Dr hab. Eligiusz Wronka

Institute of Psychology

Jagiellonian University

JAGIELLONIAN UNIVERSITY IN KRAKÓW

Faculty of Philosophy

Institute of Psychology

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Evaluation of PhD thesis of Monika Wojtczak-Kwaśniewska entitled

"Cortical sources of vergence eye movements"

The doctoral thesis under evaluation consists of 4 parts, presented in four corresponding chapters. The first chapter is a general introduction to the topic of eye movements. In the consecutive parts of this chapter various types of eye movements are described, as well as the role of attention in its execution, behavioral and electrophysiological methods of eye movements measurement are presented, and finally short review of literature related to the problem of the neural basis of different types of eye movements is provided. The chapter ends with an overview of the research questions and of the work presented in the subsequent chapters. Chapter 2 presents the experimental study that aims at answering some of the thesis questions, i.e., how the exogenously evoked eye movements differ on a behavioral level, what is the time course of the neural activity related to the processing of the stimulus eliciting eye movement and the preparation of movement itself, and activity of which cortical areas can be related to the observed changes. In Chapter 3 similar questions were raised with regard to the endogenously controlled eye movements. The answers to these questions were sought using a similar experimental paradigm, which additionally allowed for the comparison of the results in both experiments. The final chapter, Chapter 4, presents an overview and discussion of the results presented in the previous chapters.

Chapter 1.

Chapter 1 provides a good overview of the relevant literature overall, is well written, and nicely demonstrates the importance of studying the brain's activity underlying eye movements in understanding the way we visually experience the world around us. It begins with a detailed presentation of the characteristics of various types of eye movements, including the most important for work, i.e. saccades and vergence movements. The role of the attention mechanism in the process of planning and controlling eye movements is additionally presented, which allows to understand the research problem that the experiments will concern. The two main measurement methods that have been used in the research, i.e. electrooculography (EOG) and electroencephalography (EEG), are also precisely and correctly described.

The most extensive part of Chapter 1 includes a very detailed description of the two most important EEG signal analysis techniques used in the work, which are the Event-Related Potentials and the source localization technique. The first one allows to illustrate the course of bioelectric processes taking place within the cerebral cortex with

ul. Romana Ingardena 6

30-060 Kraków

tel. +48 12 663 24 15

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ms accuracy. This technique is very popular and most often used in studies of cognitive psychology, because it enables the differentiation of individual sub-processes at different stages of information processing. However, it has also important limitation which is its poor spatial resolution. The second technique overcomes this weakness. It enables the reconstruction and localization of electric field generators in the brain structures, which are the sources of electrical changes measured on the surface of the skull as ERPs. Chapter ends with a very clear overview of recent research into the problem of the brain control of various types of eye movements.

This part of the work is a pleasure to read. Each subsequent section appears in a perfectly matched sequence. I have not found any unnecessary fragment in this chapter. At the same time, all important information necessary for understanding the research problem were included.

Chapter 2

The second chapter presents the results of the experiment aimed at determining the differences between the three types of exogenously elicited eye movements: saccades, combined convergences and combined divergences. The processes related to the participants' reactions were measured by registering the latency time of the eye movements with the use of EOG, and by recording electrical activity of the cerebral cortex using EEG. The latter method has the well-known disadvantage of low spatial resolution, which makes it difficult to infer about the potential neural sources of the activity observed on the scalp. This problem was overcome by the use of BESA, advanced technique to localize sources of neural activity. The experimental design used is ingenious and allows all relevant variables to be correctly measured. The way in which the collected data was analyzed also deserves recognition. It was carried out very thoroughly and all the details necessary to understand its course were described. All analyzes were carried out independently for the chosen time windows related to the processing of perceptual information (stimulus-locked) and the preparation of the motor reaction (response-locked). It also made possible to directly compare the activities of the brain involved in both processes. Overall, the study presented in chapter 2 is advanced, well planned and carried out. I also highly assess the way the data were analyzed and the clarity of results presentation.

However, there are also some issues that need to be clarified. The first problem concerns the validity of the choice of time windows for which the analyzes were carried out. Analysis of the response-locked activity was restricted to the time interval between -180 and -60 ms before the eye movement. The reason was to minimize the possibility that the analyzed activity can reflect eye movement execution. Therefore, the choice of the end value for the interval (-60 ms before the movement) seems justified. The big problem arises when someone looks for a justification for the start value for the interval (-180 ms before movement). If we consider the differences in latency times of specific eye movements, it can be stated that at least part of the time window cover the interval before the stimulus presentation. For example, in the case of saccades, the response-locked analysis time window starts about 40 ms before stimulus. Thus, at least part of

JAGIELLONIAN UNIVERSITY IN KRAKÓW
Faculty of Philosophy
Institute of Psychology
ul. Romana Ingardena 6
30-060 Kraków
tel. +48 12 663 24 15
www.psychologia.uj.edu.pl

the activity analyzed in this window is therefore not related to stimulus processing (it has not been presented yet) nor the preparation of the reaction to it. Quite similar problem occurs in the case of the time window for the analysis of combined-divergences. The choice of such large time windows seems to be inadequate. It seems reasonable to say that this interval could be shorter by 40 ms.

Second problem is related to the fact that analysis of the stimulus-locked activity was performed within the time window which starts 20 ms after stimulus onset and ends 120 ms later. The choice of these values was determined by the necessity to select an interval of the same length as the interval chosen for the analysis of response-locked activity. However, as it was shown above, the interval selected to perform analysis of response-locked activity is incorrectly selected if it includes time before stimulus onset. Similarly, much narrow time window seems to be more appropriate when we want to analyze stimulus processing related activity. As it was presented in the thesis (page 33), the first stage of the stimulus processing is visible as C1 component in the ERPs approximately 80 ms after stimulus onset. Therefore, shortening the interval by initial 40 ms would better reflect the real activity related to the visual stimulus analysis.

Another point that is unclear to me concerns the analysis of behavioral data. The results of ANOVA comparing the latency times of different types of eye movements are presented on page 65. This section is clear for me. The saccades were performed as fastest, the longest latency times were observed for combined convergences and intermediate latencies were recorded for combined divergences. However, on the next page one can find the results of the correlation analysis that are not fully explained. It can only be guessed that this analysis was performed to determine the correlation coefficient between the latency time of eye movement and the level of activity within a specific regions of the cerebral cortex (RS1, RS2 and RS3) selected on the basis of the analysis of neural sources of activity related to the execution of eye movement (BESA). If this is the case, it is worth noting that the only correlation coefficients indicating significant relationship were obtained for the interval of -100 to -60 ms before eye movement. Thus again, it seems that time window chosen to analyze response-locked activity is probably too wide.

Another issue is closely related to all of the aforementioned problems, and also applies to the question how the cortical sources related to the execution of eye movement were determined. My experience in determining the sources of cortical activity with BESA software is limited. However, as I understand it, this method allows to determine the localization of potential activity generators that best explain the actual course of the analyzed ERP. In this case, the ERP waveform recorded in the interval -180 to -60 ms before the eye movement was analyzed and three different cortical sources (RS1 – the anterior frontal area, RS2 – the occipital cortex, RS3 – the FEF) were chosen as best fitted to the model. Thus, these three cortical sources tell us where to locate the cortical area responsible for the course of the analyzed ERP segment. So, if the time window for the analysis has been chosen incorrectly (because it also includes the ERP recorded even before the stimulus onset), then the sentence that can be found on page 67 is unfounded. This sentence is as follows: *”source analyses revealed that the following cortical areas are strongly related to the execution of the different eye movement types:*

JAGIELLONIAN
UNIVERSITY
IN KRAKÓW

Faculty of Philosophy

Institute of Psychology

ul. Romana Ingardena 6

30-060 Kraków

tel. +48 12 663 24 15

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(RS1) an anterior frontal area, (RS2) the occipital cortex, and (RS3) the FEF". I have doubts whether the activity within the selected cortical sources are really strongly related to the execution of eye movement. In my opinion, this activity can be closely related to the ERP recorded in the selected time window for sure. And that's it. However, if the time window was incorrectly selected, and this is probably the case, then we cannot say that it reflects movement execution. It is rather related to some mixture of neural processes, some occurring before the stimulus presentation, some linked to its processing, and only in part it is activity connected with movement planning or execution. This remark applies to a varying degree to all three time intervals selected for analysis for the three different eye movements. In the case of saccades with the shortest latency times, the analyzed time window covers the activity before the stimulus onset to the greatest extent. This is least true for the time window selected for the analysis of combined convergences.

It should be also noted that two different intervals selected for the analysis, one chosen as response-locked time window and other defined as stimulus-locked time window could also overlap each other, and this overlap differ between three tested types of eye movement. The overlap is most evident in the case of combined convergences, for which average latency time was about 178 ms. The time window chosen for analysis of response-locked activity starts approximately at the moment of stimulus onset and ends 120 ms later, while the stimulus-locked interval was established between 20-140 ms after stimulus onset. These two time windows cover almost identical intervals. Therefore, nearly similar neural activities were compared. It is not surprising that "*for combined convergences no differences between the stimulus- and response-locked activities were observed"* (page 78). On the other hand, the overlap was the least noticeable in case of saccades, for which average latency time was about 135 ms. Thus, if the stimulus-locked interval was chosen between 20-140 ms, then its included both stimulus processing activity as well as activity related to motor response execution. In contrast to this, response-locked interval starts about 40 ms before and ends 80 ms after stimulus onset, covering some prestimulus activity and only some early stages of its processing. This explain why significant differences between response- and stimulus-locked activities were obtained for the occipital cortex and the FEF for saccades - "*especially within RS2 concerning a time interval of about 100 ms after stimulus onset"* (page 79). It cannot be surprising that this is a time window of P1 component of visual ERPs.

The scientific speculative considerations made above do not detract from the overall high level of research. It is a very well planned and conducted experiment. Appropriately selected methods of measuring brain activity were used. The analysis of the collected data is advanced and precise.

Chapter 3

The experiment presented in Chapter 3 was aimed to identify the differences in brain activity associated with the same three types of eye movements which were previously studied in experiment reported in chapter 2: saccades, combined convergences and

ul. Romana Ingardena 6
30-060 Kraków
tel. +48 12 663 24 15
www.psychologia.uj.edu.pl

combined divergences. In this case, however, eye movements were induced endogenously, which means that participant voluntary directed his gaze towards the stimulus indicated by the instruction (different in various blocks) and the cue (color of the central LED). Methods used for participants' reactions measurement were the same as well the methods of data analysis. Eye movements were registered using EOG and brain activity was recorded by the use of EEG. And again, BESA was utilized to localize sources of neural activity. All the advantages of the earlier study are also visible in the case of this experiment. Experimental design is simple and elegant, but simultaneously allows to measure all relevant variables. Description of the experiment is clear and detailed. All analyzes were carried out thoroughly. Results were presented very clearly.

And again, analyses were performed independently for the selected time windows related to the processing of perceptual information (stimulus-locked) and the preparation of the motor reaction (response-locked). The comparison of both processes has also been made.

Unfortunately, the same doubts as in the case of the previous experiment appear again with regard to the method of selecting the intervals for analysis.

Analysis of the response-locked activity was restricted to the time interval between -300 and -100 ms before the eye movement. I believe that the choice of the end value for the interval (-100 ms before eye movement) was determined to avoid possibility that analyzed activity can reflect eye movement execution. However, this end value is different compared to the chosen in experiment reported in chapter 2. I did not found any information why the change was made.

Analysis of the stimulus-locked activity was performed within the time window which starts with stimulus onset and ends 200 ms later. However, such wide time window covers also period when "*no significant activity was observed*" (as it was indicated in legend for Figure 24, page 99). Again, it seems to be chosen with no specific justification.

If one take latency of eye movement into consideration then it is clear that response-locked activity was determined for almost the same interval as stimulus-locked activity. It is evident especially for the combined divergences with average latency about 300 ms. Thus, in case of this type of eye movements stimulus-locked activity was analyzed for the time window which starts with stimulus onset (and ends 200 ms later) and it is more less the start value for the window selected for response-locked activity.

Simply speaking, again, an inadequate choice of the time windows for the analysis was made. There is a high probability that the results of the analysis would be different if the time windows for both stimulus- and response-locked activities were selected differently. For example, time window for stimulus-locked activity can be selected to cover P1 and N1 components of visual ERP (80-200 ms poststimulus) and corresponding time window for response-locked activity can be defined as starting 170 ms before eye movement and ending 120 ms later.

Nevertheless, the study presented in chapter 3 is well planned and carried out. Also the way the data were analyzed as well as the clarity of results presentation need recognition.

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www.psychologia.uj.edu.pl

Chapter 4

Chapter 4 provides an overview of the work presented in the previous chapters, together with the corresponding conclusions. The chapter is well-written and easy to follow. However, it does not go much beyond a summary of the results and interpretations reported in the previous chapters.

Conclusions

My general evaluation of the doctoral thesis is positive, and I definitely recommend acceptance. The research questions are timely, interesting and highly relevant. The work brings together two fields of cognitive psychology and neuroscience in an elegant way. The candidate demonstrates good knowledge from both fields and takes advantage of these to propose a novel way of investigating an important but so far rarely studied issue. The experiments are well-designed and the most analyses appear sound.

Overall, the proposed interpretations of the results are well-presented and reasonable, although a more elaborated and more critical evaluation of all findings reported in the thesis and their theoretical implications would have been welcome in the general discussion. Finally, the doctoral thesis is well-structured and well-written, the figures and tables are useful and of high quality, and the relevant literature is cited and explained. I enjoyed reading the work and I am convinced that it will serve to advance our understanding of the relationship between brain activity and eye movement planning important in the process of visual exploration of the environment. Altogether then, this thesis demonstrates the candidate's general theoretical knowledge and the ability to conduct empirical research independently.

Stwierdzam więc, że rozprawa Pani mgr Moniki Wojtczak-Kwaśniewskiej zatytułowana "Cortical sources of vergence eye movements" spełnia warunki określone w określone w art. 187.1. ustawy z dnia 20 lipca 2018 r. (Prawo o szkolnictwie wyższym i nauce). W związku z powyższym wnioskuję o dopuszczenie Pani mgr Moniki Wojtczak-Kwaśniewskiej do dalszych etapów postępowania w przewodzie doktorskim.

Elig Wronka

Dr hab. Eligiusz Wronka

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Institute of Psychology

ul. Romana Ingardena 6

30-060 Kraków

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