimuli and abolish discriminability. To be informative, the neuron should respond according to one of the multiple competing stimulus sources. To be adaptive, the neuron should respond according to the most relevant stimulus source.

One of the primary functions of attention is to set preparatory *biases* to influence the competitive interaction among multiple inputs in favour of the most behaviourally relevant stimulus. Biasing competitive interactions in this way facilitates selection of the attributes of relevant objects, and filtering out of irrelevant attributes, across populations of neurons. Interactions among neurons with spatially and temporally correlated activity further aid co-selection and integration of the features of the relevant objects (Desimone and Duncan 1995). Thus, as a corollary, such biasing signals are likely to play a major role in solving the difficult 'binding problem', by helping to reconstitute features of relevant events that may come to occupy awareness (Reynolds and Desimone 1999).

Our understanding of the cellular mechanisms for biasing neuronal activity, selecting target-related attributes, and integrating them into objects to guide awareness and action remains incomplete, but progress in this area is impressive, and several pieces of the puzzle are coming into view. Competitive interactions among neurons have been well described (Reynolds et al. 1999), as well as the influence of spatial (Moran and Desimone 1985), object-based (Chelazzi et al. 1993, 1998), and feature-based (Treue and Martinez Trujillo 1999) attention in resolving competitive interactions within multiple brain areas. For detailed accounts of the mechanisms being characterized, the reader is directed to the many excellent contemporary reviews of this literature (Reynolds and Chelazzi 2004). Although most experiments have concentrated on visual areas, there is clear evidence that analogous biasing mechanisms operate across sensory areas in other modalities (Mehta et al. 2000), as well as in motor (Cisek 2007; Pastor-Bernier and Cisek 2011) regions of the brain. The findings, therefore, argue against fixed points of limited capacity, and indicate instead that selective biasing mechanisms operate at multiple stages. Furthermore, the sites and temporal characteristics of modulatory mechanisms are likely to be highly task-dependent, and to be influenced by the specific types of features that need to be discriminated and the number of competing response tendencies that need to be handled for accurate task performance (Stokes et al. 2009) (for an early articulation of this flexible proposal see Kahneman and Treisman 1984).

CONTROL MECHANISMS

What are the sources of these modulatory biases that play such a fundamental role in guiding perception and action? One generally accepted distinction is that between 'exogenous' and 'endogenous' shifts of attention. These are also referred to as 'reflexive' or 'automatic' and 'voluntary' or 'effortful' respectively. The distinction dates back at least to James, who separated passive/reflexive/non-voluntary/effortless from active/voluntary attention (James 1890/1950).

In exogenous shifts, physically salient stimuli attract attention. Biases are set 'bottom-up' by sensory-driven mechanisms that prioritize neural processing of events rendered conspicuous by virtue of their higher stimulus energy or local contrast (e.g. bigger, brighter, or faster) (Yantis and Jonides 1984; see Theeuwes (in chapter 8), this volume). These stimuli have acquired an edge through the evolution of our perceptual systems, and carry their own intrinsic biases to the competitive perceptual mechanisms. Their dominance can be considered a natural consequence of competitive interactions among unequal stimuli. Interestingly, however, these perceptually salient stimuli also leave a modulatory trail. They 'prime' their location, facilitating detection and discrimination of other events occurring at the same location over very brief intervals (Posner 1978, 1980). Unless the location turns out to be relevant or informative, the transient facilitation is subsequently replaced by suppression, thus freeing the system to explore other locations (Posner and Cohen 1984; Klein 2000; Chica et al. 2006; Lupiañez 2010).

In endogenous shifts, focus is directed voluntarily to a location of choice. Biases operate 'top-down', driven by endogenous (mental) factors computed in high-level, associative areas, and influencing perceptual processing through feedback connections. Different scholars have emphasized different mechanisms of regulation for top-down biases. The biased-competition model proposes that top-down biasing signals are primarily mediated through working-memory representations of task-relevant items (Desimone and Duncan 1995). The alternative 'premotor theory' of attention emphasizes the role of motor intention, and proposes that computations in the oculomotor, as well as other sensorimotor systems, modulate perceptual analysis through feedback connections (Rizzolatti et al. 1987; Rizzolatti and Craighero 1998). Mesulam suggested a broader conceptualization, in which sensory, representational; motor, exploratory; and limbic, motivational biases combine to direct spatial attention through the action of a large-scale frontoparieto-cingulate attentional network (Mesulam 1981, 1990, 1999).

LARGE-SCALE NETWORK FOR ATTENTION

Original description

Everyone now agrees that the control of spatial attention depends on a large-scale network of brain areas. The first network model for attention was proposed by Mesulam in 1981, and subsequently refined and extended over the years (Mesulam 1990, 1999, 2005). The original proposed network architecture was based on clinical observations of patients with hemispatial neglect as well as on multiple sources of convergent data in non-human primates (Fig. 5.2). Four sets of brain areas, three cortical and one subcortical, constituted major nodes, each introducing a different functional specialization so that spatial attention emerged as a property of the network as a whole.

In the macaque, the three cortical nodes of this network were located in the dorsolateral portion of the inferior parietal lobule and lateral bank of the intraparietal sulcus (LIP) (area PG of von Bonin and Bailey, 7a of Brodmann), frontal eye fields (FEF) (area 8 of Brodmann), and the cingulate gyrus (areas 23–24 of Brodmann and the retrosplenial cortex). Anatomical tracer studies had shown these nodes to be monosynaptically interconnected (Mesulam et al. 1977). The parietal node was proposed to provide a multisensory perceptual map of the extrapersonal space weighted by physical salience and relevance of stimuli. The frontal node provided a hub for motor integration, which contained representations of motor programs for the distribution of exploratory actions. The cingulate node acted as a region for integration of limbic signals, assigning motivational relevance to events based on previous experience and current needs. Experimental lesions to any of these cortical nodes resulted in attention-related deficits akin to neglect (Bianchi 1895; Kennard 1939; Denny-Brown and Chambers 1958; Welch and Stuteville 1958; Heilman et al. 1970; Cowey and Latto 1971; Watson et al.

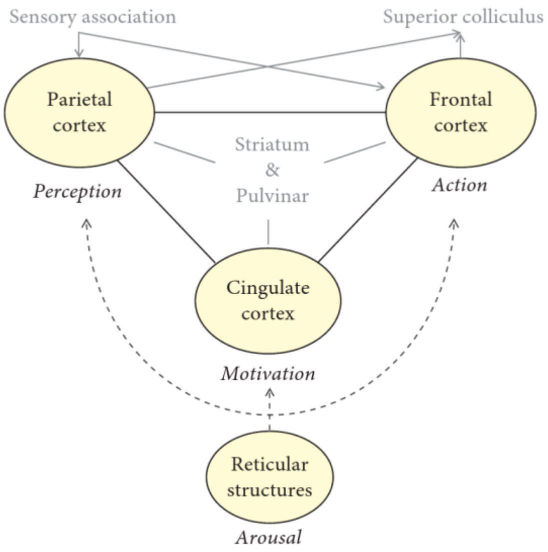


FIGURE 5.2 Large-scale network for orienting visual spatial attention proposed by Mesulam (1981, 1990, 1999, 2005). Parietal, frontal, and cingulate cortices are the three primary cortical nodes. These act as local hubs for organizing and integrating signals related to perception, exploratory action, and motivation, respectively. The three cortical nodes are directly interconnected with one another, and are additionally interconnected through participating subcortical hubs in the striatum and the pulvinar nucleus of the thalamus. In addition to their intrinsic connections, the cortical and subcortical nodes also have connections to other areas with specialized sensory, limbic, and motor functions. The main nodes of the large-scale network each also receive modulatory reticular input from brainstem nuclei.

1973) and single-unit recordings showed modulation of neuronal activity by the relevance of the stimulus and nature of orienting responses it elicited (Hyvarinen and Poranen 1974; Mountcastle et al. 1975; Lynch et al. 1977; Bushnell et al. 1981). Each of these interconnected nodes had its own pattern of connections with functionally related areas, such as sensory association areas in the case of the parietal cortex, motor and premotor regions in the case of frontal eye fields, and other limbic nuclei in the case of the cingulate cortex. In addition, all three areas receive reticular input from a common set of thalamic, basal forebrain, and brainstem nuclei (see Mesulam 1990). These subcortical inputs comprised the fourth functional node of the network, and were proposed to play a central role in regulating the state of arousal, which underpins and interacts strongly with the selective control of spatial attention (Hecaen et al. 1956). Brainstem reticular lesions have long been known to cause severe deficits in arousal and awareness, and lesions of the intralaminar thalamic nucleus in monkeys have been observed to result in neglect (Watson et al. 1974, 1978).

The network approach is intermediary to centrist approaches, in which complex functions are supported by exclusively dedicated brain areas (Spurzheim 1825), and holistic approaches, in which complex functions are equipotentially distributed across areas (Lashley 1950). It has several noteworthy properties. According to the large-scale network approach, individual cognitive domains are enabled through the interaction of interconnected areas, each with a relative specialization for a component function of that domain. Having a network of areas supporting a complex function means that impairments can arise from different lesion sites. The network also provides some protective compensatory mechanisms, so that severe and lasting impairments may not arise unless multiple nodes are damaged. The presence of multiple nodes with distinct functional specializations can also help explain the variety of deficits that arise from lesions to the different nodes, their interconnections, or their connections to other regions (see Geschwind 1965a, 1965b).

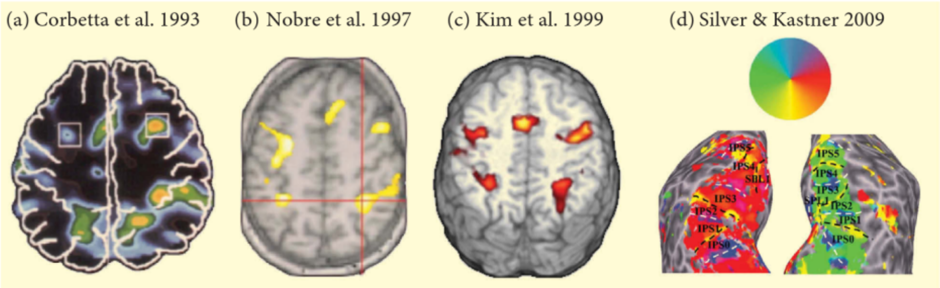
The interactions among the areas in an integrated system can blur the categorical distinctions between the functional specializations contributed by the different nodes. For example, the distinction between sensory and motor contributions across parietal and frontal nodes in the attention network was considered to be relative, with sensory and motor functions observable in each of these areas. Such a proposal, of course, is perfectly acceptable nowadays with our growing exposure to the sensory properties of neurons in the motor system, as in mirror neurons (di Pellegrino et al. 1992), and to increasing proposals of action-based active sensing mechanisms in perceptual systems (Fortuyn 1979; Schroeder et al. 2010).

Another feature of the large-scale network model is that brain areas with a given functional specialization need not be exclusively dedicated to one network. Conceivably, the same physiological specialization could underlie multiple complex functions. For example, similar neuronal profiles in posterior parietal cortex have been implicated in spatial attention, oculomotor control (Colby and Duhamel 1996; Snyder et al. 2000; Bisley and Goldberg 2010), decision-making (Leon and Shadlen 1998; Gold and Shadlen 2007; Gould et al. 2012), working memory (LaBar et al. 1999; Todd and Marois 2004; Buschman et al. 2011), and long-term memory (Wagner et al. 2005; Cabeza et al. 2008). The nodes of large-scale networks also add flexibility by acting as portals of interactions with other brain areas so as to integrate attention control with other complex functions, such as language, working memory, and long-term memory.

Imaging the attentional network

Over subsequent years, the large-scale model of attention was amply vindicated. Refinements to the model came from continued characterization of neglect symptoms and their dissociations, and from increasing knowledge about physiological properties and connectivity of brain areas (Mesulam 1990, 1999; Mesulam et al. 2005). The development of positron-emission tomography (PET), and then functional magnetic-resonance imaging (fMRI) methods, introduced a wealth of new information on the attentional network. Non-invasive brain imaging enabled the testing and extending of the network model, by mapping its constituent critical nodes and revealing areas that participate without being critical to spatial orienting. The core cortical parietal, frontal, and cingulate nodes were recognized to comprise functional mosaics of multiple areas with distinct but interrelated contributions to representational, intentional, and motivational functions. Other, highly related cortical areas for attention were also proposed to participate in some spatial attention functions, such as in the medial parietal cortex, supplementary eye fields (SEF), premotor areas in the case of orienting attention to near space, dorsolateral prefrontal cortex (BA 46), and possibly parts of temporal cortex. Also stressed was the role of subcortical areas, in particular the superior colliculus, striatum, and pulvinar nucleus of the thalamus (see also Saalmann and Kastner (in chapter 14), this volume).

The first visualization of the network for controlling spatial attention in the human brain came from studies using PET using an adaptation of Posner's visuospatial orienting task over a group of participants (Corbetta et al. 1993, 1995) (Fig. 5.3). We extended



(a) Corbetta et al. 1993 (b) Nobre et al. 1997 (c) Kim et al. 1999 (d) Silver & Kastner 2009

FIGURE 5.3 Imaging the cortical areas involved in the control of visual spatial attention with increasing resolution. All images are from an axial perspective with the posterior part of the brain on the bottom and the right hemisphere on the right. (a) The seminal study by Corbetta et al. (1993) used positron emission tomography (PET) and relied on patterns of activation across a small group of participants. Data from Corbetta, M., Miezin, F. M., Shulman, G. L. and Petersen, S. E., A PET study of visuospatial attention. *Journal of Neuroscience*, 13, pp. 1202–26 © 2003, Society for Neuroscience. (b) Nobre et al. (1997) used PET to image the network in individual participants as well as in groups. It became possible to localize cortical activations to the intraparietal sulcus, frontal eye fields, and anterior cingulate cortices. Data from Nobre, A. C., Sebestyen, G. N., Gitelman, D. R., Mesulam, M. M., Frackowiak, R. S. and Frith, C. D., Functional localization of the system for visuospatial attention using positron emission tomography, *Brain*, 120 (Pt 3), pp. 515–33 © 1997, Oxford University Press. (c) Functional magnetic-resonance imaging greatly increased the functional anatomical resolution for investigating the spatial attention networks in groups and individuals in tasks with much greater experimental control. The example illustrated is from the study by Kim et al. (1999), showing the overlap in brain areas activated by voluntary/endogenous spatial orienting based on informative central cues and by automatic/exogenous spatial orienting based on non-informative peripheral cues. Data from Kim, Y. H., Gitelman, D. R., Nobre, A. C., Parrish, T. B., LaBar, K. S. and Mesulam, M. M., The large-scale neural network for spatial attention displays multifunctional overlap but differential asymmetry. *Neuroimage*, 9 (3), 269–77 © 1999, Elsevier. (d) By adapting procedures for retinotopic mapping to produce spatiotopic maps, it has become possible to subdivide the nodes of the spatial attention networks into multiple constituent functional regions. The example shows the subdivision of posterior parietal cortex into multiple functional regions with spatial specificity. Reproduced from Silver, M. A. and Kastner, S., Topographic maps in human frontal and parietal cortex, *Trends in Cognitive Sciences*, 13 (11), 488–95, © 2009, Elsevier.

this work with the first functional anatomical characterization of the human 'frontoparietal network' using PET at the individual-subject level, which strongly supported Mesulam's model (Nobre et al. 1997). Three cortical areas were implicated in orienting spatial attention: posterior parietal cortex, straddling the intraparietal sulcus; dorsal premotor/posterior prefrontal cortex (in both lateral and medial Brodmann area 6); and anterior cingulate cortex (Brodmann area 24). We replicated these sites of activation with greater spatial resolution in an fMRI study using single-subject analyses and stringent behavioural controls (Gitelman et al. 1999). Studies investigating activity of spatial cues in isolation, separately from processing of subsequent targets, have verified that multiple brain areas participate in controlling spatial attention (Kastner et al. 1999; Corbetta et al. 2000; Hopfinger et al. 2000; Nobre et al. 2004; Woldorff et al. 2004).

By now, activation around the intraparietal sulcus and in dorsal premotor/prefrontal areas has been replicated by dozens of spatial attention imaging studies across labs worldwide (Vandenberghe et al. 1996; Fink et al. 1997; Kim et al. 1999; Hopfinger et al. 2000; Kastner and Ungerleider 2000; Corbetta and Shulman 2002; Giesbrecht et al. 2003; Pollmann et al. 2003; Woldorff et al. 2004; Molenberghs et al. 2007). Involvement of cingulate cortex in top-down regulation of behaviour according to motivational factors has also been convincingly demonstrated (Isomura and Takada 2004; Rushworth et al. 2007, 2011; Liu et al. 2011; Wallis and Kennerley 2011), and specifically noted in tasks involving spatial attention (Mesulam et al. 2001; Small et al. 2003, 2005; Dean et al. 2004; Mohanty et al. 2008; Kaping et al. 2011). Successive imaging studies have achieved increasing spatial and functional characterization of the mosaic of parietal and frontal cortical areas, as well as of the subcortical areas involved (e.g. Vandenberghe et al. 2001; O'Connor et al. 2002; Astafiev et al. 2004; Kastner et al. 2007; Kelley et al. 2008; Konen and Kastner 2008; Molenberghs et al. 2008; Silver and Kastner 2009; Szczepanski et al. 2010; Saalmann and Kastner 2011; Serences 2011; Scolari et al. 2012).

Relationship between visuospatial attention and oculomotor control

In our original PET study (Nobre et al. 1997), the parietal and frontal areas were noted to resemble those highlighted by imaging studies of oculomotor control (Melamed and Larsen 1979; Fox et al. 1985; Petit et al. 1993; Anderson et al. 1994; Darby et al. 1996; Paus 1996), and were proposed to include the human homologues of macaque lateral intraparietal area (LIP), frontal eye fields (FEF), and supplementary eye fields (SEF). The strong functional interrelationship between visuospatial orienting and oculomotor control had been, and continues to be, suggested by a number of behavioural (Allport 1987; Sheliga et al. 1994) and neurophysiological (e.g. Colby and Duhamel 1996; Snyder et al. 1997, 1998; Gottlieb et al. 1998; Kusunoki et al. 2000) studies (see Deubel (in chapter 30), this volume). Human imaging studies comparing activations during spatial orienting of attention in the absence of eye movements (covert attention) and saccade generation confirmed a high degree of overlap in activated brain areas (Corbetta et al. 1998; Rosen et al. 1999; Nobre et al. 2000a; Perry and Zeki 2000; Van der Stigchel et al. 2006). Contemporary research continues to explore the nature and degree of functional and neural overlap between eye movements and attention, as well as the mechanisms which enable the two functions to be dissociated during covert attention (e.g. Juan et al. 2004; Cohen et al. 2009; Khan et al. 2009; Lawrence and Snyder 2009; Bisley and Goldberg 2010; see also Deubel (in chapter 30), this volume, Theeuwes (in chapter 8), this volume; Gottlieb and Balan 2010; Wardak et al. 2011; Belopolsky and Theeuwes 2012; Gregoriou et al. 2012). Although oculomotor circuits may play a primary role in the network for spatial attention, studies have suggested that other sensorimotor circuits, specialized for different forms of spatially guided action (e.g. reaching or pointing movements), also display similar attentional modulations (e.g. Snyder et al. 1997, 1998; Astafiev et al. 2003; Van Der Werf et al. 2010; Deubel (in chapter 30), this volume).

Endogenous versus exogenous spatial orienting

The different characteristics of endogenous versus exogenous spatial shifts of attention (see Posner 1978, 1980; Posner et al. 1982, 1984; Müller and Rabbitt 1989; Friedrich et al. 1998; Losier and Klein 2001; Berger et al. 2005; Sieroff et al. 2007; Lakatos et al. 2008; Wright and Ward 2008; Chica et al. 2013) have led to numerous brain-imaging studies comparing the neural systems involved in these two types of orienting.

Initial studies used blocked designs to contrast experimental conditions with high versus low requirement for voluntary orienting under well controlled stimulus conditions (Nobre et al. 1997), or to contrast conditions using symbolic cues that predict subsequent target location versus non-predictive transient peripheral cues (Kim et al. 1999; Koski et al. 1999; Rosen et al. 1999; Peelen et al. 2004). Surprisingly, the patterns of activations in endogenous and exogenous conditions reported were very similar, and consistent with engagement of the dorsal frontoparietal network in both cases (see Fig. 5.3c). These studies therefore suggested that endogenous and exogenous shifts of attention rely on the same general network of brain areas (Posner 1978; Jonides and Irwin 1981; Yantis 1998), though they could be supported by different dynamics and mechanisms within a common network.

In contrast to these findings and interpretations, Corbetta and colleagues proposed that different circuits supported endogenous versus exogenous orienting of spatial attention (Corbetta et al. 2000; Corbetta and Shulman 2002). They proposed that the dorsal frontoparietal network mediated voluntary, endogenous shifts of spatial attention; whereas a ventral network, comprising the temporal parietal junction (including supramarginal gyrus and superior temporal gyrus) and inferior frontal gyrus, mediated reflexive, exogenous shifts. Their proposal was based on the different patterns of activations triggered by spatial cues versus subsequent targets in event-related fMRI tasks. In agreement with the previous literature (Kastner et al. 1999), spatial cues activated dorsal parietal and premotor/prefrontal cortices. Targets, on the other hand. engaged a more widespread network of areas, including the temporal parietal junction and inferior frontal gyrus, in addition to dorsal frontoparietal areas. Furthermore, the ventral parietal and frontal regions responded more strongly to targets that had been invalidly cued, appearing at unexpected locations. Corbetta and colleagues reasoned that unexpected (e.g. invalidly cued) targets trigger predominantly exogenous shifts of attention to their location, and do more so when voluntary attention had been directed somewhere else by the preceding cue. Their findings, but even more so their interpretations, led to their influential subdivision of attention into two functionally distinct 'dorsal' and 'ventral' attention networks (shortened to DAN and VAN respectively) (Corbetta and Shulman 2002).

The strict correspondence of the ventral network to exogenous orienting, however, could be challenged. The account does not explain the consistent similarity of cortical activation patterns between blocked endogenous versus exogenous attentional shifts (Kim et al. 1999; Koski et al. 1999; Rosen et al. 1999; Peelen et al. 2004). Furthermore, comparing the processing of unexpected targets to informative cues is not the same as comparing exogenous to endogenous orienting. The appearance of an invalidly cued target may trigger disengagement of attention from its previous site and a reflexive shift toward its location, but it may also engage a number of other processes: e.g. signalling a mismatch between current expectations about stimulus contingencies to direct action, updating learning of stimulus contingencies, switching stimulus–response associations between expected and novel patterns, as well as the motivational and emotional factors of violated expectations (see Nobre et al. 1999). The conceptualization of the 'ventral attention network' therefore conflates various putative factors that are not restricted to the control of attention (for further discussion on the 'VAN', see also Beck and Kastner (in chapter 9), this volume).

The conditions in which ventral parietal and frontal areas become activated have become better characterized through careful subsequent experiments. Findings argue clearly against the hypothesis that ventral frontoparietal regions play a special role in directing exogenous shifts of attention (Kincade et al. 2005). Using an ingenious and well controlled design, Corbetta's group compared activations triggered by predictive central cues versus non-predictive peripheral cues, as well as by validly versus invalidly cued targets in the endogenous and exogenous cueing contexts (Kincade et al. 2005). As expected, endogenous spatial cues activated the dorsal frontoparietal network. Contrary to their predictions, however, exogenous cues did not activate either dorsal or ventral frontoparietal areas. Valid and invalid targets in both endogenous and exogenous cueing conditions activated both dorsal and ventral frontoparietal regions. Furthermore, higher activation for invalid targets compared to valid targets only occurred in endogenous cueing conditions, when spatial expectations were breached. These occurred in some of the dorsal (e.g. FEF) as well as ventral (e.g. supramarginal gyrus) regions. Targets at an invalid location after a non-informative cue did not recruit frontoparietal areas (for related results see Peelen et al. 2004; Natale et al. 2009). Additional experiments have also shown that irrelevant salient events fail to engage frontoparietal areas; only task-relevant target events, or distractors sharing target features, occurring at unattended or unpredicted locations engage ventral parietal and frontal regions (Serences et al. 2005; Indovina and Macaluso 2007; Serences and Yantis 2007).

Taken as a whole, the evidence shows that the 'ventral attention network' is a misnomer. Ventral parietal and frontal areas do not participate directly in shifting attention exogenously or in resetting attentional weights. These areas are not engaged by stimuli that trigger exogenous shifts of spatial attention, such as transient non-informative cues. Instead, they are activated by the appearance of imperative target stimuli (or distractor stimuli sharing target features), which require decisions or responses; and their activation is enhanced when target appearance is unexpected. Elucidating the precise functional roles these areas play will require continued experimentation. Though the functions are likely to interact closely with the control of attention in spatial orienting tasks, they should not be construed as spatial attention functions in their own right. Many possibilities remain, such as functions related to motivational or emotional responses to breaches in expectation, sensory prediction-error signals, and/or updating representations of stimulus contingencies relevant to behaviour. Dropping the misleading nomenclature is an important first step in achieving clarity and making progress in understanding the nature of and interrelationship among the various types of control functions.

Temporal dynamics within the attention network

The high degree of interaction among nodes of the frontoparietal network has been fully supported by studies of functional connectivity in humans and macaques. The similarity in functional profiles of areas like FEF and LIP has long been noted (e.g. Chafee and Goldman-Rakic 1998), and indeed it is difficult to distinguish them other than in a relative way (e.g. Lawrence and Snyder 2009; Muggleton et al. 2011; Wardak et al. 2011). During tasks requiring spatial attention, correlations have been noted to increase among network areas (e.g. Buchel and Friston 1997; Gitelman et al. 2002; Buschman and Miller 2007; Vincent et al. 2008; Ozaki 2011; Vossel et al. 2012).

A key question in this field concerns the identity of the prime mover in shifting the focus of spatial attention. Given the high degree of proposed interaction and coordination across the nodes of the large-scale network for attention, it is unlikely that a clear and consistent temporal hierarchy of contributions can be identified. Hemodynamic imaging methods lack the resolution to measure timing differences at the scale necessary to resolve a sequence of events across the network of attention. Studies using event-related potentials show that lateralization of cortical activity triggered by predictive spatial cues starts posteriorly, suggestive of a parietal origin, and then progresses anteriorly, suggestive of frontal engagement (Harter et al. 1989; Hopf and Mangun 2000; Nobre et al. 2000b; but see van Velzen and Eimer 2003; Praamstra et al. 2005; Murray et al. 2011). A similar posterior-to-anterior progression is observed in non-lateralized brain activity triggered by cues that instruct a shift of spatial attention versus maintenance of attention at the same locations (Talsma et al. 2005, 2011;

Brignani et al. 2009), though spatial shifts compared to a cued rest period elicit a different pattern (Grent-'t-Jong and Woldorff 2007). Stepping back, it is important to realize that the sequence of effects within the attention network may largely depend on what triggers a spatial shift—an instructional cue, a working-memory representation of an anticipated target, or a salient perceptual event. Buschman and Miller (2007) neatly demonstrated this context dependency of the temporal hierarchy among spatial attention control areas. Recording simultaneously from different brain areas in the macaque, they showed that LIP was the first to signal a target within a search array when it popped out based on sensory features; but that FEF and lateral prefrontal areas took the lead when target detection required effortful matching of the target to a template held in working memory.

Interactions between the attention network and visual areas

The large-scale network for spatial attention—bringing together perceptual representations, intentions, and motivations—is proposed to act as the main source of spatial biases to prioritize the selection and integration of relevant events during the competitive processing in visual, and other sensory areas (Hopfinger et al. 2000; Kastner and Ungerleider 2000; Mendenorp et al. 2011). Single-unit and local field-potential recordings taken from multiple brain regions simultaneously in macaques show task-related correlations between visual areas and FEF and LIP (Buschman and Miller 2007; Saalmann et al. 2007; Gregoriou et al. 2009). In humans, analyses of functional interactions among brain areas using fMRI (Buchel and Friston 1997; Gillebert et al. 2012) or MEG (Siegel et al. 2008) also show enhanced coupling between frontoparietal nodes and visual areas with attention. Strong confirmation that frontal and parietal areas play a causal role in modulating excitability of visual neurons has come from studies using interference methods to change activity in FEF or posterior parietal areas while simultaneously measuring visual activity. Pioneering studies by Moore and colleagues showed that microstimulation of FEF neurons led to changes in the firing rate of V4 neurons with compatible receptive fields, and improved visual discriminability of targets therein (Moore and Armstrong 2003; Moore and Fallah 2004; Armstrong et al. 2006; Armstrong and Moore 2007). In humans, studies using transcranial magnetic stimulation (TMS) to FEF or posterior parietal areas while simultaneously measuring visual activity using fMRI or EEG have confirmed that frontal and parietal areas play a causal role in modulating visual excitability (e.g. Paus et al. 1997; Ruff et al. 2006, 2008; Taylor et al. 2007; Capotosto et al. 2009; Blankenburg et al. 2010; Driver et al. 2010).

These studies provide convincing evidence that the frontoparietal network acts as a source of top-down signals to influence perceptual analysis at sensory sites. Future work combining interference and correlational methods should help describe differences in the types and timings of top-down influences originating from different areas within the large-scale attention network. It will be equally important to test for alterations in visual excitability in patients who have sustained focal cortical lesions to different functional regions within posterior parietal, frontal, and cingulate areas (see Knight et al. 1980; Woods and Knight 1986; Woods et al. 1993; Vandenberghe et al. 2012).

The network for visuospatial attention and hemispatial neglect

Neglect, a neurological syndrome of disrupted spatial attention, is often associated with parietal lesions (Brain 1941; Vallar and Bolognini (in chapter 33), this volume), but can also occur after frontal, temporal, thalamic, or striatal damage (Karnath et al. 2002; Husain and Rorden 2003). This multiplicity of neglect-causing lesion sites is incorporated into the large-scale network model of spatial attention (Mesulam 1981, 1999). However, the fit between the location of neglect-causing lesions in neurological patients and of areas activated by attentional tasks in healthy subjects is far from perfect. Human brain-imaging studies of visuospatial attention have implicated parietal areas around the middle segment of the intraparietal sulcus (Nobre et al. 1997, 2003, 2004; Kastner and Ungerleider 2000; Nobre 2000; Corbetta and Shulman 2002; Giesbrecht et al. 2003; Woldorff et al. 2004), in the posterior segment of the intraparietal sulcus (Vandenberghe et al. 1997, 2005; Silver and Kastner 2009), and in the superior parietal lobule (Vandenberghe et al. 2001; Yantis et al. 2002; Molenberghs et al. 2007; Serences and Yantis 2007). In contrast, 'parietal' lesions, which are the most common cause for neglect, occur at more inferior locations such as the angular gyrus (Vallar and Perani 1986; Hillis et al. 2005; Verdon et al. 2010; Vossel et al. 2011), supramarginal gyrus (Committeri et al. 2007; Golay et al. 2008), the temporal–parietal junction (Driver and Vuilleumier 2001), or the posterior superior temporal gyrus (Karnath et al. 2001; Hillis et al. 2005; Verdon et al. 2010).

This potential mismatch can be partially resolved by considering that neglect is caused by lesions disconnecting the communication between network nodes or between the network and input and output areas (see Geschwind 1965a, 1965b; Gaffan and Hornak 1997; Thiebaut de Schotten et al. 2005; Bartolomeo et al. 2007). Studies using diffusion-tensor imaging methods to measure damage of white matter tracts in patients with and without neglect symptoms have confirmed that structural damage to the superior longitudinal fasciculus (SLF), linking parietal and frontal nodes of the attention network, contributes significantly in determining the occurrence of persistent neglect symptoms (Doricchi and Tomaiuolo 2003; Doricchi et al. 2008; Urbanski et al. 2008, 2011; Ciaraffa et al. 2013). In a similar vein, it has also been proposed that effective lesions exert their influence remotely (Corbetta et al. 2005; He et al. 2007; Corbetta and Shulman 2011).

Whereas it is easy to imagine how differences in the prevalence of certain brain lesions, consequences of disconnection, and remote effects could have led to the current picture of clinic-pathological associations, it remains important to verify whether lesions to the areas implicated in spatial attention functions by imaging and neurophysiology studies