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ORIGINAL ARTICLE

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Detection of motion onset and offset: reaction time and visual evoked potential analysis

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Abstract Manual reaction time (RT) and visual evoked potentials (VEP) were measured in motion onset and offset detection tasks. A considerable homology was observed between the temporal structure of RTs and VEP intervals, provided that the change in motion was detected as soon as the VEP signal has reached critical threshold amplitude. Both manual reactions and VEP rise in latency as the velocity of the onset or offset motion decreases and were well approximated by the same negative power function with the exponent close to −2/3. This indicates that motion processing is normalised by subtracting the initial motion vector from ongoing motion. A comparison of the motion onset VEP signals in two different conditions, in one of which the observer was instructed to abstain from the reaction and in the other to indicate as fast as possible the beginning of the motion, contained accurate information about the manual response.

Introduction

It has been well documented that the time required for the detection of the onset of uniform motion decreases with an increase in velocity (Ball & Sekuler, 1980; Collewijn, 1972; Mashhour, 1964; Tynan & Sekuler, 1982). According to a general theory of motion detectability (Dzhafarov & Allik, 1984), the observer's decisions about the presence of motion are made on the basis of its kinematic form: This is the dependence of the moving object's position on time. A specific property of kinematic form—the moving variance of the spatial positions passed through within a temporal window of length s—appears to be a criterion for decisions about the presence of movement, provided that the moving object's trajectory is not obscured by brightness fusion. Because the variance of passed positions is equivalent to kinematic power, the proposed theory can also be called the *Model of Kinematic Energy* or *Power*. When this model was applied to motion onset detection, it was shown that the time that it takes for moving variance to reach a critical level provides a fairly good account of reaction time (RTs) (Allik & Dzhafarov, 1984). In particular, the model of kinematic energy predicts that the mean RT to motion onset is a negative exponent power function of velocity with exponent close to −2/3 (Allik & Dzhafarov, 1984; Dzhafarov, Sekuler, & Allik, 1993).

Applied to a velocity change detection task it was shown that this task is in fact reduced to one of the motion onset detection. Indeed, subtraction of the initial velocity explains the fact that the time needed to detect motion offset is approximately equal to motion onset detection time (Hohnsbein & Mateeff, 1992). In fact detection of changes in velocity depends primarily on the absolute difference between the initial and final velocity (Dzhafarov et al., 1993). This mechanism is called subtractive normalisation. Several later studies confirmed that the initial motion vector is largely ignored when changes in velocity are detected (Amano, Nishida, & Takeda, 2006; Hohnsbein & Mateeff, 1998; Mateeff et al., 2000; Mateeff, Genova, & Hohnsbein, 1999).

Although electrophysiological and neuroimaging studies have been successful in localising networks responsible for motion analysis, there are relatively few theoretically motivated studies concerned with the neuronal substrate of motion perception (Culham, He, Dukelow, & Verstraten, 2001). In motion onset detection tasks, the problem is not only discovering the neuronal activation responsible for solving this task, but also the time course and psychological outcome of this activation. In general, electrophysiological and neuroimaging studies parallel psychophysical findings, demonstrating that the development of cortical responses to the onset of uniform motion decreases with an increase in velocity

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(e.g. Kawakami et al., 2002; Maruyama, Kaneoke, Watanabe, & Kakigi, 2002; Wang, Kaneoke, & Kakigi, 2003). The latency of the N200 component of the motion onset visual evoked potentials (VEP) is also inversely related to the velocity (Markwardt, Göpfert, & Müller, 1988; Schellart, Trindade, Reits, Verbunt, & Spekreijse, 2004). However, some other MEG studies failed to find a correlation between the first major evoked peak's latency and velocity (Bakardjian, Uchida, Endo, & Takeda, 2002). In a recent study, Schellart et al. (2004) studied discrepancies between motion-onset VEP and MEG by recording them simultaneously. In addition to consistencies between both recording methods they also found differences which indicate that the sources of MEG and VEP components are not necessarily identical.

Patzwahl and Zanker (2000) measured motion-related evoked potentials together with behavioral performance (discrimination thresholds and RT) and found a parallel rise and fall in latencies as the strength of the motion signal (a coherence in their case) changed. In another study, it was found that the difference between the latency of the evoked magnetic field and manual RT was fairly constant over a wide range of velocities (Kaneoke, Bundou, & Kakigi, 1998). However, the exact parallelism between registered brain activity and perceptual performance is not inevitable (see Whitney et al., 2003).

Because it is relatively well established that the manual RT to onset and offset of uniform motion is a negative exponent power function with exponent close to $-2/3$ our aim was to use the known relationship for the search of the equivalent patterns in the VEP signal as a possible neurophysiological substrate of motion detection.

Methods

Observers

The participants were two men (23 and 54 years) and three women (25, 26 and 29 years). All participants had corrected-to-normal visual acuity and were right-handed.

Apparatus

A 19-inch Hewlett Packard monitor with the frame rate 66 Hz driven by a PC was used for the presentation of stimulus. VEP was recorded by a *BioSemi*'s system *Active One* that uses active electrodes with built-in amplifiers. The data were analyzed by the *Vision Analyzer* (Brain Products GmbH) and *Statistica* (StatSoft Inc.) software.

Stimuli

The display was tessellated into 960 rectangular areas each of which subtended $0.15° \times 0.12°$ when viewed from a distance of 3.7 m. The luminance of each rectangle was assigned randomly from 256 possible values. The luminance of rectangles varied from zero to 58.7 cd/m^2 with the average luminance equal to 30.1 cd/m^2 and standard deviation 23 cd/m^2. A small red fixation point was in the centre of the screen.

Each trial started with the appearance of a stationary pattern of rectangular tessellation. After a random foreperiod from 0.8 to 1.6 s the whole pattern started to move to the right with one of the six uniform velocities: 0.16, 0.31, 0.62, 0.93, 1.24 or 1.85°/s. Unlike many previous motion-onset VEP and MEG studies (e.g. Kawakami et al., 2002; Schellart et al., 2004), this relatively low range of velocities was chosen to extend the difference between the slowest and the fastest mean RT. The six velocities were presented 150 times in a pseudo-random order during a session. The movement lasted up to 2 s after which the pattern stopped and was replaced with a uniform grey field until the next trial.

Procedure

The experiment was carried out in a semi-darkened room (average illumiance was 1.5 lx, *Testo 545*). The observer was instructed, in separate blocks, to press a key as rapidly as possible as soon as she/he was able to detect the onset or offset of motion. RTs that were slower than 1,000 ms and faster than 100 ms were excluded from further analysis given that they are both physiologically and psychologically unrealistic measures of detection performance.

Sixteen pin-type active electrodes were fixed on the observer's head by an elastic head-cap. Cortical responses were recorded at approximate locations O1, O2, T5, T6, P3, P4, Pz, C3, C4, Cz, F3, F4, Fz and Fpz (according to the international 10–20 system). Two electrodes were linked to the observer's ears and used as references. The Active One system replaces the traditional ground electrode with two additional electrodes, the common mode sense (CMS, an active electrode) and the driven right leg (DRL, a passive electrode). The CMS was fixed on the top of the head (in the middle between Fz and Cz) and the DRL was put on the observer's neck. Four electrodes were used for the registration of eye movements. The DC mode and sample rate of 1,024 Hz was applied for recording. *Signa gel* (*MedCaT B.V.*) was used to improve the contact between the skin and electrodes.

A single experimental session of 900 trials lasted for about an hour. In the offline analysis the signal was segmented into 1.1 s epochs (100 ms before and 1,000 ms after the event trigger coinciding with the onset or the offset of motion). Steep filters (48 dB/oct) were used to filter out frequencies below 0.3 Hz and over 70 Hz, and a 50 Hz notch filter was also applied. A pre-stimulus period of 100 ms was selected for the baseline correction. Conventional artefact-rejection criteria (like allowed range within ± 100 μV) were applied keeping, depending on electrode, approximately 90% of trials for averaging. The Gratton and Coles algorithm (Gratton & Coles, 1989; Gratton, Coles, & Donchin, 1983) was applied to remove eye movement artefact from the signals.

Results and discussion

Median RTs to the motion onsets show a progressive decrease that takes the form of a negative exponential relationship between RT and velocity of the motion. The median RT to the motion onset and offset can be well approximated by a negative exponential function (Fig. 1). Because individual data were qualitatively very similar, Fig. 1 (and all coming figures, too) shows the RT data to the motion onset (filled circles) and offset (open circles) averaged across five subjects. Continuous curves correspond to the best fitting function $\mathrm{RT}=r+cV^{b}$, where β was fixed to $-2/3$ (for the explanation see Allik & Dzhafarov, 1984; Dzhafarov et al., 1993). The coefficient of proportionality, c, was assumed to be equal for both the motion onset and offset. The best fit was found with $c=64.2$. The main difference between the motion onset and offset detection is the residual time r. The detection of motion onset was best described when $r=256.1$ ms and offset with $r=285.8$ ms. The joint approximation of the motion onset and offset data was only slightly worse than their approximation in isolation, accounting for 95.1% of the total variance.

The estimated parameters and the general shape of the motion onset/offset detection curves are close to those that were obtained in previous studies (Dzhafarov et al., 1993; Hohnsbein & Mateeff, 1992): although the shape of the functions is similar it took an average longer (about 30 ms) to detect motion offset than onset.

The smoothed VEP data for a central electrode (Cz) in the two RT conditions (the detection of motion onset and offset) are shown in Fig. 2. The electrode Cz was chosen according to factor analysis that on one hand showed that all electrodes had considerable common activity (the first unrotated factor explained 50.9% of variability in averaged VEP data for conditions and all electrodes). On the other hand, according to varimax rotated factor analysis for all conditions and velocities (separately), the parallel analysis revealed either two or three factors behind the data, with Cz having most prominent contribution as estimated by factor loadings. The upper panel represents the motion onset VEP in the motion onset task and the lower panel shows the motion offset VEP when the observer's task was to detect, as soon as possible, the motion offset.

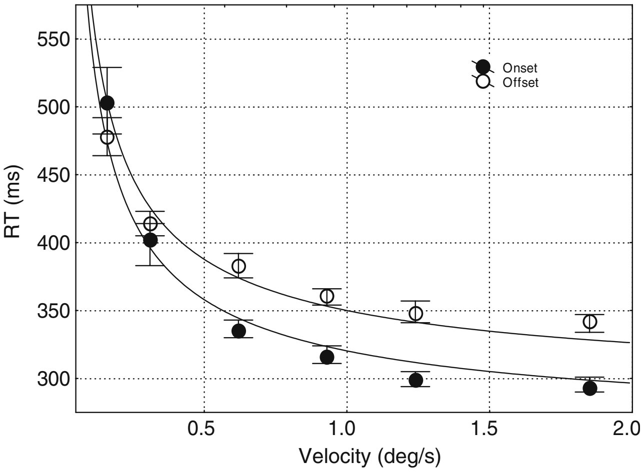

Fig. 1 Median manual RT data with 95% confidence intervals (Conover, 1980) in the motion onset (*filled circles*) and offset (*open circles*) task. Continuous curves show the best fitting negative exponential power function ($\mathrm{RT} = r+cV^{-2/3}$) with common $c = 64.2$, and separate values for r for the motion onset ($r = 256.1$ ms) and the offset ($r = 285.8$ ms)

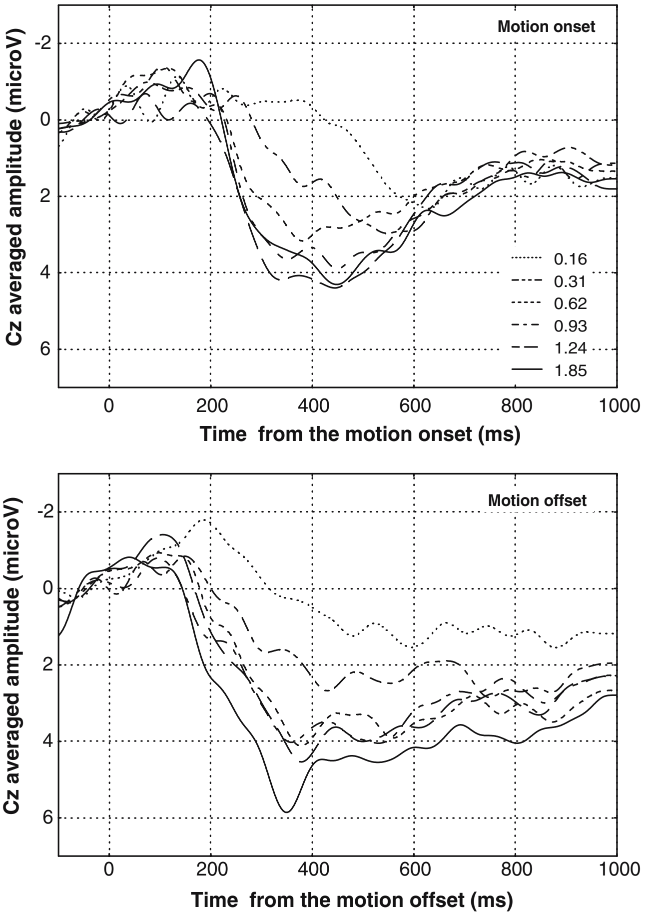

Fig. 2 Motion onset (*upper*) and offset (*lower*) VEP for the central electrode Cz for six different velocities 0.16, 0.31, 0.62, 0.93, 1.24, and 1.85°/s

Previous studies have shown that motion onset and offset VEP are characterised by a negative peak, specific to motion that occurs just prior to 200 ms post stimulus onset (Spekreijse, Dagnelie, Maier, & Regan, 1985; Kuba & Kubová, 1992; Markwardt et al., 1988; Schellart et al., 2004). This negative peak evoked by the motion onset was barely manifest in the data from the detection task (Fig. 2, upper panel) but it was clearly visible in the pure inspection condition when the observer was instructed to ignore the motion onset and react to the end of movement (Fig. 3, upper panel, *Encoding*). It seems that the first prominent negativity around N200 was masked by a massive positive wave associated with the detection of motion onset (Fig. 2, upper panel) or offset (Fig. 2, lower panel). This positive wave is known to have larger amplitude than the first negativity and it is also sensitive to the task the observer was instructed to solve (Kuba, Kremláček, & Kubová, 1998; Kubová, Kremláček, Szanyi, Chlubnová, & Kuba, 2002). To illustrate the decision-related wave, we subtracted the motion onset-related peak (Encoding in Fig. 3, upper panel) from the VEP pattern recorded in the motion onset RT condition (Fig. 2, upper panel). The resulting difference wave (Fig. 3, lower panel, *Decision*) represents the hypothetical situation of pure perceptual decision (i.e. decision about the motion in the motion detection task without motion encoding).

The growth rates of the VEP responses, in all experimental conditions, were ordered according to the target velocity: with the decrease of velocity the cortical response became more sluggish. This expected regularity is in accordance with previous data showing that the N200 wave's latency decreases with stimulus velocity (Müller, Göpfert, Breuer, & Greenlee, 1999; Schellart et al., 2004). The VEP responses to motion onset, without an instruction to respond, were negative with a characteristic -2 µV peak around 200 ms (Fig. 3, upper panel). The order of the peaks was not random. In Fig. 4 the latency of the motion onset-related peak values (Fig. 3, upper panel) is shown for the selected electrode Cz. The observed dependence was qualitatively at least very similar to the manual RT. For that reason we approximated the peak data presented in Fig. 4 (Encoding, filled triangles) with the same function, $r + c\,V^{\beta}$, as we did with the RT data. The best fit was obtained with $c = 39.2$ and r equal to 163.5 ($r^2 = 0.899$).

Unlike the magnetic response (Kaneoke et al., 1998), the difference between the RT and the latency of the VEP peak was not constant across onset velocities. In the slowest motion (0.16°/s) condition it was around 210 ms decreasing to approximately 100 ms in the fastest (1.85°/s) condition.

As with the manual RTs and the peak-value latencies in the inspection task, the positive waves in the motion onset (Fig. 2, upper panel) and offset (Fig. 2, lower panel) detection tasks are ordered according to target velocity: the higher the velocity the more rapid the VEP response. Unlike the N200 in the inspection task it is impossible to use the peak value because the positive waves do not have a definite maximum. It is possible, however, to assume that the rising edge of the VEP contains information about the motion onset and offset. The simplest assumption is that the change in motion, its start or stop, is detected as soon as the VEP signal has reached a critical threshold amplitude. Unfortunately, the value of this critical threshold amplitude is not known. Nonetheless, we may assume that this is a value, the passing by of which the VEP signal resembles, in the closest possible way, the pattern of latency intervals of the manual RTs.

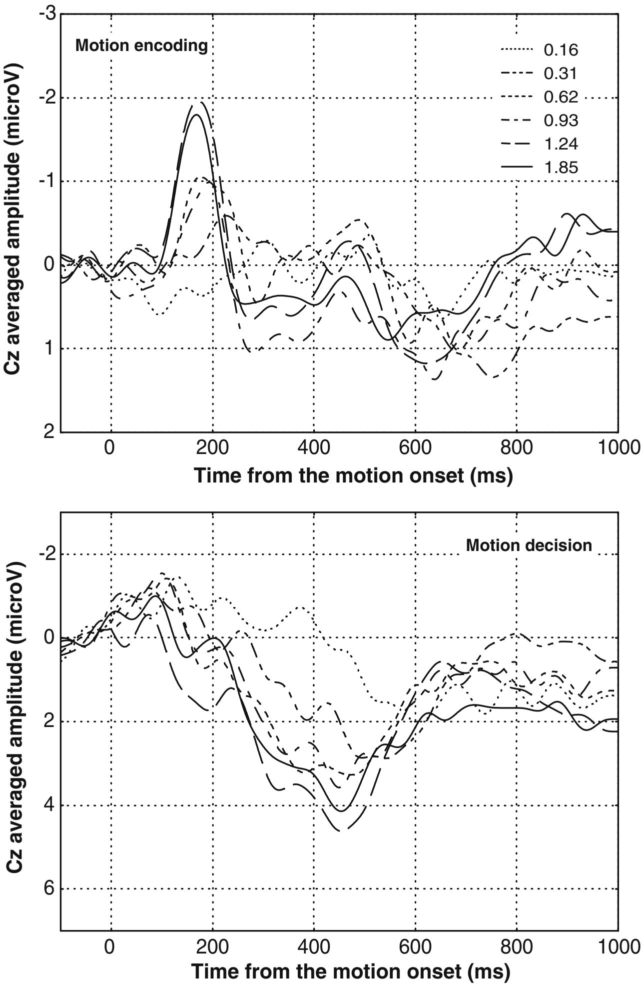

Fig. 3 VEP for the hypothetical motion encoding (*upper*) and decisions (*lower*) for the central electrode Cz. The encoding is recorded in the motion offset condition where the motion onset was not attended to and the decision-curves were found by subtracting the motion onset peak (i.e. *the upper graph*, encoding) from the motion onset VEP in the onset reaction task (Fig. 2 *upper*)

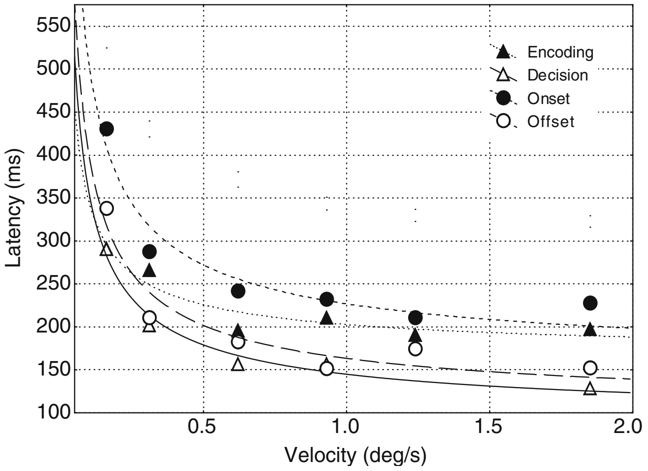

Fig. 4 The VEP latencies for the central electrode Cz that give the best fits to the manual RT temporal structure: the motion encoding related peak N200 (*filled triangles*) and hypothetical decision (*open triangles*), the detection of motion onset (*filled circles*) and offset (*open circles*). See approximation parameters in the text

In other words, we can look for the VEP signal amplitude that is reached with the set of temporal intervals that best approximates the time structure of the manual RTs (the mean difference in RT between two successive velocities). An exhaustive search through all possible threshold values was applied to find the best match between the VEP and manual RT temporal structures. The critical VEP amplitudes in the motion onset and offset condition that gave the best fits to the manual RT temporal structure were 0.35–0.3 μV for the onset and offset, respectively. Remaining curves in Fig. 4 demonstrate the approximation with the function $r + cV^{\beta}$ for the closest match with manual RT for the hypothetical process of decision (open triangles), motion onset (filled circles) and offset (open circles) VEP.

The approximation procedure for the hypothetical decision (with one missing point for the velocity of 1.24 deg/s, which appeared to be an outlier) estimated c to be 58.1, and explained 97.7% of VEP variability. Residual time (r) for the decision was 86.8 ms at Cz (see Fig. 4, open triangles). Latencies of amplitudes where the best possible similarity between the manual RT and the motion onset or offset VEP curves were found are shown in the remaining graphs in Fig. 4. Data for Cz were at least satisfactorily described by the exponential function explaining 93.5 and 91.9% the total variance, respectively. Again, an equal c for the onset and offset conditions was assumed. The fitting procedure that left less than 7% of variance of individual data points in the motion onset and offset condition (circles in Fig. 4) unexplained, estimated c to be 71.1 (indicating relatively better discrimination ability than 64.2 estimated for the manual RT). Although the manual RT to the motion offset was longer than for the onset (c.f., Fig. 1), the corresponding temporal structure was established earlier in the motion offset VEP than in the onset VEP. The estimated residual time, r, was about 60 ms shorter in the offset than in the onset VEP signal. The same pattern is also discovered in macaque V1 neurons where the motion offset latency is shorter than the motion onset latency (Bair, Cavanaugh, Smith, & Movshon, 2002). It is, however, unclear why for the manual reaction the opposite was true.

Conclusions

Besides confirming of the relatively well-established negative exponent power function between the RT to motion onset and velocity of the motion, this study also provided additional evidence in favour of an unified mechanism which determines the detection of both beginning and termination of motion and, more generally, any change in velocity. This study provides the first physiological evidence that the cortical mechanisms underlying motion detection treat motion offset in the same way as motion onsets. We demonstrated that the patterns of VEP associated with the detection of the onset and offset of motion had similar properties: specifically, their latencies are similarly ordered according to stimulus velocity and their growth rates follow the same negative exponent power function of stimulus velocity as do manual RTs.

We were less successful in the discrimination between movement encoding and decisions, the distinction proposed by Dzhafarov et al. (1993), in the VEP pattern. According to the proposed distinction, motion encoding is a general task-independent computation providing a sufficiently rich internal representation of the kinematic properties of the visual scene. This representation is achieved by a mass-action of the elementary motion encoders. The output of the encoding system is fed into the task-specific detection system which enables one to answer more specific questions about the nature and properties of the motion. Such questions include, among others, “Has the target moved at all?” and “Has it changed its speed and direction?” In the inspection condition, where no reaction was required, the motion onset VEP were characterised by the specific negative peak with its latencies ordered according to the velocity (cf., Kuba & Kubová, 1992; Markwardt et al., 1988). The structure of these latencies was very similar to that of the manual RT described by a negative exponential function with the power equal to −2/3. This indicates that the cortical VEP contained relatively accurate information about the velocity-dependent, temporal structure approximately 150 ms before the manual RT was given. In the RT task, which certainly presumes some decision and evokes some cognitive processes, the VEP signal is dominated by a later and larger positivity (Kuba et al., 1998; Kubová et al., 2002). This almost completely masks the earlier negative motion-specific peaks. However, there is no logical necessity that the difference between these two different VEP signals (RT task minus inspection condition) can characterise the encoding process as an initial representation of motion. Even considering this we need to assume that the initial representation of motion may be modified by the process of decision. Whether this modification can be equivalently re-interpreted or not in terms of re-entrant and feed-forward processing needs to be established (cf., Bachmann, 2000).

Besides a higher cognitive load the decision process can be characterised by many accompanying attributes: response preparation, perceptual set, the need to give manual response. That higher cognitive or attentional functions can modulate the VEP signal in the response to visual motion is not a new proposal (Niedeggen, Sahraie, Hesselmann, Milders, & Blakemore, 2002). Niedeggen et al. for example showed that the slow positive peak (P300), but not earlier negativity (N200), had considerably higher amplitude for correctly detected cases than misses but both were attenuated by the cue presented less than 300 ms before the motion. The general result from the VEP and fMRI studies is that several brain areas change their activity level with the observer’s changing attentional state (Culham et al., 2001; Raymond, 2000).

For example, in a study from Beauchamp, Cox, and DeYoe (1997) MT activity was higher when more attention was allocated to the motion task (attended location and speed of stimuli vs. location and colour or fixation point only).

Unfortunately, the number of electrodes (14) used in this study was too small for a precise brain mapping. One obvious task for future studies is to identify sources of cortical signals evoked by motion onset and offset. Contrary to the motion onset and offset VEP where the response to the offset is faster than to onset, the order of manual RT is reversed: on average it takes longer to detect termination of motion than its start. We do not have an explanation for this discrepancy and future mapping studies are needed to clarify this problem. Another unsolved task is to identify brain structures underlying motion encoding and decision that are characterised only by VEP pattern here.

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