Task Related Pupil Dilation Patterns in a List Lexical Decision Task Explained by the Adaptive Gain Theory

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Abstract

Adaptive Gain Theory relates modes of activity of locus coeruleus-norepinephrine (LC-NE) system to performance optimization. Recent studies suggest that the switch between LC phasic and tonic modes of activity can be traced via pupil dilation patterns. The LC phasic mode occurs during episodes of high performance and task exploitation and is accompanied by large task-related pupil dilations and lower pupil baseline. LC tonic mode occurs during episodes of poor performance and exploratory behavior and is linked to higher pupil baseline. Such pupil dilation patterns in a list lexical decision task with varying payoff schemes were examined. The three payoff schemes emphasized either accuracy of responses, speed of responses or a balance between the two factors. The correlation of pupil baseline with pupil dilation, payoff and response time throughout the task is consistent with the predictions made through the Adaptive Gain Theory. Alternations between the LC phasic and tonic mode are apparent throughout the task and are consistent with changes in one's task performance, demonstrated in payoff and response time. Moreover, LC phasic and LC tonic alterations are also apparent at a more local level, within a trial, and after fixation on word or nonword stimuli. The difference in correlation between pupil baseline and pupil dilation patterns between the three payoff categories supports the prediction that the increase in LC phasic mode when the potential cost of exploration is high, and increase in LC tonic mode when the potential cost of exploration is low.

Keywords: Adaptive Gain Theory, pupil dilation, pupil baseline, List Lexical Decision Task

Task Related Pupil Dilation Patterns in a List Lexical Decision Task Explained by the Adaptive Gain Theory

Can our eyes be a window to our souls? Over the past few decades, so much has been discovered about eye movements and pupil dilations this question may not seem too far from being answered. Studies concerning pupil dilations began more than fifty years ago with the study of task-related pupil dilation and its relation to cognitive processing and cognitive workload (Beatty and Kahneman, 1966; Beatty & Jackson, 1978; Ahern & Beatty, 1979; Beatty, 1982). More recent studies have shown similar pupil dilation patterns in response to cognitively challenging tasks such as detection of auditory stimuli (O'Neill & Zimmerman, 2000; Steinhauer, Siegle, Condray & Pless, 2004), detection of visual stimuli (Privetera, Renninger, Carney, Klein & Aguilar, 2010), the visual backward masking task (Verney, Granholm & Marshall, 2004), speech planning (Papesh & Goldinger, 2012), Stroop task (Siegle, Steinhauer & Thase, 2004) and the lexical decision task (Kuchinke, Võ, Hofmann & Jacobs, 2007). All these studies reveal that the magnitude of task related pupil dilations is directly related to the difficulty of the task and task-related cognitive processing.

Individual Variations in Pupil Dilation Patterns

Many factors such as an individual’s age, cognitive competence and psychological dysfunctions can influence the task related pupil dilation patterns on a given task. Granholm and Verney (2004) showed that in a backwards masking task, schizophrenic participants have larger pupil dilations to nontarget stimuli (the masks) and smaller pupil dilations to the target stimuli, whereas the non-psychiatric controls have larger pupil dilations to the target stimuli and smaller pupil dilations to the masks. Granhlom and Verney attributed such pupil dilations to differences in attention allocation to the task in schizophrenic participants and controls. In a similar study, Verney and colleagues (2004) showed that pupil dilation patterns could also be influenced by one's cognitive skills. In a visual backwards masking task, college students with higher Scholastic Aptitude Test (SAT) scores had larger pupil dilations to the visual targets and smaller pupil dilations to the masks compared to students with lower SAT scores. Siegle and colleagues (2004) tested the pupil dilation patterns in depressed and non-depressed controls on a coloring Stroop task. They found significant pupil dilations for incongruent compared to congruent trials in both groups, reflecting the greater cognitive load required for incongruent trials. However, although there was no significant difference in the Stroop effect on pupil dilation of the two groups, few seconds following the stimuli, depressed participants showed a smaller pupil dilation and lower prefrontal activity compared to the controls. Karatekin, Marcus and Couperus (2007) also showed an age related difference in pupil dilations during a digit recall task. When performing a digit recall and a simple reaction task simultaneously, ten year old children have smaller pupil dilations when recalling longer spans (6- and 8-digits) relative to adults. Such lower pupil dilations were attributed to children's inability to fully utilize the working memory for more cognitively compelling tasks. Overall, pupil dilation patterns in response to stimuli or cognitive stimuli are shown to be very sensitive to many biological, cognitive and psychological factors.

Adaptive Gain Theory and Cognitive Processing

The link between pupil dilations and cognitive workload has been established through many pupilometry studies. However, there are many more studies to be conducted to fully understand the actual mechanism through which the task related cognitive processing affects pupil dilation patterns. The Adaptive Gain Theory, (Aston-Jones and Cohen, 2005) which specifies the role of the Locus Coeruleus (LC) Norepinephrine (NE) system in optimizing behavioral performance and task utility could be used to relate such pupil dilations to cognitive processing. In a series of experiments with monkeys performing a signal detection task, Aston-Jones and Cohen discovered that the monkey's LC neurons fire tonically at a moderate rate throughout the experiment while firing phasically only following presentation of the target stimuli, and not the non-target stimuli. They also found that not only such LC responses are highly plastic and task selective, but they also depend on presence of a behavioral response from the monkey. LC responses do not occur in trials that are not accompanied by a manual response despite detection of the target stimuli by the monkey. These findings provide more support for the idea that the behavioral and LC responses are highly linked.

According to Aston-Jones and Cohen, the LC phasic response occurs about 100 ms following presentation of target stimuli and 200 ms preceding the behavioral response. Moreover, LC impulses take 60-70 ms to reach frontal motor areas (Aston-Jones, Foote & Segal, 1985) Thus, LC responses reach the motor cortex just in time for development of motor impulses which occur 150 ms preceding the execution of the manual response. (Mountcastle, Lamotte & Carli, 1972) In this way, the timing of LC phasic impulses and the time it takes for them to reach the frontal motor areas make it feasible for the LC responses to affect the task related behavioral response. A diagram of the sequence of task related LC response and the programming and execution of the motor response is shown in Figure 1.

Studies regarding the physiology of LC have revealed that LC activity can be described by two modes of activity: the phasic and the tonic mode. According to Aston-Jones and Cohen (2005), the LC phasic mode involves the phasic activation of LC neurons in response to task-related stimuli and moderate levels of LC tonic activation. In this mode, one exploits the selected and most optimal strategy for a given task and refrains from exploring other options. Such task selective activity leads to higher levels of performance on a given task. LC phasic mode resembles a filter that decreases the multi-dimensional system of different options, resources and strategies, each with a unique probability to enhance the performance, to a single layered system that holds only the most optimal strategy. Unlike LC phasic, LC tonic involves higher levels of LC tonic activation and lacks the task related LC phasic activity. LC tonic is associated with exploration of different options and strategies and lack of exploitation of the resources at hand, consequently, resulting in a poor performance on the task. During LC tonic mode, one explores all the different options provided by the multi-dimensional system of strategies and abstains from exploiting a selected strategy. Thus, LC tonic is associated with higher degrees of distractibility and lack of attention to the task. In sum, LC phasic mode seems to be associated with higher performance and task utilization while LC tonic mode is associated with exploration of other options and a poorer performance on the task.

According to the Adaptive Gain Theory, LC phasic mode occurs when the gain from exploitation of the resources is higher than the gain from exploration of new options, (or the cost of exploring other options is higher than cost of exploiting the current resources). LC phasic occurs with a system-wide increase in gain, driven by task relevant decision processes, which is expressed in behavioral responses. On the other hand, LC tonic mode occurs when exploitation of current resources results in a lower gain, and exploration of new resources is needed for optimal results. LC tonic mode is associated with an increase in gain of nonspecific information, resulting in an increase in the degree of noise. According to the Adaptive Gain Theory of LC-NE activity, for optimal results one has to maintain a balance between exploitation of resources and exploration of other options associated with LC phasic or tonic modes of activity.

Role of ACC and OFC Neurons in Regulation of LC Mode

The two cortical centers, orbitofrontal cortex (OFC) and the anterior cingulated cortex (ACC) have received a great deal of attention regarding their role in regulation and perception of costs and rewards. Many studies have shown that OFC plays an important role in evaluation of rewards. OFC neurons in monkeys get activated in response to rewarding stimuli and not the stimulus identification alone (Tremblay & Schultz, 1999; Rolls, 2004) , the magnitude of such activation is correlated with the magnitude of the reward (Wallis & Miller, 2003; Roesch & Olson, 2004) and diminishes after satiation with the specific reward. (Rolls, Sienkiewicz, & Yaxley, 1989; Critchley & Rolls, 1996). On the other hand, ACC activation is associated with evaluation of cost and errors in performance and negative feedback in a given task (Gehring, et al., 1993; Yeung, Botvinik & Cohen, 2004), and task difficulty and conflicts in cognitive processing of a task (Ullsperger & von Crammon, 2001). Supported by the presence of strong projections from ACC and OFC to LC, Aston-Jones and Cohen (2005) propose the potential regulatory effects of OFC and ACC on alternation of the LC modes of activity. According to their theory, high cost and low task utility causes the ACC and OFC neurons to trigger LC tonic mode and exploration of other options, whereas, high task utility and low cost causes these centers to trigger LC phasic mode and task exploitation. Such regulatory effects provide important physiological explanations for the LC activation and behavioral responses to task related feedback.

Pupil Dilations and Adaptive Gain Theory

How are pupil dilation patterns related to task utility and cognitive load? Over the past years, many studies have been conducted to shed light on the pathways that link pupil dilation patterns to variations in cognitive load. Studies of Rajkowski, Kubiak, and Aston-Jones, (1993) revealed a link between task-related pupil dilation patterns and LC tonic and phasic modes of action. Measurements of the LC-NE activity in monkeys while performing a target detection task have showed that high task performance was accompanied by LC phasic mode, a large target stimulus- related pupil dilation and a moderate non-target related pupil dilations. In contrast, low task performance was accompanied by LC tonic mode, low target stimulus-related pupil dilation and larger non-target related pupil dilations (see Figure 1). Since direct measurement of LC activity in humans during task performance is not feasible, the findings from this study forms the basis of the following studies regarding pupil dilation patterns and LC-NE activity in humans.

In their studies of pupil dilation patterns in an auditory detection task Gilzenrat, Nieuwenhuis, Jempa and Cohen (2010) showed that changes in pupil dilation follow patterns predicted by the Adaptive Gain Theory. In series of experiments, Gilzenrat and colleagues, (2010) first showed that such pupil dilations are only derived from the task and are not related to illumination of the experiment setting. Next, they examined pupil dilation patterns in an auditory detection task with increasing payoff amounts. They found that higher performance and smaller response time (RT) in trials was associated with larger task related pupil dilations and lower pupil size baseline. However, poor task performance and larger RT values were associated with smaller task related pupil dilations and larger pupil size baseline. Moreover, trials on which participants had poor performance and large pupil size baseline were followed by trials of improved performance, lower pupil size baseline and higher task related pupil dilations. Considering the fact that pupil dilation patterns are parallel with the LC-NE responses, the observed pupil dilation patterns in their study follows the Adaptive Gain Theory. Poor performance on trials leads to exploration of other options that may improve the performance

(LC tonic mode) which is associated with larger pupil size baseline and smaller task related pupil dilations. Such activity is followed by selection of the optimal strategy, exploitation of resources and higher performance (LC phasic mode), leading to lower pupil size baseline and larger task related pupil dilations.

In a more recent study Jepma and Nieuwenhuis (2011) tested the AGT in an auditory gambling task with changing pay off. As predicted, larger pupil diameter baseline was accompanied by exploratory decision making, whereas, smaller pupil size baseline was associated with exploitative decision making. They also found a shift in pupil size in the transition between exploitative and exploratory decisions. Such transitions in pupil size baseline due to task utilization directly support the Adaptive Gain Theory. Moreover, their study showed that individual variations in patterns of pupil baseline transitions were predictive of one's tendency towards exploratory or exploitative decisions.

List Lexical Decision Task

Task related pupil dilation patterns in a lexical decision task have been studied by Kuchinke and colleagues (2007). However, such changes in pupil size baseline corresponding to Adaptive Gain Theory, in a List Lexical Decision Task (LLDT) have yet to be examined. In our study, we examined the pupil dilation patterns and exploratory and exploitative behaviors in a List Lexical Decision Task. During LLDT one decides whether all the words in the given trial are actual English words or whether the list contains a non-English word (nonword). The payoff is based on the accuracy and the speed of the responses; participants gain points for being fast, and lose points for providing inaccurate responses. In our study, the degree of reward points for speed and penalty for inaccurate responses varies between the three versions of the task. In the Accuracy payoff scheme, the penalty of inaccurate responses is much larger than the other payoff schemes, whereas in the Speed payoff, the reward for fast responses is lower than the other schemes. The reward points for speed and the penalty for inaccuracy in the Balance payoff is in between that of the Accuracy and Speed payoff scheme (see Table 1). While the participants perform the task, the accuracy of their responses, their response times, the fixation duration on each word, the saccade duration and their pupil size are recorded. The participants are informed about the points gained (or lost) once after each trial and second after finishing a block of twenty trials. Consequently, the participant may change their strategy to receive better results at any point during the experiment. At the end of the experiment, participants receive a monetary bonus based on the total points gained throughout the experiment. Such monetary bonus is aimed to motivate more task engagement and efforts to gain optimal performance among participants. Overall, this is a unique task in the field of pupilometry, in that, the three payoff categories are set to manipulate the participants strategies and task performance, and consequently pupil dilation patterns.

Based on the Adaptive Gain Theory and its relation to pupil dilation pattern, we made the following prediction about pupil dilation patterns in our list lexical decision task. (1) The pupil size baseline is much larger when the participants are performing poorly on the task, since they may be exploring other strategies to maximize their reward points. This could be an indication of the LC tonic mode. (2) The pupil size baseline is lower and the task related pupil dilations are more prominent when the participants are performing well on the task. This could be an indication of LC phasic mode and exploitation of the strategy that is resulting in higher reward points. (3) Trials with larger pupil size baseline and poor performance (LC tonic) are followed by trials of lower pupil baseline and task-specific pupil dilations (LC phasic) and improved performance. In other words, poor performance results in exploration of other strategies until the strategy that results in better performance is detected and utilized. (4) In the Accuracy payoff, more frequent occurrence of lower pupil size baseline and larger task related pupil dilations could be evident of more LC phasic and exploitation behaviors. In such trials the cost of exploring other strategies may surpass the potential gain of finding a more optimal strategy, resulting in an increased exploitation of current resources (LC phasic mode) rather than exploration of other options (LC tonic). (5) In Speed payoff, higher pupil size baseline could be evident of increased LC tonic activity and exploration of different strategies for performance optimization. In such trials the gain of exploring different strategies for the most optimal one may exceed the cost of not utilizing the current resources, resulting in more exploratory behavior and LC tonic mode.

Methods

Participants

49 native English speakers, 19 to 40 years old, 23 females and 11 males, members of the University of Michigan community, participated in this study (the gender of 2 of the participants was not documented). Due to calibration errors, equipment malfunctions, and failure to finish the experiment the data obtained from 13 participants was discarded (n=36). Prior to start of the study, the participants signed a consent form, which briefly explained the procedure, risks and benefits of participating in the study. Upon participation in the study, the participants received $10 plus a bonus of $1 for each 1000 points they scored on the task. If the participants were unable to finish in the study due to complications with the device or calibration, they received $5 as compensation.

Stimuli

The task consists of 200 trials divided in 10 blocks of 20 trials, following a 10 trial practice block. Half the trials consisted of six English words (the Word trials) while the other trials consisted of five English words and one nonword (the Nonword trials). The position of the nonword in the trial was uniformly distributed between the first and sixth position. Words were 4 characters long and drawn from a 234-word subset of the Brown Corpus (Kucera & Francis, 1967), containing 117 high-frequency words (mean frequency count 239.2, SD 186.0) and 117 low frequency words (mean frequency count 5.6, SD 12.8). Nonwords were also all 4 characters long, and were drawn from a list of 53 pronounceable nonwords according to English phonotactics.

Items were presented on a CRT monitor in a 20pt Courier font, separated by 6 characters of white space. This resulted in each word covering .7 inches or 1.6 degrees of visual angle, and whitespace covering 1.48 inches or 3.4 degrees of visual angle at a distance of 25 inches from the screen.

Procedure

Participants were randomly assigned to each of the three versions of the task (Accuracy, Speed and Balance). At the beginning of the experiment, the instructions appropriate to that version of the task were displayed on the screen. For instance, the participants in the Speed version were told they would receive 5.7 points for each 1000 ms by which their response is faster than 5000 ms, and will lose 25 points for inaccurate responses. Each trial was preceded first by a drift correction and then by a gaze-contingent trial start, which required the participants to fixate on the fixation dot appearing first in the middle and then to the left of the screen, respectively. The list of six items would appear once participants pass the drift correction, and the trial ended after participants responded using a Cedrus response box. The data about the saccades, fixations and pupil size of the right eye were recorded via Eyelink II head-mounted eye-tracker operating at 500Hz (the participants' pupil size was recorded every 4 ms during each trial). At the end of each trial the participant's response time, accuracy of response and points on the trial appeared on the screen. At the end of each block, the participant's points on the last trial, total points on the whole task, and the average score on each block appeared on the screen. After completion of the last trial, the participants were informed about their total points, filled out a questionnaire, were debriefed and compensated for their participation.

List Lexical Decision Task (LLDT). A trial in the List Lexical Decision Task (LLDT) applied in this experiment consists of a list of 6 items, in which participants need to decide whether all the items in trial are English words (Word trial) or at most one of the items in the list is a nonword (Nonword trial). For each trial, the participants receive points based on their accuracy and response time. The three versions of the task differ in the amount of bonus for speed and penalty for inaccuracy (See Table 1).

Results

Almost all the participants finished the experiment without any complications. The participants who could not finish, due to calibration errors or equipment malfunction were accounted for and their data was discarded. As shown in Table 2, consistent with the predictions, the average percentage of accurate responses was much higher for participants in the Accuracy Payoff category (92%) than participants in the Balance and Speed Payoff category (87% and 88%, respectively). However, the average response time (RT) for each trial was smaller for the participants in the Speed Payoff category (RT = 1494 ms) compared to the participants in the Accuracy and Balance Payoff category (1667 ms and 1548 ms, respectively). Such RT and Accuracy tradeoff was expected due to the scheme of each payoff category. Moreover, with an average trial payoff of 16.95, participants in the Speed Payoff Category had a better performance than the participants in the other two payoff categories.

To examine the variations in pupil size in response to performance and task utility pupil baseline and the task related pupil dilation in each trial were determined. Pupil base line was defined as the mean pupil size for the first 200 ms of each trial, and the pupil dilation was determined as the maximum positive deviation from the base line in each trial. The first 200 ms period was chosen to avoid counting the potential task related pupil dilation towards calculations for the pupil baseline, in trials in which the nonword is first on the list. To minimize the effect of factors such as recalibration of the eyetracker or the participant's head movements on the recorded pupil size throughout the experiment the obtained pupil size baseline and pupil dilation value in each trial was normalized for each participant. Next, the correlation between pupil dilation and pupil baseline throughout the experiment for each participant was determined. The value of such correlation for each participant is shown in Table 3. Next, a sign test was performed to determine whether the calculated correlation values support the hypothesis that there is a negative correlation between pupil baseline and pupil dilation. With (m = - .34, p < .001) the negative correlation between the pupil baseline and pupil dilations for the participants was significant. Such negative correlation reflects the prediction of large task related pupil dilations and lower pupil baseline associated with LC phasic activity throughout the task. The changes in pupil dilation and pupil baseline patterns for three of the participants, each from one of the payoff categories, is shown in Figures 3, 4 and 5. Comparison of the correlation values in between participants in the three payoff categories revealed that on average the correlation between pupil dilation and pupil baseline is much stronger for participants in the Accuracy

Payoff category (*M* = -.41) than participants in the Balance (*M* = -.36) and Speed Payoff (*M* = -.27) categories, however, such difference is not significant ($F(2, 33) = 2.14$, $p = .13$).

Besides the pupil dilations patterns seen throughout the experiment, local pupil dilations in response to word and nonword stimuli within a trial were also present. To examine such local pupil dilations, changes in pupil size within an 800 ms period after fixation on a word or nonword stimulus was plotted. As seen in Figure 6, the difference in magnitude of pupil dilation after fixation on a nonword compared to a low or high frequency word is apparent as early as 200 ms after fixation and increase over the next 600 ms. The difference in magnitude of pupil dilation after fixation on high and low frequency words becomes more distinct at around 500 ms after fixation. Moreover, there seems to be a difference in such local pupil dilation patterns for participants in the three payoff categories. As seen in Figure 7, the magnitude of pupil dilation after fixation on the word or nonword stimulus is much greater for participants in the Accuracy Payoff category than participants in the Balance and Speed Payoff categories. Participants in the Balance and Speed Payoff categories show almost no changes in pupil size within the 800 ms period after fixation on high or low frequency words, whereas participants in the Accuracy payoff show an increase in pupil size after fixation on both high and low frequency words. Moreover, for participants in the Speed Payoff category, the pupil dilation response occurred after about 500 ms post fixation on a nonword stimulus, whereas such pupil dilation is distinct as early as 200 ms post fixation for participants in the Accuracy and Balance Payoff categories.

Next, the relationship between changes in pupil baseline and participants' performance was examined. First, the payoff on each trial was normalized for each participant, and then compared to the normalized pupil baseline on that given trial. A sign test was performed to test the hypothesis that the pupil baseline and payoff of each participant are negatively correlated.

With (m = - .024, p = .033) the negative correlation between pupil baseline and payoff was significant. Such negative correlation may reflect the negative correlation of LC tonic activity and performance. The changes in pupil baseline and payoff throughout the task in three participants, each from one of the payoff categories, are shown in Figures 3, 4, and 5. The correlation between pupil baseline and payoff was not significantly different between the three payoff categories (F(2, 33) = .38, p = .68).

Finally, the relationship between pupil baseline and response time for each participant was determined. First the response time of each trial was normalized for each participant, and then compared to the normalized pupil baseline. A sign test was performed to test the hypothesis that the pupil baseline and response time of the participants are positively correlated. With (m = .038, p = .12) such positive correlation almost reached significance. Results of the sign test for the correlation of pupil baseline with pupil dilation, response time and payoff are shown in Table 4. Though not significant, the results reflect the larger response time associated with LC tonic activity. Moreover, regression analysis revealed that the correlation between response time and pupil baseline is not significantly different between the three payoff category (F(2, 33) = .26, p = .77).

Discussion

This study was designed to examine the applicability of Adaptive Gain Theory in linking the variations in pupil dilation patterns to cognitive processing and task utility in a list lexical decision task. In this study, different payoff schemes were used to assess participants' patterns of coping with the negative or positive feedback and the strategies used to gain optimal results. As expected the participants in the Accuracy Payoff category had a higher Accuracy percentage (92%) than the Balance (87%) and Speed Payoff (88%) categories. This result is most likely due to the very large penalty set for inaccurate responses in the Accuracy Payoff scheme. Also, as predicted, the participants in the Speed Payoff category on average had lower response times and higher average payoff than the participants in the other two payoff categories. These results confirm that through creation of three different payoff schemes we were able to successfully change the participant's performance optimization strategies through either focusing on accuracy of responses, like the participants in the Accuracy Payoff, or decreasing response time, like the participants in the Speed Payoff category.

Throughout the study, a strong link between different pupil dilation patterns and task optimization strategies for each participant was observed. The significant negative correlation between pupil dilations and pupil baseline reflects presence of LC phasic and tonic modes throughout the task for each participant. As predicted, in most participants large pupil dilation accompanied by low pupil baseline and small pupil dilation accompanied by higher pupil baseline alternate throughout the task. This is evident of goal driven alternation between LC phasic and LC tonic activity for each participant. Since each participant showed a unique pattern of pupil dilation, it was not possible to make a general claim about the order of such LC phasic and LC tonic modes throughout the task. However, in most participants there was a decrease in pupil baseline in the last quarter of the experiment, which can be evident of less LC tonic activity. Thus, close to the end of the task, most participants appear to have found the best strategy to optimize their performance on the task and refrain from exploring other options (less LC tonic activity). On the other hand, in most participants there is also a decrease in payoff in the last quarter of the experiment. This could show that decrease in participant's pupil baseline and payoff may be caused by lack of task engagement and lack of motivation to engage in exploratory and exploitative behaviors to optimize one's performance.

Comparison of the correlation between pupil dilation and pupil baseline between the three payoff categories, showed an almost significant difference between these categories. As expected, such negative correlation was much stronger in the Accuracy Payoff compared to Balance and Speed Payoff categories. This provides support for the prediction that there will be more LC phasic mode of activity in the Accuracy Payoff category. Due to the high penalty for inaccurate responses (a higher potential cost of wrong choosing the wrong strategy), participants in the Accuracy Payoff maybe less inclined to engage in exploratory behavior, compared to participants in the Speed Payoff category. On the other hand, the smaller correlation between pupil baseline and pupil dilation in the Speed Payoff category supports the prediction that there will be more LC tonic mode of activity in participants in this payoff category. Lower potential cost with choosing the wrong strategy will make the participants in this category to be more inclined to engage in exploratory behavior when the gain of the current strategy is low.

The pupil dilation patterns between the three payoff categories on a local level, after fixation on nonword or word stimuli, supports the aforementioned findings. The near complete lack of pupil dilation after fixation on high and low frequency words in the Speed Payoff category maybe linked to lack of focus and engagement on the smaller components of each trial and a manifestation of LC tonic activity on a much smaller scale. However, the larger pupil dilation after fixation on nonword and word stimuli observed in participants in the Accuracy Payoff category is evident of larger task related pupil dilation and LC phasic activity on a local level. Moreover, the increase in pupil dilation after fixation on a nonword stimulus becomes distinct from pupil dilation after fixation on a word stimulus before 200 ms. This is consistent with the timing of stimuli triggered LC phasic response, which occurs 100 ms after presentation of stimuli. Since it takes the LC phasic impulse 60 -70 ms to reach frontal motor areas, task related pupil dilations are expected to occur after 170 ms after presentation of stimuli. Also, in most cases detection of the nonword leads to an immediate behavioral response (pressing the red button). Thus such differences in pupil dilation responses after fixation on nonword compared to word stimuli may reflect the association of LC responses and pupil dilations in initiation of motor response

The changes in payoff correlated with changes in pupil baseline provides more support for performance optimization efforts and the associated changes in pupil size patterns throughout the task. The significant negative correlation between payoff and pupil baseline supports the prediction that, in this task, LC tonic activity is associated with lower performance whereas LC phasic activity is associated with a higher performance. Moreover, the almost significant positive correlation between pupil baseline and response time, also supports the prediction that LC tonic activity is associated with larger response time and lower task performance. The correlation between pupil baseline and payoff or response time was not significant between the three payoff categories. To gain significance in such differences, we might have to make modifications to the payoff scheme.

Overall, in this study, pupil dilation patterns in response to different levels of task performance and task utility support the Adaptive Gain Theory. Alternations between the LC phasic and tonic mode are apparent throughout the task and are consistent with changes in one’s task performance, as demonstrated in payoff and response time. Moreover, LC phasic and LC tonic alterations are also apparent at a more local level, within a trial, and after fixation on word or nonword stimuli. The difference in correlation between pupil baseline and pupil dilation patterns between the three payoff categories supports the prediction of increase in LC phasic mode when the potential cost of exploration is high, and increase in LC tonic mode when the potential cost of exploration is much lower.

Limitations

One of the major limitations of the design of this experiment is difficulty in distinguishing task related pupil dilations as defined by Gilzenrat and colleagues. Gilzenrat (2010) defined pupil dilations as the maximum deviation of pupil size from the baseline at 2.5 s after presentation of stimulus. In our study the recording of pupil size stops after the button press, which occurs on average 1.57 s after start of the trial. Thus, the pupil size values are recorded for less than 2 s after the start of each trial, and the stimulus related pupil dilation, as defined by Gilzenrat et al. (2010), may occur after the start of the second trial or when the participant is presented with the feedback about his or her performance on the trial. To overcome this problem, pupil size recordings should be continued after the participant's response. When presenting the participants with the summary of their performance on the previous trial, to prevent interference of changes in lighting or reading sentences on pupil size, auditory feedback should be provided with at least a 3 s delay at the end of each trial.

One of the other limitations of this study is lack of correction for gaze position dependant changes in pupil size. Since the pupil size is determined as the number of pixel cells measured by the eyetracker, the magnitude of pupil size may change merely as a result of position of gaze on the screen (Gagl, Hawelka, and Hutzler, 2011). If present, it is important that such error be corrected in this task.

This study can be further modified by having each participant perform a random combination of all the three payoff schemes in one setting. In this way the effects of each of the payoff schemes on the variations in pupil dilations in response to different patterns of exploitative and exploratory behavior can be studied in each participant. The obtained pupil dilation patterns for each individual may be further used to understand other underlying factors that could influence task related pupil dilation patterns, such as mood, degree of sleepiness and other personal variables.

Conclusion

In this study, we demonstrated that pupil dilation patterns follow the Adaptive Gain Theory in a list lexical decision task. The three different payoff schemes successfully enforced exploitative and exploratory behaviors accompanied by different pupil dilation patterns in the participants. Further modifications of the task and future studies can be used to produce pupil dilation patterns characteristic to individual traits.

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Table 1

Quantitative Payoff Model for each Version of the Task

	Bonus for each 1 s bellow 5 s	Inaccuracy Penalty
Accuracy	+8.0	-150
Balance	+6.7	-50
Speed	+5.7	-25

Note. The payoff scheme is set up in a way that participants do not receive any points for accurate responses that occur later than 5 s after start of the trial.

Table 2

The Average Response Time (RT), Accuracy Percentage, and Payoff per Trial for the Participants in each Payoff Category

	RT (ms)	Percent Accuracy	Payoff
Accuracy	1667	92%	12.91
Balance	1548	87%	16.08
Speed	1494	88%	16.95

Table 3

The Correlation Between Pupil Baseline and Pupil Dilation Throughout the Experiment for each Participant

Accuracy	Balance	Speed
-0.55	-0.46	-0.096
-0.20	-0.62	-0.49
-0.63	-0.54	-0.13
-0.45	-0.051	-0.21
-0.43	-0.21	-0.36
-0.11	-0.24	-0.19
-0.44	-0.28	-0.16
-0.56	-0.32	-0.32
0.27	-0.52	-0.46
-0.32	-0.56	-0.069
-0.48	-0.31	-0.49
-0.54	-0.37	-0.30

Note. On average, the magnitude of the negative correlation between pupil baseline and pupil dilation was bigger for the participants in the Accuracy Payoff category (M= - 0.4136) than the Balance (M = - 0.3652) and Speed Payoff category. (M= - 0.2737)

Table 4

Sign Test performed for Correlation Between pupil baseline and Pupil Dilation, Response Time and Payoff

	s	*m*	*P*
Pupil Baseline and Pupil Dilation	1	- 0.34	< 0.001
Pupil Baseline and Payoff	12	- 0.024	0.033
Pupil Baseline and RT	22	-0.038	0.12

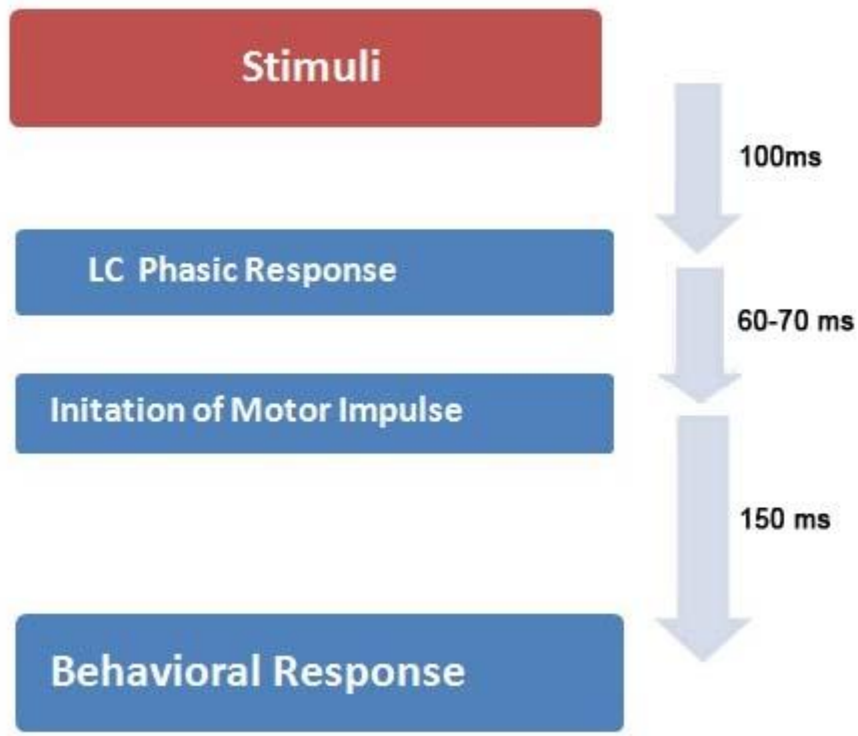


Figure 1. Sequence events occurring after stimuli presentation and prior to motor response execution.

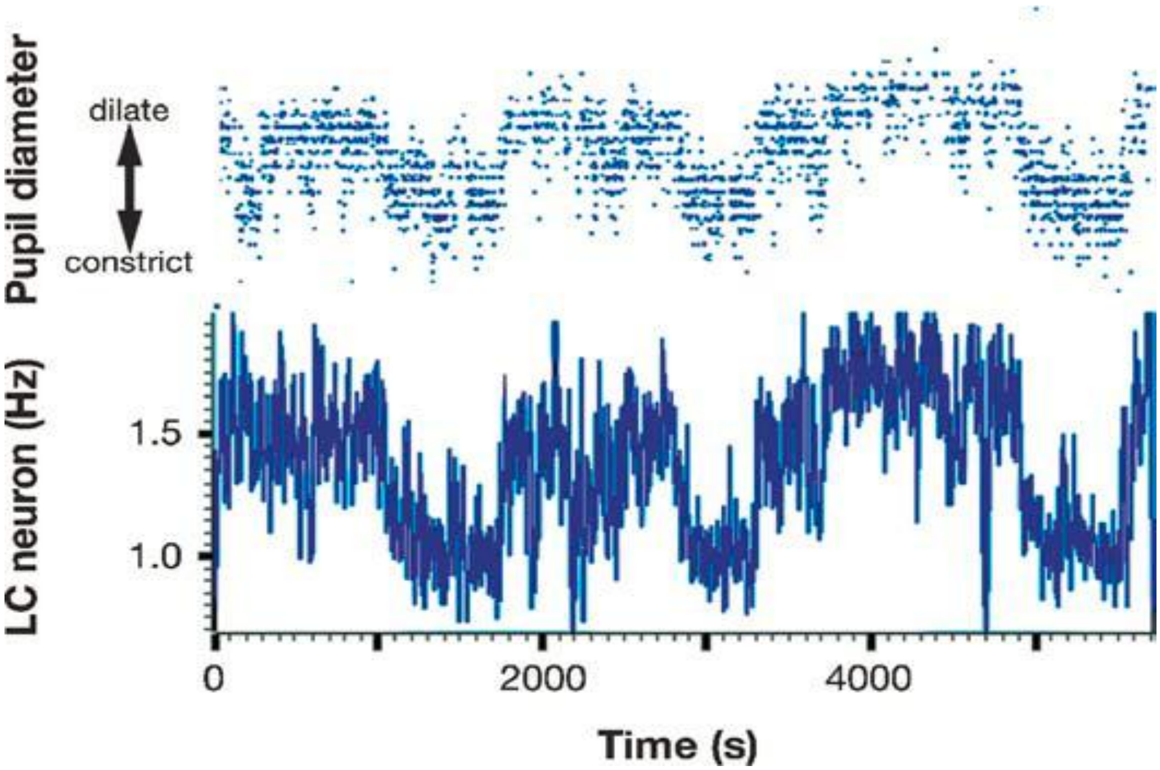


Figure 2. Relationship between tonic pupil diameter and baseline firing rate of an LC neuron in monkey.

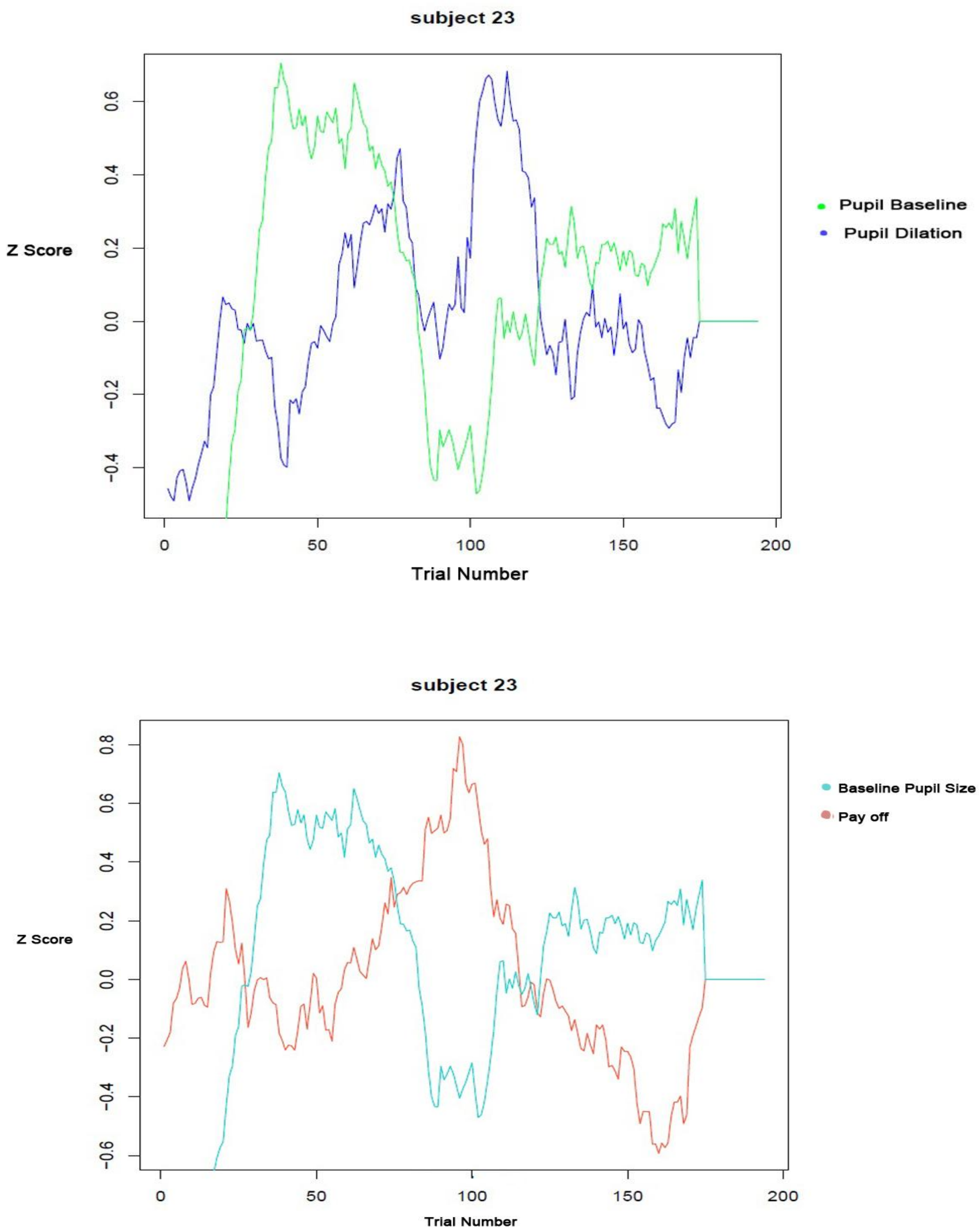


Figure 3. The running average of changes in pupil size baseline compared to pupil dilations (top) and payoff (bottom) throughout the task for participant 23, in the Accuracy Payoff category.

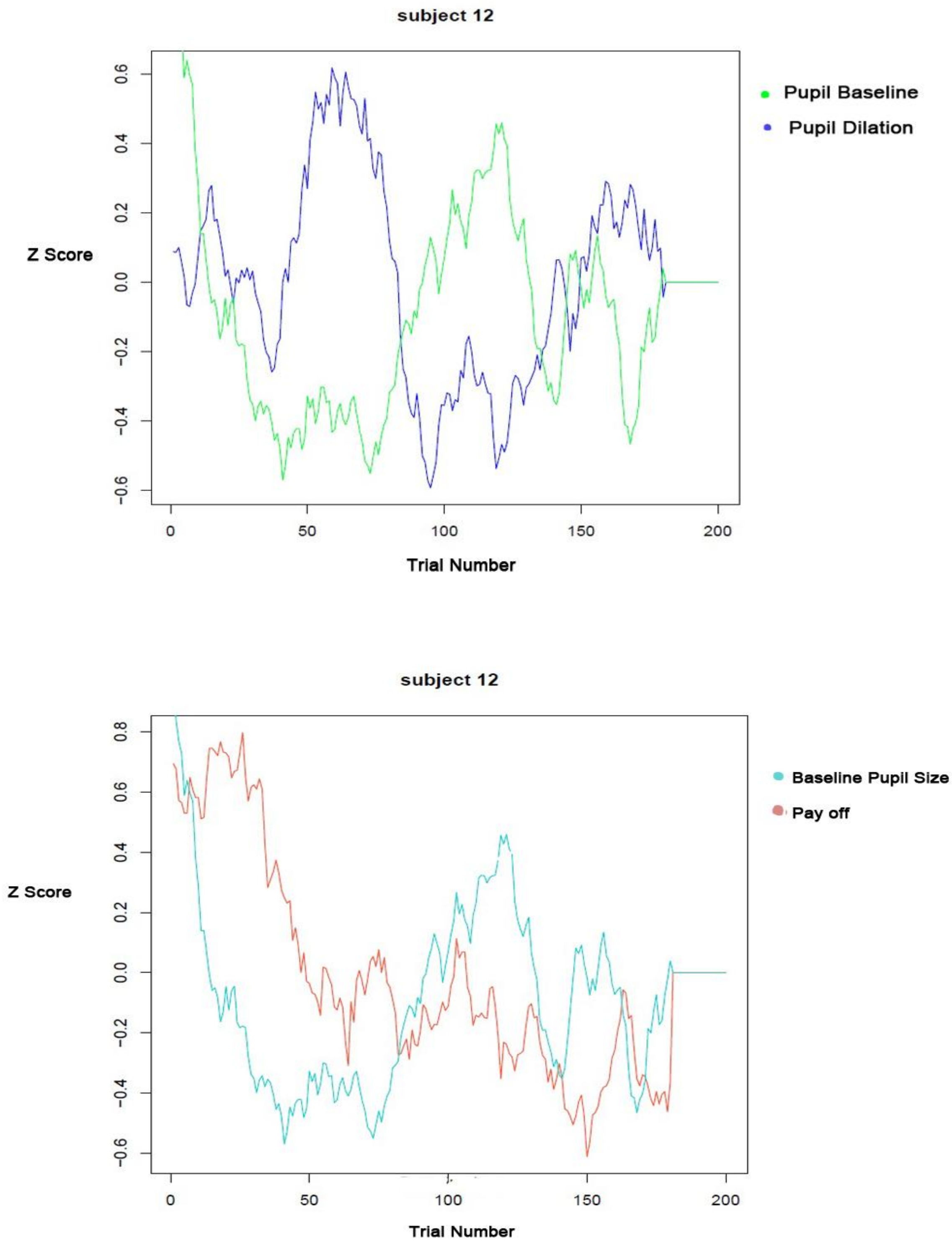
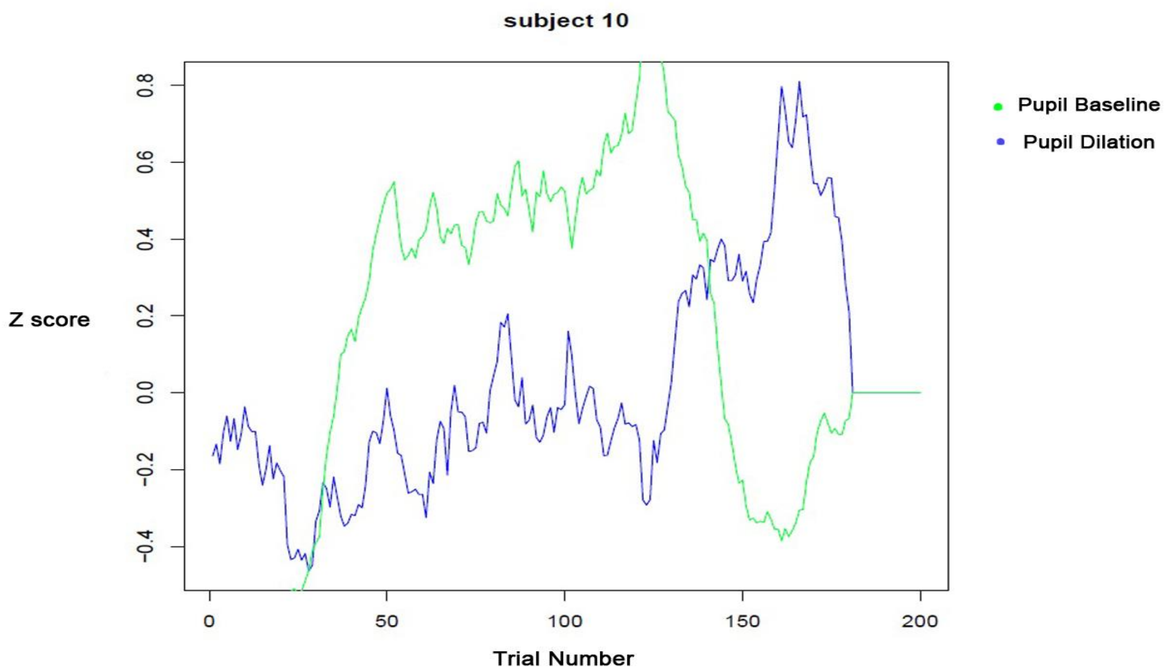


Figure 4. The running average of changes in pupil size baseline compared to pupil dilations (top) and payoff (bottom) throughout the task for participant 12, in the Balance Payoff category.



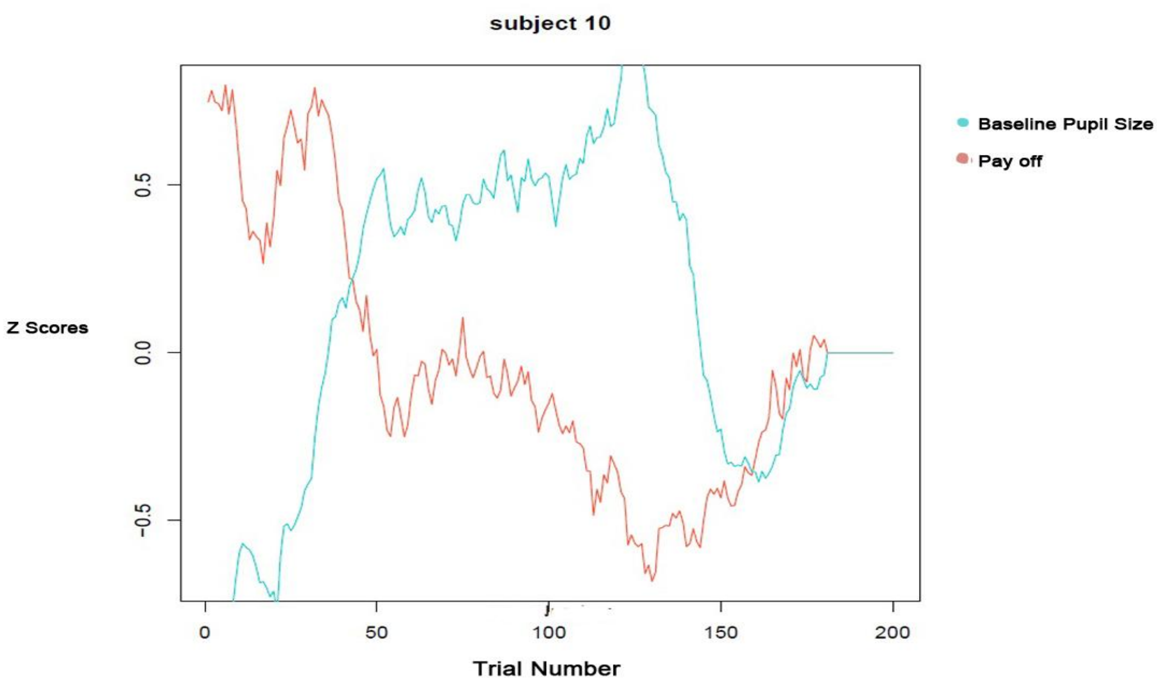


Figure 5. The running average of changes in pupil size baseline compared to pupil dilations (top) and payoff (bottom) throughout the task for participant 10, in the Speed Payoff category.

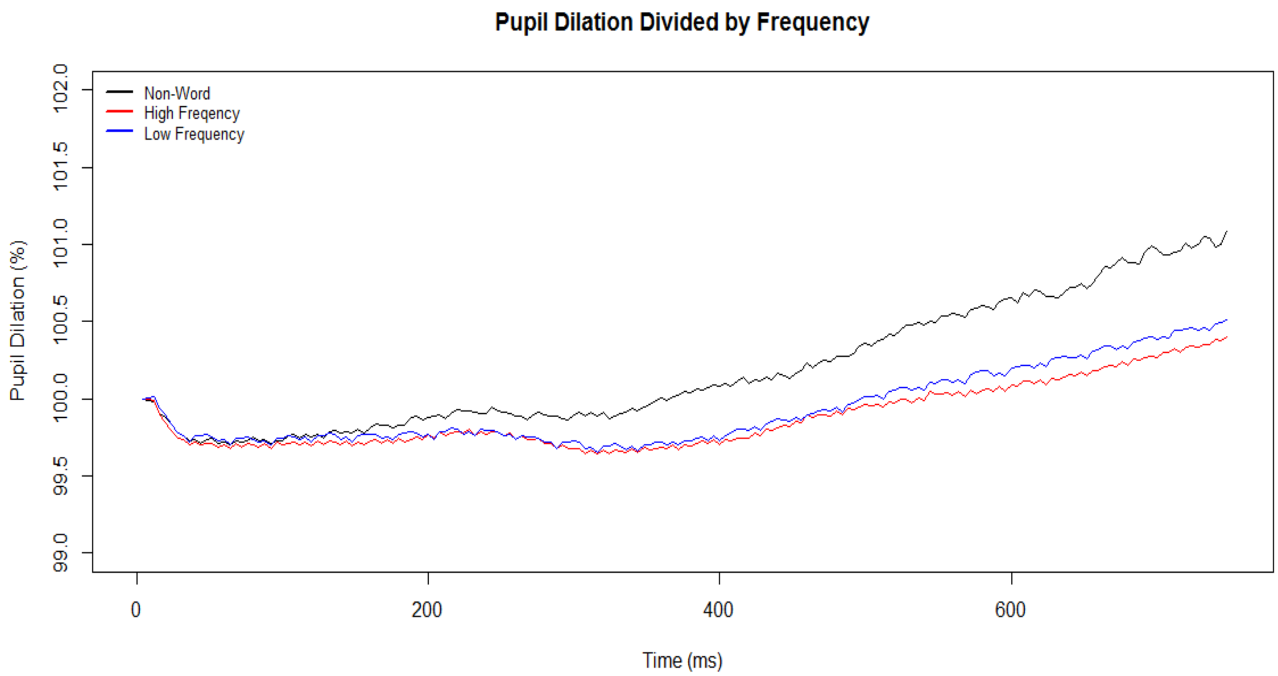


Figure 6. Changes in pupil size in the 800 ms period after fixation on nonwords, high frequency and low frequency words. The distinction between the pupil dilation after fixation on the nonword compared to the word stimuli is apparent as early as around 200 ms after fixation.

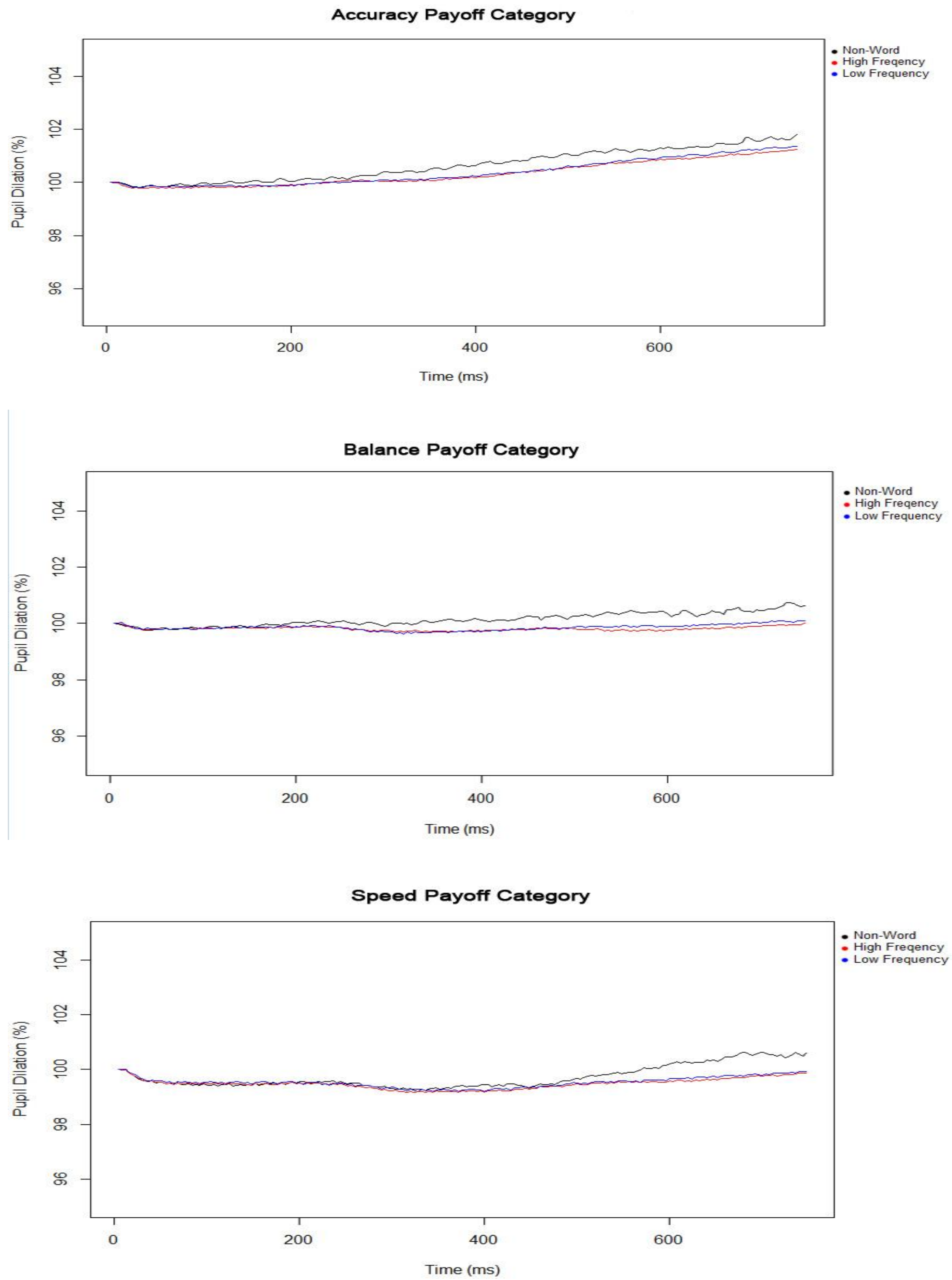


Figure 7. Changes in pupil size after fixation on the word or nonword stimuli for participants in each payoff category.