Preattentive processing of visually guided self-motion in humans and monkeys

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**Abstract**

The visually-based control of self-motion is a challenging task, requiring immediate adjustments to keep on track. Accordingly, it would appear advantageous if the processing of self-motion direction (heading) was predictive, thereby accelerating the encoding of unexpected changes, and un-impaired by attentional load. We tested this hypothesis by recording EEG in humans and macaque monkeys with similar experimental protocols.

Subjects viewed a random dot pattern simulating self-motion across a ground plane in an oddball EEG paradigm. Standard and deviant trials differed only in their simulated heading direction (forward-left vs. forward-right). Event-related potentials (ERPs) were compared in order to test for the occurrence of a visual mismatch negativity (vMMN), a component that reflects preattentive and likely also predictive processing of sensory stimuli. Analysis of the ERPs revealed signatures of a prediction mismatch for deviant stimuli in both humans and monkeys. In humans, a MMN was observed starting 110 ms after self-motion onset. In monkeys, peak response amplitudes following deviant stimuli were enhanced compared to the standard already 100 ms after self-motion onset. We consider our results strong evidence for a preattentive processing of visual self-motion information in humans and monkeys, allowing for ultrafast adjustments of their heading direction.

**1. Introduction**

Navigation through an environment is a challenging task. Signals from different sensory modalities have to be combined and motor output has to be adjusted – if needed – to keep on track. It would appear advantageous if this processing was predictive and quasi-reflexive, i.e. independent from attentional load. Predictive coding is suggested to facilitate sensory processing by attenuating responses to predictable sensory information and enhancing responses to unpredicted events like unexpected changes in heading (Rao and Ballard, 1999; Friston, 2005).

Along the same vein, a preattentive processing of self-motion direction could accelerate and thereby facilitate successful navigation irrespective of cognitive load. In this respect, heading would be different to path integration whose accuracy has been shown to be modulated by a secondary task (Glasauer et al., 2009).

A specific electroencephalography (EEG)-component, the so-called visual mismatch negativity (vMMN), has been suggested to be indicative of predictive and preattentive processing of sensory stimuli (Iberi, 2011; Stefanics et al., 2018). The MMN is typically recorded in an oddball experiment (Kimura, 2012; Stefanics et al., 2014) and computed as the difference between two event-related potentials (ERPs). Deviant stimuli elicit a more negative N2 ERP-component than frequently presented standard stimuli (Luck, 2005), which leads to the MMN (deviant-standard). The MMN typically peaks in a time window between 100 and 400 ms after stimulus onset on parietal electrodes (Kimura, 2012; Czigler, 2014). In the predictive coding framework this component has the important role of carrying the prediction error elicited by the mismatch of a sensed event with the predictions formed by prior experience (Friston, 2005; Winkler and Czigler, 2012; Stefanics et al., 2014).

**Keywords:** Self-motion, Mismatch negativity (MMN), Non-human primate, EEG, Heading

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1 Shared first authorship.
Originally the MMN was described in the auditory domain (Naatanen et al., 1978; Winkler and Czigler, 2012), but in recent years several studies reported a visual mismatch negativity (vMMN) component in humans for various stimulus features (Amenedo et al., 2007; Kimura et al., 2010; Müller et al., 2010; Hesse et al., 2017; Schmitt et al., 2018; Czigler et al., 2019). Previous studies introduced secondary tasks to distract participants’ attention away from the MMN-inducing stimulus and towards objects or features unrelated to the stimulus under study (Pazo-Alvarez et al., 2004; Stefanics et al., 2012; Li et al., 2012; Kuhlkepp et al., 2013; Hesse et al., 2017; Schmitt et al., 2018). Remarkably, MMN-components have been shown also under such experimental conditions. This led to the conclusion that the MMN is independent of attentional load or pre-attentive (Maekawa et al., 2005; Czigler, 2007; Müller et al., 2013; Yu et al., 2017; Stefanics et al., 2018).

In previous studies on the key animal model of human sensory processing, i.e. the macaque monkey, MMN-components have been found after the presentation of auditory stimuli (Javitt et al., 1992, 1994; Fishman and Steinschneider, 2012; Gil-da-Costa et al., 2013; Takaura and Fujii, 2016). In most of these studies, however, EEG was recorded with implanted electrodes (Javitt et al., 1992, 1994; Fishman and Steinschneider, 2012; Takaura and Fujii, 2016). Only a few studies so far succeeded to record non-invasive, human-like scalp-EEG (e.g. Schmid et al., 2006; Gil-da-Costa et al., 2013; Sandhaeger et al., 2019). The goal of our study was twofold: first, we wanted to probe our hypothesis that visually-based heading is processed ultrafast and unimpaired by attentional load as indicated by the occurrence of a MMN. Second, given its existence in humans, we wanted to test for such MMN in monkeys. The visual optical flow only up to a scalable factor (Bremmer and Lappe, 1997; Pelli, 1997; Kleiner et al., 2007) on a standard Windows (v7, Microsoft, Redmond, USA) PC (Dell Precision T5810, Round Rock, USA). Without references, distance and speed can be determined from visual optical flow only up to a scalable factor (Bremmer and Lappe, 1997). The simulated height of the observer was 1.6 arbitrary units (a.u.) above ground level, and simulated velocity was 8.33 a.u./s. The simulated visibility, i.e., the maximum visible distance that the observer could see from any point on the plane, was 25 a.u. Scene details beyond this point were not displayed on the screen. The ground plane stimulus was composed of 660 white dots (luminance 57 cd/m$^2$), in the attention on the ground plane condition the dots could change to light grey with a luminance of 40 cd/m$^2$ with a limited lifetime of 1 s on a black background (luminance 0.1 cd/m$^2$). It covered the full horizontal width of the screen (central 42 degrees of the visual field) and 10.9′ in the lower 25 years) with normal or corrected to normal vision participated in our study. Prior to the experiment they provided written informed consent. Our study was in accordance with the Declaration of Helsinki and was approved by the local Ethics Committee. All participants finished data collection on four different days. They were compensated with 8 € per hour.

2.1.2. Setup
Participants were sitting in a darkened, sound attenuated and electrically shielded room. The stimuli were presented on a computer monitor (VPixx Technologies Inc., Saint-Bruno, QC, Canada) 68 cm in front of them at eye level. The participants’ heads were stabilized by a chin rest. The display was 42′ wide and 24′ high and was set to a resolution of 1920 × 1080 pixels at a refresh rate of 100 Hz. Eye movements were recorded using an EyeLink 1000 system (SR Research, ON, Canada). Trials containing blinks and other movement artefacts were excluded from further offline data analysis (see below).

2.1.3. Stimulus
We presented an optic flow stimulus to our participants which simulated self-motion across a ground plane with heading directed either forward and 10′ to the left or 10′ to the right (Fig. 1). This self-motion stimulus was implemented using Matlab R2010a (v7.10) (MathWorks, Natick, USA) and the psychophysics toolbox (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007) on a standard Windows (v7, Microsoft, Redmond, USA) PC (Dell Precision T5810, Round Rock, USA). Without references, distance and speed can be determined from visual optical flow only up to a scalable factor (Bremmer and Lappe, 1997). The simulated height of the observer was 1.6 arbitrary units (a. u.) above ground level, and simulated velocity was 8.33 a.u./s. The simulated visibility, i.e., the maximum visible distance that the observer could see from any point on the plane, was 25 a.u. Scene details beyond this point were not displayed on the screen. The ground plane stimulus was composed of 660 white dots (luminance 57 cd/m$^2$), in the attention on the ground plane condition the dots could change to light grey with a luminance of 40 cd/m$^2$ with a limited lifetime of 1 s on a black background (luminance 0.1 cd/m$^2$). It covered the full horizontal width of the screen (central 42 degrees of the visual field) and 10.9′ in the lower

![Fig. 1. Self-motion stimulus for the two headings forward to the left and to the right.](image-url)
part of visual field (starting 1.1 degrees below the fovea). Dot size increased when approaching the virtual observer, ranging from 1.5 pixel radius at the furthest distance up to 25 pixels radius when being closest to the observer. In addition, a central white fixation dot with a radius of 3 pixels (57 cd/m²) was displayed throughout each trial. In the first phase of each trial ground plane dots were shown stationary for a random time between 600 ms and 1000 ms. In the second phase self-motion across the ground plane was simulated by moving the dots for 400 (+/-50) ms. One of the movement directions was shown as the standard stimulus (80 % occurrence), the other one as deviant stimulus (20 % occurrence). Across sessions, deviant and standard directions were counterbalanced. For further analysis, all data were aligned to self-motion onset.

2.1.4. Task
The main task of the participants was to fixate the central target. An additional secondary task was introduced to control the participants focus of attention. The task was one of two different attention conditions. A luminance change could affect either the fixation target or the ground plane. In the “attention on the fixation target” condition, a small black dot (radius 2 pixels) appeared in the middle of the fixation target in 10 % of all trials, i.e. in 320 trials. In the “attention on the ground plane” condition, the white dots of the ground plane changed to grey in 10 % of all trials, i.e. in another 320 trials. These changes appeared randomly in a time window from self-motion start to 100 ms before self-motion end and stayed throughout the rest of the trial. Participants were asked to press the key “S” on the numerical pad of a regular computer keyboard located in front of them as soon as they got aware of it. Trials with a luminance change were excluded from further offline data analysis. Due to the smaller number of deviant trials the attention task only appeared in standard trials. On each day of data collection we presented only one of the two attention conditions. Before the start of the experiment participants were informed about this condition.

2.1.5. Procedure
On each of the four days of the experiment we collected data from eight sessions: four of them with heading to the left as deviant stimulus and four with heading to the right as deviant stimulus. Each session consisted of 200 trials. This leads to a total number of 6400 trials per participant. The sequence of movement directions was pseudorandomized across blocks and participants. On the first two days of data collection we presented the condition “attention on the fixation target” and on the other two days the condition “attention on the ground plane”.

2.1.6. EEG recordings
We used an actiCHamp module (Brain Products GmbH, Gilching, Germany) and the software Brain Vision PyCorder (Brain Vision LLC, Morisville, NC, USA) to record the electroencephalogram (EEG) continuously throughout the whole experiment at 1000 Hz at each electrode. We used 64 active Ag/AgCl electrodes positioned according to the extended international 10–20 system. Principally the impedances of all electrodes were kept below 5 kΩ during the whole experiment.

2.1.7. Analysis
For the offline analysis of our EEG data we used the software Brain Vision Analyzer (Brain Products, Gilching, Germany). First, we redefined the average signal of the two mastoid electrodes TP9 and TP10 as our new reference electrode during data collection: Cz. Then we applied a Notch filter at 50 Hz, a low pass filter with a cut-off frequency of 80 Hz and a high pass filter with a cut-off frequency of 3 Hz. Next, we excluded all trials with blinks or eye movements as well as all trials which showed one of the two attention tasks (10 % each) from further analysis because motor responses were induced in these trials. Based on these exclusion criteria, approximately 25 % of all trials were removed.

All remaining data were aligned to the onset of the self-motion phase and epochs with a length of 550 ms (50 ms before motion onset to 500 ms after motion onset) were extracted from the continuous data stream. Each epoch was baseline corrected (centered) using the average signal from -50 ms to 0 ms relative to motion onset. In a last step all those epochs were averaged for subjects and conditions separately.

To calculate the MMN-component we compared data for a given heading direction collected in deviant trials with data for the same heading direction collected in standard trials (deviant-standard). In half of the sessions this given self-motion direction served as standard stimulus, while in the other half it served as deviant.

The onset time of the MMN was calculated on a single subject basis using the following bootstrapping procedure. For each movement direction, a random subset was drawn from the (larger) set of ‘standard’ trials, matching the number of trials in the ‘deviant’ set for the identical direction, and the resulting difference (standard-deviant) was calculated. This procedure was repeated 1000 times to obtain a statistical distribution. Subsequently, for each participant we could identify the times when the 95 % confidence interval of the mean difference did not include zero for the last time before the MMN peak time. This MMN onset time was averaged over all participants to define the analysis time window. The average was based on the participants who showed a confidence interval different from zero around the MMN-component (self-motion to the right: attention on fixation target: 10 participants; attention on ground plane: 9 participants; self-motion to the left: attention on fixation target: 9 participants, attention on ground plane: 10 participants).

For our statistical analysis we compared ERPs in a fixed temporal window from 110 ms to 160 ms after self-motion onset. We aimed to cover the full time course of the MMN-component and based the decision for this time window on the peak time of the MMN and the mean MMN onset time determined for all participants.

In order to facilitate comparison between human and monkey EEG data, we compared the total oscillatory power of the difference VEP (deviant-standard. See Section 2.2.4 for details). In order to mimic the approach concerning the monkey data, we choose a rather broad region of interest for the human data, comprising all parietal and occipital electrodes (17 electrodes in total).

2.2. EEG in monkeys
We performed scalp EEG recordings in two head-restrained male macaque monkeys (macaca mulatta, monkeys O and S, weighing 10 kg and 9.6 kg, respectively). All procedures, including housing, animal care, surgical and experimental procedures were carried out in accordance with applicable regulations and approved by the responsible regional government office (Regierungspräsidiun Gießen: V 54 - 19 c 20 15 h 01 MR 13/1, Nr. G 71/2017). Prior to the start of experiments, the animals were implanted surgically with a head-holding system. Anesthesia for this procedure was induced initially by Rompun/ketamine and subsequently maintained by i.v. propofol/fentanyl injection, and analgesics were administered postoperatively.

2.2.1. EEG procedure and electrode arrangements
The head-holding system used in this study was mounted to the skull at two baseplates located in frontal and occipital positions along the midline, allowing placement of an EEG cap and electrodes on the scalp. One monkey was additionally implanted with a recording chamber centered on a circular craniotomy (outer diameter of the chamber 21 mm) for use in a different experiment (monkey O). The chamber was located above the intraparietal sulcus on the right hemisphere, restricting placement of electrodes in this monkey. In total, data from 6 electrodes in monkey O and 15 electrodes in monkey S were recorded. For electrode placements see Fig. 5A. The same type of recording system as for the human subjects was used (BrainProducts actiCHamp amplifier with active Ag/AgCl electrodes). The electrodes were placed on the scalp using a custom-design cap (actiCAP, BrainProducts LLC), fixed with
straps to the front part of the monkey chair. Electrode impedances were kept below 5 k\(\Omega\) for the duration of the experiment. It should be noted that the electrode labels used in the monkeys are given only as an approximation of the locations relative to the standard 10–20 arrangement that was used for the human participants. As discussed in more detail below, the differences in anatomy hinder a direct transfer of electrode positions between the species. Consequently, identically labeled electrodes should not be assumed to be located above homologous cortical regions.

2.2.2. Experimental setup

Each monkey sat in a chair with its head restrained in a dark room in front of a projection screen (viewing distance 114 cm). The stimuli were presented using a PROPixx DLP LED projector (ViewPixx Technologies) at a resolution of 1920 \times 1080 pixels and 100 Hz refresh rate. The projection screen was approx. 79° wide and 49° high. Eye-movements were monitored at 500 Hz continuously using an EyeLink 1000 (SR Research, ON, Canada).

2.2.3. Stimulus and task

The stimulation procedure followed the same pattern as for the human subjects. The self-motion stimulus was built using Matlab R2012a (v7.14) (MathWorks, Natick, USA) and the psychophysics toolbox (Kleiner et al., 2007) after the stimulus used for human participants. The slightly different setups in the human and monkey experiments resulted in some parameters differing from the stimulus presented to the human participants which was described earlier. The white dots of the ground plane presented on a dark background had a luminance of 39 cd/m\(^2\). The ground plane covered the full horizontal width of the screen (central 79 degrees of the visual field) and 22.8° in the lower part of visual field (starting 1.7 degrees below the fovea). The monkey was trained to maintain fixation on a central red fixation dot (15 \times 15 pixels) throughout the trial and was given liquid reward after each successfully completed trial. Following initial fixation, the ground plane stimulus appeared and first remained stationary for 350 (+/- 100 ms).

Subsequently self-motion was simulated for 700 ms with a movement direction of forward 10 deg to the left or to the right. Like in the human EEG recordings, the directions were presented as standard and deviant (80% and 20%) in experimental blocks, and the respective standard direction was counterbalanced across blocks. The presented data were collected over multiple days and comprise between 425 and 678 trials within each sub-condition (combinations of movement direction and standard/deviant; after balancing trial numbers to account for the higher number of trials in the standard condition).

2.2.4. Analysis

Data processing and analysis were performed using MATLAB (Mathworks) and the FieldTrip toolbox (Oostenveld et al., 2011). The recorded EEG was first re-referenced to the activity from a frontal electrode (monkey S: Fz; monkey O: F1). It should be noted that the location of the reference for monkey O was not on the midline due to the asymmetrical electrode arrangement. This introduces a lateralized component to the observed potentials which should be considered in the interpretation of the results.

Like for the human data, we applied a Notch filter at 50 Hz, a low pass filter with a cut-off frequency of 80 Hz and a high pass filter with a cut-off frequency of 3 Hz to the re-referenced data. Epochs with signal artefacts (e.g. from body movements) in the relevant time window were discarded. Data from each trial were baseline-corrected by subtracting the average activity in the 150 ms immediately before movement onset. ERPs were then calculated by aligning the data to this movement onset and averaging over trials within each direction and condition (standard/deviant) as described above.

Unlike for the analysis of the human data, our comparison of standard and deviant conditions in the monkeys could not rely on grand average ERPs over the population of subjects. Therefore, we conducted the statistical analysis and the MMN onset time for each monkey using a bootstrapping procedure described above. Due to the non-standard shape of the VEP as a result of the close, frontal reference, we were not able to isolate the canonical VEP-components (as homologues to the human data) with certainty. Thus, we relied instead on the total oscillatory power of the VEP in our comparison of the two conditions. To this end, we calculated a continuous wavelet-transform of the trial-average VEP in each condition. We then determined the time-frequency window in which the VEPs were defined (0–300 ms after motion onset, 3–15 Hz), and averaged power within this window for each condition.

Owing again to the non-standard electrode arrangements, we relied on a broader region of interest in our selection of electrodes for the main analysis. This included all parietal and occipital electrodes (4 in monkey O, and 8 in monkey S), which comprised the region of the main potential in response to self-motion onset in both monkeys (cf. Results).

3. Results

In our study, we presented to humans and monkeys an optic flow stimulus simulating forward self-motion with two different headings (forward to the left and right, Fig. 1) alternately as standard and deviant stimulus in an oddball experiment. We analyzed the resulting EEG data for the existence of a heading-related vMMN-component.

3.1. Human participants

3.1.1. Behavioral performance

In order to draw the subjects’ attention away from the visual feature under study, i.e. self-motion direction, we employed them in a secondary, luminance change detection task of either the central fixation target or the moving ground-plane stimulus. This task was intended to be rather difficult to capture our participants’ attention. Our results show a correct response rate between 43% and 64% (mean: 52%) for attention directed towards the fixation target. This corresponds to 65–195 true positives per subject, while we recorded false positives in only one subject (8 false positives in total). For attention directed towards the luminance-change of the ground plane stimulus we found between 35% and 56% (mean 45%) correct performance. This corresponds to 77–178 true positives per subject, with only 0–8 false positives per subject, except for one subject who had 29 false positives, but also 144 true positives.

3.1.2. Probing for preattentive visually-based heading processing

We analyzed the EEG-activity recorded at electrode Pz averaged across all participants (Fig. 2). Data was aligned to simulated self-motion onset which induced in all cases (standard and deviant trials) a clear visual evoked potential (VEP): a first positive peak (P1) at around 85 ms, a negative peak (N2) around 150 ms and a second positive peak (P2) around 220 ms after self-motion onset. In all four experimental conditions (heading to the left or right, attention towards the fixation target or the ground plane), the N2-peak was more negative for data collected in deviant trials compared to standard trials. The difference (deviant trials compared to standard trials. The difference (deviant–standard, depicted in red) shows the resulting vMMN which peaked at around 135 ms after self-motion onset (self-motion to the left: attention on fixation target (A): 136 ms; attention on ground plane (C): 132 ms; self-motion to the right: attention on fixation target (B): 139 ms; attention on ground plane (D): 131 ms). The start of the MMN-component was determined on a single subject basis as described in the methods section. The mean across all participants ranged from 105 ms to 115 ms after self-motion onset, dependent on the experimental condition (self-motion to the right: attention on ground plane: 105 (+15) ms; attention on fixation target: 115 (+17) ms; self-motion to the left: attention on ground plane: 106 (+7) ms; attention on fixation target: 114 (+13) ms). In all four conditions, the VEP-difference, i.e. the vMMN, in a time window ranging from 110 ms to 160 ms after self-motion onset was significant (Fig. 2): (One-sided t-test: A: t(11)=-5.18,
As a second approach, we compared the total oscillatory power in a broad region of interest comprising all occipital and parietal electrodes (in total 17 electrodes). We computed for each condition the average power of the VEP in a time frequency window (3–15 Hz; 0–300 ms) of interest when investigating the VEP response to motion onset (Fig. 3).

We found a significant difference between the standard and deviant condition for both attention conditions as well as both self-motion directions (two-sided t-test of the mean power across the region of interest: attention directed towards the fixation target, self-motion to the left: t(11) = 3.25, p = 0.008; self-motion to the right: t(11) = 4.5, p = 0.0009; attention directed towards the ground plane, self-motion to the left: t(11) = 5.27, p = 0.0003; self-motion to the right: t(11) = 5.79, p = 0.0001).

3.1.3. Lateralization of the processing of self-motion information

Recent studies suggested lateralized processing of self-motion information in primates with more neurons being tuned for contraversive headings (Greenlee et al., 2016; Bremmer et al., 2017; Schmitt et al., 2020). The experimental approach of our current study allowed to further investigate this lateralization in heading processing. We determined the VEP-difference (deviant - standard) at all electrodes and show the group data in a topographic plot (Fig. 4 A and B). Negative VEP values are displayed in blue. For both headings, forward to the left and right, respectively, a vMMN-component could be observed over parietal and occipital electrodes. The vMMN was indeed slightly lateraled, i.e. shifted towards electrodes in the hemisphere contralateral to the simulated self-motion direction. This can easily be seen in Fig. 4C and E which present difference maps (heading to the left – heading to the right) for both attention conditions. They show a bi-phasic topography: positive values in the left hemisphere and negative values in the right hemisphere. This bi-phasic pattern is indicative of a lateralized vMMN.

In order to quantify this effect of a stronger contralateral vMMN-component we pooled data from four electrodes each in the left and right hemispheres: electrodes O1, P03, P1 and CP2 over the left hemisphere and electrodes O2, PO2, P2 and CP2 over the right hemisphere. These electrodes showed a significant vMMN in all four conditions (two different headings and two attention conditions) as determined using a cluster-based permutation test on the event related data. We collapsed data from both hemispheres to obtain two time courses of the vMMN: one for contra- and one for ipsiversive self-motion with respect to the EEG electrodes. This data is presented for the two attention conditions separately in Fig. 4D and F. In both cases the vMMN-component for contraversive self-motion was stronger than for ipsiversive self-motion. This effect, however, was statistically significant only for data with attention directed towards the ground plane (Paired one-sided t-tests for VEPs. Attention directed towards the fixation target: time window 110–160 ms: t(11)=1.29, p = 0.11; attention directed towards the ground plane: time window 110–160 ms: t(11)=2.86, p = 0.008).

3.2. Non-human primate participants

We recorded scalp EEG from two macaque monkeys while they were presented with similar self-motion stimuli as the human subjects. The paradigm also followed the same procedure (standard and deviant directions presented in 80 % and 20 % of the trials, respectively), with the exception that there was no additional attention task. Instead, monkeys were rewarded to keep fixation of a small central target throughout each trial.

Fig. 5 shows the average recorded activity across all occipital and parietal electrodes for both monkeys (4 and 8 for monkey O and S, respectively) and movement direction forward to the left. As expected, we found a clear VEP in response to movement onset (aligned to t = 0 ms) at latencies ranging from ~75 ms to 300 ms. The succession of VEP-components was very similar between the two monkeys, but followed an overall higher frequency oscillation than the human VEPs. We speculate that this difference is attributable to the fact that here the offline reference electrodes were located over the cortex (and in close proximity to the region of interest). The re-referenced activity thus reflects the difference between neighboring dipoles, which may have
resulted in the observed waveforms. The comparison between conditions in Fig. 5 shows that, for both monkeys, the deviant stimulus evoked peaks of higher amplitude than the standard. This effect is equally present for negative and positive deflections in the VEP, and is reflected in significant deviations of the VEP-difference (red, shaded area representing the bootstrapped 95 % CI) from zero. The same pattern was observed for the movement direction forward to the right (data not shown). The observed VEP waveforms did not allow us to isolate a single component as homologue to the human N2 with certainty. Therefore, we tested for the between-condition effect by comparing the total oscillatory power of the VEP in its corresponding time/frequency window (3–15 Hz; 0–300 ms), based on a continuous wavelet-transform of the trial-averaged data. The window boundaries were chosen post-hoc to contain the full response in both monkeys. Using a bootstrapping procedure, we calculated a 95 % CI of the power in the standard condition at individual electrodes, and compared to this the observed power for the deviant condition. For each random set of trials, the number of trials was balanced between conditions to account for the lower number of trials in the deviant condition. The topographical distribution of the VEP power difference is shown in Fig. 5 for both monkeys. Both monkeys showed a significant enhancement in VEP power for the deviant condition at occipital and parieto-occipital sites (two-sided test of the mean power across the region of interest, p < 0.01). This indicates that the responses to the deviant movement direction were overall larger than those to the standard direction within the first 300 ms after movement onset.

4. Discussion

In this study we aimed to determine if the encoding of self-motion direction (heading) is in line with the predictive coding framework (Friston, 2018). We recorded EEG data from humans and monkeys to test for a visual MMN-component with stimuli simulating forward self-motion. Here, we focused only on visual information (optic flow)
showed the expected visual motion onset stimulus response (Kuba et al.,
the resulting event-related potentials (ERPs). The observed signals
and Hannon, 1988; Lappe et al., 1999; Lich and Bremmer, 2014) and
primates. Importantly, the pure visual information during self-motion
presentations of the same movement direction, i.e. for physically iden-
tical visual stimuli. In humans, the N2-component started to be more
present before to be tuned to self-motion direction.

4.1. Visual MMN to self-motion direction

We aligned our data to simulated self-motion onset and investigated
the resulting event-related potentials (ERPs). The observed signals
showed the expected visual motion onset stimulus response (Kuba et al.,
2007). This response was compared between standard and deviant
presentations of the same movement direction, i.e. for physically iden-
tical visual stimuli. In humans, the N2-component started to be more
negative for deviant as compared to standard trials, i.e. the MMN, at
about 110 ms after self-motion onset. The peak time of this vMMN
(around 135 ms after motion onset) is in line with results from previous
studies investigating the response to motion onset of sinusoidal gratings
or a moving circular pattern (e.g. Urban et al., 2008; Kulkepp et al.,
2013; Schmitt et al., 2018). At the same time, we consider our results
highly notable. While the perception of self-motion direction (heading)
is considered to be a complex task, to our best knowledge no data are
currently available about its dynamics. Our results indicate, for the first
time, that heading is processed ultrafast, i.e. within roughly 100 ms.

Importantly, we also found a similar mismatch-signature in our EEG
recordings from rhesus monkeys. Here, the same comparison revealed
that responses to deviant stimuli were overall enhanced relative to those
to standard stimuli. While the data did not allow a targeted analysis of
VEP-components because of the oscillatory EEG pattern being different
from those of the human participants, the enhancement was significant
and also showed its maximum over posterior electrodes similar to the
human data. For the monkeys, deviant and standard responses started to
be significantly different slightly before 100 ms after self-motion onset
(97 and 83 ms for monkey O and S, respectively; cf. Fig. 5). In a final step
we repeated this form of analysis also on the data set from human par-
ticipants. Results were highly similar to those obtained from the mon-
keys. Thus, it seems likely that the two signatures (MMN as obtained
from visually evoked potentials vs. power analysis of the VEPs in a
restricted time-frequency window) represent functionally equivalent
cross species phenomena.

The neural basis for the MMN-component is heavily debated (e.g.
Garrido et al., 2009; Fitzgerald and Todd, 2020). One of the most widely
accepted hypotheses suggests that the MMN and the differences in
processing of standard and deviant stimuli are based on a prediction
error account (Kimura, 2012). Yet, if this is indeed the case and how this
prediction error would be reflected at the neural level remains unclear
until now. Alternative hypotheses suggest more basic mechanisms like
stimulus-specific adaptation (e.g. Ross & Hamm, 2020) or repetition
suppression (e.g. Amado & Kovàcs, 2016).

The MMN like component found in our monkey experiment was
elicited by the same set of self-motion stimuli. This demonstrates that
the same experimental approach can also be applied to sensorimotor
processing in the monkey. In line with a very recent approach (Sand-
hæger et al., 2019), this offers the outstanding possibility to investigate
in the future the neural signature of the self-motion related MMN by
simultaneously recording EEG and neural activity in the monkey, an
invasive method usually not applicable in humans.
4.2. Influence of attention on self-motion MMN

Our human study design employed two different attention conditions to further test for the preattentive nature of the MMN (Czigler, 2007). In both cases the task was not related to the feature under study, i.e. the self-motion direction. In 10% of all trials per attention condition the change was displayed and in about half the cases it was detected. The correct response rates of 52% for “attention on the fixation target” and 45% for “attention on the ground plane” reflect the difficulty of the task, which required focused attention throughout the experiment. The very small number of false positives (in total 8 for “attention on the fixation target” and 57 for “attention on the ground plane”) supports this view. The difference in correct response rates between the two attention conditions most likely reflects slightly different behavioral task loads, which are not expected to influence the MMN-components (Pazo-Alvarez et al., 2004; Kremlaˇcek et al., 2013).

The simplified version of the paradigm in the monkey experiment did not include any additional task for the animal except the fixation of a central target. While attention often coincides with gaze direction, both can also be spatially separated (Bisley and Goldberg, 2010). Therefore, it remains unresolved whether the observed mismatch signature is similarly invariant to the focus of attention. Importantly, the early onset of the observed enhancement (97 and 83 ms for the two monkeys, respectively) suggests that it reflects a preattentive modulation of processing, comparable to the human MMN. It is possible, however, that the sustained (up to 300 ms after stimulus onset) increase in VEP amplitude may be related to or augmented by attentional mechanisms.

4.3. Lateralized processing of self-motion direction

We found vMMN-components for the two different heading directions, forward to the left and forward to the right. Topographic analysis of the vMMN-components revealed an occipito-posterior scalp distribution which is in line with previous studies on visual processing (Kimura, 2012; Qian et al., 2014). The exact scalp distribution found in the human data, however, revealed subtle differences between the two headings. For self-motion to the left the vMMN-component was located more over the right hemisphere and vice versa. Previous studies have reported a larger N2-component over contralateral hemispheres (Pazo-Alvarez et al., 2004). Yet, while these previous studies employed visual stimuli presented only in one part of the visual field (contralateral or ipsilateral with respect to the EEG electrodes), our stimuli always covered bilaterally a large part of the visual field (the central 42 degrees) regardless of the self-motion direction. Comparing the vMMN-components pooled over electrodes on either hemisphere resulted in more negative vMMNs for the contraversive self-motion as compared to the ipsiversive. This effect, however, was statistically significant only for one of our attention conditions, in which the participants were asked to attend to luminance changes of the dots forming the ground plane. In this task, attention was on a visual stimulus with a lateralized component (ground plane with two different self-motion directions), while in the other task it was on the fixation target which was always in the middle of the screen. This probably led to the stronger lateralization effect if attention was directed towards the luminance (but not explicitly the direction) of the ground plane. In general the result of a
lateralization of the processing of self-motion direction is fully in line with recent results combining neurophysiology in the monkey with a behavioral study in humans and modeling (Bremmer et al., 2017) as well as with a study employing TMS in humans (Schmitt et al., 2020).

4.4. Commonalities across species in the processing of self-motion

Through applying the same experimental paradigm to record EEG from humans and monkeys, we found that the two species share a similar signature of a prediction-mismatch with respect to self-motion direction. This adds to previous evidence that the processing of self-motion is similar between humans and monkeys and involves functionally equivalent cortical areas (humans: medial superior temporal area (area hMST): Huk et al., 2002; ventral intraparietal area (area hVIP): Bremmer et al., 2001. Monkeys: area MST: Duffy and Wurtz, 1991; Lappe et al., 1996; Sasaki et al., 2019; area VIP: Bremmer et al., 2002; Shao et al., 2018. Humans and monkeys: Bremmer et al., 2017; Schmitt et al., 2020; for review, see e.g. Britten, 2008).

The consistent pattern of results between humans and monkeys opens new research avenues to better understand the neural basis of scalp EEG, especially in humans. However, some methodological limitations to the monkey recordings have to be considered when comparing results between the two species. As noted above, the electrode arrangements in both monkeys did not include a neutral electrode (i.e. not recording any cortical signal) to use as offline reference. A common average reference as sometimes used for human recordings is likewise not feasible due to the small head size/low number of electrodes. The referencing to frontal electrodes (chosen to maximize distance to the ROI) inevitably produces an ambiguous signal from which occipital and frontal dipoles cannot be separated. The short latencies of the response under study made it unlikely that frontal activity would have influenced our results systematically. More importantly, however, a standardized VEP waveform is necessary to identify individual components (such as the N2) in the same manner as for the human recordings. Given that the oscillatory VEP as found in the two monkeys differed from its counterpart in humans, we relied instead on the more global parameter of VEP power for the comparison of conditions. As such, this measure does not warrant inference about the source of modulation in the same way as the human MMN. The results from our monkey experiment are thus to be interpreted with reliance on the human data. Future standalone studies are needed to explore the MMN in monkeys in more detail. These should ensure a standardized VEP waveform through a neutral reference.

4.5. Potential limitations of our approach

Aside from the issue of the reference, establishing scalp EEG in monkeys as a model for the human EEG remains challenging for a variety of reasons. Arguably the most crucial factor here are the differences in anatomy. In thalamic macaques, the musculature for mastication extends much further to the top of the skull than in humans (see, e.g., Schwartz and Huelke, 1963). Over temporal regions in particular the scalp thickness increases greatly with distance from the midline, due to the pronounced temporals muscle. This limits the placement of scalp electrodes to a central region, and even there the scalp tissue is quite different from that in humans. These limitations have led many investigators in this area to rely instead on cranially implanted EEG electrodes, which provide a greatly enhanced signal-to-noise ratio. Indeed, that approach has already helped to identify commonalities in the neuronal processing between monkeys and humans through shared components in the ERP and frequency spectra (e.g. Teichert, 2016; Errington et al., 2020; Westerberg et al., 2020). However, we would argue that scalp recordings, as used in our study, are likewise a highly valid translational tool to bridge the literature between humans and monkeys since they allow the use of the same recording setup in both species.

An additional methodological factor to consider is that signal propagation in the tissue and/or the skull may be altered by implants. Both monkeys used for the EEG recordings were implanted with a head-holding system, and one monkey (O) in addition with a recording chamber (cf. Fig. 5B). The effects of these implants on the measured scalp potentials are largely unknown (and may be difficult to model for individual implant arrangements). To mitigate this potential limitation, we chose to rely on a broader region of interest for our analysis of the MMN in the monkeys than in the humans, where source localization relative to the standard electrode locations is well established.

In addition to the different attentional demands imposed on our human participants and the monkeys and the differences in EEG recordings and their follow-up analyses, as described above, also the overall experimental settings were slightly different: while the size of the display for human participants was 42° (hor.) x 24° (vert.), the screen in front of the monkeys was 79° (hor.) x 49° (vert.). Importantly, previous research has documented the importance of the central part of the visual field over its periphery for heading perception (Warren and Kurtz, 1992). A more recent study has elaborated on this issue and could reveal a slight dominance of the upper half of the visual field for heading judgements for self-motion through a 3D cloud of random dots (Iassen et al., 2015). Yet, in our study, we had simulated self-motion across a horizontal ground plane not extending into the upper half of the visual field. Accordingly, we conclude that while displays for human and non-human primate observers were differently sized, this difference most likely did not influence our EEG results.

Taken together, while providing us with promising results, our approach had clear limitations: number and location of electrodes were different in humans and monkeys. In addition, scalp EEG in monkeys comes at cost of a weaker signal-to-noise ratio as compared to cranial electrodes. Also the exact behavioral tasks were different, as were the visual displays. All these facts and circumstances can be considered a weakness of our approach. At the same time we would like to stress that despite these experimental shortcomings, our results provide evidence for a vMMN for the processing of heading information in primates. We consider this remarkable, pointing towards a strong effect worth to be considered further in future studies, ideally combined with monkey cell recordings. Such cell recordings concurrent with scalp EEG recordings could contribute to a better understanding of the neural basis of the MMN.

4.6. Conclusion

Taken together, our results derived from an identical EEG approach in humans and monkeys strongly suggest that the processing of self-motion information in the primate brain is in line with the framework of predictive coding, as indicated by the vMMN. Accordingly, although being a complex perceptual task, visual self-motion direction is processed preattentively, allowing for immediate adjustments to keep on track if needed.

Author contributions

Constanze Schmitt: Conceptualization, Software, Formal analysis, Investigation (human data), Writing – Original Draft. Jakob Schwenk: Methodology (monkey setup), Software, Formal analysis, Investigation (monkey data), Writing – Review & Editing. Adrian Schütz: Methodology (monkey setup), Investigation (monkey data), Writing – Review & Editing. Jan Churan: Methodology (monkey setup), Software, Investigation (monkey training), Writing – Review & Editing. André Kamianetz: Methodology (monkey setup), Investigation (monkey training), Writing – Review & Editing. Frank Bremmer: Conceptualization, Writing – Review & Editing.

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