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Graphical Abstract (for review)

HIGH AROUSAL

LOW AROUSAL

Saccadic Peak Velocity

Saccadic Magnitude
Research Highlights

► Saccadic metrics vary with task difficulty and time-on-task in naturalistic scenarios
► Low arousal is correlated to decreased saccadic velocity
► Saccadic velocity may signal variations in sympathetic nervous system activation
Saccadic velocity as an arousal index in naturalistic tasks

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Abstract

Experimental evidence indicates that saccadic metrics vary with task difficulty and time-on-task in naturalistic scenarios. We explore historical and recent findings on the correlation of saccadic velocity with task parameters in clinical, military, and everyday situations, and its potential role in ergonomics. We moreover discuss the hypothesis that changes in saccadic velocity indicate variations in sympathetic nervous system activation; that is, variations in arousal.

Keywords: mental workload, mental fatigue, cognitive load, main sequence, eye movements, saccades, complex tasks, neuroergonomics, warning system, sleep deprivation, driving simulation, drowsy driving, air traffic control.

Contents

1. Introduction
2. Saccadic parameters and basic influences on saccadic velocity
3. The influence of arousal on saccadic velocity
   3.1. Effects of sleep deprivation
4. Saccadic velocity in applied domains
   4.1. Pioneering studies
   4.2. Galley’s contributions
   4.3. Recent studies
      4.3.1. Saccadic velocity in the clinical domain
      4.3.2. Saccadic velocity in the military
      4.3.3. Saccadic velocity in everyday tasks
4.4. A physiologically plausible explanation for the effects of arousal on saccade velocity
5. Concluding remarks
6. Future steps
Acknowledgements
References

Saccadic peak velocity correlates with arousal during the performance of ecological tasks
1. Introduction

Eye movements are essential to visual perception. High-resolution information, crucial to many everyday tasks, is available only in the fovea. Fast ballistic eye movements called saccades bring successive regions of interest onto the fovea, and thus are critical to navigating the visual world, from reading and interacting with objects to performing demanding visual monitoring tasks such as air traffic or nuclear platform control (Wang, 1998). Saccadic mean velocity, peak velocity, and duration increase as a function of saccadic amplitude, a relationship known as the main sequence (Zuber et al., 1965; Bahill et al., 1975). Despite early interest to determine if the slope of the saccadic main sequence was correlated to time-on-task (Bahill and Stark, 1975), saccadic metrics have received little attention in applied research. Here we discuss how the field of vision science has attempted, and thus far failed, to develop an eye-movement index of cognitive demand. We identify the obstacles that remain and the gaps in knowledge that future studies must fill to achieve success. We moreover discuss the hypothesis that changes in saccadic peak velocity indicate variations in sympathetic nervous system activation (i.e. variations in arousal) (Figure 1).

<<Insert Figure 1 about here>>

2. Saccadic parameters and basic influences on saccadic velocity

Research in saccadic metrics has focused on duration, acceleration, and velocity. The saccadic velocity waveform is typically symmetric (that is, the acceleration/deceleration phases are equal in duration). This may reflect the duration of the activity of burst neurons in the pontine reticular formation projecting to oculomotor neurons (Leigh and Zee, 1999). Peak velocity is achieved contemporaneously to the end of the neural signal pulse, typically at the point of maximum firing rate of the burst neurons (Galley, 1989). Saccades larger than 10º have a skewed velocity profile: the acceleration phase comprises about 1/3 of the total duration of the saccade (Baloh et al., 1975; Takagi
et al., 1993; Lin et al., 2004). The saccadic mean velocity is the ratio between saccade magnitude and duration.

Saccadic mean and peak velocity are highly correlated and tend to exhibit a 1 to 2 ratio in their absolute values [the proportion is called Q-ratio and is approximately constant for different saccadic amplitudes (Harwood et al., 1999; Garbutt et al., 2003)]. Mean velocity is an acceptable measure of saccadic velocity only for small saccades, however, where the velocity wave shape is symmetrical. For large saccades, peak velocity is preferable, as it is connected with the maximal firing rates of burst neurons (Galley, 1989). Unlike mean velocity, peak velocity measurements are moreover invariant to different saccade detection thresholds, and thus unaffected by whether a saccade ends crisply or wobbles at the end point (i.e. as a glissade saccade does) (Becker, 1989). Despite the functional distinctions between peak and mean velocity, many studies use the terms interchangeably (i.e. De Gennaro et al., 2000) or refer merely to “saccadic velocity” (Russo et al., 2002; Thomas and Russo, 2007; Morad et al., 2009).

Saccade direction is a main source of variability in saccadic velocity (Becker, 1989). For example, the same 20° saccade may reach a peak velocity of 570 º/s in the adduction direction, but only 490º/s in the abduction direction. Further, horizontal centripetal saccades are faster than centrifugal saccades, vertical saccades are slower than horizontal ones, and upward saccades are faster than downward ones (Galley, 1989).

Visual target presence also affects the variability of mean and peak saccadic velocity. Aiming the gaze to non-visual targets results in slower saccades (Galley, 1989). Antisaccades (saccadic movements made in the direction opposite to a suddenly appearing visual stimulus) are slower than visually guided saccades, anticipatory saccades, and memory-guided saccades, whereas saccades made immediately to a suddenly appearing target are faster than delayed saccades to persistent targets (Edelman et al., 2006).
Head restraint (Collewijn et al., 1992), arm-eye coordination (Snyder et al., 2002), saccade adaptation (Iwamoto and Kaku, 2010), and neurological disease (Galley, 1989) can also affect the main sequence slope.

3. The influence of arousal on saccadic velocity

Dodge and colleagues (Dodge et al., 1915) first observed a reduction of saccadic velocity after the ingestion of alcohol, in a dose-dependent manner. Miles (1929) later concluded that drugs and fatigue lower saccadic velocity through decreased activation of the central nervous system. Recent studies have confirmed these pioneering observations (Grace et al., 2010; Di Stasi et al., 2012; Ahlstrom et al., 2013); see section on "Saccadic velocity in applied domains".

Human factors and applied psychology studies have related “mental fatigue”, “mental workload”, “attentional/cognitive state” and other such terms, to variations in saccadic velocity (Di Stasi et al., 2011). Here we explore the possibility that subjective fatigue from long and cognitively demanding tasks, as well as certain neurological disorders such as depression, may affect saccadic metrics by reducing activation of the sympathetic nervous system; in other words, by lowering arousal (Figure 1). That is, that the subject’s level of arousal is the critical variable by which time-on-task, task difficulty, neurological impairment, drugs, and sleepiness, affect the saccadic main sequence.

3.1. Effects of sleep deprivation

The influence of the sleep/wake cycle on neural activation has been investigated extensively (Oken et al., 2006), as have been the effects of sleep deprivation and sleepiness on saccadic metrics (Miles, 1929, Bocca and Denise, 2006, Ahlstrom et al., 2013). A well known effect of sleep deprivation (and the resulting increased sleepiness (Ahlstrom et al., 2013)) is the reduction of peak and
mean saccadic velocity (Miles, 1929; De Gennero et al., 2000; Zils et al. 2005, Frasson et al., 2008; Ahlstrom et al., 2013) (See sections on “Saccadic velocity in the clinical domain/military/everyday tasks” for examples). Omnidirectional pause neurons [OPNs] stop firing during sleep (Henn et al., 1984). Thus, decreased saccadic velocity from OPN inactivation (Soetedjo et al., 2002; Kaneko, 1996) is in line with the proposal that a reduction in saccadic velocity reflects diminished arousal (see section on “A physiologically plausible explanation for the effects of arousal on saccade velocity”).

4. Saccadic velocity in applied domains

Human retinas are outgrowths of the brain and thus part of the central nervous system (Hoar, 1982; Wilson and O’Donnell, 1988); therefore studies have used gaze parameters as indicators of attentional or cognitive engagement (Ahlstrom and Friedman-Berg, 2006; Schleicher et al., 2008; Dey and Mann, 2010). Such research has generally disregarded saccadic velocity, however, focusing instead on the relationship between saccadic amplitude and fixation duration (Unema et al., 2005; Graupner et al., 2007; Pannasch et al., 2008). Unlike saccadic amplitude or fixation duration, saccadic velocity is not subject to voluntary control (Leigh and Zee, 1999); thus it may represent the underlying neural activity more accurately than other gaze parameters (Rowland et al., 2005).

4.1. Pioneering studies

Dodge and colleagues observed that time-on-task affected saccade generation (Dodge and Cline, 1901; Dodge, 1917). Their findings set the stage for the discovery of the main sequence (Bahill et al., 1975). Subsequent studies found that alcohol, sedative substances, and natural drowsy states lowered eye movement speed (Becker and Fuchs, 1969), even in the absence of muscular fatigue (Schmidt et
al., 1979, Prsa et al. 2010). These observations remained controversial for several decades, however (i.e. Boghen et al., 1974): discrepancies in results were due to the disparate saccadic amplitude ranges used by different studies, and to inconsistencies in methods and recording techniques. More than half a century later, Niels Galley (1989) proposed that decreased saccadic velocity indicated deactivation (i.e. low arousal) more reliably than most other gaze parameters.

4.2. Galley’s contributions

Galley and colleagues investigated variations in saccadic velocity in applied and basic research (Galley 1989, 1993, 1998, Galley and Andrès 1996, Schleicher et al., 2008). Galley (1993) and Galley and Andrès (1996) first studied the usefulness of saccadic metrics in ecological conditions (i.e. driving a car), in which eye movements have direct consequences on task performance. Their experiments overcame the limitations of previous research conducted with artificial paradigms/tasks such as the antisaccade task (App and Debus, 1998).

Galley (1993) evaluated the sensitivity of the electrooculogram (EOG) as a measure of gaze behavior in subjects driving automobiles while they performed various secondary tasks, such as looking for information in different locations on the dashboard (i.e. several digital displays or lateral mirrors). Mean and peak saccadic velocity decreased as time-on-task increased, suggesting that saccadic velocity may be a sensitive index of (low) arousal. Saccadic velocity increased with task difficulty, a counterintuitive finding explained further below.

To test whether the secondary tasks in Galley (1993) might have produced artificial driving behavior, Galley and Andrès (1996) studied long-term city driving (presumed high difficulty) and motorway driving (presumed low difficulty) in the absence of a secondary task. Participants drove in natural conditions for at least 6 hours a day, over a 5 day period. City driving led to higher mean
saccadic velocity than motorway driving, and increased time-on-task resulted in moderately lower mean saccadic velocity.

Galley (1998) required participants to track for more than one hour a light spot that jumped with unpredictable timing. Time-on-task lowered saccadic peak velocity, and higher-frequency stimuli increased saccadic velocity.

Contrary to the results above (Galley and Andrès, 1996; App and Debus, 1998; Galley, 1993), recent studies have reported decreases—rather than increases—in saccade velocity with task difficulty (Di Stasi 2010b,c, 2011), see section on “Saccadic velocity in everyday tasks”. We propose that variations in arousal may be the critical variable to reconcile this discrepancy. Namely, that increased task difficulty may increase arousal in some cases (leading to faster saccades) and decrease arousal in other cases (leading to slower saccades), depending on factors such as motivation and reward. Further, we note that ceiling effects make decreases more likely than increases in saccadic velocity (Gijsman et al., 2002), meaning that there is an upper limit to the saccadic velocities that an awake and alert person can generate (Galley, 1998); see also section on “A physiologically plausible explanation for the effects of arousal on saccade velocity”. Thus, Galley's studies, as a whole, support the hypothesis that arousal modulates saccadic velocity. That is, that decreased arousal lowers saccadic velocity, and increased arousal speeds up saccades.

4.3. Recent studies

Few studies have relied on saccadic velocity as an index of arousal/cognitive demand, despite the above observations (Parasuraman and Rizzo, 2007; Schleicher et al., 2008). Saccade metrics, and peak velocity in particular, may have failed to gain traction in applied ergonomics due to the technical and methodological difficulties of measuring saccades in naturalistic settings (though advances in the last
decade have obviated such difficulties). Traditionally, cognitive ergonomists and risk management experts used subjective tests and questionnaires to arousal/cognitive demand (Cooper and Harper, 1969). Main sequence analyses are highly technological in comparison, and were published originally in engineering or physics journals, such as Bahill et al.’s 1975 study in *Mathematical Biosciences*. In recent years, user-friendly commercial eye-trackers have overcome these barriers. Numerous psychological studies currently rely on off-the-shelf eye-tracking systems to record eye position non-invasively at high speed—via unobtrusive video cameras positioned in front of the operator or located on a lightweight headband—and on automated software analysis of the data, eliminating the need for intensive engineering training (McCamy, et al., in press).

### 4.3.1. Saccadic velocity in the clinical domain

Diefendorf and Dodge (1908) were the first to study the main sequence in mentally ill patients, anticipating that saccadic metrics might help to diagnose psychiatric disease. They found abnormal mean saccadic velocities in a number of diseases, such as slow saccades in extremely depressed patients, and unusually fast saccades in manic patients. The overall effects were weak, but they provided the basis for future saccadic research in psychiatric populations (Gooding and Basso, 2008).

Melancholic and non-melancholic depression are subtypes of major depressive disorder, each having distinct cognitive and motor impairments (Winograd-Gurvich et al., 2006). Winograd-Gurvich and colleagues found abnormal main sequences in patients with melancholic depression and relatively normal main sequences in patients with non-melancholic depression (Winograd-Gurvich et al., 2006). They postulated that decreased saccadic peak velocity in melancholic depression was due to dopamine dysfunction, whereas the relatively minor effects of non-melancholic depression on saccadic velocity might be a byproduct of prefrontal cortex dysfunction in response to changes in serotonin levels.
(because perturbations in the serotonergic system are thought to underlie the non-melancholic symptoms of depression (Malhi et al., 2005)). Large serotonergic axons projecting to the superior colliculus and several brainstem nuclei that control eye movements could modulate peak velocity, a possibility consistent with peak velocity increases after the administration of the serotonin-receptor agonist dexfenfluramine (Gijsman et al., 2002).

Drugs that affect the GABA/benzodiazepine receptor influence attention and cognitive activity (Barker et al., 2004; Stewart, 2005). Glue et al. (1991) found that α2-adrenoceptor agonists (clonidine) and antagonists (idazoxan) altered peak velocity, but not other saccadic parameters such as accuracy or latency. Clonidine, which generally causes sedation, led to peak velocity decreases; idazoxan, which generally increases arousal, led to peak velocity increases. Ball et al. (1991) also found that midazolam (benzodiazepine receptor ligands) concentration was inversely proportional to peak velocity. Later, Gijsman et al. (1998) reported that meta-chlorophenylpiperazine (a psychoactive drug) increased peak velocity in a dose-dependent manner, in correlation to increased arousal. More recently, Grace and colleagues (Grace et al., 2010) determined that morphine-induced sedation and sleep deprivation lowered peak velocity. Drug effects on peak velocity suggest that saccadic metrics may aid the diagnosis of neurological dysfunction and help assess the effectiveness of drug therapies.

4.3.2. Saccadic velocity in the military

The development of non-invasive methods to monitor and detect cognitive impairment (i.e. poor judgment, decreased situational awareness) in soldiers, and thus prevent catastrophic outcomes in operational environments (Friedl et al., 2007), is an area of great interest to the military (Tennison and Moreno, 2012). Military medical departments have investigated the effects of sleep deprivation and time-on-task on saccadic velocity and task performance (Porcu et al., 1998; Russo et al., 2003; LeDuc
et al., 2005; Rowland et al., 2005; Morad et al., 2009; Hirvonen, et al., 2010). Their studies follow similar experimental designs.

Hirvonen et al. (2010) compared the sensitivity of EOG versus the Fitness Impairment Test (FIT, Pulse Medical Instruments, Inc., Rockville, MD) in detecting variations in peak velocity. FIT is a self-contained, fully automated, computer-controlled, commercial optical recording system, which combines infrared pupillometry with eye movement tracking. The system measures four variables: pupil diameter, pupil constriction, saccadic latency, and velocity (Morad et al., 2009). Hirvonen et al. (2010) used a mobile FIT device with 600 Hz sampling rate and 0.1 mm resolution. Eleven navigators of the Royal Norwegian Navy remained awake for 60 hours, while performing vision and oculomotor tests, and filling in subjective questionnaires (i.e.: Karolinska Sleepiness Scale [KSS], Åkerstedt and Gillberg, 1990) every 6 hours. Saccadic velocity, calculated as the average peak velocity of four 20º saccades, decreased progressively as a function of time-on-task, and EOG measurements detected fatigue with more sensitivity than the FIT tool (when compared to the results from the subjective questionnaire).

Saccadic velocity also decreased with increased sleep deprivation in FIT studies conducted by other groups (Russo et al., 2003; LeDuc et al., 2005; Rowland et al., 2005; Morad et al., 2009). It is important to note that most FIT studies report saccadic velocity values without specifying whether they indicate mean or peak velocity. Further, the use of percentage values, instead of the original values expressed in deg/s, makes it impossible to ascertain if the results refer to peak or mean velocity.

### 4.3.3. Saccadic velocity in everyday tasks

Few studies have investigated the validity and sensitivity of saccadic velocity as an index of arousal/cognitive demand during ecological behaviors. Schleicher et al. (2008) applied the original
ideas from (Galley, 1993; Galley and Andrés, 1996) to study changes in various oculomotor variables (including saccadic parameters and blinking, as measured by EOG) as a function of increasing sleepiness in a simulated traffic situation. Participants drove for two hours on a monotonous road circuit, without any secondary tasks. Blinking behavior (blink duration, delay of lid reopening, blink interval, and lid closure speed) was the best indicator of subjective (measured by the KSS) and objective (rating of facial behaviour) sleepiness. Among the saccadic parameters (mean velocity, amplitude, and duration), only duration increased moderately with sleepiness.

Di Stasi and colleagues (Di Stasi et al., 2010b; Di Stasi et al., 2010c; Di Stasi et al., 2011; Di Stasi et al., 2012) studied saccadic metrics (peak velocity, amplitude, and duration) in applied tasks, including simulated air traffic control, driving simulations, and microworld simulations (i.e. simulations of real tasks that change dynamically to reproduce the important characteristics of real situations). The experiments combined performance, subjective, and eye movement-based measures. Eye positions were tracked via infrared video-oculography (SR Research's EyeLink, 500 Hz), and peak velocity analyzed as a function of saccade length.

Di Stasi and colleagues (Di Stasi et al., 2012) showed that peak velocity can serve as a screening tool (i.e. an online real-time measure of arousal) in drivers. Subjects performed a guided saccade task and completed subjective questionnaires before and after driving for 2 hours. Stanford Sleepiness [SSS, (Hoddes et al., 1973)] and Chalder Fatigue [CFS, (Chalder et al., 1993)] scores were higher after the driving task. The peak velocity of saccades larger than 7.5° decreased from the first to the second measuring time. The same tendencies were present during the driving task (Figure 2).

<<Insert Figure 2 about here>>
In Di Stasi et al. (Di Stasi et al., 2010b), a simulated air traffic control setting required participants to perform two simultaneous tasks with differing perceptual and task demands: a button decision task with the non-writing hand and a paper-and-pencil task with the writing hand. The experimental conditions induced varied task difficulty levels, confirmed by subjective ratings (Mental Workload Test (Di Stasi et al., 2009)) and correlated behavioral results (number of response errors and delayed answers): saccadic peak velocity decreased with increased task difficulty—contrary to Galley's studies (1993, 1998)—though saccade duration and mean velocity were not affected. The experimental design did not distinguish between the effects of task difficulty and time-on-task, however. Di Stasi et al. (2011) overcame this limitation in a follow-up experiment using the Firechief incident simulator (microworld) (Omodei and Wearing, 1995) as a complex and dynamic problem-solving task. Task difficulty differed between subject groups, whereas time-on-task was manipulated within groups. Saccadic peak velocity was a more sensitive index of task difficulty and time-on-task than both performance and subjective measures of task difficulty. Consistent with Di Stasi et al., 2010b, peak velocity decreased with increased task difficulty and increased time-on-task, whereas saccade duration and mean velocity did not change.

Di Stasi et al. manipulated task difficulty independently from time-on-task, and found that peak velocity is sensitive to variations in task difficulty during short driving periods (Di Stasi et al., 2010c). Increased task difficulty resulted in lower saccadic peak velocity, but it did not affect either saccade duration or mean velocity. Time-on-task (over a 45 minute time period) had no effects on saccadic metrics.

The combined results from the above studies indicate that increased task difficulty and time-on-task (exceeding ~60 minutes) lower saccadic peak velocity.
4.4. A physiologically plausible explanation for the effects of arousal on saccade velocity

The effects of arousal on saccadic parameters such as peak velocity may arise at a late stage of oculomotor processing, such as at the level of the excitatory burst neurons, whose firing rates encode the velocity signal of saccades (Edelman and Goldberg 2001; Sparks, 2002; Zils et al., 2005). Munoz and Everling (2004) proposed that changes in attentional processing (for instance, due to variations in arousal) can affect the strength of the excitatory connections from the frontal cortex to the brainstem reticular formation, thus modifying the characteristics of the main sequence.

Following from Munoz and Everling’s model (2004), arousal may affect peak velocity via the inhibitory connections between the sleep-regulating centers (i.e. nucleus raphe magnus, nucleus raphe dorsalis, and locus coeruleus) and the superior colliculus on the reticular formation and cerebellum. Straube and colleagues (Straube et al., 1997) found saccadic performance was worse (saccadic latency increased and saccadic accuracy and peak velocity decreased) when rhesus monkeys performed a task in the dark than when they performed it in dim light. Most of the experiments we have reviewed here were conducted in darkened laboratory conditions; therefore it is possible that decreases in peak velocity during long duration experiments were mediated by the activation of the brain’s sleep centers, thus supporting a key effect of arousal on saccadic metrics.

Excitatory connections from hypothetical arousal neurons to OPNs (Grossberg and Kuperstein, 1986; Moschovakis, 1994; Gancarz and Grossberg, 1998; Rahafrooz et al., 2008; see Girard and Berthoz, 2005 for a review) might mediate changes in saccadic velocity due to time-on-task. In agreement with this possibility, OPN inactivation produces slower saccades (Miura and Optican, 2006; Soetedjo et al., 2002; Kaneko, 1996), and decreased activation of hypothetical arousal neurons results in saccadic metrics “similar to those observed in case of fatigue state” (Grossberg and Kuperstein, 1986). Further, experiments have shown that OPNs stop firing during sleep (Henn et al., 1984),
lending additional support to the proposal that variations in arousal lead to changes in saccadic velocity.

In summary, reduced arousal due to task features (Di Stasi et al., 2010b, c), sleepiness (Hirvonen et al., 2010), and diseases of the central nervous system (Winograd-Gurvich et al., 2006) leads to decreased saccadic velocity, perhaps due to decreased activation of the OPNs. Conversely, increased arousal due to drug use (Gijsman et al., 1998), increased motivation (i.e. due to reward) (Takikawa et al., 2002), and perhaps increased effort (Galley, 1998, 1993) can raise saccadic velocity. Future studies should investigate how the interaction between motivation and task features affects saccadic metrics, especially in relationship to arousal.

5. Concluding remarks

Our analysis supports the proposal that peak velocity is a good index of arousal, with potentially important applications in ergonomics and in the clinic. Galley’s early studies (1989; 1998) and recent work by other groups (Hirvonen et al., 2010, Grace et al., 2010) should encourage further studies to uncover how variations in task demands influence saccade metrics in applied scenarios (ranging from emergency call center offices to air traffic control towers).

Recent research has begun to address how attentional fluctuations impact the characteristics of microsaccades (small involuntary saccades that occur during attempted fixation, see Martinez-Conde, et al., 2009; 2013; Rolf, 2009, for reviews). A few studies have started to investigate the effects of task difficulty on microsaccade parameters during free-viewing (Otero-Millan et al., 2008; Benedetto et al., 2011) and attention cueing tasks (Pastukhov and Braun, 2010). The initial results suggest that microsaccade production increases with task difficulty (Otero-Millan et al., 2008; Benedetto et al., 2011; but see Pastukhov and Braun, 2010). Future applied research should combine the analysis of
micro- and macro-saccades in ecological contexts. Such research may prove fruitful, given that operators of video display terminals need to scan reduced areas of interest and as a consequence generate smaller-amplitude saccades (see Di Stasi et al., 2010b).

6. Future steps

As society’s technological abilities grow, it remains a challenge to determine the most helpful type and level of automated assistance that operators/users/drivers need in demanding environments. Peak velocity, as a valid and sensitive index of arousal variations in complex and real conditions, may help us to overcome this challenge. Foreseeing that “the vehicles of the future will be equipped with a cognitive prosthesis…” (Cacciabue and Carsten, 2010), the next step will be to create systems with the ability to measure physiological data (Casucci, et al., 2010). Real-time detection of changes in arousal could help design systems that may allocate tasks to operator and/or machine in an optimal and dynamic way (i.e. Kaber et al., 2006).

Critically, these objectives must be achieved without interfering with the task or compromising its safety. The automotive industry has been very productive in this sector (AIDE, 2012; ISi-PADAS, 2012, ITERATE, 2012). Numerous studies on intelligent transport systems have focused on safety over the last two decades (Piao and McDonald, 2008), with recent studies addressing the effects of the temporal and physical features of warning systems on driver performance and attitudes (Wiese and Lee, 2004; Cacciabue, 2007). New results are beginning to reduce the gap in knowledge concerning how subjects in highly demanding situations respond to warning alarms (Jou et al., 2009; Di Stasi, et al., 2010a).
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Figure Captions

Figure 1. A possible effect of arousal on saccadic velocity.
Schematic diagram of the effect of arousal on the midbrain/brainstem saccade circuit. The superior colliculus’ caudal poles drive the burst neurons, which in turn project to oculomotor neurons, giving rise to saccades. The superior colliculus’ rostral poles drive omnipause neurons (OPN) during fixation. Burst neurons and OPN are mutually inhibitory (Yoshikazu et al., 2011). OPN, which are critical to encoding saccadic velocity, fire at a relatively constant rate during fixation, but stop during saccades and also during sleep. Hypothetical arousal neurons [A] project onto OPN and modulate their activation (Grossberg and Kuperstein, 1986; Moschovakis, 1994; Gancarz and Grossberg, 1998; Rahafrooz et al., 2008). Reduced levels of arousal may decrease the firing rates of OPNs, leading to slower saccades.

Figure 2. Effect of time-on-task on the main sequence.
Saccadic peak velocity decreases with driving time. Each dot represents a saccade. Two hours of driving time are divided into four 30-minutes sections: green (first 30 minutes), yellow (second 30 minutes), orange (third 30 minutes), and red (last 30 minutes). The curves are the exponential fits to the data from each block (data from Di Stasi et al., 2012b).
HIGH AROUSAL

Saccadic Peak Velocity

LOW AROUSAL

Saccadic Magnitude

Omnipause Neurons [OPN] Activity

Saccade

Superior Colliculus
Caudal  Rostral

Burst Neurons

Motor Neurons

Figure 1
Figure 2

Saccadic Peak Velocity (deg/s) vs. Saccadic Magnitude (deg) for different time intervals: 0-30 min, 30-60 min, 60-90 min, and 90-120 min.