1. Introduction

1.1. Attention

1.2. Human Research

Every organism faces the challenge of perceiving and representing information that impinges on it through its different sensory channels. However, living organisms are continually being bombarded with external and internal stimuli. With an information processing system of limited capacity (Glass and Holyoak, 1986), perceiving and representing all incoming information is impossible. Thus, biological systems have evolved information processing mechanisms that selectively perceive and represent "relevant" inputs. Theoretically, this filtering process must maintain a fine balance between leaving enough processing capacity for other important tasks (such as motor control, problem solving, etc.) and the possibility of not detecting or processing important information that is provided by the environment. Logically, therefore *adjustable* filter mechanisms must exist that allow for optimization of the processing capacity to the ever-changing challenges of the environment. This system of filter mechanisms is referred to as attention (Davies & Parasuraman 1982).

1.2.1. Historic definition

William James (1890) was the first to recognize the role of attention and the need for distinguishing between different forms and functions of attention: *"everyone 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 on order to deal effectively with others"* (pp 403-404). Intense interest in understanding the processes of attention arose during World War II for pragmatic reasons. The Royal Airforce had radar operators monitor radar screens to detect enemy submarines. During these procedures it became clear that some of the possible contacts were missed, prompting the Airforce to determine the optimal length of a watch for their operators without overstraining them. The Airforce commissioned Norman Mackworth to design experiments towards these goals. Mackworth (1950) had human subjects detect infrequent and unpredictable double jumps of a clock hand (signals) embedded in single jumps (non-signal). During these tests, the signals had a fairly low probability of occurrence (3 – 5%). Mackworth found that signal detection declined mainly from the first half hour to the second half hour of the test and only gradually thereafter. This deterioration of performance during the task has become known as *vigilance decrement*.

Follow-up studies of vigilance decrement (e.g. Teichner, 1974) indicated that the largest decrement appears at about 15 minutes into the task. After verifying the vigilance decrement phenomenon, Mackworth investigated methods to prevent this effect. He showed that vigilance decrement could be extinguished by providing subjects with feedback about the accuracy of their reactions, (e.g. a sound would tell them whether they had a "hit", a "miss" or a "false alarm"). A 30-minute rest after the first sequence of tests also extinguished the decrement. Based on these findings, Mackworth developed the "*inhibition theory*" (1950) of vigilance. The theory explained vigilance decrement as an extinction of a conditioned response if the response is no longer reinforced. Although classical conditioning theory predicts that the curve, which describes extinction of a response, is negatively accelerated (which is consistent with the obtained data), it does not explain the residual performance later on in the task that was found in the clock test. Mackworth's findings, that knowledge of the results by the subjects did prevent decrement, was seen by him as one of the main supporting factors of his theory. With this feedback, the reinforcement was restored and extinction of the conditioned response was prevented.

Since Mackworth's initial studies, several modifications and variations of the inhibition theory of vigilance have been proposed (e.g. Deese, 1955; Broadbent 1953b, 1958; McCormack 1962). However, none were able to explain the effects of changes in signal frequency on vigilance decrement. Studies showed that an increased signal frequency did not *accelerate* the vigilance decrement in performance, as would be expected if inhibition were the reason for the decline (McCormack 1958, 1960). Instead, increased signal frequency *reduced* the decrement in vigilance performance.

Other theories of attention and vigilance have also emerged. Baker (1959c, 1963c) developed the *expectancy theory* of vigilance to take into account the findings that increased signal frequency resulted in a decrease in vigilance decrement. According to expectancy theory, a subject devises expectancies about the probability of a signal occurring in the future based on its previous experience in the task and these expectancies determine the level of performance accuracy. The subject is performing a constant averaging process of the times in between signals in order to predict future signals. Here, knowledge of the results is theorized to provide accurate information about the temporal distribution of signals. The level of expectancy is then determined by the signal probability. Thus, the theory predicts that if the probability of signal occurrence is low the expectancy should be low to and if the probability is high the expectancy should be high as well.

Broadbent (1957a, 1958, 1971) developed the *filter theory* of attention, which stated that a filter exists, that selects information from the environment. This filter has a bias to select information from resources that have recently been neglected. In this theory, vigilance decrement is attributed to periodic failure to take in task-relevant information, and these failures become more frequent as the task progresses. In his experiments, Broadbent used "unlimited hold" tasks in which a signal remains present until a subject detects it. Thus, there are no missed signals. The parameter measured is the change in reaction time or the numbers of signals detected within a certain time period. With limited–hold tasks, only a performance decrement can be observed – but not with unlimited-hold tasks, although the reason for the change in performance is the same. The duration of the signal thus determines the vigilance decrement, and a drop in performance is more likely to be observed in experiments with short signal durations because short signals are more likely to be missed in a period of non-observation. In this theory, increasing event rate enhances the decrement because if more events are presented during a certain time the probability for a signal to be missed increases. Furthermore, increases in signal intensity decrease the decrement, which is explained by the fact that more intense signals are recognized faster. Although some studies provide the results that are predicted with Broadbent's filter theory (Broadbent, 1971), others do not (Hatfield &

Soderquist, 1970). Nevertheless, there is evidence that increased signal duration and intensity and reduced event rate improve performance accuracy.

Another theory of vigilance is the *arousal theory* (Duffy 1951,1957,1962: Malmo, 1959). This theory states that the brain maintains a certain level of arousal during the task, which gradually declines as the task progresses. This decline is due to the monotonous and repetitive nature of the task. Arousal theory proposes that behavior varies along a spectrum of intensity (e.g. from sleep to extreme excitement) and that the level of arousal determines the performance in the task. As the task progresses the level of arousal deteriorates because of the repetitive nature of the task and hence the performance of the subject drops to lower levels.

Habituation theory is a variant of the arousal theory, which states that with repeated exposure to the stimulus, the response decreases and might be extinguished over a longer time period. Sharpless and Jasper (1956) suggested that vigilance decrement is caused by such a habituation process. However, the negative acceleration of detection accuracy that is normally associated with this process was not found in the typical vigilance task where the detection efficiency (d') does not decay exponentially.

Finally, *Motivation theory* states that vigilance decrement is caused by differences in motivation with certain subjects being more conscientious observers than others. Smith's vigilance theory (1966) stressed the point that "typical experimental subjects differ not so much in their ability to maintain attention as in their *willingness* to do so (page 2)". The subjects that are less willing to participate are termed "periodic participators" whose performance in a vigilance task depends on external factors such as reward and punishment and the overall performance of all subjects depends on the number of motivated participators. Furthermore, the main external factor that effects performance decrement is "knowledge of results" (KR) which seems to improve overall performance but does not eliminate vigilance decrement completely.

In summary, each of these early theories of attention were able to explain some of the factors influencing vigilance experiments. However, none was able to present a general model that would account for all of the various results.

1.2.2. Modern theories

Modern theories of attention (e.g. Parasuraman 1998, Treisman 1964, Parasuraman and Davis, 1984; Posner and Boies, 1971) recognize at least three different components: *Selection*, *Vigilance* and *Control*. Selection is the component that serves as a filter mechanism to process only important or relevant information. Vigilance or sustained attention describes the control of attention over time and is sometimes seen as an opponent process to selection that might be competing with selection for the same computational resources. If, for example, an attentional process is very demanding, vigilance cannot be sustained over time. If long and sustained vigilance is necessary to monitor the environment, less processing capacity is available for other tasks. Control, as the third component, allows for the allocation of computational resources according to the need of the organism in changing situations. Priorities in processing information, necessary for optimal interaction with the environment will shift as new situations occur (e.g. bouts of feeding versus monitoring the environment for predators). These three components are viewed as part of the information processing system that allows a biological system to optimize its interaction with the environment and therefore maximize its chances for survival.

In the type of experiments described above vigilance decrement is represented by either a steady decline in performance rate over time where performance includes both correctly detected signals and correctly rejected non-signals, or an increase in reaction time for the correct detection of signals (see Figure 1).

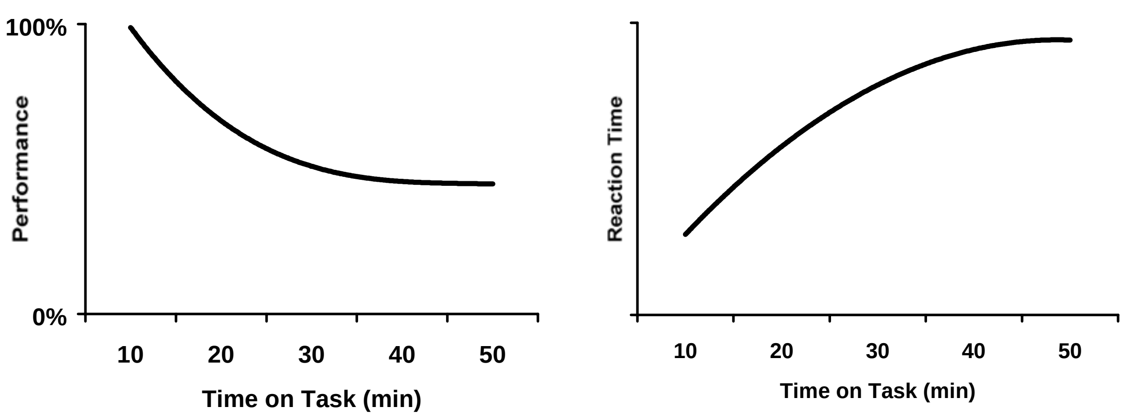

Figure 1: Schematic of performance and reaction time results in a typical vigilance task.

Typically, significant performance decrements are not apparent until 25 or 30 min into the vigilance task. However, depending on the demands of the task, vigilance decrement can occur as early as within the first five minutes. Nuechterlein et al (1983) designed an experiment in which subjects had to monitor for the appearance of a "0"-digit that was presented among other single digits (i.e., 1 to 9). Stimuli were presented for 40 ms every second and the subjects had to indicate the presence of a "0" with three different levels of confidence ("sure", "not so sure" and "unsure"). The target probability was set to 25%. Three different levels of degradation were used to increase the processing demand: a) images appeared clear (no degradation), b) moderate blur and c) highly blurred. Overall vigilance decrement was observed in the moderate and high degradation conditions and the main influence of the degradation was on the perceptual sensitivity rather on the response criterion. This experiment showed that under certain conditions vigilance decrement can occur as early as 5 minutes into the task compared to 30 – 40 minutes in normal conditions. Furthermore the decrement was more rapid than observed in experimental settings where vigilance decrement is observed later into the task.

Performance in vigilance tasks also depends on the subject's detection goals, expectation about the nature of the stimuli, and consequences of correct and incorrect behavior (e.g. is a reward given or not). These factors influence the vigilance decrement and thus it is difficult to determine whether the observed decrement is caused by a drop in perceptual sensitivity, by the previous mentioned factors (event rate, signal duration and signal probability) or by a combination of all. In order to separate the effects of perceptual and non-perceptual factors the Signal Detection Theory (Macmillan & Creelman, 1991; Green & Swets, 1966) has been used to analyze the results of vigilance experiments.

1.2.3. Signal Detection Theory

Signal Detection Theory (SDT) is a general psychophysical approach for measuring performance. In the general setup a correspondence experiment is used in which each possible stimulus is assigned a "correct" response from a finite set (see Table 1). A correspondence provides an objective standard against which to evaluate the performance. Detection theory measures the discrepancy between the two: a technique to understand errors. Errors are assumed to arise from inevitable variability either in the stimulus input or in the observer. The occurrence of errors describe the observers sensitivity: a perfect subject has a hit rate of 1 and a false alarm rate of 0. An insensitive subject has a hit rate of 1 and a false alarm rate of 1and responds therefore independent of the stimulus presented. Under normal conditions the hit rate is always higher than the false alarm rate but not perfect (H=1).

Table 1: Matrix of the stimulus classes versus the possible responses as described in Signal Detection Theory.

Stimulus class	**Response**	
	"yes"	**"no"**
Critical	***Hit***	***Miss***
Non-Critical	***False Alarm***	***Correct Rejection***

The parameter d\` is defined as a measurement of sensitivity with d'= z(Hit)-z(False Alarm) in the classic model (which assumes a normal distribution of signal and signal-plus-noise). Figure 2 shows possible Isosensitivity curves for d\`=0 (chance performance – the subject cannot discriminate signals from non-signals) to d\`=2.0 (subject is performing significantly above chance). Data points that lie on the same curve are characterized by the same sensitivity (d\`) but may describe different biases towards more hits or more false alarms. Vigilance decrement can be due to a change in the decision criterion (β) or to loss in sensitivity to the signal (d′, see Figure 3).

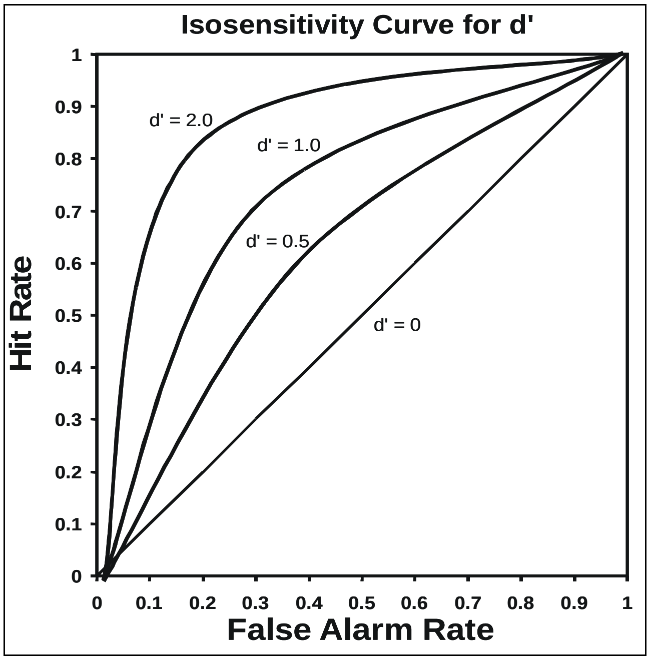

Figure 2: Isosensitivity curve for d'.

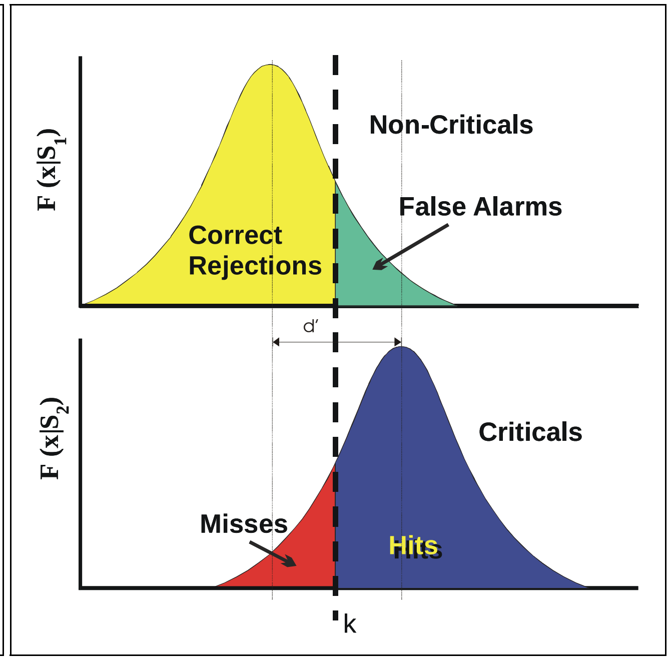

Figure 3: Rendering of the decision space as described by the signal detection theory.

1.2.4. Vigilance Taxonomy

Parasuraman and Davis (1977) were the first to attempt a classification of the various parameters that influence performance in a vigilance task. Two different variables were identified: 1) the type of discrimination – a successive task is an absolute discrimination in which *successively* presented stimuli have to be compared to a standard that is kept in working memory and a simultaneous task where presented stimuli are judged simultaneously for being either "same" or "different".

2) Event rate refers to the rate in which non-signals and signals are presented and are classified as either high or low with presentation rates of more or less then 24 stimuli per minute. This cutoff was established based on prior evidence, which showed that performance decreased significantly with event rates higher than 24 per minute.

This taxonomy was then expanded by Koelega et al (1986) to include the distinction between sensory and cognitive vigilance tasks in which they defined sensory tasks as changes in the physical characteristics of the stimuli (e.g. intensity or color etc.) and cognitive tasks by the use of symbols or alphanumeric stimuli. In their analysis, the researchers found that a sensitivity decrement was only found in sensory but not in cognitive tasks. Moreover, other experiments (e.g. Deaton and Parasuraman, 1993) indicated that performance efficiency actually increased or remained stable under certain conditions if cognitive stimuli were used. In their analysis, See et al (1995) enlarged the taxonomy to include the following factors:

Type of discrimination: Successive-absolute versus simultaneous-comparative: Only successive tasks impose a memory demand on the subject and may thus contribute to decrement in vigilance performance.

The *Event rate* determines how many stimuli (targets or non-targets) are presented in a given time period.

Sensory modality: most of the experiments conducted with humans use the visual sense, a smaller percentage of experiments test the auditory performance.

Signal regularity: determines whether a signal is presented in a regular fashion in exactly timed intervals, thus enhancing the predictability of the occurrence of a signal or in randomly timed intervals where a prediction when the next stimulus might occur is not possible. Generally, performance accuracy is higher with regular occurring signals and vigilance decrement is, if present, less pronounced than in experimental setups where stimuli are presented irregularly.

Event asynchrony: events that occur on an irregular basis tend to create a more pronounced decrement in performance then signals that occur on a regular basis and which are therefore more predictable.

Signal amplitude: higher signal amplitude normally yields better performance and less decrement because the signal to noise ratio is better. Signal detection theory states that a larger signal amplitude is represented in the decision space by a higher and steeper distribution curve, thus the separation between the signal and the noise distribution is more distinct.

Spatial uncertainty: stimuli can be either presented always at the same spatial position or the position can be randomly varied.

Signal probability: signal probability describes the probability that any randomly occurring event is a signal event. In general tasks with higher signal probability yields better performance than tasks with lower probability.

1.3. Animal Research

1.3.1. Function

Sustained attention has been investigated to a much lesser extend in non-humans. In general two different approaches have been employed: the first uses vigilance in a *descriptive* way to analyze the behavioral changes of an animal in the wild such as bouts of feeding versus resting (Lima & Bednekoff, 1999). Within these settings, changes in behavior are investigated by their dependency on other factors such as group size, environment or time of the day. Generally, an animal can utilize two different types of vigilance: a) the animal can monitor its environment directly or b) it can rely on warnings by other members of a group or even warnings from different species. Although in many species a trend towards lower vigilance in larger group sizes has been observed (Dehn 1990, McNamarra & Houston 1992, Roberts 1996, Bednekoff & Lima 1998a) some residual vigilance must remain to monitor the immediate surrounding environment. Although these studies describe the factors influencing vigilance behavior of animals in the wild, they do not explain the underlying mechanisms of sustained attention and vigilance. Laboratory studies, which manipulate variables in sustained attention tasks can help to elucidate these underlying mechanisms of vigilance.

1.3.2. Application

Most of the research published on animal vigilance in the laboratory has focused on pharmaceutical drug testing in which animals (mainly rats or primates) are tested for effects of drugs on their attention (Bushnell, 1998, 1997, 1994; McGaughy et al, 1999; McGaughy & Sarter 1995; Aston-Jones et al, 1991; Callahan et al, 1993; Amsten, 1992). These experiments investigate the role that intoxication or brain damage has on attention and try to locate the neural basis of attentional behavior. The goal of these studies is to develop a model based on animal experiments that can help in developing new treatments for brain damage in humans caused by injury or neurological diseases. Although several of these studies employ methodology that is similar to that used in human experiments on vigilance the questions remains whether an animal model of attention can be developed at all, given the fact that no single definition of attention is accepted throughout the field.

1.3.3. Dolphins and vigilance

1.3.3.1. Social structure

Many species of dolphins live in large schools with complex social hierarchies and structures. In any given situation an animal might have interactions with several other individuals simultaneously with shifting alliances and relationships. Furthermore the social structure will change over time and each member of a particular group has to take into account its position within the group hierarchy and in regard to non-members of the group in order to cope with any situation that might occur. Social structures may vary from a small tight family-type structure as seen in Orcas (*Orcinus orca*) to very loose large-scale aggregations as observed in spinner dolphins (*Stenella longirostris*) where group sizes vary throughout the day and animals may change associations with particular groups very often (Norris and Dohl, 1980). With complex and changing social hierarchies, the necessity to obtain food resources and need for protection from predators the animal must have a well-developed filter system that is able to process the incoming information (visual, auditory or other) and select relevant events.

1.3.3.2. Sensory system

Bottlenosed dolphins (*Tursiops truncatus*) have well-developed visual, auditory and echoic sensory systems (e.g. Madsen & Herman, 1980; Herman et al., 1975; Au 1993, 2000). Physical limitation to these senses act as a first filter mechanism to reduce the amount of incoming information. For example, the retina of a bottlenosed dolphin does not perceive red light and therefore any information arriving through this channel will not be processed.

1.3.3.2.1. Visual Sense

Bottlenosed dolphins have a well-developed visual sense (Herman et al., 1975) that allows them to see well both in air and underwater. Their vision is shifted towards the blue end of the spectrum and they possess several adaptations to the aquatic environment such as a double slit pupil (Herman et al 1975), and a large lens. As the eyes are placed laterally the overlapping field of view is only about 10 degrees at the body axis, allowing for an almost complete 360-degree field of view. Each eye is used independently from the other: it can be rotated, protruded and focused without affecting the contralateral eye. Depth perception is achieved with a slit pupil that closes in a half-moon shaped form, thus creating two pinholes through which light can enter the eye. These two pinholes create two images in two different areas of the retina thus enabling the brain to have depth perception of the environment by using only one eye. This feature enables the dolphin to have good depth perception even though the overlapping field of view for both eyes is only approximately 10 degrees from the body axis. The visual acuity of dolphins has been measured at 7-8 min of arc (Herman et al., 1975) and is best at 1 m distance under water and at 2.5 m distance in air. Therefore, the visual resolution is comparable to that of a dog or a cat, where as humans can resolve objects that are spaced at 1 min of arc.

1.3.3.2.2. Auditory Sense

Bottlenosed dolphins have been tested for hearing between 100 Hz and 150 kHz (Johnson, 1966,) and are able to discriminate very small differences in pitch and frequency (Jacobs 1972, Herman & Arbeit 1972, Thompson & Herman, 1975). Their most sensitive area in the frequency range lies between approximately 10 and 110kHz (Au 1993). Bottlenosed dolphins produce two different types of vocalizations: frequency modulated whistles, which are narrow-band and have harmonics and short broad-band clicks which include burst pulse sounds and echolocation signals. This complex repertoire of vocalizations is being received through sound reception system that includes the lower jaw, the middle and inner ear, and a large part of the brain where the signals are processed. Sound enters the dolphin’s head through the lower jaw that contains a fatty channel, which has a similar density to saltwater and is then transferred to the typanoperiodic bone, which in turn is connected to the oval window of the inner ear. Functionally, there is no difference in the mechanisms of the inner ear between dolphins and land vertebra, although a higher range of frequencies has to be represented on the basilar membrane. Overall, this system is well adapted and fine-tuned for underwater hearing and allows the dolphin to utilize the auditory information that is present in the aquatic environment.

1.3.3.3. Dolphin Attention Abilities

Previous research with dolphins has shown excellent short-term memory for things seen and heard (Herman & Gordon, 1974; Herman et al. 1990, 1989). Dolphins can also report accurately the presence and absence of a probe “sound” in a previously heard list of sounds (Thompson & Herman, 1977; Herman, 1980). Furthermore, the dolphin has been shown to have a capacity for understanding a gestural language where objects and actions are represented by hand signals and an auditory-based language in which different sounds represent objects, actions, and relationships and sequences of sounds convey instructions (Herman et al, 1984). These studies indicate that through the visual as well as the auditory channel, dolphins can successfully attend and respond to successively presented stimuli. However, the processes and mechanisms involved in attending to these stimuli have not yet been explained. The current suite of vigilance studies was designed to investigate these attention mechanisms in the bottlenosed dolphin using vigilance tasks similar to those used successfully with humans. The dolphins’ principal task was to monitor its visual or auditory environment for one or more “key” stimuli presented within successive lists of distractor stimuli. Within this task, we could ask several questions:

a) Is the dolphin able to perform the task over an extended period of time?

b) Can vigilance decrement be shown within the tested time period?

c) Are differences in performance accuracy between the visual and the auditory sense detectable?