

Candidate number: 10048

Efficiency in visual processing: A high-density EEG study investigating N2 responses to structured optic flow and random visual motion

Bachelor's thesis in Psychology: PSY2900

Supervisor: Seth Bonsu Agyei

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Preface

They say that the devil is in the details.

EEG analysis has a lot of details, I've found. Thank you to the supervisor of the research project, Seth Bonsu Agyei, for guiding me and the rest of the bachelor group through the process. I would also like to thank the PhD student involved for helpful feedback and patience.

A big part of this thesis was not only writing, but collecting, cleaning, and analysing the EEG-data. The bachelor group tested three of the participants and used seven already collected raw data sets. After getting the necessary training for cleaning and analysing the data using BESA, each member of the group did this part independently. This is also true for the statistical analyses. That said, learning to analyse EEG data is no easy task and I am grateful to Seth and the PhD student for being available to answer my many questions.

When it comes to the research question, the focus was inevitably going to be on latencies of the N2 component. Still, I was free to choose which themes to incorporate into the thesis. I was also responsible for finding all relevant literature.

Finally, I would like to thank caffeine in moderate doses for existing, lofi hip hop radio for keeping me in the flow (no pun intended), and, though he probably never will read this thesis, Haruki Murakami, for showing me that the process of writing is like doing a long run: A slow and steady rhythm does the trick.

Abstract

As we move through our environment, we experience a constantly changing optic array. This dynamic scene, called optic flow, gives us information about our position relative to the environment around us. However, we process different types of optic flow with various efficiency. This study used high-density EEG to examine the N2 component's latencies in response to optic flow stimulation in an adult population. This was done by examining the visual evoked potentials (VEPs) to three conditions: forwards optic flow, reversed optic flow, and random visual motion. The analysis revealed shorter latencies in both optic flow conditions compared to random visual motion, and shorter latencies in the forwards optic flow conditions compared to reversed. As the latencies indicate signal processing efficiency, our visual pathways seem to be better in processing ecologically relevant information. A main implication is that our latencies may mirror the environments we have actively engaged in. If we manage to change the environment we act in, we might also be able to lower the latencies. In turn, this can potentially be helpful in populations struggling with motion categorization.

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1. Introduction

1.1. Optic flow's role in navigation

As the toddler walks toward her parent, she knows when she is close enough to start reaching her arms out, wanting to be lifted. When she, as an adolescent, rides downhill on her bicycle, she sees an obstacle and avoids it. Finally, as an adult, she smoothly breaks her car as the traffic light ahead becomes red. In all these cases, prospective control, meaning the ability to perceive what is just about to happen (van der Weel et al., 2022), is crucial to make the right adjustments to reach one's destination. In order to make the right adjustments, however, one needs to use information coming from the ever-changing pattern of visual information, called optic flow (Gibson, 1966). This is a central term in the field of ecological psychology, where researchers investigate at perception and action in natural environments (Gibson, 1979/2015; Fajen et al., 2008). Fittingly, Lee (1980) described optic flow as spatio-temporal: as we move in space, the optic flow changes. And being able to spot these changes is fundamental if we successfully want to navigate our environment.

Early studies investigating optic flow's role in navigation did not manage to isolate it from other navigation strategies (Li & Niehorster, 2014). Conversely, some questioned optic flow's role in guiding our locomotion, arguing instead for results consistent with egocentric direction strategies (Harris & Rogers, 1999; Wann & Land, 2000), where one is thought to use own motion as a reference to the goal to navigate (Rusthon et al., 1998). However, with new technology, researchers could isolate optic flow from to other stimuli and thus examine its role in locomotion. For instance, Warren et al. (2001) used a virtual environment where they were able to separate whether participants relied on egocentric motion strategies or optic flow in steering their walking. They found that as they added optic flow to the environment, participants increasingly relied on it to guide their locomotion. Said differently, while we

may use ego-centric direction strategies when there is little optic flow, we rely increasingly on it as it becomes available (Fajen & Warren, 2000; Warren et al., 2001). Later studies have gotten similar results, supporting optic flow's role in steering our locomotion (Sarre et al., 2008; Salinas et al., 2017). Even if we could use egocentric direction strategies, we seem to use optic flow to steer towards a target (Li & Cheng, 2013), especially if the travel speed and thus magnitude of flow increases (Chen et al., 2018).

Steering towards a target is, however, only one aspect of how we use optic flow. For example, consider the complex situation of intercepting a ball. The literature suggests that we will use optic flow to adjust our movement speed (Ludwig et al., 2017), modify our posture (Stoffregen, 1985), and use our own motion relative to the target motion to anticipate time-to-contact (TTC) with the ball (Geri et al., 2010). In learning perceptual-motor skills, a central part is also learning to combine novel patterns of optic flow with specific movement (Fajen, 2008). Building on this, Fajen (2005) also suggests that the optic flow gives rise to different action possibilities (affordances) for each individual. That is, we use optic flow relative to our own abilities. Ultimately, the information that optic flow provides us with, which we use to make complex decisions, is based in our previous experiences. To put it simply: a Formula 1 racing driver and an average commuter may experience the same optic flow while driving, but they will perceive different possibilities for when and how they should break.

1.2. Neural basis and the use of EEG

Given the role of optic flow in everyday life, much research has also investigated the neural underpinnings. Here, the dorsal stream, responsible for motion information processing, is crucial (Perry & Fallah, 2014). Many papers have found that the dorsal medial superior temporal (MST) in the dorsal stream is central in processing optic flow in both primates and

humans (Smith et al., 2006; Wall & Smith., 2008; Yu et al., 2010; Perry & Fallah, 2014). Later parts in the dorsal stream, for instance the posterior parietal cortex, processes more complex aspects of optic flow (Perry & Fallah, 2014) such as forwards or backwards flow (Siegel & Read, 1997) and integrates the flow with regard to the position of the head and the eyes (Raffi et al., 2014). Furthermore, other parts of the dorsal stream, such as the human temporal/visual area 5 (hMT/V5) processes radial motion (Tohyama & Fukushima, 2005; Sack et al., 2006), while global motion elicit responses in visual area 3a and visual area 6 (V6) (Wattam-Bell et al., 2010; Furlan & Smith, 2016; Nakhla et al., 2021). In sum, then, the dorsal stream is central in processing motion, and while some areas seem to be more responsive to movement types such as radial flow or global motion, others are more specialized in processing optic flow.

To understand the cortical responses to optic flow, it is not only important to look where it is processed, but also how. Many researchers have used electroencephalography (EEG) to do this. While EEG has poor spatial resolution and therefore cannot accurately infer the source of signals (Srinivasan, 1999; Luck, 2005, p. 10), its strength lies in the high temporal resolution which allows it to accurately monitor specific patterns of task-dependant activity (Luck, 2005, p. 10). This means that EEG allows researchers to look at the responses in neural networks to specific tasks as they happen. More accurately, researchers can see the response of pyramidal neurons within those networks (Cohen, 2017). This can be useful information, as for instance looking at changes in latencies and amplitude to different kinds of stimuli can indicate in difficulty in processing (Agyei et al., 2015), which in turn can give indication of how one's brain is developing (Blystad & van der Meer, 2022).

EEG studies looking at visual evoked responses (VEPs) have found that the N2 component dominates the response in responsive optic flow (van der Meer et al., 2008; Agyei et al., 2015; Rasulo et al., 2021). This component is involved in categorization of visual stimuli

(Woodman, 2010) and is sensitive to changes in visual motion (Kuba et al. 2007). One can mostly observe it in the parietal and occipital areas, peaking after stimuli onset between 225-250 ms in adult participants (Woodman, 2010). Further research suggests that its origin is in the hMT/V5 area (Probst et al., 1993). Van der Meer et al. (2008) have also argued that this is the origin due to transcranial magnetic stimulation (TMS) studies which have found impaired motion perception when putting it over the MT area. Such impairments have included a reduced perceptual ability when it comes to speed perception (McKeefry et al., 2008), accuracy in motion-directed tasks (Laycock et al., 2007), and motion prediction (Vetter et al., 2015), all of which are related to changes in visual motion.

1.3. The present study

Many of the mentioned studies have focused on infants' development (e.g. Agyei et al., 2015; Rasulo et al., 2021) and those who have studied adults have often looked at responses to different optic flow velocities (e.g. Vilhelmsen et al., 2015; Vilhelmsen et al., 2019). This study, however, aimed the spotlight on adults' N2 responses to different types of optic flow versus random motion. Now, previous studies, both in infants and adults, show shorter latencies for the N2 component in optic flow simulations compared to random motion (van der Meer et al., 2008; Agyei et al., 2015; Blystad & van der Meer 2022). Additionally, the same studies have also found shorter latencies for forward optic flow compared to reversed. Aligned with principles of experience-dependant neuroplasticity (Kleim & Jones, 2008), the interpretation of the shorter latencies has been that we are more efficient in detecting stimuli which we often encounter. That is, latencies are shorter for structured optic flow than random motion as we encounter the former more often. Similarly, because we move more forwards than backwards, we are also more efficient in detecting forward optic flow. In sum, there

seems to be a difference in how efficiently we process visual motion, with motion that we often encounter being easier to detect.

While several studies have gotten similar results regarding the N2 component's involvement in detection of optic flow (e.g. van der Meer et al., 2008; Agyei et al., 2015; Rasulo et al., 2021), there is still a need to replicate such findings. Some might argue against the need for replication, arguing that these results have been found multiple times and are robust. After all, what is the point in using resources when we are quite sure what will happen? At the same time, however, it is important to consider the lack of replication in psychology. A known example is Open Science Collaboration (2015), who, in short, found that most psychological findings could not be replicated. This is also relevant for experiments done in cognitive neuroscience, such as the present study. EEG analysis can easily give significant, yet false effects (Luck & Gaspelin, 2016). The analytical freedom might also steer results into the wanted results (Pavlov et al., 2021). Considering such challenges, there is always a need for replications even for well-established results such as the characteristics of the N2 component. Said differently, even studies which investigate simpler aspects of VEPs have their use.

The goal of this study was to try to replicate previous findings regarding the N2 component. Specifically, the hypothesis was that structured optic flow would elicit shorter N2 latencies compared to random motion. Within this, that the N2 latencies for forward optic flow would be shorter compared to reversed optic flow. As described, the rationale behind this is that we encounter more structured optic flow than random motion, and more forward optic flow than reversed. Thus, there should be a difference in the processing efficiency.

Support for this hypothesis will suggest, as other studies have argued, that we process patterns of motion that we encounter in everyday life faster than less-encountered stimuli

(van der Meer et al., 2008; Agyei et al., 2015; Vilhelmsen et al., 2015). As neurons become more specialized and effective in response to repeated stimuli (Kleim & Jones, 2008), a more basic interpretation would also be that our neurons specialize on stimuli which we encounter in our environment. Some would also argue that such data would support the ecological view. That is, if our visual system is highly specialized to detect stimuli we often encounter, it would support the proposed tight link between the subject and environment put forward by Gibson (1979/2015). All these perspectives would ultimately endorse, however, that support for this hypothesis would suggest that we pick up ecological relevant information more easily. Thus, this would give support to the notion that a subject's perception is shaped by the environment, meaning that we are more effective in detecting stimuli that we often encounter.

2. Methods

2.1. Participants

The study had a cross-sectional design with 10 participants tested (7 woman, 3 men). All were adults and had either corrected-to-normal or normal eyesight. None had any known neurological defects. The participants were recruited from the university campus and the age range was 21- 37 years ($M = 28$, $SD = 6$).

We, meaning the project leader and students involved, used high-density electroencephalography (HD-EEG) to conduct a series of repeated measures using the optic flow paradigm. As a measurement tool for psychological research, EEG is non-invasive and does not have any known negative effects. The participants had signed an informed consent form and could withdraw from the experiment at any time. Both the Norwegian Data Services for the Social Sciences (NSD) and the Norwegian Regional Ethics Committee (REC Central) had approved the study.

2.2. Experimental stimuli and paradigm

E-Prime software (Psychological Software Tools, Inc.) showed an optic flow pattern on a Microsoft Surface Hub 84" (108 cm width x 70 cm height) with a 60 Hz refresh rate. The participants sat 80 cm from the screen with a 70 cm distance from the screen to the eyes. Furthermore, they looked at the screen with an approximately 90° degree angle at a fixation cross with a width of 1.69 mm (1 pixel). The fixation cross was at the horizontal centre and around 3/4th of the screen's height. The angle by the fixation cross was 0.161°, the angle by the width of the screen was 68.0° with the height at 46.7° (see Figure 1).

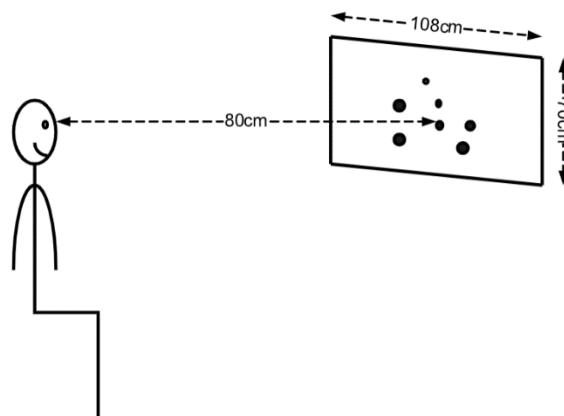


Figure 1: Physical dimensions of the experiment. Illustration of a participant resting her vision on the fixation point in the optic flow paradigm.

There were four conditions in the optic flow experiment: forwards optic flow, reversed optic flow, random non-flow, and static non-flow. They were presented in a random order and lasted for 1500 ms each. All four conditions had the appearance of 100 black dots on a white surface, and a red dot representing the fixation cross. While each had a radius of 5 mm in the virtual space, they appeared as big as 17 mm when they were “close” and as small as 2 mm when they were “far away”. For the forwards optic flow, 100 dots moved towards the

participant with a constant speed (30 mm per frame with a rate of 60 fps) from the centre of the screen, giving the impression of forward self-movement. The effect is comparable to looking through the front window when in a moving car while it is snowing. Dots that “passed” the participant were immediately replaced at the back, keeping the number of dots on the screen at a constant (100 dots). The second simulation of optic flow was the reversed condition. In contrast to forwards optic flow, the dots moved towards the centre of the screen and gave the participant the impression of moving backwards. To use the snow analogy again, this gave the impression of looking through the back window while in a moving car. The speed was the same as the forward conditions and there were always 100 dots present; Those that disappeared in the horizon spawned in front of the participant.

The last two simulations were non-flow conditions. One of these, random non-flow, did have constant movement, yet there were not any structure or coherence in the dots’ movement. The motion was completely random and hence gave no impression of self-movement. Lastly, in between each otherwise randomly presented condition, there was a static non-flow condition where there was no movement at all. This frozen state was designed to avoid motion adaptation and functioned as a baseline condition for the later analyses. In total, the experiment had 40 trials for each motion condition with a total of 120 static trials.

2.3. Data acquisition

EEG activity was recorded with a Hydrocel Sensor Net 200 (Electrical Geodesics). The net consisted of an arrangement of 256 Ag/AgCl sponge sensors, spread out evenly over the participant’s scalp. Consistent with the optimal signal-to-noise ratio, the high-input EGI amplifier connected to the net was set at a maximum of impedance at 50 k Ω (Picton et al., 2000; Ferree et al., 2001). The amplifier was further connected to a Macintosh computer

which used NetStation software to record the signals with a sampling rate of 500Hz. The filters were set at a 0.1 Hz high pass and 200 Hz low pass.

To record the participants' gaze, an infrared Tobii X50 camera was used. This tracked where the participants were looking during the experiment. ClearView software processed this data. There was also a video camera which recorded the participant's behaviour. This gave the experimenters the opportunity to ensure that the participants did not move in a way which distorted the EEG-signals too much. Additionally, the video could also be of help to explain noise in the data set (if a participant scratched her head, for instance).

2.4. Procedure

Before every trial, the experimental room was prepared. This included ensuring that the chair and table were placed on the marked spots, that the Microsoft Hub screen functioned, and that the computer used for viewing the impedance of the electrodes was functional. In short, it was checked that each experiment had the same standardized conditions set by the lab.

When preparing the EEG net, the participant's head size was first measured and the suitable net was selected. The net was then soaked in an electrolyte solution consisting of potassium chloride and baby soap for a minimum of minutes to optimize electrical conductivity.

Additionally, the participant's inter-aural and inter-pupillary distance was measured, trying to find the approximate centre of the skull as the point of the reference electrode. After marking the middle part where they crossed, the participants were asked to point at the centre of their skull. If it deviated from the previous markings, a new mark in the middle of these two points was made. This new point was then used at the point of the reference electrode.

After soaking, the net was slightly padded with a dry towel and put carefully on the participant's head. To ensure good impedance, the electrodes were fastened, focusing on the

backside of the head where the visual cortex is as it was the main area of interest for the study. When satisfied, the participant was taken to the experimental room and the net was connected to the amplifier. Then, the impedance was checked to ensure that the net showed a minimum requirement of 90% electrodes of adequate impedance. If needed, electrodes were adjusted, and in some cases, extra electrolyte solution was added with a pipette.

When the EEG net had the required impedance, it was checked that the ClearView settings for eye tracking were according to the lab's standard. Afterwards, the eye movement was calibrated using five different reference points. Several assistants were always in the control room and could respond to issues regarding if the participant moved too much, had any questions, or if there were any technical issues. To limit external artefacts, the experimental room were lit only by the screen. The chair, which was electric, was unplugged. The participant left any electrical equipment outside the experimental room.

Although this study focuses on the optic flow paradigm, the session for each participant consisted of four different paradigms. Each of the paradigms were related to perception of visual motion. Of these, optic flow was shown first. After finishing the testing, the net of the participant was soaked for 10 minutes in an anti-bacterial solution. When the time was up, it was rinsed with water from the sink, patted, and lastly hung up for drying.

2.5. Analyses

2.5.1. Data analyses

To analyse the raw EEG data, the 7.1 version of the research software Brain Electrical Source Analysis (BESA, GmbH) was used. To facilitate the analyses, the NetStation software first segmented the EEG datasets which then were exported to a different offline server. Likewise,

the data eye tracking data from ClearView and E-Prime data containing the information of the optic flow paradigm was transferred to the offline server.

Averaging epochs were set from -200ms to 800 ms with the baseline definition was at -100 to 0 ms. To remove both the channels which were contaminated high frequency activities, and those with slow drift in the data, the high and low cut off-filter were at 80 Hz and 1.6 Hz, respectively. To avoid line interference, the notch filter was at 50 Hz. Artefact-contaminated electrodes caused by head/body movement were visually inspected, and either removed from further analysis or re-estimated using spherical line interpolation (Perrin et al., 1989; Picton et al., 2000). While bad channels were excluded, there was always a maximum of 10% exclusion. When doing manual artefact correction to separate the eye movement artefacts from the brain signals, the threshold values were 0.1 μV for the low signals and 75 μV for gradients and the maximum amplitude was at a threshold of 120 μV (Berg & Scherg, 1994; Ille et al., 2002).

2.5.2. VEP peak analyses at electrode level

To be able to do the VEP analysis, the EEG-data was exported into the standard 81-electrode configuration of the 10-10 international system. To get the reference-free (10-10) montage signal, spherical line interpolation was used to estimate the signal (American Electroencephalographic Society, 1991). To obtain a grand average, the individual averages were first analysed and then combined. This functioned as a reference for the selection of the individual N2 components. By showing the maximum N2 activity for the waveform which was most dominant over the occipito-parietal areas, the 3d spherical whole head voltage maps allowed the identification of the individual averages of the N2 components (Perrin et al., 1989). In other words, the maps showed spatially where the N2 activity was the strongest.

The latency of the individual averages was recorded from the stimulus onset to the peak of the N2 component. These latencies were used in the further analyses.

3. Results of VEP analysis

To find channels to use for the analysis, the method as put forth by van er Meer et al. (2008) was used. This included first using the individual participant averages and then combining them into a grand average. This functioned as a reference for picking the four electrodes in the forward optic flow condition which had the highest N2 amplitudes for further analysis. Of these four, when choosing one electrode from each participant, the one with the highest mean N2 amplitudes in the forwards optic flow condition was chosen. Thus, while the electrode varied with the different participants, it was always one of the following four: PO4, PO8, O2, Oz. In the electrodes used, the mean latencies for forwards optic flow were 227.00 ms ($SD = 45.03$), reversed had a mean latency of 268.4 ms ($SD = 53.37$), and random visual motion had 344.60 ms ($SD = 70.56$). When it comes to amplitude, the mean for forwards optic flow was -0.49 μ V ($SD = 0.40$), -0.42 μ V ($SD = 0.65$) for reversed optic flow, and -0.11 μ V ($SD = 0.45$) for random visual motion.

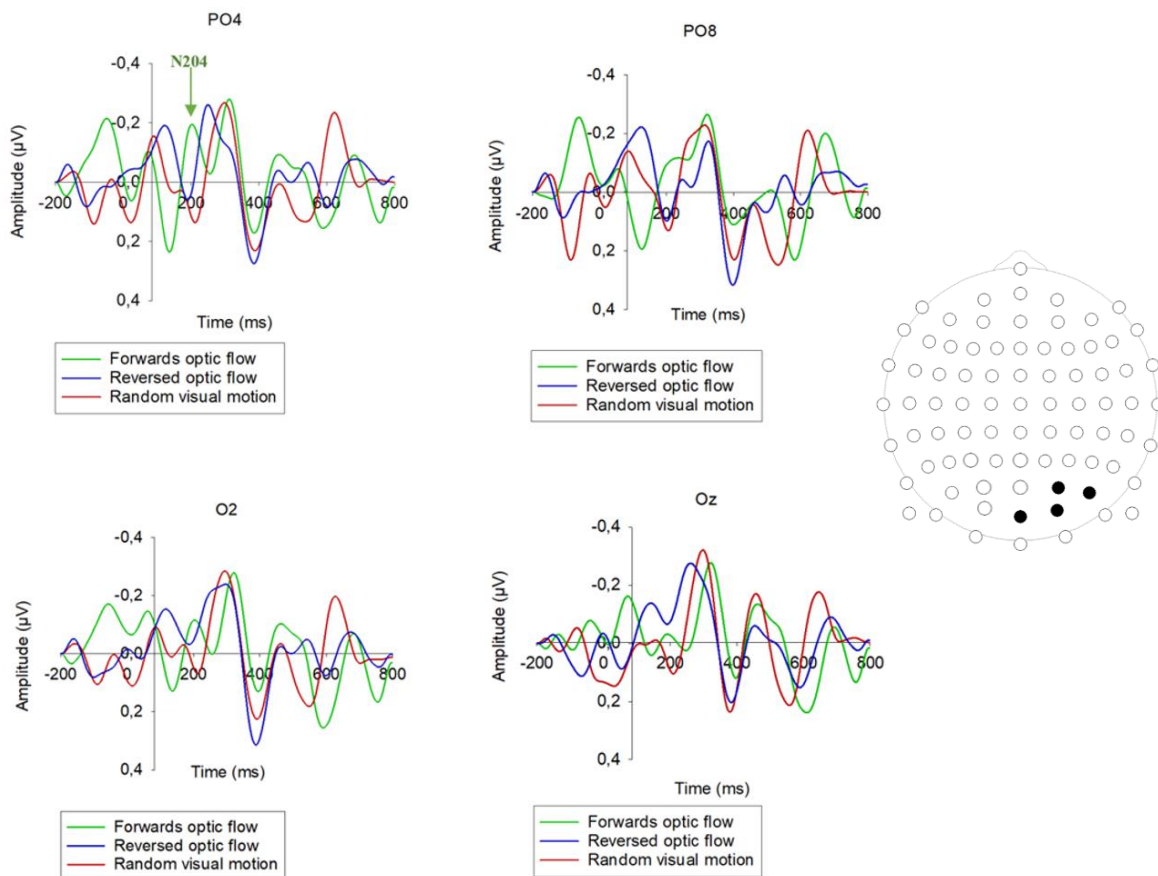


Figure 2: Grand average VEPs for the different motion conditions in the four electrodes with the highest mean amplitude (Top row: PO4, PO8. Bottom row: O2, Oz). The X-axis shows the epoch from -200 ms to 800 ms, while the Y axis shows amplitude in μV . The vertical arrow shows where the N2 component was judged to be based on both amplitude and the signature of the activation distribution in the head model in the BESA analysis. The forwards optic flow is shown in green, the reversed optic flow in blue, and the random visual motion in red. On the right is the scalp localization of the standard 81 electrodes with the mentioned electrodes marked as black circles. Oz is in the bottom left, with O2 on its right. PO8 is on the furthest right and PO4 on is on the top.

A repeated measures analysis of variance (ANOVA) was used with the conditions (forwards, reversed, random visual motion) as within-subject variables and latencies of the N2 component as between subject variable. To adjust for multiple corrections, Bonferonni correction was used. The analysis showed a main effect of group, $F(2, 9) = 18.97, p < .001$, indicating significant differences between the different conditions. Further post hoc tests (see Figure 3) showed that the biggest difference was between forwards optic flow and random

visual motion, $\Delta M = -116.60$, $p = .002$, followed by reversed optic flow and random visual motion, $\Delta M = -76.20$, $p = .012$. Lastly, forwards optic flow also had shorter mean latencies compared to reversed optic flow, $\Delta M = -41.40$, $p = .044$. This means that forwards optic flow and reversed optic flow had on average 117.60 ms and 76.20 ms shorter latencies, respectively, compared to random visual motion. This indicates an enhanced ability to detect the optic flow conditions. Meanwhile, the participants were also more efficient in detecting forwards optic flow compared to reversed optic flow, with forwards optic flow having on average 41.40 ms shorter latencies. Similarly, this also indicates a difference in efficiency of processing the two conditions.

For the amplitudes, a repeated measures ANOVA was used with the conditions (forwards, reversed, random visual motion) as within-subject variables and the amplitude as between-subject variables. This revealed no significant differences between the conditions, $F(2, 9) = 1.98$, $p = .167$. However, a post hoc analysis (see figure 3) showed a significant difference between in amplitudes between the forwards optic flow and random visual motion, $\Delta M = -.38$, $p = .043$.

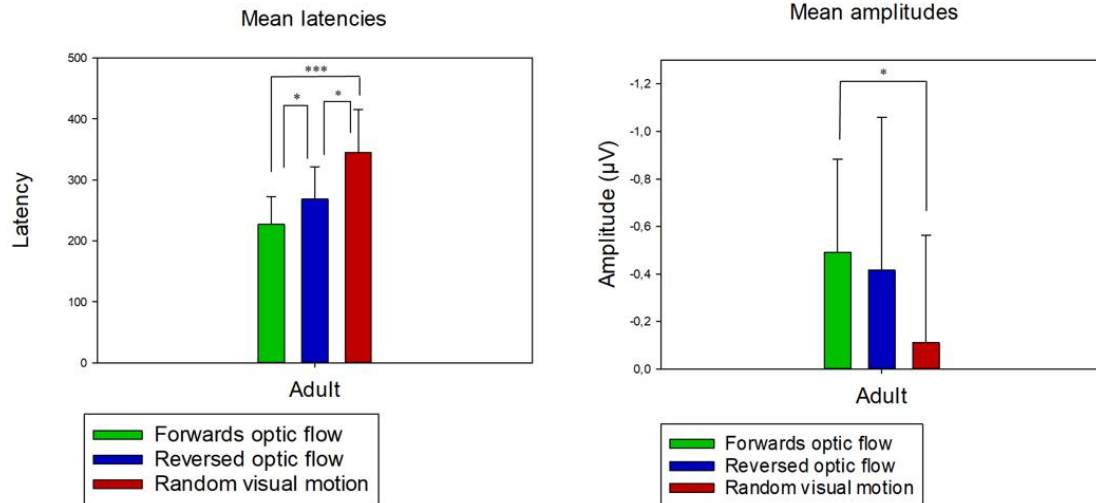


Figure 3: Group mean latencies and group mean amplitudes for the different motion conditions. The X-axis shows bars representing the different conditions. Forwards optic flow is shown in green, reversed optic flow in blue, and random visual motion in red. Meanwhile, the Y-axis is the latencies. The bars thus show the differences in mean latencies between the conditions, with significant differences at the, $p < .001$, level between forwards optic flow and random visual motion, and significant differences at the, $p < .05$, level between forwards optic flow and reversed, and reversed optic flow and random visual motion. * Significant at the, $p < .05$, level, *** at the, $p < .001$, level.

4. Discussion

This study used high-density EEG in an adult population to investigate differences in responses for structured optic flow and random visual motion. VEP analyses were used with the focus being on latencies of the motion sensitive N2 component. The main results were two-part. First, both structured optic flow conditions had shorter latencies compared to random visual motion. Second, forwards optic flow had shorter latencies compared to reversed. Both results were in accordance with the previous described hypothesis. As mentioned, there was also a significant difference between the forwards optic flow amplitude and random visual motion. However, given that both other studies looking at N2 responses to optic flow have had no significant within-group differences in amplitude (e.g. van der Meer et al., 2008; Agyei et al., 2015) and that the N2 component peak's amplitude seems less clear

compared to such studies (see figure 2), this may suggest that the results are due to distortions in the data set. Therefore, my focus in this discussion will be on the latency differences.

4.1. Neuroplasticity and latencies

When it comes to the shorter latencies for both optic flow conditions compared to random visual motion, my interpretation is that this represents more efficient processing of the optic flow stimuli. This means that we detect the optic flow structures faster. The literature also seems to agree when it comes to what such shorter latencies means, both in the optic flow paradigm (van der Meer et al., 2008; Agyei et al., 2015; Blystad & van der Meer, 2022) and in other fields (e.g. ElleMBERG et al., 2003; HÜLSDÜNKER et al., 2018). While there may be a consensus, it is also important to discuss why we see the differences in this study. Based in experience-dependent plasticity, meaning how the brain reorganizes its function and structure as a response to internal and external pressure (Kleim & Jones, 2008), there are two main points which I want to highlight here: importance and action. Both are central in explaining why we see the differences in latencies, yet they differ in meaningful ways.

As van der Meer et al. (2008) discusses, the differences in latencies may reflect the importance of optic flow. Another way to look at “importance” is high ecological relevance, meaning that we use and encounter the stimuli often. We know that the brain adapts through environmental pressures and experiences (Pascual-Leone et al., 2005), with high use, repetition, and intensity of stimuli being crucial (Kleim & Jones, 2008). Now, part of the reason why we use optic flow so much may be because it has a reliable structure which gives meaningful information. As mentioned, we use it in various ways as we drive (Lee, 1980), walk (Warren et al., 2001) and adjust our posture (Stoffregen, 1985). By allowing us to, for example, reliably predict time-to-collision with an object (Fajen et al., 2005), we rely on optic

flow to adjust our behaviour correctly. There seems, in other words, to be enough incentive for the brain to induce plasticity when it comes to the pathways involved in detecting optic flow based on what we know sparks such changes. On the other hand, the explanation for random visual motion's reliably longer latencies (van der Meer et al., 2008; Agyei et al., 2015; Blystad & van der Meer, 2022) may be that it lacks this ecological relevance. Random visual motion may still have a structure which we are able to detect, yet it is unreliable by nature. It is true that the pathways become more effective in detecting the structure, as the latencies are lower from early infancy to late infancy (Agyei et al., 2015; Agyei et al., 2016a) and from late infancy to adulthood (van der Meer et al., 2008). However, this might be due to general brain maturation, which enhances visual motion perception (Agyei et al., 2016a), and may not benefit from the further efficiency which comes due to experience with using the information embedded within optic flow (Agyei et al., 2016b; Blystad & van der Meer, 2022). Either way, the high frequency and intensity of the optic flow conditions seems to have a higher ecological relevance to us. Meanwhile, outside normal neurobiological development, there is less incentive for increasing the efficiency of detecting random visual motion. Thus, the latency differences between the optic flow conditions and random visual motion can be partly explained by how important the types of stimuli are to us.

A second explanation which can explain the latencies in this study is previous action. This overlaps with the latter point, where I discussed that we gain more experience in using optic flow as it is more important to us. However, action is crucial as it highlights that we must actively engage in our environment, and not just passively experience it. For instance, when it comes to infants, they might be able to react at approaching motion at 1-2 months of age (Nanez & Yonas, 1994) and discriminate between large changes in optic flow when they are 3-4 months old (Gilmore et al., 2004). However, pre-locomotor infants at 3-6 months of age infants have a minimal improvement in optic flow discrimination (Gilmore et al., 2004) until

they gain experience in self-generated locomotion, where the latencies in response to optic flow show a similar pattern to that of adults (van der Meer et al., 2008; Agyei et al., 2015; Agyei et al., 2016a; Agyei et al., 2016b). This suggests that self-generated locomotion is an activity with a high enough rate of repetition and intensity that it helps induce developmental changes, such as increased white matter myelination (Bells et al., 2019), local glucose metabolic rate maturation (Klaver et al., 2011), and axonal pruning (Low & Cheng, 2006). Again, I want to emphasize that part of the explanation shortened latencies in infants is due to rapid maturation of the pathways that processes motion information (Agyei et al., 2016a; Agyei et al., 2016b). Still, as I've argued, self-generated action is crucial for enhancing the effectiveness of such processing (James & Swain, 2011; Agyei et al., 2016a). Consequently, this results in more efficient neural pathways responsible for detecting optic flow but not random visual motion. Overall, I would argue that this helps explain why this study observed the differences between the optic flow conditions and random visual motion. Action seems to be a catalyst for the infants to get a response pattern to optic flow similar to adults'. As we as adults have more experience with optic flow than random visual motion, this suggests that previous action is an important reason behind why we see the relative differences in latencies.

4.2. Differences between forwards optic flow and reversed optic flow

The second finding was that forwards optic flow induced shorter latencies compared to random visual motion. Just as with the previous result, my interpretation is that this reflects a difference in signal processing efficiency due to a different amount of experience. Previous studies have also come to the same conclusions (van der Meer et al., 2008; Shirai et al., 2009; Agyei et al., 2015), arguing for the importance of experience. As with the last result, what I have called importance and action is just as important in explaining the differences. However, I also want to highlight another factor which is useful in explaining the latency differences:

specificity. Combined with importance and action, specificity also has especially important implications.

Specificity is important as the latencies for forwards and reversed optic flow are experience-dependent (Agyei et al., 2015; Blystad & van der Meer, 2022). Thus, it seems likely that the latencies for each can change based on our actions in our environment. In fact, we do see such specific changes due to actions in other parts of the visual system (Schoups et al., 2001; Draganski et al., 2004; Sigman et al., 2005; Baroncelli et al., 2013). And, though it would be difficult to conduct a study where one experiences more reversed optic flow than forwards over a longer period of time, one can find support that it is similar for the N2 latencies in the study by Blystad and van der Meer (2022). Here, among other things, they found shorter N2 latencies for infants which had received extra visuo-motor stimulation compared a control group. The extra-stimulated group went to baby swimming once a week and the authors argued that this had an indirect effect: Because of more motor training, the infants achieved earlier self-produced locomotion. As I will discuss, this is relevant for this study as it indicates that specific practice in using optic flow may underly the found differences in latencies.

Although both mentioned groups had shorter latencies for forward optic flow compared to reversed, the extra-stimulated group had reversed optic flow latencies comparable to the control group's latencies for forward optic flow. This means that the extra-stimulated group was as efficient in detecting reversed optic flow as the control group was in detecting forwards optic flow. I would argue that this suggests that there does not have to be an asymmetry in our ability to detect the two conditions. While we may be prone to experiencing more forwards optic flow relative to reversed (Shirai et al., 2009; Agyei et al., 2015), the results gotten by Blystad & van der Meer (2022) emphasize that our actions in the

environments we are in shape our latencies. However, as most will use forwards optic flow more than reversed, we are more efficient in detecting the forwards optic flow structure.

In short, by demonstrating that our actions in our environment can shape the N2 latencies, the study by Blystad & van der Meer (2022) can help explain the relative shorter latencies for forwards optic flow compared to reversed in this study. Indeed, a central reason seems to be one's active engagement with the stimuli. The alternative is that the difference is innate, but as I have discussed, it seems more likely that they reflect our experience in different environments. In turn, this has several important implications considering that we use optic flow in a wide arrange of activities (Stoffregen, 1985; Fajen, 2005; Geri et al., 2010; Ludwig et al., 2017). Some specific examples are that this can potentially be useful to intervene with pre-terms (Agyei et al., 2016a), whose dorsal stream specialisation may be disrupted (Taylor et al., 2009). Additionally, this might also be helpful for older people, who are less sensitive to global motion (Conlon & Herkes, 2008). Other groups, such adults who want to improve their decision making in sports, might also benefit. As mentioned, the neuroplastic changes come partly due to use, frequency, and intensity of the stimuli (Kleim & Jones, 2008). If we can manipulate these factors, the study by Blystad & van der Meer (2022) may suggest that we can lower the N2 latencies.

Yet the critical reader will probably point out that the findings in Blystad & van der Meer (2022) is based on infants. While this may show that the N2 component is malleable with practice in infants, it does not necessarily translate to an adult population. While I concede that infants' N2 latencies may be more malleable due to a general higher capacity of plasticity (Gao et al., 2017), I also want to point out that there is evidence to suggest that this is the case for adult population as well. Clark et al. (2015) found, for instance, that the N2 latencies shortened after a five-day period of practice in a discrimination task. They concluded that these changes represented a faster shift of attention to the relevant target.

Though this did not look explicitly on the optic flow paradigm, it does coincide well with Blystad & van der Meer (2022), showing that one can enhance the ability to discriminate stimuli with deliberate practice. Considering how many findings in psychology that have not replicated (Open Science Collaboration, 2015), I am of course open to the possibility that the findings may not generalize and more studies are without a doubt needed. Yet, combining what we know induces plasticity and that Clark et al. (2015) found the N2 latencies in adults to be trainable, it does seem likely that the findings in Blystad & van der Meer (2022) are generalizable to an adult population.

4.3. N2 latencies and ecological psychology

Overall, the notion that the ability to detect optic flow depends on one's previous experience with different environments may support the ecological perspective of a tight link between the subject and the environment. That is, how good we are at detecting optic flow depends on how we have used it previously. This also combines an ecological view of psychology and neuroscience, a combination which has been understudied (de Wit & Withagen (2019).

Neuroscience has had a more mechanistic view (de Wit et al., 2017), meaning that the field have focused on more narrow neural circuits or cells. In these studies, the ecological focus points, such interaction between the subject and environment, has been largely ignored (de Wit & Withagen, 2019). The ignoring has also been reciprocal: the ecological view has historically not been interested in the neural underpinnings (de Wit & Withagen, 2019). In other words, while two fields are highly relevant for each other, have not paid attention to the opposite part.

Until recently, that is. This study is part of an emerging literature (e.g. van der Meer et al., 2008; Agyei et al., 2015; van der Weel et al., 2022) that tries to combine the two

perspectives. For instance, from an ecological perspective, when Agyei et al. (2015) show the close association between being able to detect optic flow and engaging in self-generated locomotion, this may suggest that action is central in the interaction between the environment and the subject. Blystad & van der Meer (2022) further develops this, showing evidence for that action can further enhance the link by making optic flow more available following extra stimulation. The present study's replication of more basic findings regarding the N2 component and optic flow is important as it further increases the validity and reliability of these studies. That is, an assumption in the mentioned studies is that the latencies for the different motion conditions will vary based on how ecological relevant the stimuli are to us. In getting results consistent with this, this study helps making those findings more robust. Importantly, the present study also supports a major implication from such studies with an ecological perspective of psychology: we seem to attune to our environment. In short, based on the literature in neuroplasticity and optic flow, it seems likely that the N2 can change if our active engagement in our environment changes.

Now, as I mentioned in the introduction, one can go away from an ecological perspective and rather look at the results from a more mechanistic neuroplastic perspective. As specific, intensive, and frequent stimulation is known to induce neuroplasticity (Kleim & Jones, 2008), this may spark the question if we need the ecological perspective with its focus on how the one can attune to the environment through actions. However, by examining the neural underpinning from an ecological perspective, one can gain more practical insights for how to use such principles. We do need knowledge of what drives plasticity in general, but it is equally important to understand which specific neural processes which underly our perception. For instance, take my argument regarding the latencies reflect our previous active engagement with optic flow stimuli. If extra optic flow stimulation can shorten the N2 latencies, this may give a suggestion how we can more mechanistic principles of experience-

dependent plasticity if one encounter cases where someone lacks an ability to categorize motion. Ultimately, my point here is the ecological view gives an important perspective in suggesting that behaviour is central in neurally attuning to our environment. Further, this may enhance our understanding of how to intervene in specific situations. Subsequent studies of the N2 component should look at the different ways to see how optic flow stimulation and its effect on the latencies may help various groups of people. If researchers are interested in longitudinal effects, it would be interesting to investigate if adults still benefit from extra stimulation as a child. As the brain operate on a “use it or lose it” principle (Kleim & Jones, 2008), this might indicate that one has to continue with active engagement with optic flow to keep the latencies relatively short. However, even if one is more passive as an adult, it is also possible that extra stimulation as child could have protective effects.

5. Conclusion

This study further supports that we vary in how efficiently we process various motion conditions. As the shorter N2 latencies show, we seem to be more efficient in processing optic flow conditions compared to random visual motion, and more efficient in processing forwards optic flow compared to reversed. A main reason for this may be the asymmetry in the amount of experience. From infancy, optic flow is fundamental to predict the best option for action. Deciding when to turn on a bicycle, stretch out our foot to intercept a ball, or break our car, are all dependant on the incoming visual array. In these processes, we also use more forwards optic flow than reversed, which may explain the relative shorter latencies. As random visual motion may not provide any information which we can use regularly, we seem to be less efficient in detecting such stimuli. Thus, the pathways which process the different conditions vary in how efficient they are. These results are also a part of an emerging

literature looks at the neural aspect of ecological psychology. From this perspective, the differences in latencies may ultimately reflect how attuned we are to different kinds of environments. Taking into considerations how much we use optic flow, the suggestion that the N2 component is malleable might have several important implications. To conclude, we differ in our ability to detect the structure in different types of visual array. A central reason for this might be that our previous active engagement in our environment shape how effective our neural processing is.

6. References

- 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. *Developmental Science*, *18*(3), 436-451.
<https://doi.org/10.1111/desc.12221>
- Agyei, S. B., van der Weel, F. R. & van der Meer, A. L. H. (2016a). Development of visual motion perception for prospective control: Brain and behavioural studies in infants. *Frontiers in Psychology*, *7*. <https://doi.org/10.3389/fpsyg.2016.00100>
- Agyei, S. B., van der Weel, F. R. & van der Meer, A. L. H. (2016b). Longitudinal study of preterm and full-term infants: High-density EEG analyses of cortical activity in response to visual motion. *Neuropsychologia*, *84*, 89-104.
<https://doi.org/10.1016/j.neuropsychologia.2016.02.001>
- American Electroencephalographic (1991). Guidelines for standard electrode position nomenclature. *Journal of Clinical Neuropsychology*, *8*(2), 2000-2202
- Baroncelli, L., Braschi, C. & Maffei, L. (2013). Visual depth perception in normal and deprived rats: Effects of environmental enrichment. *Neuroscience*, *236*, 313-319.
<https://doi.org/10.1016/j.neuroscience.2013.01.036>
- Bells, S., Lefebvre, J., Longoni, G., Narayanan, S., Arnold, D. L., Yeh, E. A. & Mabbott, D. J. (2019) White matter plasticity and maturation in human cognition. *Glia*, *67*(11), 2020-2037. <https://doi.org/10.1002/glia.23661>
- 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/10.1016/0013-4694\(94\)90113-9](https://doi.org/10.1016/0013-4694(94)90113-9)

- Blystad, B. J. & van der Meer, A. L. H. (2022). Longitudinal study of infants receiving extra motor stimulation, full-term control infants, and infants born preterm: high-density EEG analyses of cortical activity in response to visual motion. *Developmental Psychobiology*, 64(5). <https://doi.org/10.1002/dev.22276>
- Chen, R., Niehorster, D. C. & Li, L. (2018). Effect of travel speed on the visual control of steering toward a goal. *Journal of Experimental Psychology: Human Perception and Performance*, 44(3), 425-467. <https://doi.org/10.1037/xhp0000477>
- Clark, K., Appelbaum, L. G., van den Berg, B., Mitroff, S. R. & Woldorff, M. G. (2015). Improvement in visual search with practice: mapping learning-related changes in neurocognitive stages of processing. *Journal of Neuroscience*, 35(13), 5351-5359. <https://doi.org/10.1523/jneurosci.1152-14.2015>
- Cohen, M. X. (2017). Where does EEG come from and what does it mean? *Trends in Neurosciences*, 40(4), 208-218. <https://doi.org/10.1016/j.tins.2017.02.004>
- Conlon, E. & Herkes, K. (2008). Spatial and temporal processing in healthy aging: Implications for perceptions of driving skills. *Aging Neuropsychology and Cognition*, 15(4), 446-470. <https://doi.org/10.1080/13825580701878008>
- Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U. & May, A. (2004). Neuroplasticity: Changes in grey matter induced by training- Newly honed juggling skills show up as a transient feature on a brain-imaging scan. *Nature*, 427(6972), 311-312. <https://doi.org/10.1038/427311a>
- De Wit, M. M. & Withagen, R. (2019). What should a “Gibsonian neuroscience” look like? Introduction to the special issue. *Ecological Psychology*, 31(3), 147-151, <https://doi.org/10.1080/10407413.2019.1615203>

- Elleberg, D., Lavoie, K., Lewis T. L., Maurer, D., Lepore, F. & Guillemot, J.-P. (2003). Longer VEP latencies and slower reaction times to the onset of second-order motion than the order of first-order motion. *Vision Research*, 43(6), 651-658.
[https://doi.org/10.1016/S0042-6989\(03\)00006-3](https://doi.org/10.1016/S0042-6989(03)00006-3)
- Fajen, B. R. & Warren Jr., W. H. (2000). Go with the flow. *Trends in Cognitive Sciences*, 4(10), 369-370. [https://doi.org/10.1016/S1364-6613\(00\)01532-1](https://doi.org/10.1016/S1364-6613(00)01532-1)
- Fajen, B. R. (2005). Calibration, information and control strategies for braking to avoid a collision. *Journal of Experimental Psychology-Human Perception and Performance*, 31(3), 480-501. <https://doi.org/10.1037/0096-1523.31.3.480>
- Fajen, B. R. (2008). Learning novel mappings from optic flow to the control of action. *Journal of Vision*, 8(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/10.1016/S1388-2457\(00\)00533-2](https://doi.org/10.1016/S1388-2457(00)00533-2)
- Fuggetta, G. & Duke, P. A. (2017). Enhancing links between visual short term memory, visual attention and cognitive control processes through practice: An electrophysiological insight. *Biological Psychology*, 124, 48-60.
<https://doi.org/10.1016/j.biopsycho.2017.04.004>
- Furlan, M. & Smith A. T. (2016). Global motion processing in human visual cortical areas v2 and v3. *Journal of Neuroscience*, 36(27), 7314-7324.
<https://doi.org/10.1523/JNEUROSCI.0025-16.2016>

- Gao, W., Lin, Weili, Grewen, K. & Gilmore, J. H. (2017). Functional connectivity of infant human brain: Plastic and modifiable. *The Neuroscientist*, 23(2), 169-184.
<https://doi.org/10.1177/1073858416635986>
- Geri, G. A., Gray, R. & Grutzmacher, R. (2010). Simulating time-to-contact when both target and observer are in motion. *Displays*, 32(2), 59-66.
<https://doi.org/10.1016/j.displa.2009.11.002>
- Gibson, J. J. (1966). *The senses considered as perceptual systems*. Houghton Mifflin.
- Gibson, J. J. (1979/2015). *The ecological approach to visual perception*. Psychology press & routledge classic editions. (1979)
- Gilmore, R. O., Baker, T. J. & Grobman, K. H. (2004). Stability in infants' discrimination of optic flow. *Developmental psychology*, 40(2), 259-270.
<https://doi.org/10.1037/0012-1649.40.2.259>
- Harris, J. M. & Rogers, B. J. (1999). Going against the flow. *Trends in Cognitive Sciences*, 3, 449-1998. [https://doi.org/10.1016/S1364-6613\(99\)01411-4](https://doi.org/10.1016/S1364-6613(99)01411-4)
- Hülsdünker, T., Strüder, H. K. & Andreas, M. (2018). The athletes' visuomotor system- Cortical processes contributing to faster visuomotor reactions. *European Journal of Sport Science*, 18(7), 955-964. <https://doi.org/10.1080/17461391.2018.1468484>
- 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://doi.org/10.1097/00004691-200203000-00002>

- James, K. H. & Swain, S. N. (2011). Only self-generated actions create sensori-motor systems in the developing brain. *Developmental Science*, 14(4), 673-678.
<https://doi.org/10.1111/j.1467-7687.2010.01011.x>
- Klaver, P., Marcar, V. & Martin, E. (2011). Neurodevelopment of the visual system in typically developing children. *Progress in Brain Research*, 189, 113-136.
<https://doi.org/10.1016/B978-0-444-53884-0.00021-X>
- Kleim, J. A. & Jones, T. A. (2008). Principles of experience-dependant neural plasticity: implications for rehabilitation after brain damage. *Journal of Speech, Language, And Hearing Research*, 51(1), 225-239. [https://doi.org/10.1044/1092-4388\(2008/018\)](https://doi.org/10.1044/1092-4388(2008/018))
- Kuba, M., Kubova, Z., Kremlacek, J. & Langrova, J. (2007). Motion-onset VEPs: Characteristics, methods, and diagnostic use. *Vision Research*, 47(2), 189-202.
<https://doi.org/10.1016/j.visres.2006.09.020>
- Laycock, R., Crewther, D. P., Fitzgerald, P. B. & Crewther, S. H. (2007). Evidence for fast signals and later processing in human V1/V2 and V5/MT+: a TMS study of motion perception. *Journal of Neurophysiology*, 98(3), 1253-1262.
<https://doi.org/10.1152/jn.00416.2007>
- Lee, D. N. (1980). The optic flow field: the foundation of vision. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 290(1038), 169-179. <https://doi.org/10.1098/rstb.1980.0089>
- Li, L. & Cheng, J. C. K. (2013). Visual strategies for the control of steering toward a goal. *Displays*, 34(2), 97-104. <https://doi.org/10.1016/j.displa.2012.10.005>

Li, L. & Niehorster, D. C. (2014). Influence of optic flow on the control of heading and target egocentric direction during steering toward a goal. *Journal of Neurophysiology*, 112(4), 766-777. <https://doi.org/10.1152/jn.00697.2013>

Low, L. K. & Cheng, H. J. (2006). Axon pruning: an essential step underlying the developmental plasticity of neuronal connections. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 361(1473), 153-1544. <https://doi.org/10.1098/rstb.2006.1883>

Luck, S. J. (2005). *An introduction to the Event-Related Potential technique*. Cambridge, MA: MIT Press

Luck, S. J. & Gaspelin, N. (2016). How to get statistically significant effects in any ERP experiment (and why you shouldn't). *Psychophysiology*, 54(1), 146-157. <https://doi.org/10.1111/psyp.12639>

Ludwig, C. J. H., Alexander, N., Howard, K. L., Jedrejewska, A. A., Mundkur, I. & Redmill, D. (2017). The influence of visual flow and perceptual load on locomotion speed. *Attention, Perception & Psychophysics*, 80, 69-81. <https://doi.org/10.3758/s13414-017-1417-3>

McKeefry, D. J., Burton, M. P., Vakrou, C., Barrett, B. T. & Morland, A. B. (2008). Induced deficits in speed perception by transcranial magnetic stimulation of human cortical areas V5/MT and V3A. *Journal of Neuroscience*, 28(27), 6484-6857. <https://doi.org/10.1523/JNEUROSCI.1287-08.2008>

Nakhla, N., Korkian, Y., Krause, M. R. & Pack, C. C. (2021). Neural selectivity for visual motion in macaque area V3A. *eNeuro*, 8(1). <https://doi.org/10.1523/ENEURO.0383-20.2020>

Nanez Sr. J. & Yonas, A. (1994). Effects of luminance and texture motion on infant defensive reactions to optical collision. *Infant Behavior and Development*, 17(2), 165-174.

[https://doi.org/10.1016/0163-6383\(94\)90052-3](https://doi.org/10.1016/0163-6383(94)90052-3)

Open Science Collaboration (2015). Estimating the reproducibility of psychological science. *Science*, 329(6251). <https://doi.org/10.1126/science.aac4716>

Pascual-Leone, A., Amedi, A., Fregni, F. & Merabet, L. B. (2005). The plastic human brain cortex. *Annual Review of Neuroscience*, 28, 377-401.

<https://doi.org/10.1146/annurev.neuro.27.070203.144216>

Pavlov, Y. G., Adamian, N., Appelhoff, S., Arvanet, M., Benwell, C. S. Y., Beste, C., Bland, A. R., Bradford, D. E., Bublatzky, F., Busch, N. A., Clayson, P. E., Cruse, D., Czeszumski, A., Dreber, A., Dumas, G., Ehinger, B., Ganis, G., He, X., Hinojosa, J. A., ... Mushtaq, F. (2021). #EEGmanylabs: Investigating the replicability of influential EEG experiments. *Cortex*, 144, 213-229.

<https://doi.org/10.1016/j.cortex.2021.03.013>

Perrin, F., Pernier, J., Bertrand, O. & Echallier, J.F. (1989) Spherical lines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology*, 72, 184-187. [https://doi.org/10.1016/0013-4694\(89\)90180-6](https://doi.org/10.1016/0013-4694(89)90180-6)

Perry, C. J. & Fallah, M. (2014). Feature integration and object representation along the dorsal stream visual hierarchy. *Frontiers in Computational Neuroscience*, 8(84).

<https://doi.org/10.3389/fncom.2014.00084>

Picton, T. W., Bentin, S., Berg, P., Donchin E., Hillyard, S. A., Johnson R., Miller., G. A., Ritter, W., Ruchkin, M.D. & Rugg, 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/10.1111/1469-8986.3720127>

- Probst, T., Plendl, H., Paulus, H., Wist, E. R. & Scherg, M. (1993). Identification of the visual motion area (area V5) in the human brain by dipole source analysis. *Experimental Brain Research*, 93(2), 345-351. <https://doi.org/10.1007/BF00228404>
- Raffi, M., Persiani, M., Piras, A. & Squarito, S. (2014). Optic flow neurons in area P_{EC} integrate eye and head position signals. *Neuroscience Letters*, 568, 23-28. <https://doi.org/10.1016/j.neulet.2014.03.042>
- 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. *Experimental Brain Research*, 239, 3143-3154. <https://doi.org/10.1007/s00221-021-06195-5>
- Rushton, S. K., Harris, J. M., Lloyd, M. R. & Wann, J. P. (1998). Guidance of locomotion on foot uses perceived target location rather than optic flow. *Current Biology*, 8(21), 1191-1194. [https://doi.org/10.1016/S0960-9822\(07\)00492-7](https://doi.org/10.1016/S0960-9822(07)00492-7)
- Sack, A. T., Kohler, A., Linden, D. E., 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>
- Salinas, M. M., Wilken, J. M. & Dingwell, J. B. (2017). How humans use visual optic flow to regulate stepping during walking. *Gait & Posture*, 57, 15-20. <https://doi.org/10.1016/j.gaitpost.2017.05.002>
- Sarre, G., Berard, J., Fung, J. & Lamontagne, A. (2008). Steering behaviour can be modulated by different optic flows during walking. *Neuroscience Letters*, 436(2), 96-101. <https://doi.org/10.1016/j.neulet.2008.02.049>

- Schoups, A., Vogels, R., Qian, N. & Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. *Nature*, 412, 549-553.
<https://doi.org/10.1038/35087601>
- Shirai, N. Kanazawa, S. & Yamaguchi, M. K. (2004). Asymmetry for the perception of expansion/contraction in infants and adults. *Infant Behavior and Development*, 23(3), 315-322. <https://doi.org/10.1016/j.infbeh.2003.12.004>
- Shirai, N., Birtles, D., Wattem-Bell, J., Yamaguchi, M. K., Kanazawa, S., Atkinson, J. & Braddick, O. (2009). Asymmetrical cortical processing of radial expansion/contraction in infants and adults. *Developmental Science*, 12(6), 946-955.
<https://doi.org/10.1111/j.1467-7687.2009.00839.x>
- Siegel, R. M. & Read, H. L. (1997). Analysis of optic flow in the monkey parietal area 7A. *Cerebral Cortex*, 7(4), 327-346. <https://doi.org/10.1093/cercor/7.4.327>
- Sigman, M., Pan, H., Yang, Y., Stern, E., Silbersweig, D. & Gilbert, C. D. (2005). Top-down reorganization of activity in the visual pathway after learning a shape identification task. *Neuron*, 46(5), 823-835. <https://doi.org/10.1016/j.neuron.2005.05.014>
- Smith, A. T., Wall, M. B. Williams, A. L. & Singh, K. D. (2006). Sensitivity to optic flow in human cortical areas MT and MST. *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(5), 554-564. <https://doi.org/10.1037/0096-1523.11.5.554>

- Srinivasan, R. (1999). Methods to improve spatial resolution in EEG. *International Journal of Bioelectromagnetism*, 1(1), 107-116.
- Taylor, N. M., Jakobson, L. S., Maurer, D. & Lewis, T. L. (2009). Differential vulnerability of global motion, global form, and biological motion processing in full-term and preterm children. *Neuropsychologia*, 47, 2766-2778.
<https://doi.org/10.1016/j.neuropsychologia.2009.06.001>
- Tohyama, K. & Fukushima, K. (2005). Neural network model for extracting optic flow. *Neural Networks*, 18(5-6), 549-556. <https://doi.org/10.1016/j.neunet.2005.06.039>
- 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. *Experimental Brain Research*, 186, 493-502.
<https://doi.org/10.1007/s00221-007-1251-2>
- Van der Weel, F. R., Sokolovskis, I., Raja, V. & van der Meer, A. L. H. (2022). Neural aspects of prospective control through resonating taus in an interceptive timing task. *Brain Sciences*, 12(12). <https://doi.org/10.3390/brainsci12121737>
- Vetter, P., Grosbras, M. & Muckli, L. (2015). TMS over V5 disrupts motion prediction. *Cerebral Cortex*, 25(4), 1052-1059. <https://doi.org/10.1093/cercor/bht297>
- Vilhelmsen, K., van der Weel, F. R. & van der Meer, A. L. H. (2015). A high-density study of differences between three high speeds of simulated forward motion from optic flow in adult participants. *Frontiers in Systems Neuroscience*, 9.
<https://doi.org/10.3389/fnsys.2015.00146>
- Vilhelmsen, K., Agyei, S. B., van der Weel, F. R. & van der Meer, A. L. H. (2019). A high-density EEG study of differentiation between two speeds and direction of simulated

optic flow in adults and infants. *Psychophysiology*, 56(1).

<https://doi.org/10.1111/psyp.13281>

Yu, C. P., Page, W. K., Gaborski, R. & Duffy, C. J. (2010). Receptive field dynamics underlying MST neuronal optic flow selectivity. *Journal of Neurophysiology*, 103(5), 2394-2808. <https://doi.org/10.1152/jn.01085.2009>

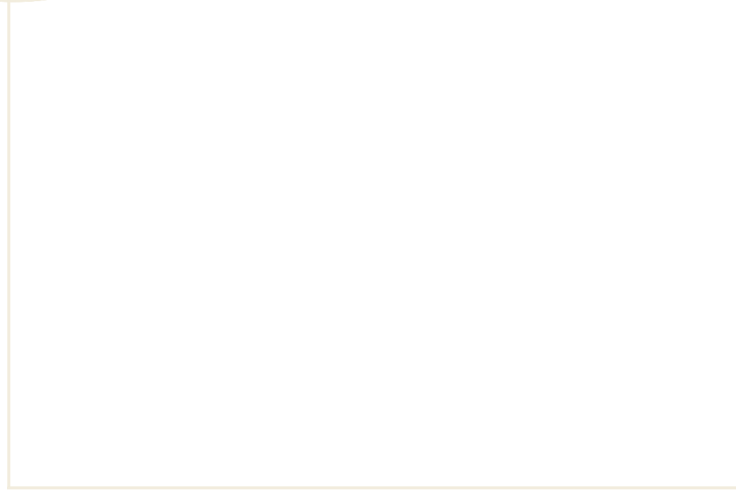
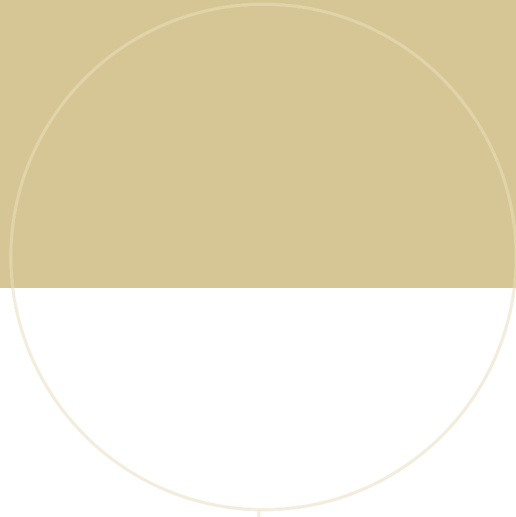
Wall, M. B. & Smith, A. T. (2008). The representation of egomotion in the human brain. *Current Biology*, 18(3), 191-194. <https://doi.org/10.1016/j.cub.2007.12.053>

Wann, J. & Land, M. (2000). Steering with or without the flow: is the retrieval of heading necessary? *Trends in Cognitive Sciences*, 4, 319-324
[https://doi.org/10.1016/S1364-6613\(00\)01513-8](https://doi.org/10.1016/S1364-6613(00)01513-8)

Warren Jr., W. H., Kay, B. A., Zosh, W. D., Duchon. A. P. & Sahuc, S. (2001). Optic flow is used to control human walking. *Nature Neuroscience*, 4, 213-216.
<https://doi.org/10.1038/84054>

Wattam-Bell, J., Birtles, D., Nyström, P., von Hofsten, C., Rosander, K., Anker, S., Atkinson, J. & Braddick, O. (2010). Reorganization of global form and motion processing during human visual development. *Current Biology*, 20(5), 411-415.
<https://doi.org/10.1016/j.cub.2009.12.020>.

Woodman, G. F. (2010). A brief introduction to the use of event-related potentials in studies of perception and attention. *Attention Perception and Psychophysics*, 72(8), 2031-2046. <https://doi.org/10.3758/APP.72.8.2031>



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