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Abstract

High-density electroencephalogram (EEG) was used to investigate brain electrical activity as a functional response mechanism to visual motion stimuli in adults. Participants were healthy adults from the age 21 to 37. Motion stimuli consisted of an optic flow pattern simulating forwards and reversed self-motion, and unstructured random visual motion. Analyses of visual evoked potential (VEP) was performed. VEP results showed that N2 latencies for structured optic flow were significantly shorter for all adults, with the largest latency difference being between forward optic flow and random visual motion. The significant latency difference is attributed to the fact that structured optic flow provides more coherent and relevant visual information than random visual motion. The findings indicate that adults have a developed visual processing system that allows for faster processing of structured optic flow compared to random visual motion.

1 INTRODUCTION

Imagine travelling through space at a super high velocity while looking straight ahead (Figure 1). When examining the visual image as you “travel” through space, take note of how the stars seem to move outward in your visual field, becoming more peripheral as you approach and pass them. This is because, in your visual image, all objects appear to move radially away from an optically static point in the direction that you are heading. This type of motion pattern is called “optic flow”, and it occurs as the observer moves through his/her environment (Warren, 2008). In general, the pattern of light reflected from objects in the world to the point of observation undergoes a continuous perspective transformation, resulting in these global motion patterns.



Figure 1. Impression of the optical motion by an observer travelling through space at a high velocity without rotating their eyes, head, or body. Adapted from “Space Travel Through Stars Trails. Hyper Jump Into Another Galaxy” [animation], by Cherayut000, 2023, Pond5 (<https://www.pond5.com/stock-footage/item/134450160-space-travel-through-stars-trails-hyper-jump-another-galaxy>).

This phenomenon is known as optic flow, referring to the motion pattern generated at an eye that is moving relative to the environment (Warren, 2008). The optic flow pattern provides data about the three-dimensional (3D) layout of the surroundings and the relative motion between the observer and their environment. In a static environment, the observer can utilize the optic flow pattern to guide their self-motion or heading (Gibson et al., 1955). When we fixate our gaze on an object of interest and move forward, we need to track that object to keep it in view. However, the eye movement used to track that object can disrupt the optic flow generated by other objects in the background. These objects provide information about our direction of motion and enable us to navigate effectively (Forrester et al., 2016). Optic flow is crucial on several functions for behaving observers. For instance, effective navigation in the real world as it conveys important information about how objects are moving relative to the observer and their speeds (Vilhelmsen et al., 2019), balance and posture control (Stoffregen, 1985) and avoiding or achieving collisions (Fajen, 2008). The perception of object shape and environmental layout is also significantly influenced by optic flow (Koenderink, 1986). As we develop and gain an understanding of the optic flow in our environment, we can begin to perceive and use this to our advantage. Prospective control is the term used to describe the ability to perceive the visual environment and use that information, along with cognitive processes, to guide actions towards a desired destination in the near future (Van der Meer & van der Weel, 2019). Successful navigation requires the integration of perceptual information, cognitive processing, and motor execution to achieve effective results. A practical example of successful navigation could be a driver in traffic. The driver uses visual information about upcoming road conditions and adjusts their speed and steering accordingly. If an object such as an animal were to suddenly appear on the road, they might have to make a sharp turn to avoid collision. This study focuses on the visual movement perception as an important element in prospective control.

Over the years, there has been a significant focus on utilizing non-invasive electroencephalogram (EEG) during motion perception and analyse the specific functions of cortical structures (Berg & Scherg, 1991; Sakkalis et al., 2008). The recording techniques of EEG and functional magnetic resonance imaging (fMRI) offer complementary advantages in terms of the temporal and spatial resolution of brain activity, respectively (Debener et al., 2006). Morrone et al. (2000) used fMRI to demonstrate how areas in the human cortex respond selectively to components of optic flow like radial and circular motion. Their findings revealed that the area commonly known as the V5/MT complex region, demonstrated a selective response to these components. However, the region responding to optic flow is separate from the part that responds to translation. A physiological study have indicated that in humans, the hMT/V5+ area of the brain contains neurons that are mainly specialized in processing radial motion through the dorsal visual pathway (Duffy & Wurtz, 1991).

To investigate the responses to visual motion and optic flow, EEG is a useful non-invasive technique which provides precise temporal information and can be used in conjunction with other physiological methods. The N2 component, which is a known component sensitive to motion, has been primarily observed in occipital and parietal regions and dominates the waveform activity of EEG in response to visual motion. The occipital and parietal brain regions are cortical areas involved in the dorsalstream. Visual motion perception is a function of the dorsalstream (Pitzalis et al., 2012; Probst et al., 1993).

The use of visual-evoked potentials (VEPs) has been widely used in investigating the processing of motion and integrity of the visual system (Pitzalis et al., 2012). EEG studies measuring VEPs found the N2 component to be generated at approximately 130-150ms after stimulus onset in adults (Kremláček et al., 2004). This negativity (N2) is suggested to have its origin in the MT+ area of the human brain (Probst et al., 1993). The fact that transcranial magnetic stimulation (TMS) applied over MT+ at 130-150ms after the motion stimulus

impairs motion perception provides evidence for support (Sack et al., 2006). Numerous studies on optic flow have been carried out to explore the neurological foundation of visual motion perception and examine the brain regions engaged in this process. The V5/MT and MST regions have been recognized as particularly sensitive to optic flow (Holliday & Meese, 2005; Morrone et al., 2000; Smith et al., 2006). The N2 component is linked to various cognitive processes, such as attention, object recognition and categorization. It is a negative deflection in the ERP waveform that typically occurs around 225-250ms (Folstein & Van Petten, 2008). In adults, a recent study demonstrated that in response to higher driving speeds, N2 latencies were longer, and amplitudes were lower compared to lower driving speeds (Vilhelmsen et al., 2015). This study, however, did not account for changes in optic flow direction.

A high-density EEG study demonstrated how infants' and adults' brains respond to structured forward optic flow and random visual motion (van der Meer et al., 2008). The researchers observed that infants appeared to process information at a slower pace than adults, demonstrated by higher N2 latencies. This is thought to reflect the general slower information processing in infants, because of lesser degree of neuronal myelination of white matter tracts compared to adults. However, both groups had shorter N2 latencies for structured optic flow as opposed to random motion, which suggested that structured motion reflects a higher importance for both infants and adults (van der Meer et al., 2008). Using a similar optic flow stimuli, Agyei et al. (2015) discovered that 12-month-old infants exhibited shorter latencies for forward optic flow in comparison to reversed and random motion.

This study aimed to utilize EEG to investigate the brain electrical activity as a function of perception of structured optic flow and random visual motion. Based on previous research on EEG and optic flow the hypothesis for this thesis is that structured optic flow stimuli produce shorter latencies compared to random motion stimuli, and specifically, forward optic flow

results in shorter latencies compared to reversed optic flow, due to our greater exposure to structured optic flow and forward motion in everyday environments. By gaining insight into how the brain responds to real-world plausible stimulus moving at different speeds, we could learn more about how our brain handles real life events and speed fluctuations.

2 METHOD

2.1 Participants

A total of 10 healthy adult participants took part of the study. Most of the participants were recruited from Dragvoll University campus at the Norwegian University of Science and Technology (NTNU) and were mostly students. All participants had normal or corrected-to-normal eyesight. Mean ages for the participants were 28 ($SD = 5.9$, range 21-37). The high-density (HD-) EEG is non-invasive with no known harmful repercussions. All the participants gave their informed consent and were given the opportunity to withdraw at any point in time during the study without any adverse consequences. This study was approved by the Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences.

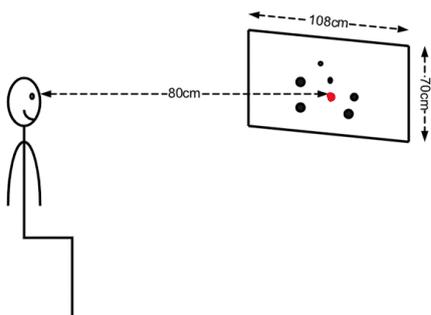


Figure 1. *Optic flow pattern with intent to emulate self-movement in space. The subject is sitting in a chair looking at the fixation point in the middle of the screen.*

2.2 Experimental stimuli and paradigm

The experimental paradigm was generated by E-Prime software (Psychological Software Tools, Inc.) and projected onto a Microsoft Surface Hub 84'' (1.08m x 0.705m) through an Athen Masterview CS1782 DVI-KVMP switch, with a refresh rate of 60 Hz. Participants were placed so the distance between the eyes of the subject and screen is 80.0cm. The software generated an optic flow pattern with intent to emulate an impression of self-movement in space. The pattern is rectilinear and consists of a constant number of 100 black dots on a white background with constant speed (30 mm per frame with a rate of 60 fps) across motion conditions. The virtual radius of one dot is 5 mm, meaning that they appear small when they are far away from the eye, and large when they are near the eye. Subjects were also instructed to look at a fixation point in the shape of a red dot in the centre of the screen (see Figure 1).

The number of black dots remains the same. The experiment consists of four conditions, e.g., four variations in the stimulus, where one condition constitutes one 1500ms-lasting trial. One is forwards optic flow, where 100 black dots appear to move towards the subject with a constant velocity simulating an impression moving through the dots in a forward motion. As mentioned in the introduction, an analogy for this condition is to imagine travelling through space with high velocity. The stars seem to spawn in the far distance in front of you, and move towards you, before disappearing. Another condition is the reversed optic flow. This condition is similar to the forwards flow, but the dots move in the opposite direction, e.g., appearing closer the perceiver, and moving towards the horizon with constant velocity. The same analogy applies, but this time you look behind you, giving the perception of moving backwards through space. The third condition is the random non-flow; dots moving with the same constant speed through space like the prementioned conditions, but the direction of the dots is random. This leads to the subject not getting the impression of self-movement. The fourth condition is the static non-flow. In this condition the dots are the same as in the other

conditions, but in this case, they stay in the same position for the duration of the trial. This is used as a baseline condition in the analysis of the EEG-data and also used to avoid motion adaptation. The motion conditions are presented randomly throughout the experiment, and the static non-flow trial is in between all the other conditions in the sequence of trials.

2.3 Data acquisition

EEG activity was recorded through Electrical Geodesics Inc. (EGI) sensor net 200 (Tucker, 1993) consisting of an array of 256 Ag/AgCl sponge sensors. The net was evenly distributed across the scalp of the participants. A high-input EEG amplifier connected to the net allowed for amplification of signals at maximum impedance of 50 k Ω as recommended for an optimal signal-to-noise ratio (Ferree et al., 2001). A Macintosh computer used a NetStation software to record amplified EEG signals at a sampling rate of 500 Hz (200 Hz low-pass and 0.1 Hz high pass online filters). The gaze of the participants was monitored using an infrared Tobii X50 camera to keep track whether they were looking straight ahead at the screen during the experiment. Behaviour was monitored throughout the experiment using two digital cameras for all participants.

2.4 Procedure

The experiment took place at the Developmental Neuroscience Laboratory (Nu-Lab) at the Department of Psychology at the Norwegian University of Science and Technology (NTNU) in Trondheim, Norway. Participants arrived some time before the experiment and were seated

in the waiting room to receive explanations and instructions about the procedure, and afterwards asked to sign the consent form. Participants heads were measured to select an appropriate net. Measurement tape and markers were used to pinpoint the centre of the subject's head. This is to help with the alignment of the net. The net was soaked in a saline solution to provide good impedance. After the net had soaked for a few minutes, it was slightly dried with a towel and carefully fitted on the head of the participant. Electrodes were carefully "massaged" towards the scalp of the participant to create good impedance. Participants were guided into the experimental room and instructed to remain seated in the chair in front of the screen. The net was connected to the amplifier and impedance was checked. If the impedance was unsatisfactory, extra saline solution could be added, together with adjustment of the relevant electrodes. Three students were controlling the computers in the adjoining room, separated from the experimental room by a soundproof window. All stimulus conditions had a number of 40 trials each, with the exception of the static condition that appeared between all the other conditions, with a total of 120 trials in a successful and completely performed test. The experiment lasted about 6 minutes and 40 seconds. As the experiment was finished, participants were guided to the fitting room and the net was carefully removed. The net was then washed and soaked in an alcoholic solution before being rinsed and dried.

2.5 Analyses

2.5.1 Data analyses

The EEG raw data were segmented using Net Station Tools software and exported to another server for offline analysis with Brain Electrical Source Analysis (BESA, GmbH) 7.0 research

software. Averaging epochs were set from -200 ms to 800 ms with a baseline definition set at -100 to 0 ms. Notch filter was set at 50 Hz to remove line interference, and low cutoff filter was set at 1.6 Hz in order to remove slow drift in the data. High cutoff filter was set at 60 Hz to remove channels contaminated with high-frequency activities. Channels and epochs that were contaminated with artifacts due to movements of the head and arms and eye activity were either removed from further analysis or repaired using spherical spline interpolation (Perrin et al., 1989; Picton et al., 2000). A manual artifact correction procedure was carried out using spatial filters with threshold values of 0.1 μV for low signals and 75 μV for gradients to separate brain activity from eye movement artifacts (Berg & Scherg, 1994; Ille et al., 2002). Maximum amplitude for all participants was set at 120 μV . Bad channels were excluded, with a limit of 10% per participant. If more than 10% channels were bad or less than 50% accepted trials after scanning, the participant would be excluded from further analysis.

2.5.2 Peak analyses at the electrode level

To investigate responses of visually evoked potentials (VEP), the electrode level was analysed through peak analysis. EEG data was referenced to an artificial reference calculated from scalp-averaged potentials and exported to the standardized 81-electrode configuration of the 10-10 International system. To obtain individual averages, reference-free (10-10) montage was established using spherical line interpolation (Perrin et al., 1989). The individual averages were then computed and analysed for all participants, before being combined into a grand average to serve as a reference while selecting individual N2 components. Using 3D spherical spline whole-head voltage maps, N2 components of individual averages over posterior areas were selected by identifying maximum N2 activity for the most dominant waveform (Perrin et

al., 1989). Peak latency was then measured from stimulus onset to the peak of each scalp N2 component.

3 RESULTS

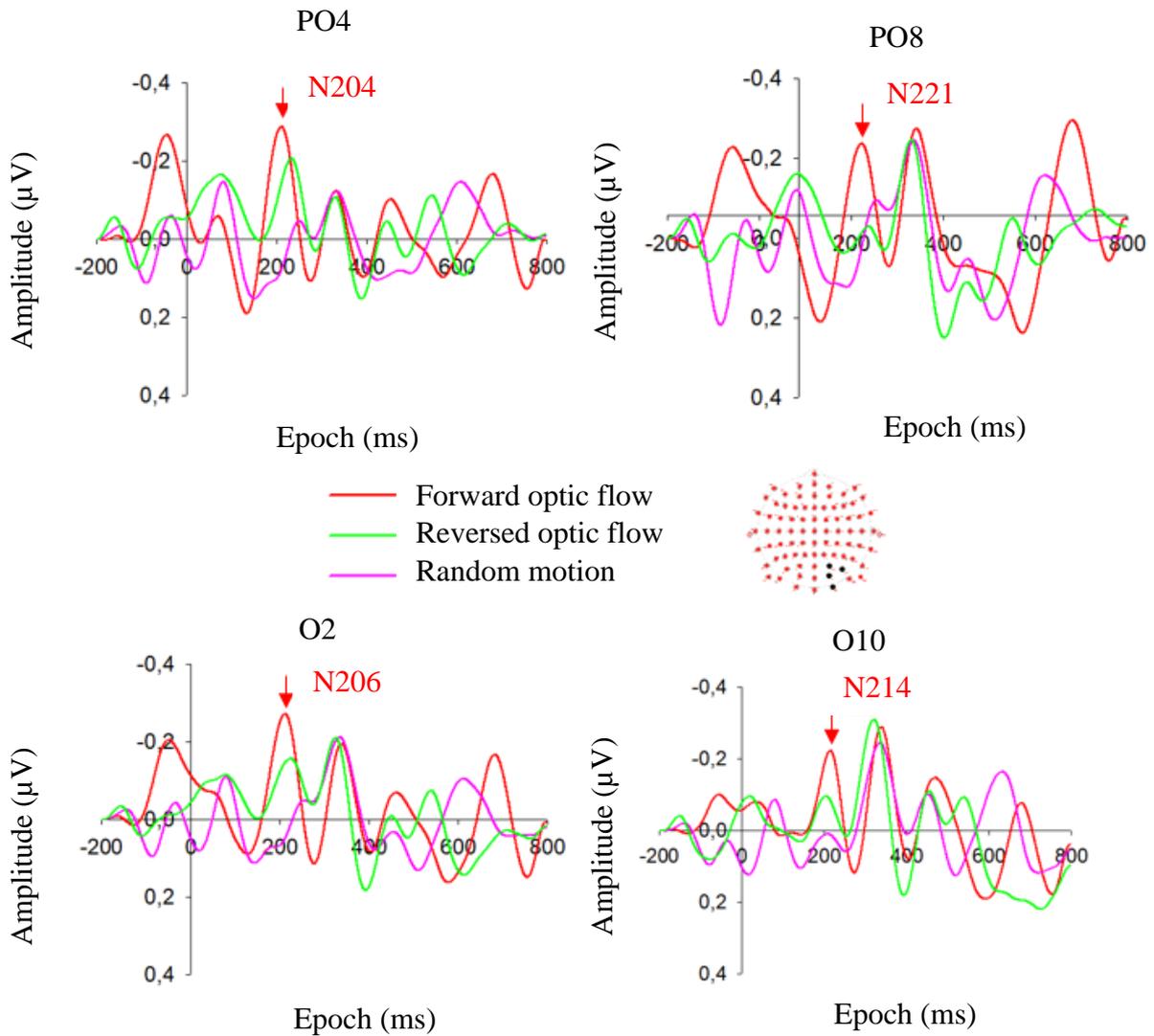


Figure 1: Grand average waveforms in adults. Epoch is from -200 to 800ms (x-axis), and y-axis shows amplitude (μV). The N2 peak for forward optic flow is marked for all electrodes (red arrows). Scalp localization of the electrodes (PO4, PO8, O2 and O10) is indicated with black circles on the head drawing (nose up).

3.1 VEP responses

After averaging the VEP responses to all ten participants, a grand average procedure was performed in BESA. Based on the grand-averaged waveforms a total of four electrodes were selected for each of the participants. The four electrodes were chosen based on their high mean activation values in the forwards optic flow condition of the VEPs grand average. Peak amplitude and peak latency were recorded and further analysed. The chosen electrodes were PO4, PO8, O10 and O2 (see figure 1).

Among the four electrodes that were selected, the electrode exhibiting the highest amplitude value in the forwards optic flow condition for each participant was specifically utilized in the ANOVAs. As shown in figure 2, N2 mean peak latencies (ms) for the participants after stimulus onset for forwards optic flow, reversed optic flow, and random visual motion were 222ms (SD = 31), 265ms (SD = 40) and 325ms (SD = 47), respectively. Mean N2 peak amplitudes for participants were $-0.11 \mu\text{V}$ (SD = 0.55) for forwards optic flow, $-0.01 \mu\text{V}$ (SD = 0.59) for reversed optic flow, and $0.16 \mu\text{V}$ (SD = 0.61) for random visual motion.

Repeated measure analysis of variance (ANOVA) was used to separately test for differences in N2 peak latencies and amplitudes. The adult participants were between subject factor and stimulus (optic flow, random visual motion) within subject factor. Bonferroni correction was used to adjust for multiple comparisons. Two separate tests were performed for amplitude and latencies.

For N2 peak latency, the results showed a significant effect between the stimulus in adult participants, $F(1,9) = 41.78$, $p < 0.01$, indicating that there is a significant difference in N2 peak latency between structured optic flow and random visual motion. Pairwise comparisons revealed a mean latency difference between structured optic flow and random visual motion of 103ms, $p < .01$, indicating that there is a large difference in how quickly the brain responds to structured optic flow compared to random visual motion.

For N2 peak amplitude, a small non-significant effect of amplitude between the stimulus in the adult participants was found $F(1,9) = 0.49, p = .623$. This is a pattern that may indicate some noise across the amplitude among the participants, but also reflect some of the challenges within ERP research such as variability in ERP-responses, lack of expertise in data analysis and interpretation of results (Woodman, 2010).

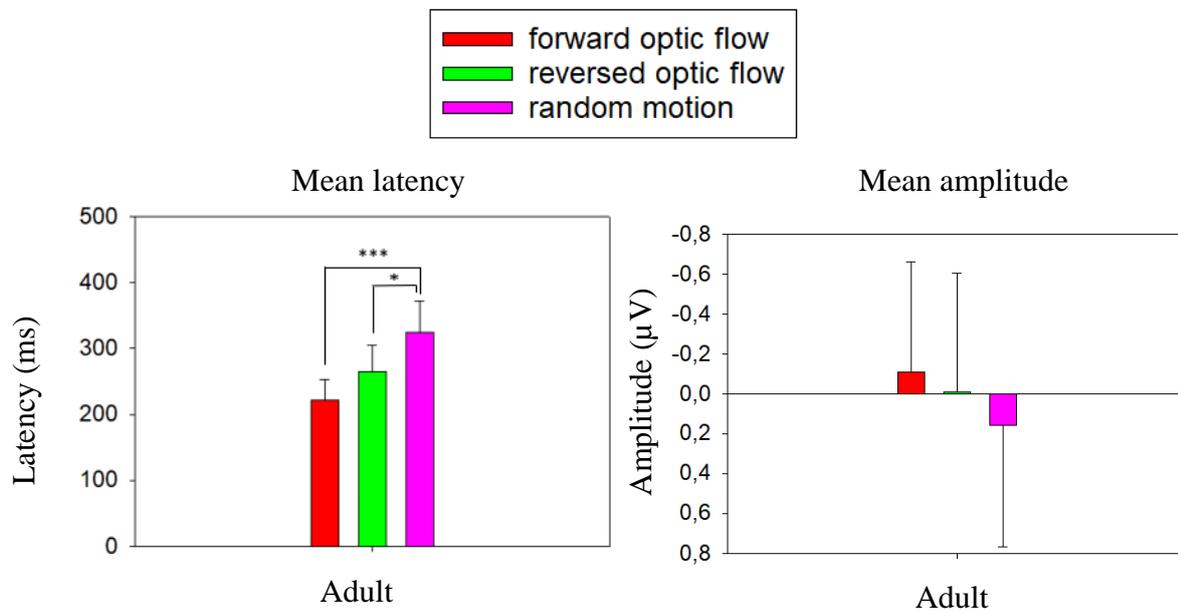


Figure 2: Group mean latencies and amplitudes (with SEs) for forward optic flow, reversed optic flow and random visual motion for adults. * Significant at the $p < 0.05$ level, *** significant at the $p < 0.001$ level.

4 DISCUSSION

In this study, EEG was used in adult participants to study brain electrical activity as a function of perception of structured optic flow and random visual motion. It was investigated whether there were any differences in brain activity related to the two types of motion stimuli using VEP analyses.

In this study, significant differences were observed between latencies regarding structured optic flow compared with random visual motion in the adult participants. Participants showed a faster N2 component latency for forwards optic flow, and a slower response to reversed optic flow and random visual motion respectively. The largest latency difference was found between forward optic flow and random visual motion. These results consistent with previous research on N2 motion components, where latencies are found to be generated around the 130-150ms mark (Kremláček et al., 2004), with N2 peaks around 225-250ms (Folstein & Van Petten, 2008).

The differences in latency between the structured optic flow and random visual motion can be thought to reflect the fact that the structured optic flow provides more predictable and coherent visual information compared to random visual motion (van der Meer et al., 2008). Hence, random visual motion may require additional processing time to extract important information, and as a result the N2 peak latency may appear at a later interval/time.

Structured optic flow also provides cues on the direction and speed of objects in the environment, which can be rapidly processed and used by the visual system to guide our behaviour. Random visual motion, however, does not provide the same informative cues which makes it more difficult to detect coherence in the optic flow (van der Meer et al., 2008).

The latency difference between forward and reversed optic flow, where the N2 component of reversed optic flow appears around 40ms later than forward is thought to reflect the fact that most of everyday optic flow comes from the individual moving forwards. Occasionally we move backwards, or we can perceive reversed optic flow when looking in the rear mirror in a driving car. This gives us some form of experience in the different visual inputs. Random visual motion, on the other hand, is not something we experience through our everyday normal visual input. This could be one explaining factor as to why the N2 component for random visual motion appears later than structured optic flow.

Another argument that strengthens the hypothesis is when we compare the same EEG experiment done on infants as on adults. Infants had a significant slower response (about 60ms) in optic flow VEP, and longer latencies than adults for the N2 in random visual motion VEPs (van der Meer et al., 2008). These findings are interpreted to reflect the slower level of information processing in infants. White matter changes and myelination are known to be associated with learning and experience in people, and is a process that continues for decades (Fields, 2008).

The development of motion processing may be constrained by slow transmission through an incompletely myelinated system, since detecting motion relies on comparing the time-of-arrival of rapidly changing visual signals from different locations (Braddick et al., 2003). The slower information transmission in infants can come as a result of the absence myelination of the visual pathway (Braddick et al., 2005).

Infants who are given the opportunity to engage in self-generated actions, such as reaching and grasping, appear to show faster development of their sensorimotor systems than infants who are not given the same means/environment. Sensory feedback created by self-generated actions is essential for the development of the sensorimotor maps in the brain (James & Swain, 2011). By receiving better postural control, infants can better use optic flow to

regulate their balance instability to navigate. Studies on development have shown that infants demonstrate a significant increase in sensitivity to optic flow when they begin crawling (Anderson et al., 2001).

Rasulo et al. (2021) included prelocomotor infants at 4-5 months, crawling infants at 9-11 months, primary school children at 6 years, adolescents at 12 years, and young adults, in a study, using a simulated forward motion through optic flow paradigm, with three ecologically valid speeds representing walking, jogging and cycling (slow, medium and high). The VEP peak analysis showed the N2 latencies for motion decreased significantly with age, from around 400ms in prelocomotor infants to 325ms in crawling infants, and from 300 and 275ms in 6- and 12-year-olds, respectively, to 250ms in adults. These results on VEP peak analysis are relatively compatible with our research on adults. Infants at 4-5 months had the longest latencies and were unable to differentiate between motion speeds. However, crawling infants at 9-11 months and 6-year-old children were able to differentiate between low, medium, and high speeds, with the shortest latency for low speed. The results indicate the importance of locomotion when it comes to understanding motion speed perception. This can also cause implications for the design of school routes for children, in countries like Norway the speed limits on these routes are often 50km/h with some children riding their bicycles on roads without a proper sidewalk.

Similar results were found in a study by van der Weel and van der Meer (2009), where they found that infants at 10-11 months were able to differentiate between different looming speeds, while younger infants, especially those at 5-7 months, were unable to. This suggests that older infants have more mature neural networks for processing impending collision information compared to younger infants. The study also suggests that neural networks for processing looming danger may start to develop around 8-9 months, which is when infants begin to crawl and have better control over their self-produced locomotion. Authors suggest

that the improvement in perceptual ability could help infants recognize and avoid impending collisions.

Both these studies help argue the fact that experience in locomotion and being able to crawl/walk in an environment could facilitate for prospective control and navigation through different environments. This ability could also be one explaining factor into how we are able to discriminate between structured optic flow and random visual motion, and why we can observe N2 component latency differences between them.

With the importance of self-induced locomotion in relation to development in visual processing, one should keep in mind the many different environments infants and children are surrounded by. One factor that influences children's motor development is their upbringing and culture. While Western caregivers generally believe that infants are fragile and require careful handling, certain African and Caribbean cultures maintain that rough handling and intentional exercise are crucial for promoting healthy motor development (Adolph & Hoch, 2019). A longitudinal high-density EEG study showed that infants who received extra stimulation during their first year of life showed greater sensitivity to visual motion and more developed functional networks involved in visual motion processing compared to traditionally raised control infants. This improvement was attributed to the caregivers' enriched motor activities, such as baby swimming and body massage, resulting in accelerated brain development for visual motion perception (Olafsen, 2022). Different cultural upbringings can influence the development of visual processing in infants and young children and contribute to individual differences within the N2 component latency responses, in structured optic flow versus random visual motion.

A study investigating the effects of aging on the processing of visual motion using motion-onset VEPs found that the amplitude and latencies were different between older adults and younger adults, with older adults showing reduced amplitudes and longer latencies (Langrová et al., 2006). As our population ages, it's important to gain insight into how cognition changes with age because it impacts functional independence and effective communication. With normal aging, measurable changes in cognition occur, particularly in cognitive tasks that involve quick processing or transformation of information to make decisions. This includes declines in speed of processing, working memory, and executive cognitive function. This refers to changes in the structure of neurons, such as modifications in their shape or connectivity, which occur without neuronal death, loss of synapses, or dysfunction of neuronal networks (Murman, 2015).

Research on visual perception and prospective control using high-density EEG is of great importance for advancing our understanding of how the brain processes and integrates sensory information to guide actions in a goal-directed manner. By using high-density EEG, researchers can gain insights into the neural mechanisms underlying visual perception, such as motion, depth, and colour processing, and how these mechanisms contribute to the generation of predictive models of the environment. These predictive models can be used to anticipate the consequences of future actions, allowing for more efficient and adaptive behaviour.

Applying findings within research on prospective control and optic flow could also have beneficial attributes on traffic and road safety. The design of roads and intersections could be improved to provide better optic flow cues to the drivers. For instance, road signs and lane markings could be designed in a way that provides clear and more consistent optic flow cues, making easier for drivers and anticipate and adjust their driving accordingly. It has also been shown that children are less accurate than adults in judging the time-to-contact and that this was due, in part, to their reduced sensitivity to visual looming (Wann et al., 2011). Although

looming is not the same as forwards optic flow, they share similarities in terms of their dependence on motion cues and can provide complementary value in research by providing more comprehensive information on how visual information is processed and used to guide action in different contexts.

In conclusion, this study has highlighted how the brain responds differently to structured optic flow and random visual motion stimuli using high-density EEG and VEPs. All adults detected structured optic flow faster than random visual motion. Within the structured optic flow, participants had faster latencies for forward optic flow compared to reversed optic flow. Studies on infants have shown the importance of experience with self-produced locomotion for creating healthy and normal development within visual processing, as well as the effects of cultural upbringing in relation to extra motor stimulation. More coherence in the structured optic flow and a developed specialized visual processing system in adults allows for faster detection of structured optic flow compared to random visual motion.

References

- Adolph, K. E., & Hoch, J. E. (2019). Motor Development: Embodied, Embedded, Enculturated, and Enabling. *Annu Rev Psychol*, *70*, 141-164.
<https://doi.org/10.1146/annurev-psych-010418-102836>
- Agyei, S. B., Holth, M., van der Weel, F. R., & van der Meer, A. L. H. (2015). Longitudinal study of perception of structured optic flow and random visual motion in infants using high-density EEG. *Dev Sci*, *18*(3), 436-451. <https://doi.org/10.1111/desc.12221>
- Anderson, D. I., Campos, J. J., Anderson, D. E., Thomas, T. D., Witherington, D. C., Uchiyama, I., & Barbu-Roth, M. A. (2001). The flip side of perception–action coupling: Locomotor experience and the ontogeny of visual–postural coupling. *Hum Mov Sci*, *20*(4), 461-487. [https://doi.org/10.1016/S0167-9457\(01\)00063-X](https://doi.org/10.1016/S0167-9457(01)00063-X)
- Berg, P., & Scherg, M. (1991). Dipole modelling of eye activity and its application to the removal of eye artefacts from the EEG and MEG. *Clin Phys Physiol Meas*, *12*(A), 49-54. <https://doi.org/10.1088/0143-0815/12/A/010>
- Berg, P., & Scherg, M. (1994). A fast method for forward computation of multiple-shell spherical head models. *Electroencephalography and Clinical Neurophysiology*, *90*(1), 58-64. [https://doi.org/https://doi.org/10.1016/0013-4694\(94\)90113-9](https://doi.org/https://doi.org/10.1016/0013-4694(94)90113-9)
- Braddick, O., Atkinson, J., & Wattam-Bell, J. (2003). Normal and anomalous development of visual motion processing: motion coherence and ‘dorsal-stream vulnerability’. *Neuropsychologia*, *41*(13), 1769-1784. [https://doi.org/10.1016/S0028-3932\(03\)00178-7](https://doi.org/10.1016/S0028-3932(03)00178-7)
- Braddick, O., Birtles, D., Wattam-Bell, J., & Atkinson, J. (2005). Motion- and orientation-specific cortical responses in infancy. *Vision Research*, *45*(25), 3169-3179.
<https://doi.org/https://doi.org/10.1016/j.visres.2005.07.021>

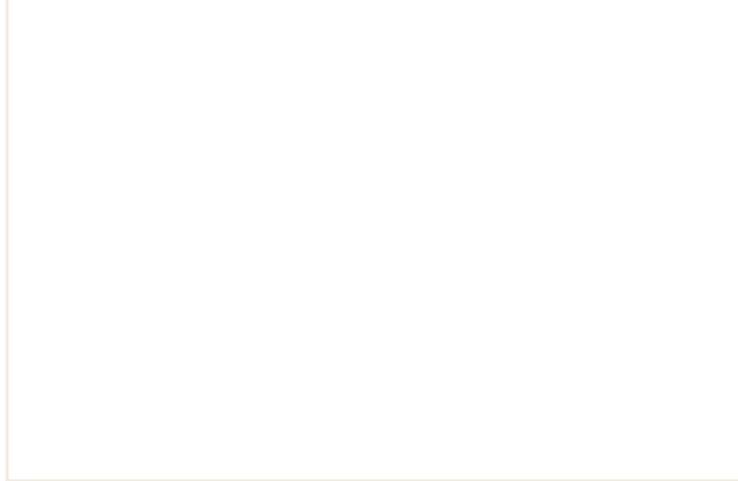
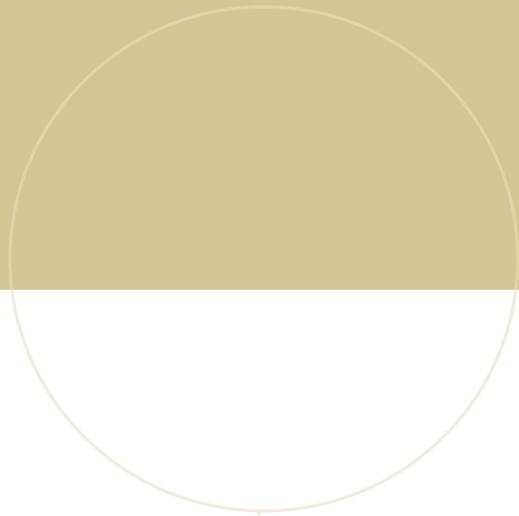
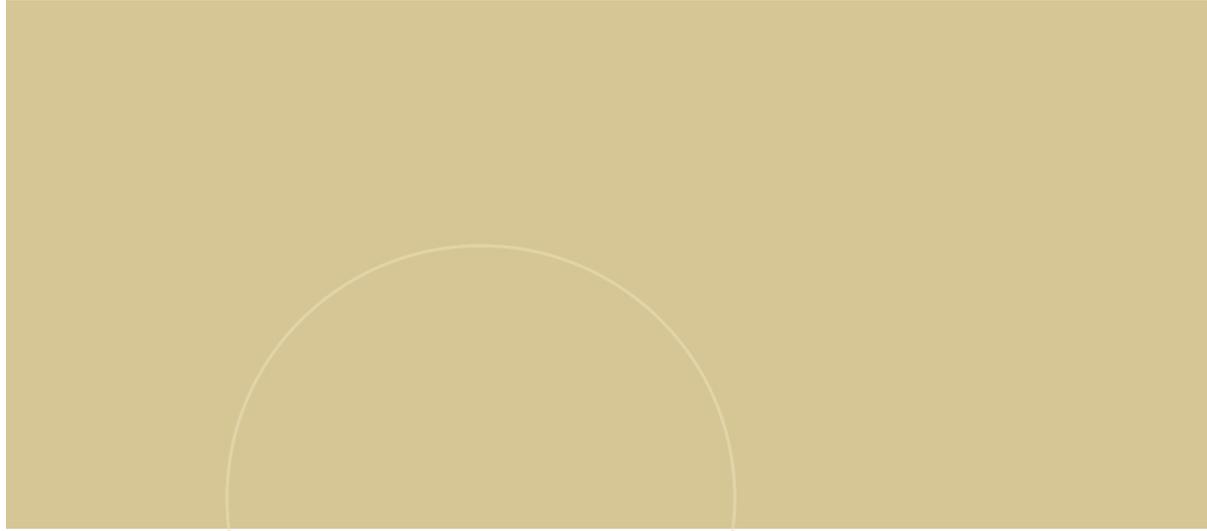
- Debener, S., Ullsperger, M., Siegel, M., & Engel, A. K. (2006). Single-trial EEG–fMRI reveals the dynamics of cognitive function. *Trends Cogn Sci*, *10*(12), 558-563.
<https://doi.org/10.1016/j.tics.2006.09.010>
- Duffy, C. J., & Wurtz, R. H. (1991). Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli. *J Neurophysiol*, *65*(6), 1346-1359. <https://doi.org/10.1152/jn.1991.65.6.1346>
- Fajen, B. R. (2008). Learning novel mappings from optic flow to the control of action. *Journal of Vision*, *8*(11), 12-12. <https://doi.org/10.1167/8.11.12>
- Ferree, T. C., Luu, P., Russell, G. S., & Tucker, D. M. (2001). Scalp electrode impedance, infection risk, and EEG data quality. *Clinical Neurophysiology*, *112*(3), 536-544.
[https://doi.org/https://doi.org/10.1016/S1388-2457\(00\)00533-2](https://doi.org/https://doi.org/10.1016/S1388-2457(00)00533-2)
- Fields, R. D. (2008). White matter in learning, cognition and psychiatric disorders. *Trends in Neurosciences*, *31*(7), 361-370.
<https://doi.org/https://doi.org/10.1016/j.tins.2008.04.001>
- Folstein, J. R., & Van Petten, C. (2008). Influence of cognitive control and mismatch on the N2 component of the ERP: A review. *Psychophysiology*, *45*(1), 152-170.
<https://doi.org/10.1111/j.1469-8986.2007.00602.x>
- Forrester, J. V., Dick, A. D., McMenamin, P. G., Roberts, F., & Pearlman, E. (2016). Chapter 5 - Physiology of vision and the visual system. In J. V. Forrester, A. D. Dick, P. G. McMenamin, F. Roberts, & E. Pearlman (Eds.), *The Eye (Fourth Edition)* (pp. 269-337.e262). W.B. Saunders. <https://doi.org/https://doi.org/10.1016/B978-0-7020-5554-6.00005-8>
- Gibson, J. J., Olum, P., & Rosenblatt, F. (1955). Parallax and Perspective during Aircraft Landings. *Am J Psychol*, *68*(3), 372-385. <https://doi.org/10.2307/1418521>

- Holliday, I. E., & Meese, T. S. (2005). Neuromagnetic evoked responses to complex motions are greatest for expansion. *Int J Psychophysiol*, 55(2), 145-157.
<https://doi.org/10.1016/j.ijpsycho.2004.07.009>
- Ille, N., Berg, P., & Scherg, M. (2002). Artifact Correction of the Ongoing EEG Using Spatial Filters Based on Artifact and Brain Signal Topographies. *Journal of Clinical Neurophysiology*, 19(2), 113-124.
https://journals.lww.com/clinicalneurophys/Fulltext/2002/03000/Artifact_Correction_of_the_Ongoing_EEG_Using.2.aspx
- James, K. H., & Swain, S. N. (2011). Only self-generated actions create sensori-motor systems in the developing brain. *Dev Sci*, 14(4), 673-678.
<https://doi.org/10.1111/j.1467-7687.2010.01011.x>
- Koenderink, J. J. (1986). Optic flow. *Vision Research*, 26(1), 161-179.
[https://doi.org/https://doi.org/10.1016/0042-6989\(86\)90078-7](https://doi.org/https://doi.org/10.1016/0042-6989(86)90078-7)
- Kremláček, J., Kuba, M., Chlubnová, J., & Kubová, Z. (2004). Effect of stimulus localisation on motion-onset VEP. *Vision Res*, 44(26), 2989-3000.
<https://doi.org/10.1016/j.visres.2004.07.002>
- Langrová, J., Kuba, M., Kremláček, J., Kubová, Z., & Vít, F. (2006). Motion-onset VEPs reflect long maturation and early aging of visual motion-processing system. *Vision Res*, 46(4), 536-544. <https://doi.org/10.1016/j.visres.2005.06.024>
- Morrone, M. C., Tosetti, M., Montanaro, D., Fiorentini, A., Cioni, G., & Burr, D. C. (2000). A cortical area that responds specifically to optic flow, revealed by fMRI. *Nat Neurosci*, 3(12), 1322-1328. <https://doi.org/10.1038/81860>
- Murman, D. L. (2015). The Impact of Age on Cognition. *Semin Hear*, 36(3), 111-121.
<https://doi.org/10.1055/s-0035-1555115>

- Olafsen, M. G. (2022). *Longitudinal study on receiving extra motor stimulation in early infancy: High-density EEG analysis of cortical responses to visual motion* [Masters, Norwegian University of Science and Technology]. Department of psychology. <https://hdl.handle.net/11250/3000380>
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology*, 72(2), 184-187. [https://doi.org/https://doi.org/10.1016/0013-4694\(89\)90180-6](https://doi.org/https://doi.org/10.1016/0013-4694(89)90180-6)
- Picton, T. W., Bentin, S., Berg, P., Donchin, E., Hillyard, S. A., Johnson JR., R., Miller, G. A., Ritter, W., Ruchkin, D. S., Rugg, M. D., & Taylor, M. J. (2000). Guidelines for using human event-related potentials to study cognition: Recording standards and publication criteria. *Psychophysiology*, 37(2), 127-152. <https://doi.org/https://doi.org/10.1111/1469-8986.3720127>
- Pitzalis, S., Strappini, F., De Gasperis, M., Bultrini, A., & Di Russo, F. (2012). Spatio-temporal brain mapping of motion-onset VEPs combined with fMRI and retinotopic maps. *PLoS One*, 7(4), e35771-e35771. <https://doi.org/10.1371/journal.pone.0035771>
- Probst, T., Plendl, H., Paulus, W., Wist, E. R., & Scherg, M. (1993). Identification of the visual motion area (area V5) in the human brain by dipole source analysis. *Exp Brain Res*, 93(2), 345-351. <https://doi.org/10.1007/BF00228404>
- Rasulo, S., Vilhelmsen, K., van der Weel, F. R., & van der Meer, A. L. H. (2021). Development of motion speed perception from infancy to early adulthood: a high-density EEG study of simulated forward motion through optic flow. *Exp Brain Res*, 239(10), 3143-3154. <https://doi.org/10.1007/s00221-021-06195-5>
- Sack, A. T., Kohler, A., Linden, D. E. J., Goebel, R., & Muckli, L. (2006). The temporal characteristics of motion processing in hMT/V5+: Combining fMRI and

- neuronavigated TMS. *Neuroimage*, 29(4), 1326-1335.
<https://doi.org/10.1016/j.neuroimage.2005.08.027>
- Sakkalis, V., Tsiaras, V., Michalopoulos, K., & Zervakis, M. (2008). Assessment of neural dynamic coupling and causal interactions between independent EEG components from cognitive tasks using linear and nonlinear methods. *2008 30th Annual International Conference of the IEEE Engineering in Medicine and Biology Society*, 3767-3770.
<https://doi.org/10.1109/IEMBS.2008.4650028>
- Smith, A. T., Wall, M. B., Williams, A. L., & Singh, K. D. (2006). Sensitivity to optic flow in human cortical areas MT and MST: Sensitivity to optic flow in human MT and MST. *The European journal of neuroscience*, 23(2), 561-569. <https://doi.org/10.1111/j.1460-9568.2005.04526.x>
- Stoffregen, T. A. (1985). Flow structure versus retinal location in the optical control of stance. *Journal of Experimental Psychology: Human Perception and Performance*, 11, 554-565. <https://doi.org/10.1037/0096-1523.11.5.554>
- Tucker, D. M. (1993). Spatial sampling of head electrical fields: the geodesic sensor net. *Electroencephalography and Clinical Neurophysiology*, 87(3), 154-163.
[https://doi.org/https://doi.org/10.1016/0013-4694\(93\)90121-B](https://doi.org/https://doi.org/10.1016/0013-4694(93)90121-B)
- Van der Meer, A., & van der Weel, F. (2019). The Optical Information for Self-Perception in Development. In (pp. 110-129). <https://doi.org/10.4324/9780429316128-8>
- van der Meer, A. L. H., Fallet, G., & van der Weel, F. R. (2008). Perception of structured optic flow and random visual motion in infants and adults: a high-density EEG study. *Exp Brain Res*, 186(3), 493-502. <https://doi.org/10.1007/s00221-007-1251-2>
- van der Weel, F. R., & van der Meer, A. L. H. (2009). Seeing it coming: infants' brain responses to looming danger. *Naturwissenschaften*, 96(12), 1385-1391.
<https://doi.org/10.1007/s00114-009-0585-y>

- Vilhelmsen, K., Agyei, S. B., van der Weel, F. R. R., & van der Meer, A. L. H. (2019). A high-density EEG study of differentiation between two speeds and directions of simulated optic flow in adults and infants. *Psychophysiology*, *56*(1), e13281. <https://doi.org/10.1111/psyp.13281>
- Vilhelmsen, K., Van Der Weel, F. R., & Van Der Meer, A. L. H. (2015). A high-density EEG study of differences between three high speeds of simulated forward motion from optic flow in adult participants. *Front Syst Neurosci*, *9*(OCTOBER), 146-146. <https://doi.org/10.3389/fnsys.2015.00146>
- Wann, J. P., Poulter, D. R., & Purcell, C. (2011). Reduced Sensitivity to Visual Looming Inflates the Risk Posed by Speeding Vehicles When Children Try to Cross the Road. *Psychol Sci*, *22*(4), 429-434. <https://doi.org/10.1177/0956797611400917>
- Warren, W. H. (2008). 2.12 - Optic Flow. In R. H. Masland, T. D. Albright, T. D. Albright, R. H. Masland, P. Dallos, D. Oertel, S. Firestein, G. K. Beauchamp, M. Catherine Bushnell, A. I. Basbaum, J. H. Kaas, & E. P. Gardner (Eds.), *The Senses: A Comprehensive Reference* (pp. 219-230). Academic Press. <https://doi.org/https://doi.org/10.1016/B978-012370880-9.00311-X>
- Woodman, G. F. (2010). A brief introduction to the use of event-related potentials in studies of perception and attention. *Atten Percept Psychophys*, *72*(8), 2031-2046. <https://doi.org/10.3758/APP.72.8.2031>



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