Chapter 1

The Working Brain

by Addie Johnson, Jacob Jolij, Raja Parasuraman and Paolo Toffanin

A neuroergonomic approach requires an understanding of the neural markers of performance. This chapter gives the background for understanding the modules and processing systems that feature in the rest of the book and describes the major techniques used to visualize or influence cognitive processing. Particular attention is given to the brain areas underlying the auditory and visual systems, emotion, decision making and social interaction, and the neural systems for attention and arousal.

Neuroergonomics has been defined as the study of the brain and behavior at work (Parasuraman & Rizzo, 2007). The major goal of this new field is to use existing and emerging knowledge from the neurosciences to inform understanding of human behavior and performance in work-relevant tasks. As such knowledge is gained, the hope is that we can design systems and work environments that are safe, efficient, and enjoyable for their users. Reaching such a goal is made even more important by the relentless march of new, small information technologies in the marketplace–iPhones, GPS, voice-operated devices, and so forth impose new information-processing demands on their users. These devices can impair safety if they are used by people while they are simultaneously engaged in other activities such as driving or walking across a busy intersection (e.g., Strayer & Drews, 2004).

Such technological advances are affecting not only civilian life, but the military as well. For example, the United States Air Force Chief Scientist recently released a report that details the expanding mismatch between human "warfighters" and the technology available to them (Chief Scientist Air Force, 2010). The report attempts to make the case that as technological capacity continues to increase, it will become increasingly important to examine the role of the human as a link in security and other systems. It is evident that now more than ever, the military needs ergonomics research to enhance human-machine systems. The Air Force Chief Scientist report goes on to identify "augmentation of human performance" as one of two key areas where substantial growth is possible in the coming decade (p. vii), and specifically calls for "direct augmentation of humans via drugs or implants to improve memory, alertness, cognition, or visual/aural acuity" (p. viii) as well as "direct brainwave coupling between humans and machines, and screening of individual capacities for key specialty codes via brainwave patterns and genetic correlators" (p. 58). In other words, cognitive science and cognitive neuroscience must be combined with traditional ergonomics to create new neuroergonomic applications.

Although much of the interest in and funding for neuroergonomic research has come from the military, key areas of neuroergonomics such as operator-state based adaptive automation and brain-computer interfaces have applications in a range of work, transportation, and leisure environments. The development of neuroergonomic applications requires an understanding of the tasks to be performed, the cognitive processing involved in their performance, and the existence of a set of techniques to measure or influence cognitive processing. Many books and articles have been devoted to task analysis and cognitive work analysis (e.g., Diaper & Stanton, 2004; Vicente, 1999). It can be argued that neuroergonomics, in seeking to apply neuroscience to system design, starts where cognitive task analysis leaves off. Instead of describing cognitive processing activities as, for example, "memory" or "decision making", an understanding of functional neuronal networks is applied to assess the quality of information processing and to intervene to improve system performance.

Much of what we know or hypothesize about neuronal networks comes from single cell studies with animal subjects (e.g., Buzsaki, 2006; Kandel, Schwartz, & Jessel, 2000). Developments in neuroimaging are, however, making it increasingly possible to test hypotheses about how information is processed in the brain in healthy humans. Neuroimaging methods allow us to infer neuronal activity in terms of localized changes in blood flow or metabolism (positron emission tomography, or PET), in terms of changes in blood oxygenation level dependent (BOLD) responses (functional magnetic resonance imaging, or fMRI). Tracers that bind to different receptors have been used in combination with PET to examine transmitter density, and pathways of activation can now be imaged using diffusion tensor imaging (DTI), in which MRI is used to trace white matter tracts. Lesion studies have played an important role in mapping brain regions to function, and in addition to the study of naturally occurring lesions, transcranial magnetic stimulation (TMS) is being used to induce, on a short timescale, disruptions in normal brain processing to test conclusions about causal relations between brain activity and behavior. Finally, measurement of electric (electroencephalogram, or EEG) or magnetic (magnetoencephalogram, or MEG) signals at the scalp can be used to provide detailed information about the time-course of information processing and, increasingly, its locus. Used separately or together, these methods, and others (e.g., transcranial Doppler sonography, near-infrared spectroscopy, deep brain stimulation) form the toolkit of the neuroscientist studying the physiology of human brain networks.

These various neuroimaging techniques have been used extensively in cognitive neuroscience studies in which nave participants, typically college undergraduates, are tested while performing simple laboratory tasks of perception and cognition (Gazzaniga, 2009). In contrast to cognitive neuroscience, one of the goals of neuroergonomics is to examine brain function in the more complex and dynamic tasks representative of everyday, naturalistic environments at work, in the home, or in transportation, and–where possible–in expert populations such as pilots, physicians, or military personnel. From small beginnings, following the initial call for such research (Parasuraman, 2003), a growing number of studies have examined human brain function in work-relevant tasks. Examples include fMRI studies of frontal and parietal cortical networks involved in simulated driving (Just, Keller, & Cynkar,, 2008) and how they are altered in intoxicated drivers (Calhoun & Pearlson, 2012); EEG investigations of pilot mental workload during actual and simulated flight (Wilson, 2001); ERP studies of the usability of hypermedia systems (Schultheis & Jameson, 2004); and fNIRS studies of frontal lobe activation in experts performing simulated minimally-invasive surgery (James et al., 2011).

Brain stimulation techniques such as TMS and transcranial direct current stimulation (tDCS) can supplement the use of neuroimaging techniques in neuroergonomics. Such techniques are of interest because of their potential for showing that brain networks that have been identified in neuroimaging studies are not only active, but are necessary for performance of a given task. This is typically achieved by showing that task performance is impaired when the associated brain region is- momentarily inhibited using TMS (Walsh & Pascual-Leone, 2005) or tDCS (Jacobson, Koslowsky, & Lavidor, 2012). Of the two techniques, tDCS has some advantages over TMS for neuroergonomic studies because of its relative non-invasiveness, greater portability, and lower cost. These methods also allow for the possibility of enhancement of human performance through electrical or magnetic stimulation of the brain. Again, whereas these techniques have primarily been used in studies of basic perception and cognition, they are making their way into neuroergonomic research. Examples include TMS investigations of reasoning and complex decision making (McKinley, Bridges, Walters, & Nelson, 2012) and tDCS studies of detection of military threats in naturalistic scenes (Clark et al., 2012).

Imaging tells us much more about the brain than simply "where things are happening" (but see, e.g., Uttal, 2001, for a dissenting view). For example, measurements of brain activity before a stimulus is presented can tell us how well subjects will remember a stimulus (Otten, Henson, & Rugg, 2002; Turk-Browne, Yi, & Chun, 2006) or are prepared for a task (Leber, Turk-Browne, & Chun, 2008; Toffanin, Johnson, de Jong, & Martens, 2007). Posner and Rothbart (2007) argue that imaging is just beginning to realize its potential in elucidating (a) different brain networks, (b) neural computation in real time, (c) how assemblies develop over the lifespan, and (d) neural plasticity following brain insult or training. As will be discussed in Chapter 9, a new development, the mapping of the human genome (Venter et al., 2001), offers great potential for understanding the physical basis for individual differences. Molecular genetics provides a set of methodological tools that can inform many issues concerning human brain function. Methods such as single nucleotide polymorphism association (SNP), genome wide association (GWAS), and proteomics are being used to relate genetic differences to individual performance in tasks involving the network influenced by particular types of genes.

1.1 Brain Structures and Networks

The starting point for neuroergonomics is the brain. A comprehensive introduction to the structure and workings of the brain is beyond the scope of this book, but it is helpful to sketch the major structures and processing networks involved in perceptual, cognitive, motor, and emotional processing. A rough guide to the brain ascribes executive function to the frontal lobe; motor planning and execution to primary motor cortex (somatomotor cortex) and pre-motor areas of the frontal lobe; the integration of sensory information from different modalities, particularly when the spatial location of objects must be determined, to the parietal lobe–and to the temporal lobe when objects must be identified; visual processing to the occipital lobe; and auditory processing to the temporal lobes. The temporal lobes are also involved in semantic processing of both speech and vision, and the hippocampus, located in the medial portion of the temporal lobes, is involved in memory formation. The cerebellum, or "little brain", plays an important role in the integration of sensory perception and motor output. The cerebellum interacts with the motor cortex and spinocerebellar tract (which provides proprioception) to fine-tune equilibrium, posture, and motor learning. The brain stem (pons, medulla oblongata, and midbrain) is a small structure but is involved in sensation, vision, arousal, consciousness, motor function, emotion, alertness, and autonomic reflexes. [figure]

Assigning cognitive functions to brain areas has heuristic value, but most information processing involves multiple areas of the brain and depends on dynamic changes in the brain itself. Perhaps the most important dynamic process in the brain (other than neural transmission, itself) is long-term potentiation (LTP), a long-lasting enhancement in signal transmission between two neurons that results from synchronous firing of the neurons. Long-term potentiation enhances synaptic transmission, improving the ability of pre- and postsynaptic neurons to communicate with one another across a synapse, and thus contributes to synaptic plasticity such as that underlying learning and memory. Another aspect of brain dynamics is synchronization of brain areas. Many recent hypotheses of how information is transmitted between brain areas (e.g., Donner & Siegel, 2011) suggest that it occurs via synchronization of oscillations in different frequency bands.

1.1.1 A Default Mode of Brain Function

A relatively recent discovery (Raichle et al., 2001; Raichle & Synder, 2007) is that the brain not only increases in activity during information processing, but also that there is a "default mode" of brain function supported by a processing system which includes the posterior cingulate cortex and adjacent precuneus. Evidence for a default mode of brain function comes from neuroimaging studies that show task-specific deactivation. Many neuroimaging techniques rely on the comparison of task and control conditions, and almost always report an increase in activity in the task as compared to the control condition. However, subtracting task-state data from control-state data in some cases reveals negative activity, or task-specific deactivation (e.g., Petersen et al., 1998; Raichle et al., 1994). Surprisingly, these activity decreases have been found even when the control condition is resting with the eyes closed or simply keeping the eyes at fixation. In other words, even when people are assumed to be refraining from information processing activity, engaging in some other activity results in a reduction of brain activity. This reduction relative to baseline is the key piece of evidence pointing to a default mode of brain function.

How does one characterize activity in a passive or resting condition? Raichle et al. (2001) answer this question with regards to activity observed during task processing. They argue that the regional decreases seen during the performance of a task represent the presence of functionality that is ongoing in the resting state and attenuated only when resources are temporarily reallocated during goal-directed behavior. Default activity can thus be defined only in reference to task activity. The fact that the spatially coherent, spontaneous BOLD activity that is the hallmark of intrinsic activity is also present under anesthesia (Vincent et al., 2007) suggests that the activity is not associated with conscious mental activity, but rather may reflect a fundamental property of the functional organization of the brain. An intriguing idea is that the default network reveals the maintenance of information for interpreting, responding to, or even predicting environmental changes. In this sense, understanding the default network may help us to understand much more about how we adapt to and learn from the environment.

1.2 Assessing and Influencing Brain Function

Of the techniques available for neuroimaging and mapping brain function, the ones with the most direct application in neuroergonomics are transcranial magnetic stimulation (TMS), transcranial direct current stimulation (tDCS), functional near infrared (fNIR) spectroscopy, and electroencephalography (EEG). However, even though techniques such as MRI and DTI are relatively expensive to use, the development of magnet-compatible virtual reality systems has led to fMRI studies of complex cognition, including simulated driving (Calhoun & Pearson, 2012) and complex spatial navigation (Maguire, 2007). Moreover, structural MRI and DTI are important for training studies, such as in quantifying the effects of training methods such as emphasis change (Boot et al., 2010), video game training (Voss et al., 2012), or working memory training (Takeuchi, Taki, &

Kawashima, 2010).

1.2.1 Transcranial Magnetic Stimulation and Transcranial Direct Current Stimulation

Transcranial Magnetic Stimulation (TMS) has been used since 1985 to manipulate brain function in a noninvasive, focal manner (Barker et al., 1985). Designed on the principle of electromagnetic induction, TMS involves passing an electrical current through a magnetic coil placed close to the head of the subject. The magnetic field penetrates through the skull and into the outer layers of cortical tissue where it induces electrical activity in neurons in the targeted area. Although the technique has been used primarily to explore the function of various brain regions, an important observation is that exposure to TMS sometimes leads to enhancement in perceptual or cognitive abilities. Exactly how TMS influences brain function is not completely clear, but it is thought to work by changing the membrane potential in neurons. When cognitive abilities are enhanced, this may be through neuronal preactivation or priming. According to this view, stimulating a region of the brain pre-activates the neurons in that region, increasing their propensity to fire. Support for this view comes from the finding that TMS applied to an area leads to an increase in regional blood flow (as measured by fMRI) and metabolism (George & Belmaker, 2007).

Most cognitive research has used single-pulse TMS, in which only one magnetic pulse is delivered. Clinical work, on the other hand, has focused on the possibility of using repetitive-pulse TMS (rTMS). Just a single pulse of TMS can momentarily interfere with the functioning of a region or enhance excitability in a region for a short amount of time (less than 500 ms), although these stimulations may have longer lasting effects on more distant cortical regions (Pascual-Leone, Walsh, & Rothwell, 2000). Repetitive-pulse TMS often has longer lasting effects (Hallet, 2007). Unfortunately, the possibilities of rTMS with respect to enhancing cognitive function (or ameliorating the effects of a disorder) are offset by questions about the safety of the technique and the risk of unpleasant side-effects. A related technique, transcranial direct current stimulation (tDCS) involves passing a mild direct electrical current between electrodes on the scalp to modify neuronal membrane resting potential. This is done in a polarity-dependent manner, such that neuron excitability in a given region is either elevated or lowered (Paulus, 2004; for details see Wagner et al., 2007). Both TMS and tDCS might be used to enhance perceptual and cognitive performance (see Chapters 3 and, for a review, Thut, Schyns, & Gross, 2011).

1.2.2 Functional Near Infrared Spectroscopy

A relatively new technique which shows promise as a field-deployable, non-invasive monitor of prefrontal cortex activity is functional near infrared (fNIR) spectroscopy. This technology uses light to measure changes in blood oxygenation as oxy-hemoglobin (HbO2) converts to deoxy-hemoglobin (HbR) during neural activity (i.e., the hemodynamic response). Because the light can be introduced at the scalp via a sort of headband, the technology is portable and relatively non-intrusive. The spatial resolution of fNIR is about 1 cm2, making it possible to test hypotheses about changes in the use of brain regions as a function of learning, in addition to testing general mental activity (Ayaz et al., 2012). Moreover, fNIR can be combined with EEG to achieve better temporal resolution (Gratton & Fabiani, 2008). In one implementation of fNIRS (Ayaz et al.), light sources and detectors for 16 optodes are placed in a flexible sensor pad which is worn over the forehead. Source detectors are separated by 2.5 cm, allowing for approximately 1.25 cm penetration depth. The light emitting diodes (LEDs) are activated one at a time with a temporal resolution of 500 ms per scan. The placement of the detectors allows the monitoring of dorsal and inferior frontal cortical areas. Changes in light absorption are analyzed using spectroscopy for the detection of the chromophores of HbO2 and HbR. As will be discussed in Chapter 4, fNIRS shows promise as a means to measure mental workload and changes in level of expertise.

1.2.3 Electroencephalography

The electroencephalogram (EEG) is a graph of electrical brain activity in which the vertical axis represents the difference in voltage between two different scalp locations (as measured by electrodes attached to the scalp) and the horizontal axis time (Fisch, 1999). The EEG is composed of three types of neural activity (Hermann et al., 2005): (1) Spontaneous activity uncorrelated with any particular task, (2) induced activity related to the task but unrelated to particular events (not phase-locked), and (3) evoked activity related to particular events (phase-locked).

Event-related potentials. Much EEG research relies on the event-related potential (ERP; see Luck, 2005). To compute the ERP, a sample of the EEG activity is recorded just prior to and after a discrete stimulus event. Many (usually at least 100) such samples are taken and are averaged offline, thus "averaging out" spontaneous EEG activity and resulting in an ERP waveform containing activity that is phase-locked to the stimulus onset. Changes in the amplitude and latency of the different positive and negative peaks in the ERP are used to draw conclusions about the mental operations associated with the task.

A number of components of the ERP have been identified and linked to information processing (Handy, 2005; Luck, 2005; Regan, 1989; see Table 1.1). ERP components can be roughly divided into early, exogenous components which reflect the processing of stimuli and late-onset, endogenous components related to cognitive processing. For example, the latency and amplitude of the P1 and N1 (where P stands for positive polarity, N for negative polarity, and 1 for the order of the two components in the time-line of the ERP) depend on stimulus properties and the amplitude of P1 and N1 are linearly related to the amount of attention allocated to the stimulus (Mangun & Hillyard, 1990). In addition to amplitude and latency differences as a function of task demands, the scalp distribution of ERP components can be informative. For example, although a P1 is observed for both visual and auditory stimuli, the spatial distribution of P1 in these two cases is different, with the auditory P1 being largest at frontocentral electrode sites (i.e., perpendicular to the primary auditory areas) and the visual P1 being largest at occipito-lateral electrode sites (i.e., perpendicular to the primary visual areas; Luck).

Time-frequency analysis

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Table 1.1: Components of the ERP, their onset, topography, and the functionality they reflect

Component	Onset (ms)	Topography (cortex)	Functionality
Early Stimulus Processing			
C1	65-90	striate	visual processing
P1	80-120	extrastriate	visual processing + attention
N1-a	80-120	fronto-central	auditory processing + attention
Stimulus-processing Related			
ELAN	100-300	frontal (left)	violation of word-category or phrase structure
N1-v	150-200	occipito-parietal/temporal	visual processing + attention
N170	130-200	occipito-temporal (right)	processing of faces
IIN	200-300	Posterior-ipsilateral	Attention disengagement and reorienting
P2	150-275	centro-front parieto-occipital	comparison with internal representation
MMN/N2a	150-250	primary auditory/visual	detection of change (oddball)
N2b	200-350	anterior	response inhibition/conflict, error monitoring
N2c	200-300	posterior	degree of attention allocated to stimulus
N2pc	200-300	posterior-contralateral	attention allocation
LDAP	-200-0[a]	Posterior-contralateral	Preparatory activation visual cortex
EDAN	xxx-xxx	Occipital-contralateral	Decoding of the attentional cue
ADAN	300-500	frontal-contralateral	Initiation of an attentional shift
Stimulus-categorization Related			
P300/P3b	300-600	parietal	stimulus evaluation and categorization
P3a	250-280	fronto-central	attention engagement, processing of novelty
N400	250-500	centro-parietal	semantic processing
P4pc	350-450	posterior-contralateral	deallocation of attention
RON	400-600	Fronto-central	Reorienting towards target
P600	500-1200	centro-parietal	syntactic processing
Response Related			
CNV	260-470	vertex	contingency between two stimuli
LRP	260-470	centro-contralateral	response preparation
ERN/Ne	80-150	fronto-central	error processing

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[a] The LDAP is measured before target onset

& Bertrand, 1999; Pfurtscheller & Lopes da Silva). Moreover, the range of frequencies that compose the EEG is better covered with frequency analysis than ERP analysis because the computation of ERPs requires filtering, with the result that frequencies outside the range of the filter are lost (see e.g., Luck 2005). On the other hand, filtering the EEG to isolate the ERP removes movement artefacts (such as microsaccades, see Fries et al, 2008).

In the earliest known documentation of the EEG signal, Berger (1929) described a relatively slow (8–12 Hz) rhythmic oscillation which he termed the alpha band. Subsequently, oscillations with a periodicity of 12-30 Hz (the beta band), 30-80 Hz (the gamma band), less than 4 Hz (the delta band), and 4-8 Hz (the theta band) have been described. A very general way to link the activity of the nervous system with the cognitive demands imposed by a task is to observe the intervals of synchronization and desynchronization in a given band. Synchronization indexes the state of cortical rhythmicity (i.e., that the nervous system is synchronized with a certain frequency band), whereas desynchronization refers to the interruption of cortical rhythmicity. For example, Nunez et al., (2001) showed that alpha desynchronization correlated with mental effort, such that the alpha rhythm decreased with increases in mental effort. In other words, in a state of relaxation or “idling” state, alpha waves were of relatively high amplitude, or synchronized. Desynchronization is not always associated with an increase in mental effort. For example, Nunez et al. showed that theta tends to increase (i.e., synchronize) with increased mental effort.

1.3 Information Processing in the Brain

1.3.1 Perception

Information from the different senses is processed in dedicated brain areas, which have a roughly similar functional organization in the case of vision, audition, and somatosensation (Penfield & Rasmussen, 1972). Sensory information arrives from the senses in a deep brain structure called the thalamus, which may be thought of as the brains switchboard for incoming information. Sensory information then propagates to the so-called primary sensory cortices: Visual information is sent to V1 in the occipital lobe, auditory information to A1 in the temporal lobes, and somatosensory information to S1 in the parietal lobe. These primary sensory cortices process information at a very basal level, such as brightness in the case of vision, or tone frequency in the case of audition. The early sensory areas are topically organized in feature space–that is, in the somatosensory cortex, the brain cells processing input from the index finger are next to the brain cells processing input from the middle finger, and so forth. In the primary visual area, neurons are retinotopically organized. Activity in these neurons shows a one-to-one relation with the image projected on the retina. In the primary auditory cortex, the organization is tonotopic: Neurons are organized according to the frequency they respond to. After processing in the sensory cortices, information is fed forward to so-called association cortices in the temporal and parietal lobes, where sensory information is integrated in higher-level processes, such as memory and decision making.

Of the sensory brain systems, the visual system has been studied most extensively. The visual system consists of two separate pathways, the ventral and dorsal routes. The ventral route is from the occipital lobe to the temporal lobe. This pathway is sensitive to objects (that is, this pathway processes constellations of features, e.g., a face). The dorsal route leads from the occipital lobe to the parietal lobe and is involved in processing the location of objects, and guiding movements. The two pathways are organized into distinct visual areas in both hierarchical and parallel fashions. The organization is hierarchical in that the complexity of the represented object increases as the information is passed on from area to area, but also parallel in the sense that distinct areas are specialized in distinct features (e.g., there are areas specializing in color, in motion, and even specifically in recognizing faces).

The traditional view of visual perception is that visual images are "decomposed" into composite features in the early visual areas, and subsequently "recomposed" in higher visual areas (Marr, 1982). This view, however, has been challenged in the past decade. Visual areas higher up in the hierarchy of processing not only receive information from lower areas (so-called feedforward information processing) but also send back information to lower visual areas, thus influencing information processing at more basal levels (Lamme, Super, & Roelfsema, 1998). This feedback, or recurrent processing plays an important role in contemporary theories of visual processing, attention, and awareness (Lamme, 2003, 2006; Roelfsema, 2009). Interestingly, other sensory modalities appear to have a similar structure, though far less is known about the role of cortico-cortical interactions in modalities other than vision (see Raizada & Grossberg, 2005).

Processing of sensory information appears to be fairly modality-specific: Information presented in separate modalities tends to result in less interference than when that same information is presented within one modality, which suggests that each of the five senses has its own capacity limits (wickens, ???). Information from the various senses does seem to be subject to interference (or crosstalk) at more central stages of processing (Spence & Driver, 2004). For example, tactile stimulation can affect visual attention, suggesting that multimodal parietal areas receive tactile input and project to visual cortex, which can result in attentional enhancement of visual signals (Macaluso et al., 2000). Moreover, recent studies point to the possibility of direct interactions between primary sensory areas. For example, direct connections from A1 to V1 have been demonstrated in the primate brain (ref) and are believed to play an important role in the so-called sound-induced flash illusion (Shams et al., 2001), in which a single flash of a visual stimulus is perceived as two flashes when it is accompanied by two auditory beeps. Moreover, in conditions of sensory deprivation, early visual cortex dynamically adapts to the absence of visual stimulation and will process auditory information as well, as rapidly as after one day of visual deprivation (Pascual-Leone et al., 2008), suggesting that multimodal integration may also occur at very early levels of processing.

1.3.2 Working Memory

One of the most important ways to enhance performance in complex environments is to aid the operator in directing attention to relevant elements so that this information can be selected for representation in working memory. Working memory influences selection and holds task goals, and thus has a key role in decision making and action selection. Because of the position of working memory as an interface between external stimulation and internal states, it is sometimes considered a process fundamental to attention (Knudsen, 2007). Working memory holds the objects of attention (Cowan, 2005). In turn, attention is needed to maintain representations in working memory. More evidence of the interaction between memory and attention is that maintenance of spatial locations in working memory biases attention to those locations (Awh & Jonides, 2001).

Many studies have been conducted to elucidate the neural underpinnings of working memory. The pre-frontal cortex (PFC), in particular, seems to play a central role in working memory, as evidenced by selective interference with working memory of lesions in the PFC (Goldman-Rakic, 1995; Duncan & Owen, 2000). However, working memory is likely widely distributed in the brain, with the PFC acting as an executive controller that engages with cortical and sub-cortical regions involved in the processing of sensory, motor, and internally generated information (e.g., Miller & Cohen, 2001). Marois, Chun & Gore, 2000) proposed that a fronto-parieto-temporal network is involved in raising perceived information into awareness and working memory; synchronization between the areas involved in this network may be especially informative (Dehaene, Sergent, & Changeux, 2003; Gross et al., 2004). Visual working memory (VWM), which supports the maintenance of visual information for relatively short periods, is, in particular, supported by sustained neuronal activity in a cortical network involving frontal, parietal, occipital, and temporal areas (Palva, Monto, Kulashekhar, & Palva, 2010). Sustained, stable, and VWM-load dependent interareal phase synchrony is found among frontoparietal and visual areas during a VWM-retention period in alpha (10–13 Hz), beta (18–24 Hz), and gamma (30–40 Hz) frequency ranges, consistent with the idea that interareal synchrony has the function of sustaining object representations in VWM.

An interesting and important phenomenon is the “delay-period” or “persistent” neural correlate of working memory first described by Fuster and Alexander (1971). Namely, neurons in the PFC of monkeys that had been trained to remember target stimuli for a brief period of time responded both when the target was present and in the seconds between target disappearance and the making of a response–even when visual distractors were shown after the target (Fuster, 1995). In tasks such as this, brain dopamine (DA) in the PFC seems to play a role in the stabilization of the earlier presented stimulus across the short delay. Brain dopamine has further been implicated in working memory, and cognitive control processes, in general. Cools and D’Esposito (2011) suggest that cognitive control, such as exercised by working memory, requires a dynamic balance between cognitive stability (i.e., the “on-line” stabilization of task-relevant representations), and cognitive flexibility (i.e., flexible updating of task representations in response to novel information), and that these distinct components of control might call upon the prefrontal cortex and the striatum, respectively. They note that whereas the effects of DA on cognition have often been ascribed to modulation of the PFC, recent data suggest a complementary role for DA in the striatum for working memory and cognitive control. In the striatum, DA might have a qualitatively different function from that of DA in the PFC, with striatal DA being more important for the ability to flexibly update goal representations when new information becomes available.

1.3.3 Attention and Arousal

Michael Posner, one of the leading pioneers in the neuroscience of attention, defines attention as "the regulating of various brain networks by attentional networks involved in the alert state, orienting, or regulation of conflict" (Posner & Rothbart, 2007, p. 2; see Figure 21; Posner & Fan, 2007). This definition emphasizes the importance of temporal correspondence between multiple cell assemblies (Hebb, 1949; cf. synchronization, Womelsdorf, Fries, Mitra, Desimone. 2006). Other definitions or models of attention emphasize that control can be stimulus-driven (bottom up) or under voluntary control (top down), or focus on whether attention must be focused or divided in order to perform a task.

Alerting refers to achieving and maintaining a state of high sensitivity to incoming stimuli. Alerting is often studied by presenting warning signals before stimuli appear, and the effects of such warning signals have been related to modulation of neural activity by the neurotransmitter norepinephrine (Marrocco & Davidson, 1998). Alerting has been associated with the thalamus, as well as frontal and parietal cortex (Fan, McCandliss, Fossella, Flombaum, & Posner, 2005). Alerting is similar to the older concept of arousal, which refers to an individuals level of activity, whether reflected in general behavioral states such as active wakefulness or sleep, or in subjective experience such as alertness or drowsiness. Changes in arousal can be indexed by recording brain activity. For example, increased EEG theta activity recorded from posterior electrode sites on the scalp is associated with lowered arousal and poor performance on prolonged, monotonous tasks (OHanlon & Beatty, 1977). Also, fMRI studies have shown that variations in arousal are linked to activation in the brain stem and in widespread frontal-parietal networks in the right hemisphere (Sturm & Wilmes, 2001).

Posner and Rothbart (2007) define orienting as "the interaction of a brain network with sensory systems designed to improve the selected signal" (p. 7). Orienting, in this sense, is well-captured by the model of attention proposed by Knudsen (2007) in which attention can be controlled externally, by salient features or objects in the environment, or voluntarily, by working memory, top-down sensitivity control, and competitive selection. In the case of visual attention (see Figure 1-2), information that falls within the visual field is processed according to its salience, with infrequent or important stimuli being differentially responded to (e.g., Koch & Ullman, 1985). These representations and any other activated information are selected according to a competitive process whereby information with the highest signal strength enters working memory (c.f., Desimone & Duncan, 1995). The results of competitive selection can influence top-down sensitivity control without the involvement of working memory, or working memory can bias the top-down signals that modulate the sensitivity of neural representations competing for entry into working memory (e.g., Egeth & Yantis, 1997). Thus, voluntary attention can be described as a recurrent loop involving working memory, top-down sensitivity control and competitive selection. Moreover, competitive selection and working memory directly influence eye movements, thus determining what future input is possible, and neural discharges associated with gaze control modulate sensitivity control.

Orienting has been related to the frontal eye fields (FEFs) , the superior parietal lobe and temporoparietal junction, and also to the pulvinar in the thalamus and the superior colliculus. Event-related fMRI studies have linked cuing effects specifically to the superior parietal lobe (Corbetta & Schulman, 2002), an area that is closely related to the lateral intraparietal area (LIP) in monkeys, an area that is involved in the production of eye movements. When attention must be disengaged from one location and moved to another location, activity is seen in the temporal parietal junction (Corbetta & Schulman).

Neuroscientific evidence that working memory, top-down sensitivity control and competitive selection are dissociable is accumulating. For example, whereas PFC is associated with executive control, the posterior parietal cortex (PPC) seems to be more associated with top-down sensitivity control and competitive selection. Top-down bias signals have been observed directly in monkeys trained to discriminate between sensory stimuli: When a given stimulus is relevant on a given trial, the responses of neurons representing that stimulus are greater than when the same stimulus is presented in a behaviorally irrelevant context (Desimone & Duncan, 1995). Sensitivity control can be described as utilizing space-specific bias signals that improve localization (see Chapter 3). The fact that the PPC receives inputs from the senses, as well as movement-related corollary discharges and proprioceptive feedback (Anderson et al., 1997), makes it a tenable candidate for the translation of spatial information from the retinotopic frames of reference of the visual cortex to the more abstract frames of reference of working memory. An interesting hypothesis is that attentional selection of items for representation in working memory may be associated with oscillations in the gamma band (40-70 Hz) that are synchronized in higher-order sensory areas, PFC and PPC (e.g., Bauer, Oostenveld, Peeters, &

Fries. 2006; Womelsdorf et al., 2006).

Top-down, goal-directed attention is associated with prefrontal areas, whereas bottom-up, stimulus driven attention is associated with more parietal activity. Voluntary spatial shifts to task-relevant locations are directed by areas in the parietal cortex that contain representations in topographic maps of attentional foci (Sereno, Pitzalis, & Martinez, 2001; Silver, Ress, & Heeger, 2005). Reorientation to a target in an unattended location relies on a circuit that includes the right temporoparietal junction (Corbetta, Patel, & Shulman, 2008). According to Corbetta et al., ”reorienting”, or the ability to change a current course of action to respond to potentially advantageous or threatening stimuli, is supported by the coordinated action of a right hemisphere dominant ventral frontoparietal network that interrupts and resets ongoing activity and a dorsal frontoparietal network specialized for selecting and linking stimuli and responses. The two networks are distinct and internally correlated when the organism is at rest, but when attention is focused, the ventral network is suppressed to prevent reorienting to distracting events.

Executive attention, such as that involved in responding in so-called conflict tasks, in which irrelevant, to-be-ignored information causes interference with the information to be responded to, is commonly associated with the prefrontal cortex and the anterior cingulated cortex (ACC; Botvinick, Braver, Barch, Carter, & Cohen, 2001; see Chapter 5). Connections between the ACC and sensory areas suggest that the ACC regulates sensory input (Crottaz-Herbette & Menon, 2006). The ACC has large-scale connectivity to many brain areas, which suggests that it is ideally situated to exercise cognitive control over other brain networks. The more dorsal part of the ACC has been associated with the regulation of cognitive tasks whereas the more ventral part of the ACC is involved in the regulation of emotion (Bush, Luu, & Posner, 2000). Dorsal ACC is strongly connected to the frontal and parietal areas involved in cognitive processing and is active during task performance. For example, during a visual selection task, dorsal ACC activity correlates with visual brain areas and during an auditory task the activity of the dorsal ACC correlates with auditory areas (Crottaz-Herbette & Menon).

Cognitive control is by definition attentional in the sense that it involves maintaining task goals. Switching between tasks, response selection, and retrieval from long-term memory all require cognitive control (Chun & Turk-Browne, 2007), and it is likely that all are subject to a common processing bottleneck in lateral frontal cortex

(Marois & Ivanoff, 2005), although task switching may be subject to additional limitations on selection. Internal control requires that one response or task goal be given priority above others, and therefore implies inhibition of competing options. Prefrontal, parietal, and basal ganglia regions are involved in internal control (e.g., Braver, Reynolds, & Donaldson, 2003). As will be discussed at more length in Chapter 5, there is a close connection between attentional control and lapses of attention. In fact, reduced prestimulus activity in attentional control regions such as the anterior cingulate and right prefrontal cortex has been associated with attentional lapses (Weissman, Roberts, Visscher, & Woldorff, 2006).

1.3.4 Decision Making

Making decisions is an important aspect of human life. Even simple decisions, such as deciding whether or not to take an umbrella with you on a cloudy day, depend on many factors (e.g., the distance to be travelled, the weight of the umbrella, and the actual chance of rain). Decision making has long been dominated by behavioral economics (ref). The past decades, however, have seen growing interest in the neural basis of decision making, and this has led to the emergence of the new field of "neuroeconomics". Neuroeconomics studies the brain processes underlying optimal decision making (Sanfy et al., 2006).

Numerous studies have shown that our decision making is guided not only by rational considerations, but also by emotion. For example, what we choose is for a large part guided by our expectations of how we would feel as a consequence of our actions (Kahneman & Tversky, 1990). The question what the best option is in a particular case is thus a complicated one. Different brain mechanisms are responsible for weighing relatively more rational and more emotional considerations in decision making, with the dorsolateral prefrontal cortex being involved in more rational aspects of decision making, and the orbitofrontal cortex and the limbic system playing a role in the evaluation of the emotional aspects of decision making (Sanfy, 2006; Damasio, xxxx).

The concept of reward is a key factor in understanding why people make specific decisions. Reward is most easily understood (and studied) in terms of monetary gains, but comes in many forms. Research in behavioral economics has shown that the value associated with a reward is not fixed, but is strongly influenced by the temporal context in which it is offered. For example, if people are given the choice between receiving $100nowor110$ tomorrow, most people would opt for receiving $110 tomorrow (ref). If the interval is extended from a day to a year, however, most people would opt for immediate payment, even though the objective reward value of waiting for payment remains the same. It has been suggested that two different processes underlie how short-term and longer-term rewards are evaluated, and that the two processes operate fairly independently (Sanfy, 2011). A recent, controversial line of investigation suggests that choices between alternatives may be more rational when the pros and cons of the different options are not consciously deliberated than when they are (e.g., Dijksterhuis et al., 2009). The suggestion that distraction during decision making can lead to better decisions points to the need to clarify the roles of emotion and unconscious thought in the decision making process. Emotion and Social Interaction

Emotions play a major role in cognitive processes such as decision making (Damasio, 2001), and an even greater role in social interactions. Our capacity to feel emotion influences the way we make decisions, as is demonstrated by the seminal work of Bechara and co-workers (Bechara et al., 1998). In a now classic experimental paradigm, the Iowa Gambling Task, participants repeatedly draw a card from one of two stacks. The cards indicate the win or loss of a given amount of money. The critical manipulation is that one of the two stacks is more profitable than the other in the long run. Healthy participants notice this quite easily, but patients with prefrontal damage have significant difficulty in learning which stack is the more profitable one. Interestingly, learning which stack to choose is associated with a so-called somatic marker: Winning or losing evokes an emotional response in participants that is associated with increased autonomous activity. In patients with prefrontal brain damage, however, this emotional response is absent. According to Damasios somatic marker hypothesis, these faint emotional feelings play an important role in regulating behavior. The somatic marker hypothesis has been applied to everyday behaviors such as driving (Damasio, 2008; Lewis Evans et al., 2012), where it has been shown that even emotions that people are not aware of can make people adjust their behavior: Unconscious negative emotions, signaling danger, make people drive slower.

Emotions can also play a role in how we perceive the world: Perceptual, attentional and mnemonic processes are all influenced by how we feel. A well-known phenomenon is the shift in global-local focus that occurs as a function of positive or negative mood. People in a positive state of mind tend to have a global focus, focusing on the gist of a visual scene or remembering the overall outline of a story, whereas people in a negative mood adopt a more local focus, focusing on the details of an image or remembering the details of a story (Clore & Huntsinger, 2006). Moreover, perception itself is altered by mood such that people are better in detecting images that are congruent with their present mood. For example, when in a happy mood, people are quicker in reading positive words and tend to interpret ambiguous facial expressions as happy, whereas the opposite is true for people in a negative mood (Bouhuys et al, 1992; Niedenthal, 1992; Jolij, in press; Jolij & Meurs, 2011).

A better understanding of the emotional brain, and of how emotional responses can be monitored, is therefore of great importance in the field of neuroergonomics. Emotions, and in particular physical emotional responses, are regulated by the limbic system, in particular by the amygdala, a nucleus that regulates emotional behavior and processes the emotional content of sensory input. Activity in this emotion network does not necessarily lead to conscious emotional experience, but does alter autonomous activity and can prime fight or flight decisions (Jolij, in press; LeDoux, 1992).

How we feel emotions is less well understood that the physical correlates of emotion. Studies in patients have shown that the orbitofrontal cortex seems to play a critical role in the ability to feel emotions, but little evidence links particular brain areas to the feeling of specific emotions. However, there seems to be some hemispheric localization of emotions, with the left hemisphere seeming to mediate positive moods, and the right hemisphere being more active in a negative state. The only emotion that has been linked to a specific brain area is disgust, which appears to be localized in the insular cortex (Keysers & Gazzola, 2006).

Emotions form an important aspect of social communication. Recent studies on the perception of emotional expressions have shown that seeing an emotion induces that emotion, possibly by triggering mimicry of the perceived expression, as if we try to understand the emotional state of someone by emulating what we see (Keysers & Gazzola, 2006; Neville et al., 2011). The idea that mimicry is crucial to understanding the emotions of others fits well with the recent discovery of mirror neurons, the neurons of the motor areas of the brain that fire if an action is observed that would normally require the involvement of the same neurons. For example, neurons that would normally trigger a movement of the arm will also fire if an observer sees someone else moving an arm (Rizzolatti & Sinigaglia, 2006). Mirror neurons are supposed to play an important role in social communication by allowing us to understand the intentions of others by virtue of simulating the mental state of the other (Keysers, 2011).

In the context of neuroergonomics, the agents people interact with may not be human agents, but computer agents. It has been shown that humanoid robots–and even computer programs–may evoke brain activity in observers that is consistent with such interactions being treated as if they were social interactions. Interacting with something that looks even remotely human activates the so-called social brain network that includes the temporal-parietal junctions and the superior temporal sulci, and that is involved in the processing of social information such as trustworthiness and agency (Heussen et al., in press; Krach et al,. 2006). A better understanding of the functioning of this brain network may therefore allow the optimization of interface design. Given that recent research suggests that our brain is optimized for social interaction, modeling human-computer interaction on social interaction may prove to be an efficient way of optimizing human-computer interaction.

1.4 Prediction of Prospective Activity

From the standpoint of the ergonomist, one of the most important questions regarding neural activity is whether we can use it to predict how the operator will perform within a relatively short period of time. If we see, for example, that attentiveness is flagging, a signal or even some direct “refreshment” such as a stimulating odor (Kato, Endo, Kobayakawa, Kato, & Kitazaki, 2012)) could be given to reorient the operator to the task. Non-intrusive, real-time computation of the neural correlates of internal states that precede changes in performance is a holy grail of adaptive technologies. How can looking at the time period before an action (whether an attention shift or the selection of a response) is performed inform us about the action that will be taken or the quality of information processing that will occur? One line of research geared towards answering this question is to develop pattern classification algorithms that predict future performance on the basis of the analysis of antecedent states (see Chapters 4,and 5).

Much of the proof of concept that performance prediction is possible comes from studies using fMRI. Because fMRI is non-invasive, it is possible to scan repeatedly in order to examine changes that occur with learning. Generally, learning on a task is associated with a decrease in the number and amount of activation of associated brain networks, although the rate of change of these networks may vary from milliseconds to years depending on what is being learned

(Posner, 2012) and connectivity within networks may be enhanced with practice (McNamara et al., 2007). The EEG signal has also been extensively studied in this regard. Synchronous EEG activity has been shown to predict enhanced visual perception (Hanslmayr et al., 2007), or to relate to anticipatory attention when an event can be predicted (Rohenkohl & Nobre, 2011). Moreover, various studies have shown that the EEG signal can be used to predict participants actions before they initiate them (Libet, Gleason, Wright, & Pearl, 1983), and that fMRI can reveal which decision will be taken up to 10 seconds before the decision is actually made (Falk, Berkman, Mann, Harrison, & Lieberman, 2010; Soon, Brass, Heinze, & Haynes, 2008).

1.5 Direct Augmentation of Human Performance

Neural augmentation has its roots in research conducted in animals and in people with severe psychiatric disorders. An early pioneer in the field, Jose Delgado, showed that electronic devices could be implanted in the brain to manipulate actions or emotions by receiving signals from or transmitting them to neurons (Horgan, 2005). Although his attempts to treat disorders with brain implants met with some success, results were variable across patients and even for individual patients. To date, the most reliable results have been obtained for Parkinsons disease patients (Weaver et al., 2009) and severe depression (Kennedy et al., 2011), both using deep brain stimulation. Cochlear implants, in which the auditory nerve is stimulated directly, can also be considered brain implants. Brain implants are also being explored as input for brain-computer interfaces for locked-in patients (see Chapter 4). Direct augmentation of human function via drugs or brain implants is probably the most controversial and emotionally charged topic in neuroergonomics. Although few would seem to begrudge Parkinsons disease patients the brain implant that allows them respite from tremor, the possibility that brain implants will someday–perhaps soon–enhance healthy function has led to heated debate. From a neuroergonomic point of view, enhancement of normal function is exactly what researchers hope to achieve. Farah et al. (2004) summarize many of the arguments for and against such neurocognitive enhancement. They note that prescription stimulants such as methylphenidate and dextroamphetamine are already used by healthy high school and college students hoping to boost test scores (Babcock & Byrne, 2000), that drugs that target either the onset of long-term potentiation or memory consolidation are being developed to improve memory, and that drugs targeting the dopamine and noradrenaline neurotransmitter systems not only improve deficient executive function, but may improve normal executive function (although such improvements may be limited to low-performing individuals; Mehta et al., 200; Elliott et al., 1997). Major ethical and practical issues are: Who should decide whether or not performance enhancing drugs will be administered and how should the performance of people benefitting from enhancement be evaluated? At a more basic level, safety, coercion, distributive justice, and personhood are major concerns. Safety is a concern with all health interventions, but neurocognitive enhancement involves intervening in a complex, not fully understood system. Coercion refers to explicit or implicit pressure to engage in neurocognitive enhancement either because of pressure from an employer who recognizes the benefits of a more attentive and less forgetful workforce or because of fears of competing against enhanced co-workers. Distributive justice is a concern because there will likely be cost and social barriers to neurocognitive enhancement, as there are for other benefits, such as health care and schooling. Finally, because modifying brains affects individuals, it is important to consider how neurocognitive enhancement affects our understanding of "what it means to be a person, to be healthy and whole, to do meaningful work, and to value human life in all its imperfection" (Farah et al., 2004, p. 424). Although it can be argued that the quest to improve on natural endowments brings with it the risk of "pathologizing" normal function, ardent coffee drinkers can attest to the capacity of individuals to become adapted to some kinds of enhancement and to how widespread societal acceptance of such enhancement is.

1.6 Chapter Summary

Since Parasuramans (2003) call for a neuroergonomic approach to improving safety and efficiency at work there have been many new developments. Our understanding of the brain networks underlying memory, attention, and decision making is continuing to grow, and as our understanding grows, so do the possibilities of enhancing function.

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