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Attention: Time Capsule 2013

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The Oxford Handbook of Attention
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[–] Abstract and Keywords

‘Attention’ is a core and fundamental aspect of cognition. Accordingly it engages a sizeable and thriving research community. The field has precious theoretical and empirical seeds left by the pioneering investigators of mental functions in the nineteenth and early twentieth centuries such as Franciscus Donders (1818–89), Hermann von Helmholtz (1821–94), Wilhelm Wundt (1832–1920), and William James (1842–1910). It re-emerges in full strength in the 1950s with the cognitive revolution and Broadbent’s publication of *Perception and Communication* (1958). Since then, we have made tremendous progress in understanding the functional consequences of attention, its behavioural and neural mechanisms, its neural systems and dynamics, and its implications for neurological and psychiatric disorders. We are also making headway in understanding its interactions with other cognitive domains, and its applications to healthy cognition in the ‘real world’ more generally.

Keywords: attention, cognition, time capsule, functional consequences, behavioral mechanisms, neural mechanisms

IN this Handbook, we have pooled together some of the active researchers investigating different aspects of the field to provide a broad coverage and overview of contemporary attention research. Their combination forms a kind of scientific ‘time capsule’ for attention research today. The various researchers bring along their own assumptions, theories, experimental questions, tasks, methods, and models. Looking at all these elements together, it may be possible to gain clearer and deeper insights into the general principles of attention, as well as an intuition of the trajectory of attention research. In this epilogue, we provide a sketch of the patterns we glimpse in the time capsule.

You may be reading this epilogue because you read some of the chapters in the Handbook already. Or, who knows, like us, you may have read it cover to cover? Or perhaps you are still wondering whether to delve in? We hope you enjoy(ed) your reading. We have both greatly enjoyed working on this laborious project, and we have learned a lot along the way. Of course, we don’t agree with everything in the Handbook, nor do we expect you will. But we bring the offerings to the fore to encourage and facilitate the continued active and lively discussion of ideas, issues, and data that is essential for the health of any scientific discipline.

Bottlenecks in Perception and Cognition

Our mental interface with external reality is likely to remain perennially wondrous and puzzling. Over the centuries, we have come to accept that our grasp of our physical surroundings is neither immediate nor complete. Instead, our perception and cognition are highly selective and oriented towards the stimuli and events that are relevant to our current goals. Traditionally, it has been recognized that there are ‘limits’ to how much of the transduced external energy we can process to guide our conscious awareness, actions, and memories. Bottlenecks along the information-processing stream have been (p. 1202) proposed. Their exact nature and location have been the subject of enduring speculation and theorizing.

What exactly is limited? In the 1950s and 1960s, scholars talked of limitations in ‘capacity’ or ‘resources’ along a given critical stage of information processing. What was meant by capacity or resources was not always clear, but the terms imply some generic fuel or currency for information processes. Contemporary expressions of this view can still be found. For example, Carrasco (in chapter 7) suggests ‘limits are likely imposed by the fixed amount of overall energy available to the brain and by the high-energy cost of the neuronal activity involved in cortical computation’. Furthermore, in the early conceptualizations, single bottlenecks were envisaged. Different theories emphasized limitations in early stages of perceptual analysis (e.g. Broadbent 1958) versus late, post-perceptual stages (e.g. Deutsch and Deutsch 1963). The question regarding the locus of resource limitations framed much of the early empirical work in the field of attention; its seminal role is attested by the many summaries and discussions of this debate in numerous chapters of this handbook (see Lavie and Dalton (in chapter 3); Serences and Kastner (in chapter 4); Nobre and Mesulam (in chapter 5); Theeuwes (in chapter 8); Yu (in chapter 39)).

Over time, we have come to realize that there is much more flexibility in the process of prioritizing relevant information to guide cognition and action. Kahneman and Treisman (1984) took the first important step in pointing out that empirical evidence for early versus late selection coincided with the use of experimental tasks in which there was strong competition among perceptual streams of information (e.g. dichotic listening; Cherry 1953) versus response tendencies (e.g. Stroop task; Stroop 1935). They suggested that bottlenecks might reflect points of competition and thus move in its location depending on task demands. Following on this influential work, Lavie (1995) developed the perceptual load theory, positing a central role for resource limitations at perceptual stages in determining whether early modulation of information processing takes place (see Lavie and Dalton (in chapter 3), this volume).

Box 40.1 Quotes from contributors to this volume expressing the view that modulatory mechanisms of attention operate at multiple levels of processing

‘As with nearly all dichotomies in psychology, the emerging consensus is that neither extreme is correct. Instead, depending on task demands, the mechanisms of selective attention can flexibly operate on the quality of low-level sensory representations as well as on later stages of semantic analysis and decision making’ (Serences and Kastner (in chapter 4)).

‘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 and Mesulam (in chapter 5))

‘Neural competition is likely to take many forms throughout the central nervous system…’ (Stokes and Duncan (in chapter 6))

‘Evidence from functional brain imaging reveals that attention operates at various processing levels within the human visual system and beyond.’ (Beck and Kastner (in chapter 9))

‘Shifts in spatial attention have been associated with changes in the responses of individual neurons in every visual cortical area that has been examined, including primary visual cortex…’ (Cohen and Maunsell (in chapter 11))

‘The new consensus is that the locus of attentional selectivity can be shifted flexibly and rapidly between stages and subsystems, in accordance with a variety of factors that include stimulus parameters, current task demands, and top-down selection intentions.’ (Eimer (in chapter 10))

‘One area of growing research interest relates to the question of how attention spreads across the various modality-specific features of an object…or event as a function of the semantic relationship…between the component parts…’ (Spence (in chapter 16))

‘the emerging consensus is that feature-based and object-based attentional mechanisms…operate along a continuum and the extent to which selection is based on a specific feature or an object depends on both the complexity of the stimulus array and on the specific behavioral goals of the observer’. (Scolari, Ester and Serences (in chapter 20)) 'feature-based and object-based attention are selective modulation processes that, just like spatial attention, affect the responses of sensory neurons throughout the visual cortex of primates'. (Treue (in chapter 21))

'there may be multiple sources of temporal expectation, which can bias multiple stages of stimulus analysis depending on the stages of information-processing that are critical for task performance'. (Nobre and Rohenkohl (in chapter 24))

'Rather, at every stage of memory, processing constraints are present and selection is required...we argue that the ways in which we form, retrieve, and work with our memories largely represent *acts of attention*...' (Kuhl and Chun (in chapter 28))

'attention influences perception, as well as learning and memory'. (Scerif and Wu (in chapter 31))

'In attention research there is a long-standing debate on whether selection takes place before or after perceptual recognition...TVA takes a different view and assumes that the two processes occur simultaneously.' (Bundesen and Habekost (in chapter 37))

The consensus in contemporary research is that prioritization of information processing occurs at multiple stages. Many statements to this regard appear throughout the Handbook (see Box 40.1). In addition to revealing where the critical, process-limiting steps are located, current scholars are interested in characterizing the nature of process limitations at the various stages. A full picture is yet to form, but several candidate mechanisms are under investigation. Most researchers recognize that one major type of bottleneck is the competition among multiple stimuli occurring within the receptive fields of individual neurons (Desimone and Duncan 1995; see Serences and Kastner (in chapter 4); Stokes and Duncan (in chapter 6); Beck and Kastner (in chapter 9); Eimer (in chapter 10); Gottlieb (in chapter 12); Saalmann and Kastner (in chapter 14); Pessoa (in chapter 25); Soto and Humphreys (in chapter 26); Miller and Bushman (in chapter 27); Deubel (in chapter 30); Bundesen and Habekost (in chapter 37); Itti and Borji (in chapter 38)). Competitive interactions among stimuli occur throughout the visual system, especially in areas with large receptive fields (Reynolds et al. 1999; see chapters by Cohen and Maunsell (in chapter 11); Treue (in chapter 21)). Though less well studied, (p. 1203) (p. 1204) stimulus competition within receptive fields is also likely to limit processing in other perceptual systems and at later, post-perceptual stages of analysis (e.g. see Deubel (in chapter 30)). Many other types of process-limiting steps exist beyond receptive-field competition, which could act as targets for modulation. Contributors to the Handbook highlight a few, such as: overcoming the intrinsic noise of sensory neurons (see Serences and Kastner (in chapter 4); Cohen and Maunsell (in chapter 11)), integrating both simple and complex high-level features into coherent object representations (see Wolfe (in chapter 2); Nobre and Mesulam (in chapter 5)), indexing and keeping track of targets (see Cavanagh, Battelli, and Holcombe (in chapter 23)), selecting and executing an appropriate response among competing response tendencies (see Serences and Kastner (in chapter 4)), and encoding information into short-term memory (see Shapiro and Hanslmayr (in chapter 22)).

Defining Attention

The limitations in our perception and cognition, however we come to characterize them, are what bring us to notions of (selective) attention. But getting from notions to crisp definitions has been problematic. The field starts well, with a clear definition by William James that everyone knows (Box 40.2). Perhaps surprisingly, this well-loved definition does not make too many appearances in the Handbook (but see Zanto and Gazzaley (in chapter 32) for its insinuation). This definition emphasizes *functions* of prioritization among various simultaneously competing objects or trains of thought, including both selecting and inhibiting. Many contemporary definitions echo or try to refine this original proposal (see Box 40.2). Indeed, if one were to distil a core definition of attention out of the contemporary literature, it would be something like: the prioritization of processing information that is relevant to current task goals. Some researchers incorporate specific proposed mechanisms of prioritization functions into their conceptualizations. For example, the biased competition framework proposes the raison d'être of attention is to help resolve competitive interactions in perception (Desimone and Duncan 1995), Yu (in chapter 39) proposes a Bayesian computational framework for optimizing learning or prediction and inference, Bundesen and Habekost (in chapter 37) emphasize perceptual categorizations and competition for limited short-term memory capacity. Other researchers argue for consideration of a broader scope of prioritization functions. For example, Nobre and

Mesulam (in chapter 5) propose that there may be multiple sources of top-down modulatory signals related not only to task goals, but also to expectations, motivations, and memory (see also Pessoa (in chapter 25); Kuhl and Chun (in chapter 28); Summerfield and Egner (in chapter 29)). Furthermore, a number of researchers also consider other, closely related functions that are not strictly involved with prioritization of information processing to represent other 'kinds' of attention—such as sustained attention and executive control (see Posner, Rothbart, and Rueda (in chapter 19); Robbins (in chapter 18); Zanto and (p. 1205)

Box 40.2 Definitions of attention by William James and by contributors to this volume

'Every one knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others...' (William James 1890: 404)

'ability to prioritize relevant over irrelevant information'. (Serences and Kastner (in chapter 4))

'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.' (Nobre and Mesulam (in chapter 5))

'Attention allows us to selectively process the vast amount of information with which we are confronted, prioritizing some aspects of information while ignoring others by focusing on a certain location or aspect of the visual scene...' (Carrasco (in chapter 7))

'Visual attention allows people to select information that is relevant for their ongoing behaviour, and ignore information that is irrelevant.' (Theeuwes (in chapter 8))

'Attention is associated with improved performance on perceptual tasks and also with changes in the way that individual neurons in the visual system respond to sensory stimuli.' (Cohen and Maunsell (in chapter 11))

'Covert spatial attention prioritizes the processing of stimuli at a given peripheral location, away from the direction of gaze, and selectively enhances visual discrimination, speed of processing, contrast sensitivity, and spatial resolution at the attended location.' (Clark, Noudoost, Schafer, and Moore (in chapter 13))

'Selective attention attacks this problem, by modulating sensory-evoked neuronal responses so as to enhance the processing of task-relevant stimuli while suppressing that of irrelevant stimuli...This "active control" processing is essential to normal perception and cognition because it enables information processing to adapt to the immediate goals of the observer.' (Schroeder, Herrero, and Haegens (in chapter 17))

'Broadly speaking, the term "selective attention" refers to a collection of mechanisms that insulate patterns of neural activity evoked by relevant stimuli from the deleterious effects of stochastic synaptic transmission and interference generated by other, irrelevant stimuli...' (Scolari, Ester, and Serences (in chapter 20))

'Visual attention...allows us to select a small subset of the information picked up by our eyes and enhance its processing, thus concentrating scant resources onto those aspects of the incoming deluge of sensory data that we momentarily deem most relevant.' (Treue (in chapter 21))

'In order to process the events around us we must select and keep track of the objects of current interest, ignoring others around them. This indexing or individuation of targets is a central function of attention...' (Cavanagh, Battelli, and Holcombe (in chapter 23))

'Selective attention, understood as the processes that focus neural processing in service of current goals and requirements, is inherently and necessarily dynamic.' (Nobre and Rohenkohl (in chapter 24))

'The central challenge of executive control, then, is how finite cognitive resources are brought to bear on the information (sensory inputs, stored memories, action plans, and strategies, etc.) that is currently important for the goal at hand and how potential distractions are excluded. When this is applied to the external world, we call it attention.' (Miller and Buschman (in chapter 27))

'Attention has been defined in a variety of overlapping ways typically in terms of a mechanism that preferentially allocates processing resources to percepts, memories, or tasks on the basis of a current goal...A related definition of attention...is that it constitutes a mechanism by which sensory information is weighted according to its motivational relevance.' (Summerfield and Egner (in chapter 29))

'attention enables us to select relevant objects and locations over less important ones'. (Deubel (in chapter 30))

'attention operates as a set of biases on information processing...' (Scerif and Wu (in chapter 31))

'Selective attention refers to goal-directed focus on task-relevant information while ignoring other irrelevant information.' (Zanto and Gazzaley (in chapter 32))

'Attention is what allows one stream of information from the internal or external environment to be selected over others and therefore pervades almost any thought or action we take in our daily lives.' (Robertson and O'Connell (in chapter 36))

'Selectively filtering these sensory inputs and maintaining useful interpretations for them are important computational tasks faced by the brain.' (Yu (in chapter 39))

(p. 1206) Gazzaley (in chapter 32); Manohar, Bonnelle, and Husain (in chapter 34); Robertson and O'Connell (in chapter 36)). Finally, many simply leave the term undefined, relying on a you-know-what-I-mean approach.

Overall, it must be admitted that the field of attention could do better in terms of providing explicit and consistent definitions of its topic. The term 'attention' is often used in a vague manner, or multiple technical meanings can be juggled inconsistently or used incorrectly. Notions from folk psychology also creep in. Across the literature, 'attention' can indicate prioritization, target selection, mental effort, a mental state, the availability of resources, executive control functions, awareness, or simply 'thinking'. In addition to the core concept at stake, many other important concepts remain poorly defined or misused. We have already mentioned 'capacity' and 'resources'. Examples of other terms or concepts that prove challenging are: 'automatic', 'salience', 'relevance', 'top-down', and 'bottom-up'. In some cases, the premature coining of functional or mechanistic labels for phenomena, brain areas, or circuits can also cause confusion, and derail research and theorizing.

Several authors in the Handbook lament the state of our current nomenclature and urge for more care. Developing precise terminology and working towards an accepted taxonomy are important aims for the field at this stage. Clearly stated definitions and concepts would help kick-start the essential iterative process between theory and experimentation—guiding future experimentation and discussion, which in turn leads to refinement of definitions and concepts, which in turn guide experimentation and discussion...Having said this, it is also remarkable how much progress the field has achieved with its flexible and somewhat erratic terminology.

(p. 1207) Classical and Contemporary Experimental Questions

The questions that have framed and guided 'attention' research have evolved over the years. In addition to questions regarding the locus at which attention operated to overcome capacity limitations, another important question regarded the 'units' of attentional selection. Rival proposals held that attention operated on spatial locations (Posner 1978; Treisman and Gelade 1980) versus on representations of objects (Duncan 1984; Kahneman and Treisman 1984). Subsequent experimentation considered whether modulation could also occur at the level of feature values or dimensions, independently of objects and spatial location (see Scolari, Ester, and Serences (in chapter 20); Treue (in chapter 21)). The close intrinsic relationship between space, objects, and their constituent features naturally gives mileage to such controversies.

Nowadays, we accept a multiplicity of modulatory mechanisms, which can operate upon different types of representations in a non-mutually exclusive manner (see Wolfe (in chapter 2); Nobre and Mesulam (in chapter 5); Scolari, Ester, and Serences (in chapter 20); Treue (in chapter 21); Shapiro and Hanslmayr (in chapter 22); Zanto and Gazzaley (in chapter 32); Bundesen and Habekost (in chapter 37); Itti and Borji (in chapter 38)). It is clearly established that modulatory mechanisms can influence processing according to the various types of properties coded in neuronal receptive fields. Thus, spatial, object-based, and feature-based attention can all occur. Much current research is devoted to understanding the mechanisms of attentional modulation at the cellular level (see Cohen and Maunsell (in chapter 11); Gottlieb (in chapter 12); Clark, Noudoost, Schafer, and Moore (in chapter 13);

Saalman and Kastner (in chapter 14); Krauzlis (in chapter 15); Treue (in chapter 21); Miller and Bushman (in chapter 27)). In addition, it is important to recognize that attention can also operate on attributes that may not be directly related to neuronal receptive field properties, such as on the timing of events (see Nobre and Rohenkohl (in chapter 24); Zanto and Gazzaley (in chapter 32); Bundesen and Habekost (in chapter 37)) and meaning representations (Neely 1977; see Nobre and Mesulam (in chapter 5)). Contemporary research is also beginning to investigate the types of modulatory mechanisms that may be involved in these cases (see Schroeder, Herrero, and Haegens (in chapter 17)). There is also increasing interest in linking neuronal mechanisms with specific consequences for behavioural performance on a trial-by-trial basis (see Cohen and Maunsell (in chapter 11); Bundesen and Habekost (in chapter 37)). Typically, the mechanisms related to different types of attention have been studied in isolation. This has proven a pragmatic first step, yielding many relevant and tractable discoveries. However, in the real world, multiple types of attentional bias co-occur (see Itti and Borji (in chapter 38)). Depending on the particular stimulus parameters and task demands, a given type of attention may dominate, or multiple mechanisms may contribute in complementary ways. Moving forward, it will be increasingly important to compare and contrast the mechanisms involved in the different types of attention, and to **(p. 1208)** investigate their interactions (see Cohen and Maunsell (in chapter 11); Scolari, Ester and Serences (in chapter 20); Treue (in chapter 21); Nobre and Rohenkohl (in chapter 24)).

One useful distinction that has emerged is that between mechanisms involved in controlling the shifts of attention (between locations, objects, features, or other attributes) versus those involved in modulating ongoing processing along the information-processing stream (Corbetta 1998). As with all such categorizations, in the limit the boundary between these two aspects can become fuzzy. Nevertheless, separating the 'source' of attention signals from the 'site' where they act has been of great heuristic value for organizing research in the field. In investigating the source of attention control, the focus has moved from individual brain areas to large-scale networks (Mesulam 1981, 1990; see Nobre and Mesulam (in chapter 5); Beck and Kastner (in chapter 9); Vallar and Bolognini (in chapter 33); Manohar, Bonnelle, and Husain (in chapter 34)). Accordingly, studies of the contributions of individual brain areas (see Gottlieb (in chapter 12); Clark, Noudoost, Schafer, and Moore (in chapter 13); Krauzlis (in chapter 15)) are increasingly supplemented by investigations of how information across different network regions is coordinated and integrated (see Saalmann and Kastner (in chapter 14); Spence (in chapter 16); Schroeder, Herrero, and Haegens (in chapter 17); Miller and Buschman (in chapter 27)). Similarly, researchers characterizing mechanisms of modulation at the sites of attention increasingly consider the dynamics of modulation and information flow in neuronal assemblies, between sensory areas, and between sensory and control areas (see Cohen and Maunsell (in chapter 11); Clark, Noudoost, Schafer, and Moore (in chapter 13); Miller and Buschman (in chapter 27)).

Since their earliest descriptions (James 1890), shifts of attention are known to have different possible origins: endogenous/controlled/voluntary/active or exogenous/automatic/reflexive/passive. These shifts are often characterized as involving modulatory signals moving in a *top-down* versus *bottom-up* direction through the processing hierarchy. Understanding the relative contributions of these types of shifts to behavioural performance and charting the overlap, differences, and interactions in their mechanisms, continue to be of great interest (see Wolfe (in chapter 2); Nobre and Mesulam (in chapter 5); Carrasco (in chapter 7); Theeuwes (in chapter 8); Eimer (in chapter 10); Gottlieb (in chapter 12); Clark, Noudoost, Schafer, and Moore (in chapter 13); Miller and Buschman (in chapter 27); Kuhl and Chun (in chapter 28); Zanto and Gazzaley (in chapter 32); Vallar and Bolognini (in chapter 33); Manohar, Bonnelle, and Husain (in chapter 34)).

For researchers of spatial attention, one enduring issue has been the relationship between the mechanisms involved in the control and eye movements and of covert shifts of attention (see Theeuwes (in chapter 8); Gottlieb (in chapter 12); Clark, Noudoost, Schafer, and Moore (in chapter 13); Krauzlis (in chapter 15); Deubel (in chapter 30)). The close relationship in the computational demands and functional dynamics of eye movements and spatial attention has been long noted (Rizzolatti, Riggio, Dascola, and Umiltà 1987). Research has also revealed striking similarities in the brain areas and neuronal mechanisms involved in both cases. Indeed, within network models of attention control, it becomes very difficult to separate signals related to action intention, which can readily **(p. 1209)** enhance perceptual codes of the target items, from signals related to perceptual prioritization, which can readily activate associated action codes (see Nobre and Mesulam (in chapter 5)). Current research employs increasingly shrewd experimental designs and sophisticated methodology to measure and model behavioural performance and brain activity to understand the nature of the relationship between eye movements and spatial attention and the dynamics of their mutual influence (see Theeuwes (in chapter 8); Gottlieb (in chapter 12); Clark, Noudoost, Schafer, and Moore (in chapter 13); Krauzlis (in chapter 15); Deubel (in chapter 30)).

Experimental Paradigms and Methods

Over the years, the dominant experimental paradigm for attention investigations has moved from dichotic listening (Cherry 1953) to visual spatial orienting (Posner 1978) and visual search (Treisman and Gelade 1980). In orienting tasks, the experimental subject uses predictive or instructive cues to focus on a region of space to identify or discriminate relevant, target stimuli. Variations of this task can be used to investigate the orienting of attention to objects, features, actions, temporal instants, semantic categories, and more. In visual search tasks, participants are required to identify a pre-specified target, or a stimulus with certain pre-specified attributes, among a set of other, distracting stimuli. These tasks can also be modified to investigate attention in other modalities or across multiple sensory modalities. The prevalence of visual studies in attention naturally follows the same prevalence in research concerned with basic perceptual mechanisms. The same bias is reflected in this Handbook. Over the years, it will be imperative to increase efforts in understanding mechanisms of attention and perception in other modalities, as well as their integration across sensory modalities (see Eimer (in chapter 10); Spence (in chapter 16); Zanto and Gazzaley (in chapter 32)).

Methodological tools for investigating cognitive and brain functions have changed radically, probably in unimaginable ways, since the early empirical studies of attention. We have mostly left behind methods of introspection, which admittedly provided an incredibly fertile foundation (James 1890). In developing experimental tasks, scientists built ingenious mechanical devices to control stimulation and measure responses with increasing flexibility and chronometric control. We can now routinely rely on digital control of stimulus presentation and data collection devices—so that the main limit of the quality of the tasks we use and the behavioural data we collect is our own imagination. The most significant advances have been made in our ability to measure brain activity with increasing precision as participants perform attention tasks. In humans, structural imaging methods, such as computerized tomography and magnetic-resonance imaging (MRI), greatly facilitated linking attention-related deficits to sites of neurological lesions in patients. Hemodynamic imaging methods, positron-emission tomography, and then functional MRI (fMRI) revealed networks of brain areas correlated with attention control and modulation in the healthy brain. Event-related potentials provided rich (p. 1210) dependent variables enabling the investigation of attention-related modulation at different stages of information processing independently of responses. Time-frequency analysis of the electrocencephalogram is beginning to reveal the role of oscillatory brain activity in coordinating and integrating activity within and between brain areas during attention-related functions. With its increased spatial resolution and sensitivity, magnetoencephalogram is taking these electrophysiological studies to new levels. Non-invasive brain-stimulation methods, such as transcranial magnetic stimulation, provide the means to test the causal involvement and timing of brain areas within attention-related functions. By combining stimulation and correlational imaging studies, researchers can also start to investigate the causal interactions among brain areas and the dynamics of attentional control and modulation. Developments in analysis methods have kept pace with those in data acquisition methods, so that it is routinely possible to investigate fluctuations or influences in brain activity at the single-trial level.

In animal-model studies, the move from anaesthetized preparations that laid the foundations for neurophysiological systems explorations in the 1950s–1970s to awake behaving preparations has paved the way towards developing detailed physiological models for cognitive functions such as attention. Initially, studies focused on recording spiking activity in single neurons from a variety of brain areas. These revealed attentional modulation throughout many cortical and subcortical areas, such as the superior colliculus (Goldberg and Wurtz 1972), frontal eye fields (Bruce and Goldberg 1985), lateral intraparietal area (Robinson et al. 1978), and visual extrastriate cortex (Moran and Desimone 1985). More recently, methodological upgrades enable recordings from neuronal ensembles and from multiple interconnected sites simultaneously (see Saalmann and Kastner (in chapter 14); Schroeder, Herrero, and Haegens (in chapter 17); Miller and Buschman (in chapter 27)). Field-potentials, reflecting the neural activity of local populations, are now routinely recorded. Data analysis has advanced beyond quantifying spike counts and histograms, to consider the timing and variability in spiking, the degree of local and inter-areal synchronization, and statistical measures of causal influences between areas. Microstimulation of individual neurons is also coupled to recordings of neurons with congruent receptive fields in order to investigate causal neural dynamics of attention at the cellular level (see Clark, Noudoost, Schafer, and Moore (in chapter 13)). Increasingly, these properties and effects are considered for different neuronal subtypes, sorted according to their spiking characteristics. The methodological innovations keep coming. We stand at the dawn of optogenetic methods (Deisseroth 2010) being adapted for stimulating individual neurons within local microcircuits in behaving non-human primates in attention tasks (Gerits and Vanduffel 2013). Together, these methods will lead to a thorough understanding of the neural circuitry that subserves attentional selection. Great challenges will remain in relating the different neuronal effects to behavioural performance and in understanding the way information is coded and communicated across cognitive networks. Methods for modelling behavioural and brain activity at the various levels of analysis in humans and in animal models (see Bundesen and Habekost (in chapter 37); Itti and Borji (in chapter 38); Yu (in chapter 39)) will continue to be essential for putting the various findings together, (p. 1211) guiding the interpretation of experiments, generating new hypotheses, and building computational theories of attention.

Neural Systems and Mechanisms

Increasingly sophisticated behavioural experimentation has revealed many consequences of focused attention (see Carrasco (in chapter 7); Theeuwes (in chapter 8); Beck and Kastner (in chapter 9)); for example: reduction of spatial or stimulus uncertainty (Eckstein et al. 2002; Palmer 1994), enhancement of signal strength, increased discrimination sensitivity (Lu and Dosher 1998), improved acuity (Carrasco and Yeshurun 1998), increased contrast senstivity (Cameron et al. 2002), increased speed and efficiency of processing (Posner et al. 1980), increased temporal integration (Yeshurun and Marom 2008), suppressed masking of attended stimuli (Enns and Di Lollo 1997), inhibition of distracting information (Shiu and Pashler 1995; Theeuwes 1991), reduction of external noise (Lu et al. 2002), reduction of internal noise (Wyart et al. 2012), reweighting of information used for decision-making (Kinchla et al. 1995), improved encoding into short-term memory (Gazzaley 2011), and effective maintenance in short-term memory (Cowan 1995; Awh and Jonides 2001). Many of these effects are mutually compatible, and may occur simultaneously. Which effects take place may depend on a variety of factors involving stimulus parameters, task demands, and intentions (see Eimer (in chapter 10); Scolari, Ester, and Serences (in chapter 20)). As experimentation continues, it is hoped that these effects become better catalogued and the factors contributing to their occurrence become better understood.

The relentless methodological advances have enabled the field to make enormous progress in characterizing the neural systems and mechanisms involved in attention control and modulation. Converging lines of evidence from the various methods have substantiated network models for the control of attention (Mesulam 1981, 1990). Particularly implicated and heavily investigated are cortical and subcortical areas that are also involved in oculomotor control—posterior parietal area LIP (see Gottlieb (in chapter 12)), frontal eye fields (see Clark, Noudoost, Schafer, and Moore (in chapter 13)), and superior colliculus (see Krauzlis (in chapter 15)). Other frontal and parietal regions may also contribute, and their contributions continue to be parcellated (see Beck and Kastner (in chapter 9)). Subcortical areas in the thalamus and basal ganglia related to the coordination and integration of activity across large-scale neural circuits also play an important role (see Nobre and Mesulam (in chapter 5)). New insights into their role are coming from renewed research efforts fuelled by the interest in network dynamics and the availability of methods with which to investigate them (see Saalmann and Kastner (in chapter 14)). Network investigations are also increasingly considering the contribution of pharmacological agents (see Robbins (in chapter 18); Miller and Buschman (in chapter 27); Scerif and Wu (in chapter 31); Manohar, Bonnelle, and Husain (in chapter 34); Robertson and O'Connell (in chapter 36); Yu (in chapter 39)).

(p. 1212) As researchers investigate the physiological properties of neurons and neuronal assemblies in perceptual and attention-control areas, they also reveal an increasing number of modulatory effects that contribute to the prioritization of information processing. In perceptual areas, one of the first attention-related effects described was that competition among stimuli within receptive fields of neurons in extrastriate cortices (areas IT, V4, and V2) became resolved in favour of the task-relevant stimulus (Moran and Desimone 1985). Also reported were increases in firing rates of neurons coding relevant object-related features (Chelazzi et al. 1993) and spatial locations (Luck et al. 1997) in anticipation of their preferred targets and during sustained attention (Motter 1993). These effects suggested that one of the main mechanisms of selective attention was the biasing of competitive perceptual interactions towards relevant stimuli by filtering out the influence of irrelevant, unattended stimuli (biased competition model; Desimone and Duncan 1995). Though biasing competition is undoubtedly an important effect of attention, it is not the only one. Selective attention has been shown to enhance signals related to isolated stimuli, in the absence of competition (see Cohen and Maunsell (in chapter 11); Treue (in chapter 21)). Various types of gain control in firing rates have been reported in different visual areas as well as in the same area across experiments, including changes in response gain, contrast gain, and additive gains. Computational theories, considering the basic perceptual mechanisms of neuronal sization, have been proposed to reconcile the various findings (Boynton 2009; Lee and Maunsell 2009; Reynolds and Heeger 2009; see Cohen and Maunsell (in chapter 11); Treue (in chapter 21)). In addition to changes related to firing rates, recent studies have discovered attention-related changes in the levels of intrinsic and correlated noise of neurons (Cohen and Maunsell 2009; Mitchell et al. 2009; see Cohen and Maunsell (in chapter 11); Serences and Kastner (in chapter 4)).

In control areas, firing is enhanced when stimuli gain behavioural relevance or indicate the focus of attention for responding to subsequent targets (see Colby and Goldberg 1999; Schall 2004; see Gottlieb (in chapter 12); Clark, Noudoost, Schafer, and Moore (in chapter 13); Miller and Buschman (in chapter 27)). Changes in baseline firing rates have also been reported (e.g. Chafee and Goldman-Rakic 1998). The degree of overlap between the cellular mechanisms involved in attention and oculomotor functions continues to be investigated in these regions (see Gottlieb (in chapter 12); Krauzlis (in chapter 15); Clark, Noudoost, Schafer, and Moore (in chapter 13)). Furthermore, neurons in lateral prefrontal cortex flexibly adapt to code task-relevant stimulus attributes to guide top-down biasing signals (Duncan 2001; see Stokes and Duncan (in chapter 6); Miller and Buschman (in chapter 27)).

More recent studies of changes in baseline rates have suggested that these can be extremely dynamic, following spatiotemporally specific patterns of activation (e.g. Crowe et al. 2010; see Stokes and Duncan (in chapter 6)). Current research has also been trying to tease apart whether changes in baseline firing that have commonly been observed in working-memory tasks reflect the maintenance of memoranda, the anticipation of upcoming targets, or the transition between these two states (Lepsien and Nobre 2007; LaRocque et al. 2013; see Soto and Humphreys (in chapter 26); Kuhl (p. 1213) and Chun (in chapter 28)). Furthermore, in addition to sustained or dynamic changes in firing rates, short-term synaptic plasticity has also been proposed to play a role in maintaining the content of past experience and rules to guide goal-directed processing (Stokes et al. 2013; see Stokes and Duncan (in chapter 6); Miller and Buschman (in chapter 27)).

Perhaps the most salient new line of investigation in deciphering the mechanisms of attention is aimed at revealing the role of neural oscillations (see Saalman and Kastner (in chapter 14); Schroeder, Herrero, and Haegens (in chapter 17); Shapiro and Hanslmayr (in chapter 22); Rohenkohl and Nobre (in chapter 24); Miller and Buschman (in chapter 27)). There is great interest in forming a cohesive picture of how oscillations contribute to the neural organization of cognitive functions in general, and of selective attention in particular. Though still not fully proven or accepted (e.g. Shadlen and Movshon 1999), many present-day researchers believe that oscillations may provide conduits for the regulation of neural excitability in functional cell assemblies within or between brain areas (see Buzsaki 2009). In a ground-breaking study, Fries and colleagues (2001) showed that spatial attention greatly increased synchronization of neuronal activity in the gamma band. Computational and theoretical models suggest that increased gamma-band synchronization can greatly potentiate the throughput of the signals from the neuronal populations onto their efferent structures (Fries 2009). Many researchers are currently busy trying to extract the general principles through which oscillations aid prioritization and integration of information processing. In attention, a central question is the contribution of different frequency bands to top-down versus bottom-up signals (Buschman and Miller 2009; Bosman et al. 2012; Lee et al. 2013). Of increasing interest is whether and how oscillations may regulate neural excitability according to temporal expectations generated by the temporal regularities or associations of ongoing stimuli (see Schroeder, Herrero, and Haegens (in chapter 17); Nobre and Rohenkohl (in chapter 24)).

As this brief sampling shows, the field has revealed a dizzying collection of attention effects at the behavioural, network, and cellular level. More effects are certain to be reported. As Serences and Kastner (in chapter 4) observe: the ‘major challenge for future investigators is to meld the multiple mechanisms that support selective attention into a unified framework’.

Attention and Other Cognitive Domains

Attention is not an isolated cognitive domain. Indeed, if we accept the narrow, consensus definition of attention—the prioritization of processing information relevant to current task goals—one can immediately intuit how these functions interface with perception, action control and decision-making, motivation and emotions, memories at different time scales, and awareness. Various chapters in the Handbook consider these (p. 1214) relationships. Working across the categorical boundaries in cognitive psychology and neuroscience is fundamental for cross-fertilization of methodological advances and insights, and for reaching a cohesive and well-integrated understanding of the general principles of cognition.

The close relationship between spatial attention and action (and especially oculomotor) control has already been mentioned (see Theeuwes (in chapter 8); Gottlieb (in chapter 12); Clark, Noudoost, Schafer, and Moore (in chapter 13); Krauzlis (in chapter 15); Deubel (in chapter 30)). The field of action control is being advanced significantly by current efforts to investigate the mechanisms of choice and decision-making. Many of the factors being considered in decision-making research overlap or relate closely to those in attention research, such as notions about prediction, expectation, value, and informativeness of stimuli (see Gottlieb (in chapter 12); Scolari, Ester, and Serences (in chapter 20); Summerfield and Egner (in chapter 29); Yu (in chapter 39)). It will be essential to enhance the dialogue between these fields of research to avoid reinventing or undermining wheels. As Gottlieb (in chapter 12) notes, one 'key question for future [attention] work therefore is to integrate this work with a reinforcement learning framework...' It will also be important for researchers coming from the decision-making field to take into account the rich stock of modulatory mechanisms unveiled by attention research in order to broaden and enrich predictive-coding models.

Like attention, motivation and emotion modulate information processing (see Pessoa (in chapter 25); Scerif and Wu (in chapter 31)). Whereas the field of attention tends to home in on the influences on perception, the field of motivation has often considered effects on decision-making and responses, and the field of emotion has emphasized the effects on memory. But these preferences are somewhat arbitrary. Attention, motivation, and emotions probably all influence perception, decision-making, responses, and memories (see Nobre and Mesulam (in chapter 5); Pessoa (in chapter 25)). This realization prompts reflection into what characterizes the differences among these different types of modulatory mechanisms, the extent to which they are common, or the degree to which they interact with one another to influence ongoing perception and cognition.

Memory is another long acknowledged source of influence on our present perception and cognition. From the time of Helmholtz, memories have been considered fundamental in shaping and guiding the construction of sensible percepts (Helmholtz 1867). With some notable exceptions, attention research has not traditionally considered the prioritization of information processing by long-term memories, but this is changing (see Nobre and Mesulam (in chapter 5); Kuhl and Chun (in chapter 28); Scerif and Wu (in chapter 31)). Current research is investigating the networks and mechanisms by which memories modulate perception, and looking at the relationship of the networks and mechanisms associated with attention. Ultimately, memories are also formed about attended events, those that were prioritized for being relevant of interesting at their time. Therefore, there is a continuous, bidirectional interplay between long-term memory and attention (e.g. see Fuster 2009).

Attention also has an intimate relationship with memories on a much shorter time-scale, held in the 'rearward portion of the present space of time' (James 1890: 647). (p. 1215) Many theoretical accounts consider the contents of short-term memory, or working memory—maintained and manipulated to guide future action—to be the vital source of top-down modulatory signals in attention (Desimone and Duncan 1995; see Nobre and Mesulam (in chapter 5); Soto and Humphreys (in chapter 26); Kuhl and Chun (in chapter 28); Zanto and Gazzaley (in chapter 32); Bundesen and Habekost (in chapter 37)).[1] Again, the relationship is not unidirectional, but multifaceted. Attention, in turn, gates what comes to be encoded into short-term memory, helps maintain information in short-term memory, and dynamically modulates the information being maintained (see Kuhl and Chun (in chapter 28); Gazzaley and Nobre 2012). As with long-term memory, a virtuous cycle forms between short-term memory and perception with attention-related modulatory mechanisms facilitating prioritization and selection of relevant information at multiple stages along both directions of influence.

Missing from the Handbook is a chapter on the relationship between attention and conscious awareness. This was not deliberate, but the inevitable misfortune of being let down by a contributor. Attention and awareness are undeniably entwined, but research increasingly suggests that they are not synonymous or always coexistent. Some researchers propose that attention is a prerequisite for conscious awareness, and that the contents of awareness are mainly determined by top-down biasing of competing object representations by frontoparietal networks involved in attention (e.g. Rees 2007; Rees and Frith 2007). But others emphasize functional dissociations between attention and awareness (e.g. Koch and Tsuchiya 2007; Wyart and Tallon-Baudry 2008; Kentridge 2011). For example, Kentridge and colleagues have shown that it is possible to enhance detection and discrimination of unconscious stimuli by attention, such as in the case of blindsight (Kentridge et al. 1999, 2004). Continuing to make progress charting the relationship between these two fundamental but slippery domains will rely on having much clearer and accepted definitions as well as criteria for their measurement.

Applications of Attention Research

The widespread effects of attention on our cognition are probably evident by now. Prioritization and selection of information influence what we perceive, hold in mind, decide, do, and remember. Arguably, no other cognitive domain has as much reach in terms of applicability to real-world situations. Attention is fundamental to how we navigate through the world, how we learn, how we cope with the multiple demands and distractions as we perform our jobs, and how we focus on the things we enjoy in our moments of leisure. As technology continues to proliferate the amount of stimulation and data that surround us, our attentional mechanisms become more and more essential for coping at every step of life.

Given the pervasive influence of attention in our dealings with the environment, it is vital for the experimental field to step up its engagement with applied fields in education, industry, information and communication technologies, sports, and health. The academic **(p. 1216)** field of attention has amassed tremendous know-how of direct and important practical implications for these diverse sectors of our society. The field also stands to benefit from these various disciplines. They can tell us about particular challenges in improving or maintaining efficient performance under specific contexts. In some cases, the dialogue is beginning. For example, current research is testing the contribution of attention functions to the ability of children to maintain information in mind and to follow instructions in the classroom (see Gathercole and Alloway 2006; see Posner, Rothbart, and Rueda (in chapter 19); Scerif and Wu (in chapter 31)). But there is much further to go in terms of applying attention research to education as well as to other fields. Quick brainstorming should easily bring many areas for potential contributions, for example: design of web and other interfaces, effective advertisement, airport screening, diagnosis in medical images, sensory recognition in robots, cinema and television production, software and game design…

An important first step is for academic researchers to start investigating the dynamics of attention and selection under naturalistic conditions. What happens in the brain when we cross the street and look for cars? Do the mechanisms established using our simplified experimental paradigms apply to complex and ever-changing contexts of natural scenes? Are there important shortcomings in our understanding that we need to address? Recent behavioural and imaging studies have begun to increase ecological validity of experimental paradigms (e.g. Summerfield et al. 2006; Peelen and Kastner 2011) and to tackle questions of attention in real-life contexts (e.g. Ho, Reed, and Spence 2007; Drew, Evans, Võ, Jacobson, and Wolfe 2013; Evans, Birdwell, and Wolfe 2013). To complement studies embracing the complex and dynamic nature of real-life contexts, it will also be important to consider individual differences. Variations in genetics, environmental experience, and their interaction play important roles in how attention functions develop and operate across the lifespan (see Posner, Rothbart, and Rueda (in chapter 19); Scerif and Wu (in chapter 31)).

Deficits in Attention

The importance of attention functions to cognitive health is obvious. Unilateral spatial neglect is the neurological condition that has been most closely associated with deficits in attention. As with our conception of attention functions in the healthy brain, neglect has come to be understood as a syndrome of multiple symptoms related to spatial and non-spatial deficits in different modalities and levels of processing, underpinned by damage to nodes or connections of a large-scale network of brain areas (see Vallar and Bolognini (in chapter 33); Manohar, Bonnelle, and Husain (in chapter 34); Robertson and O'Connell (in chapter 36)). Symptoms in Balint's syndrome are also related to deficits in allocating attention across visual objects (simulanagnosia) and in spatially orienting and organizing eye movements (oculomotor apraxia) and manual responses (optic ataxia) (see Hécaen and De Ajuriaguerra 1954; Robertson (in chapter 35)).

(p. 1217) Contemporary work in neurology, psychiatry, and clinical psychology is greatly broadening our understanding of how deficits in attention contribute to cognitive health. In neurological cases, attention deficits do not only result after damage to brain areas caused by stroke, but they can also contribute to behavioural deficits after traumatic brain injury and in neurodegenerative conditions such as Parkinson's and Alzheimer's diseases (see Manohar, Bonnelle, and Husain (in chapter 34)). A number of psychiatric and psychological conditions are also currently believed to include attention-related factors. For example, individuals with anxiety or mood disorders display distorted patterns of attention (see Bar-Haim et al. 2007; MacLeod et al. 2002; Pessoa (in chapter 25)). Accordingly cognitive and behavioural interventions are being developed to redress attentional biases (see Bar-Haim 2010; Browning et al. 2010). The reasons why prioritization and selection of information can become pathological and dysfunctional in certain individuals are many, including genetic predispositions as well as environmental factors. Revealing the interplay of factors in determining individual differences in susceptibility to psychiatric and psychological conditions should prove a fruitful area for research.

Attention can also fail in the healthy brain. We all experience momentary lapses. An important new line of investigation suggests that deficits in attention become more frequent as we age (see Zanto and Gazzaley (in chapter 32))—as implied by the term 'senior moment'. Given the important role that attention plays in supporting cognition, deficits in attention may result in or greatly exacerbate deficits in other psychological functions, such as memory and decision-making. Deficits in attention are also implicated in compromising other psychological functions on the other side of the age spectrum, during early development (see Scerif and Wu (in chapter 31)). These observations suggest that interventions that are effective at enhancing attention-related functions may hold great promise in boosting healthy cognitive development in the early years and in waylaying cognitive decline during ageing (e.g. Anguera et al. 2013; Bavelier et al. 2011; see Zanto and Gazzaley (in chapter 32); Robertson and O'Connell (in chapter 36)). The race is on to devise viable and effective interventions that have reproducible and generalizable benefits.

Conclusions

As we pack up the attention time capsule and muse over its contents, we cannot help but be impressed by the industry of the field. It is true that some key elements are still missing. The field is still a bit disorganized on the nomenclature and taxonomy front. That makes it difficult to put all the findings and insights in their proper place. But the advances in revealing the mechanisms of attention at the behavioural, systems, and cellular levels remain remarkable nevertheless. Multiple effects have been documented that contribute to the prioritization, selection, and integration of information across all stages of the information-processing stream. Findings have come from convergent methodologies used across species and levels of analysis. The various aspects of the field **(p. 1218)** move ahead in a harmonious fashion. In this sense, 'attention' may be considered a role model within the fields investigating cognitive function.

But, of course, this is still the beginning. One major challenge ahead is weaving together the various findings into a cohesive and comprehensive framework. Although incomplete, our current understanding is ripe for incorporating principles of attention into the investigation of other cognitive domains. The other major challenge is reaching out to real-world applications. The role of attention in maintaining a healthy and balanced cognitive life is beginning to be recognized, and there will be important activity in understanding how best to translate our empirical work to the benefit of individuals. Attention research is poised to contribute to enhancing human experience through open dialogue and collaborative efforts with various other sectors of society.

Beyond this snapshot are so many possibilities… But for now it is a good start.

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Notes:

(1) . Most of these accounts consider the ‘content’ representations related to the target goal to be doing most of

the work during top-down guidance. However, one may also expand this notion by recognizing that representations about the current context, task set, rules, intentions, expectations, etc. are also maintained in short-term memory. These are also likely to exert influence.

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