Control of velocity in the sensorimotor area during a visually guided
joystick movement: A high-density EEG study

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Summary

The sensorimotor area in cerebral cortex is involved in processing visual motion information and the subsequent execution of visually guided hand movements. Electroencephalogram (EEG) recordings of 10 adult subjects were applied to examine the brain electrical activity accompanying a visually guided joystick movement intercepting with a moving target. While the velocity of the target varied, the direction of the joystick movement was constant and it was expected that increased stimulus` velocity would be accompanied with larger EEG activity. The EEG data analysis showed that a positive potential, evolving across the medial frontal – posterior region, immediately succeeded the joystick movement. The source model indicated that the activity primarily could be explained by two dipoles, one located medial in the sensorimotor area and another one in the visual areas in the occipital lobe. Further, by increasing the stimulus` velocity the EEG activity in the sensorimotor area also increased. The corresponding relationship between the movement–related potentials (MRP) and the velocity of the stimulus indicate that the sensorimotor area is involved in controlling velocity, which can apply to both visual motion processing and the execution of the motor response. However, the positive potential did not evolve until the actual joystick movement began suggesting that the MRPs reflect neural activity participating in the motor response in which the differentiated EEG activity can be related to a neural network in the sensorimotor area responding to increased velocity by gradually increasing the discharge rate.

1. Introduction

How does the brain process visual information and how is that information utilized to perform visually guided hand movements successfully? To be able to grasp an object in our surroundings visual information about position, orientation and the velocity of the target with respect to the observer is processed by the brain and integrated with the motor complex that initiates, executes and controls the hand movement. The execution of the movement is regulated by sensory feedback which is affected by changes that the action itself inflicts on the external environment. Further the motor areas executing the movement also feedback to the sensory structures to modulate future sensory input in this perception-action cycle (Fuster, 2008).

The visual field consists of the entire area that can be seen with both eyes at the same time, and it is further divided into the right and left hemifield. Retinal neurons in one eye respond to both visual fields but at the optic chiasm the axons that make up the retinofugal projection goes through a partial decussation in which those originating in the left nasal retinal regions cross over to the contralateral side of the brain whereby the left visual field is processed in the right hemisphere while the right visual field is processed in the left hemisphere (Figure 1).
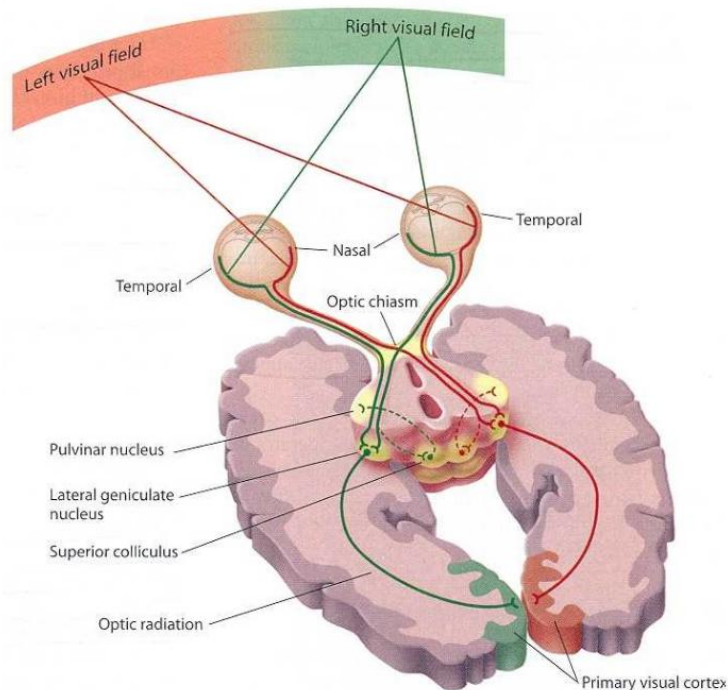

Figure 1. Graphic illustration of the visual pathways connecting the retinal neurons with the primary visual cortex.

The visual pathways are connected to the latereal genicualate nuecleus (LGN) which relay the information to the primary visual cortex (V1) located in the occipital lobe. The primary visual cortex (figure 2) propagates visual information through two interconnected visual pathways in which the ventral stream primarily process perceptual information involved in object recognition to the temporal lobe, while the dorsal stream, terminating in sensory areas in the parietal lobe, is involved in the processing of movements (Goodale, Meenan, Bülthoff, Nicolle, Murphy & Racicot, 1994). Milner and Goodale (2008) make the distinction between vision for perception and vision for action. They suggest that the ventral stream is involved in constructing perceptions which they define as our conscience experience of seeing and the pre-conscience mental representations that could reach conscious awareness and influence later cognitive operations. The link between perception and action is indirect as the ventral stream is involved in selecting possible goal objects and deciding how they should be approached but is not engaged in the action itself. The dorsal stream on the other hand process visual information to specify, execute and control the movements that constitute the action in real time. The visual information that is processed by the dorsal stream does not form perceptual representations of the world but rather it constitutes a stream of bottom-up information that is propagated from the retina to execute visuomotor guidance of movements and because of the non-perceptual character of the dorsal stream processing, it is not accessible to the conscious mind (Goodale & Milner, 1992, 2004; Milner & Goodale, 1993, 1995).
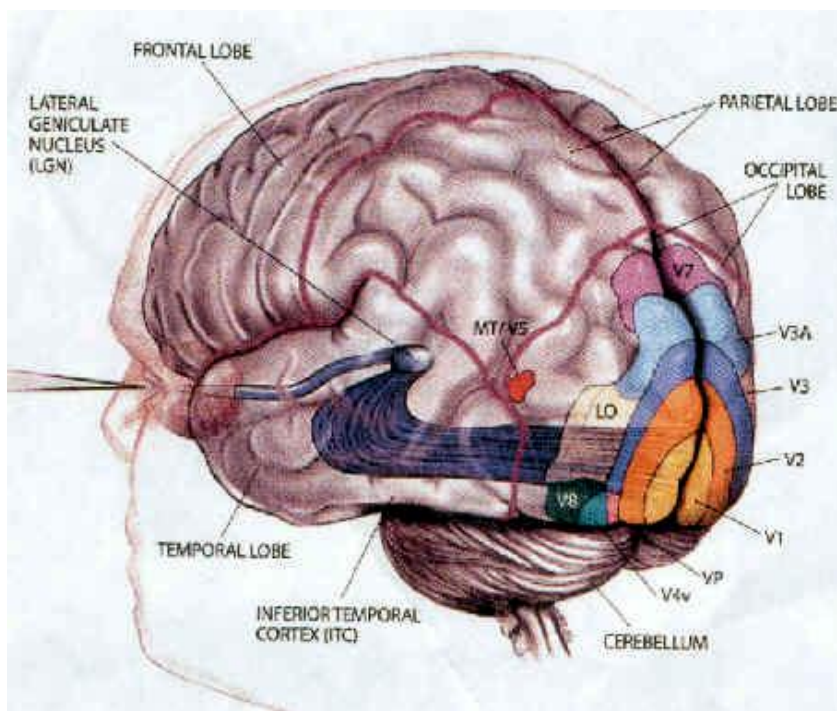

Figure 2. The visual areas V1, V2 and V3 of the occipital lobe. The ventral stream propagates information from V1, terminating in the inferior temporal lobe, while the dorsal stream connects V1 to the sensorimotor area in the parietal lobe.

Located at the temporo-parieto-occipital junction in extrastriate cortex is the middle temporal visual area 5 (MT/V5) which receives input from V1 and V3 and is activated during processing of visual motion (Zeki, 1974; Zeki, Watson, Lueck, Friston, Kennard & Frackowiak 1991; Watson, Myers, Frackowiak, Hajnal, Woods, Mazziotta, Shipp & Zeki, 1993). Although it was originally assumed that the functional significance of the MT/V5 complex was an unimodal involvement in perception of visual motion, later research indicated that it is also activated by tactile motion (Hagen, Franzen, McGlone, Essick, Dancer & Pardo, 2002; Beauchamp, 2005). But this doesn`t necessarily imply a polymodal engagement of MT/V5 in motion processing including a tactile module as the activation could also reflect visual imagery enabling tactile discrimination of orientation (Sathian, Zangaladze, Hoffman & Grafton, 1997). MT/V5 is also associated with the temporal characteristics of motion perception. Sack, Kohler, Linden, Goebel and Muckli (2006) showed that motion processing was impaired when neuronal activity in MT/V5 was disrupted by applying transcranial magnetic stimulation in two critical time periods, about 40-30 ms before stimulus onset and 130-150 ms after.

Research on the posterior parietal cortex (PPC), located between the sensorimotor fields around the central sulcus in the frontal lobe and the visual areas in the occipital lobe, have established the areas` involvement in motion processing and reaching. Single-unit recording studies on macaque monkeys have shown that the different subdivisions of PPC hold cells that are selective for reaching movements (Johnson, Ferraina, Bianchi & Caministi, 1996; Eskandar & Assad, 2002). In a task that required the monkey to use a joystick to guide a spot to a target, neurons in the medial intraparietal area (MIP) responded mainly directionally with respect to the hand movement. The neurons in the medial superior temporal area (MST) displayed directional activity to visible movements that were projected on a screen before the monkey but not to the hand movement it-self (Eskandar et al., 2002). In humans, damage to parietal cortex may result in optic ataxia, a deficit in visually guided hand movements (Perenin & Vighetto, 1988). Reaching towards objects in the peripheral vision field, often contralateral to the lesion is impaired in patients with optic ataxia while reaching for targets in the central vision is not affected. Further they may be able to accurately saccade to targets in the peripheral vision field and successfully reach for targets on their own body indicating that the disorder is not strictly a sensory or a motor deficit (Culham & Kanwisher, 2001). Neuroimaging studies also show that the PPC is involved in planning and execution of visually guided hand movements. Chaminade and Decety (2002) demonstrated in a task resembling reaching that the intraparietal sulcus is involved in visuomotor coordination of

hand movements and target, and the activity is stronger contralateral to the movement. Further the intraparietal sulcus is associated with motion processing in different modalities such as visual, tactile and auditory and the activation is bilateral in either intraparietal cortex (Bremmer, Schlack, Shah, Zafiris, Kubischik, Hoffmann, Zilles & Fink, 2001).

The functional significance of the motor cortex has been debated, relating it to direct control of muscles and force as well as to spatial encoding of motor output which includes parameters such as direction, velocity and position. Single cell recordings on rats have shown that certain neurons in hippocampus respond to specific directional information by increasing the rate of firing when the rat is moving in the direction corresponding to the place field of the cell and declining as the rat gradually moves in the opposite direction (O`Keefe & Dostrovsky, 1971). Equivalent experiments performed on monkeys reveal that cells in motor cortex also display the same directional preferences (Georgopoulos, Kalaska, Caminiti & Massey, 1982). Research on posterior parietal areas conducted by Andersen, Essick & Siegel (1985) showed that the response pattern of certain neurons could be explained by the product of a gain factor in which the total response of the neuron accounts for the eye position and the response profile of the visual receptive field. The corresponding response pattern is also present in motor cortex in which the discharge activity of single neurons can be attributed to a gain factor that accounts for direction and velocity (Moran & Schwartz, 1999) and position and velocity (Paninski, Fellows, Hatsopoulos & Donoghue, 2004). Paninski et al. (2004) further stated that the activity of neuronal ensembles provides more precise encoding of position and velocity compared to the effort of the individual cell. This is in concordance with research on neuronal networks stating that the individual neuron makes a vectorial contribution to the population code that generates the motor output (Georgopoulos, Kettner & Schwartz, 1988; Kruse, Dannenberg, Kleiser & Hoffmann, 2002). The single cell does not discharge to specific movements only; on the contrary it discharges for movements in many directions but at different rates and therefore a large number of cells will be active in movements in any particular direction. In a three-dimensional reaching experiment Georgopoulos et al. (1988) showed that the direction of the arm movement was close to the direction of the population vector for the neuronal ensemble and proposed that it is the entire activity of the neuronal ensemble that encodes for the direction of an upcoming movement. Further, in a second study it was established that the attribution of the single cell in the neuronal network is not necessarily restricted to one kind of information only as the same cells responded to different parameters such as direction, velocity, position and acceleration (Ashe & Georgopoulos, 1994).

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In order to examine how visually guided hand movements are processed by the brain in healthy human subjects single cell recordings cannot be applied. An EEG recording of brain electrical activity on the other hand does not cause any harm to the subjects or otherwise obstruct the arm movement, and although the spatial resolution is limited it provides a detailed measure of the activity of a neuronal population in the temporal domain. An event such as a sensory or motor stimulus can induce both time-locked and phase-locked changes in a neuronal population and the subsequent EEG activity is called an event-related potential (ERP). It is assumed that the evoked activity has a fixed time-delay to the stimulus while the ongoing EEG background activity constitutes random fluctuating noise which implies a higher signal-noise ratio when the ERPs are averaged. Research on externally - and internally paced finger movement show that primary sensorimotor areas (M1-S1) in both hemispheres are activated in addition to the pre motor areas (PMA) and supplementary motor area (SMA) of the frontal lobe, suggesting that both hemispheres are involved in planning and execution of unilateral finger movements although the activity is stronger contralateral to the movement (Kim, Ashe, Georgopoulos, Merkle, Ellermann, Menon, Ogawa & Ugurbil, 1993; Urbano, Babiloni, Onorati & Babiloni, 1996; Gerloff, Richard, Hadley, Schulman, Honda & Hallet, 1998). A series of cerebral potentials preceding and succeeding voluntary finger flexions and extensions have been identified starting with a slow negative EEG activity called the readiness potential (RP) which begins about 2 seconds pre movement onset before the gradient suddenly increases at 400 ms (Vaughn, Costa & Ritter, 1967; Shibasaki, Barrett, Halliday & Halliday, 1980). The RP is followed by a negative motor potential immediately preceding movement onset located to the contralateral central scalp and probably caused by the activity of pyramidal tract neurons in the primary motor cortex (M1) (Shibsaki & Hallet , 2006). Shibsaki et al. (1980) further described four post-movement components, namely N+50 which is a negative frontal peak, followed by P+90 and N+160; both predominant over the contralateral parietal region. The fourth component, peaking about 300 ms after movement onset was a large widely distributed positive potential located in the precentral region contralateral to the movement. The P+300 corresponds to the P2 component of Vaughn et al. (1967) who described it as a "complex positive wave (P2) which accompanies and follows for a brief period the movement it-self".

In the present study high density EEG recording is applied to examine the brain electrical activity accompanying a visually guided joystick movement intercepting with a target moving in one of three different velocities. The main focus of interest is how the velocity of the stimulus affects the EEG activity in motor cortex. Further we investigate the

regions in the occipital, temporal and parietal lobe that are associated with visual motion processing for any brain electrical activity that display different characteristics with regards to the velocity of the stimulus or connecting these regions temporally to the activity in motor cortex and the execution of the joystick movement. Georgopioulos et al. (1988) proposed that the direction of an arm movement can be encoded by the neuronal population vector in which the discharge rate of the single cell is proportional to changes in direction relative to that cells` preferred direction and the sum total of all single cell contributions constitutes the population vector. Further the single cell can account for both velocity and direction during reaching, with velocity acting as a gain factor on the cells` directional turning curve by affecting the firing rate of the individual cells in which increased velocity results in increased firing rate of the cells with preferred direction close to the direction of the actual movement (Moran et al., 1999). In our study the direction of the joystick movement is fixed while the velocity of the stimulus varies. On the basis of velocity acting as a gain factor while the direction of the movement remains constant, we expect higher brain electric activity accompanying increased velocity of the stimulus.

2. Method

2.2 Subjects

10 subjects (4 females) were recruited among students and teachers at the Norwegian University of Science and Technology. All subjects had normal or corrected to normal vision and according to their self report they were all right handed but one who was ambidextrous. The mean age of the subjects were 27.1 ± 4.8 years (age range from 19 to 37). They had all signed the written consent before the experiment began informing them that they could withdraw at any time. The study was approved by The Norwegian Regional Ethics Committee and The Norwegian Data Services for the Social Sciences.

2.3 Apparatus

The EEG activity was recorded with Geodesic Sensor Net (GSN 200) (Tucker, 1993) using Net Station software on a Macintosh computer. The GSN 200 contains an array of 256 Ag/AgCI electrodes which are evenly distributed across the scalp, each connected to a corresponding amplifier channel. The sample rate of the high density EEG recording was 500 Hz using a 100 Hz low-pass filter and 0.1 Hz high-pass filter.

As it is advised for high-input impedance EGI amplifier systems, the electrode-scalp impedance were kept below 50 kΩ in order to achieve an optimal signal to noise ratio (Ferree, Luu, Russell & Tucker, 2001; Picton, Bentin, Berg, Donchin, Hillyard, Johnson et al., 2000). The joystick movements were executed with Current Designs` Fiber Optic Joystick (HH-Joy 4) and recorded with E-prime (Psychology Software Tools, Inc) software. Tags marking stimulus onset/offset and successful/unsuccessful trials were transferred to the EEG data using E-prime and they were stored on hard disk for off-line analyses.

In order to monitor the direction of gaze during the experiment, eye movements were recorded with Tobii x50 infra red camera running on Clear View software. The subjects` overall behavior was monitored with 2 digital cameras.

2.4 Stimuli

The subjects visually tracked a stimulus-car (stm-car) moving horizontally from left to right over a wide screen on which it was mirror-reversed projected with an ASK M2 projector. The final approach of the car was occluded before it reappeared in a gap on the far right of the screen. By the means of a joystick the subjects controlled an identical car (joy-car) moving vertically between the starting point in the upper right corner and the touchdown area in the middle of the gap after the occlusion. The subjects were instructed to crash the joy-car into the stm-car (see figure 3).
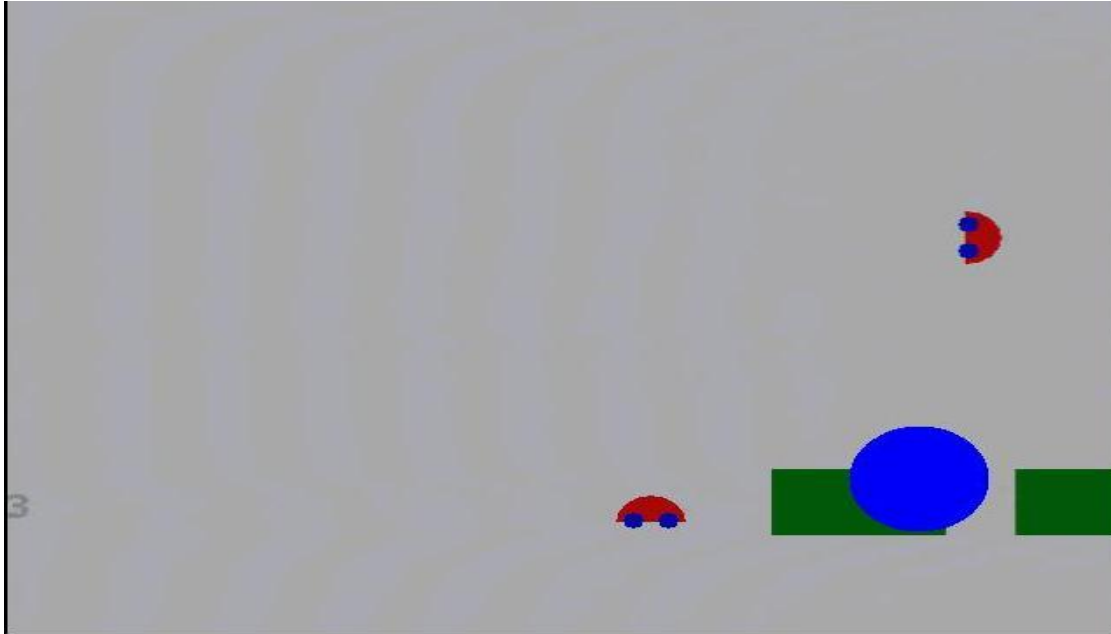
Figure 3. The stimulus car drives horizontally from left to right while the joy-car follows the vertical axis to the open gap between the two green occlusions on which the subjected were instructed to focus their eyesight. Their gaze was recorded for back up purposes with the Tobii infra red eye camera and monitored on the experimenters screen as a blue ball.

A crash was achieved when the centre of the stimulus car was at the centre of the gap between the two obstructions. The length of the stm-car and the gap were both 40 pixels (px) which is approximately 6.5 cm when projected on the screen while the front of the joy-car was 20 px wide. Further the centre of the joy-car had to reach the bottom of the chassis of the stm-car. Both vertically and horizontally a deviation of 30 px around the centre of the gap was tolerated. The distance of the whole horizontal plane was 620 px, (100 cm) and the occlusion began at 440 px (71 cm). The total horizontal visual angel was 64°. The vertical plane on the other hand was 360 px (58 cm) with a total vertical visual angel of 40°.

The initial velocity of the horizontal moving car was 0.5 px/ms or 0.84 m/s. Subsequently it would decelerate in one of 3 constant ways: "fast" (10% deceleration), "medium" (50% deceleration) and "slow" (90% deceleration). In the "fast" condition the occlusion lasted for 131 ms, 194 ms for "medium" and 283 ms for "slow". The total length of any trial did not exceed 2400 ms and the inter-trial interval was 1500 ms.

2.5 Procedure

The subjects were seated 80 cm away from the screen (108 x 69 cm) on which the experimental conditions were projected. The impedance of the electrodes was checked and corrected if necessary with the use of saline electrolyte or by repositioning them slightly to improve the contact with the scalp. The participants were instructed to keep the joystick in their lap and to use their dominant hand. In order to avoid unnecessary cortical activation due to head or eye movements, the subjects were further instructed to focus their eyesight on the gap between the two occlusions. Even though the approach of the horizontal car was accessible through peripheral vision only the subjects did not report this as a complicating matter. The subjects were then instructed to crash the joy-car into the stm-car employing one continuous swift downward joystick movement thereby preventing them from applying cognitive strategies such as moving the joy-car close to the gap first and then wait for the stimulus-car before executing the impact or hitting it on the upward rebound. Finally the eye movements in visual space were calibrated to the Tobii X50 eye camera.

To get familiar with the joystick the subjects were allowed to run through 24 test trials (8 for each condition). They then carried out the experiment completing 210 trials; 70 for each condition in randomized order.

2.6 Joystick data analysis

The joystick data were processed off line using custom designed software to further edit the selection of trials. The beginning of each movement was defined by joy-car reaching 10 % of the maximum velocity for that trial. Tags marking the beginning of the single joystick movement and the velocity of the stm-car (fast, medium, slow) were generated. Video recordings of the experiments were also examined, omitting trials in which the subjects did not focus their eyesight on the gap or otherwise used cognitive problem solving strategies to execute the crash. An event file with tags for the remaining trials was then transferred back to the EEG data. In all 113 trials were discarded because the subjects used different cognitive strategies and one subject was rejected because of repeatedly occurring eye movements.

2.7 EEG data analysis

Only trials resulting in a successful crash were segmented and accepted for EEG-data analysis using the software program Brain Electrical Source Analysis (Besa) version 5.3. All channels that were characterized by noise because of head/body movements were rejected by visual inspection while artifacts due to vertical ocular movements were removed with a principal component analysis (PCA) method identifying the overall eye- blink pattern based on manually selected segments. None of the subjects included in the analysis had more than 10 % of the channels defined as bad. The events for stimuli onset and joystick movement begins were the triggers of interest. Time-locked epochs were generated to stimuli onset [-200, 2400] ms and joystick movement begins [-1200, 1200] ms. Baseline for the time-locked stimuli onset was [-200, 0] ms while the response-locked joystick movement begins baseline was [-1200, -1000] ms. It is not a straightforward matter to set the baseline for a response-locked trigger because the activity that precedes the response sometimes is stronger than the activity that follows (Luck, 2005). In order to avoid pre-motor activity influencing the baseline for the response-locked joystick movement begins, baseline was estimated by calculating the difference between triggers for stimuli onset and joystick movement begins in a random sample of single trials. However the beginning of the joystick movement varies both in trials and between the subjects and it is therefore possible that the baseline is contaminated with either pre-motor activity or post-motor activity from previous trial as well as brain electric activity related to the visual stimulus. The joystick-movement generated epochs were therefore only used as a roadmap by which they were compared with the epochs computed at stimulus onset. Although the epochs grounded in the joystick triggers could be contaminated by noise and the effect weakened, it is likely that a response in the EEG data corresponds to actual brain electrical activity generated by the movement. The effect should also be detectable in the EEG data belonging to the stimulus onset generated triggers thereby creating a link between the movement and the less contaminated stimulus onset data.

To remove slow drift in the data the low cut-off filter was set to 1.6 while the notch filter was set to 50 Hz and the high cut-off filter was set to 40 Hz. Since time-frequency analysis was not applied the 40 Hz high cut-off filter was engaged during the artifact scan but turned off for averaging. The difference between maximum and minimum amplitude did not exceed 200 µV and the gradients were lower than 75µV/sample for any channels or trials that were accepted for further analysis. In addition signals below 0.1 were rejected. Altogether 1233 time-locked stimuli onset trials were analyzed and on average each subject contributed

with 34 (SD = 11.5) in the fast condition, 44 (SD = 13.1) in the medium condition and 45 (SD = 13.8) in the slow condition. Further 1250 response-locked joystick onset trials were analyzed and the average individual contribution was 35 (SD = 11.6) in the fast condition, 45 (SD = 12.4) in the medium condition and 45 (SD = 13.6) in the slow condition.
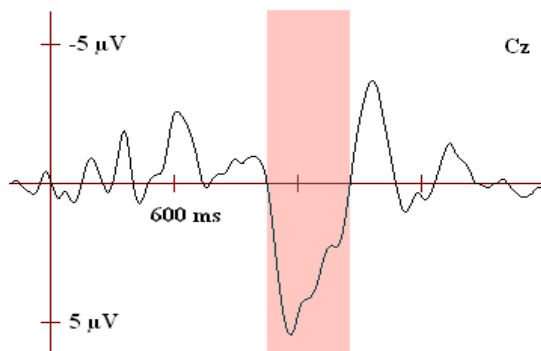

Figure 4. Identifying the MRP in the individual averages . The borders of the positive MRP was defined by y > 0 µV. Then peak amplitude, mean amplitude and area for the selected region were calculated.

2.7.1 MRP analysis

Individual averages were computed for fast, medium and slow in both trial onset and joystick-onset and they were analyzed with a 10 Hz high cut-off filter engaged. The averages were referenced to an artificial reference calculated from the average potentials over the scalp. The averages were then interpolated to 81 standard electrode positions and combined to generate a grand average in which the MRPs were identified. Next, the equivalent MRPs were identified in the individual averages and peak amplitude was calculated. The positive MRPs were defined by Y > 0 µV and the area (µV*ms) of the block interval and mean amplitude was computed (figure 4). Although the block interval was defined by Y > 0 µV a certain visual estimate was applied as sometimes sudden voltage fluctuations would be included in a selected region. Mean amplitude corrects for these voltage deviations while the area does not and therefore both units of measurement were used because they complement each other.

2.7.2 Source analysis

Although the accuracy of high density EEG spatial resolution is debated because of the inverse problem involved in estimating source localization founded on the distribution of potentials at the scalp surface (Luck, 2005; Snyder, 1991) it was performed to establish a possible connection between the MRPs and the brain regions that could cause the activation. Filters for the source analysis were set to 1.6 Hz for the low cut-off, 40.0 Hz for the high cut-off and 50 Hz for the notch filter.
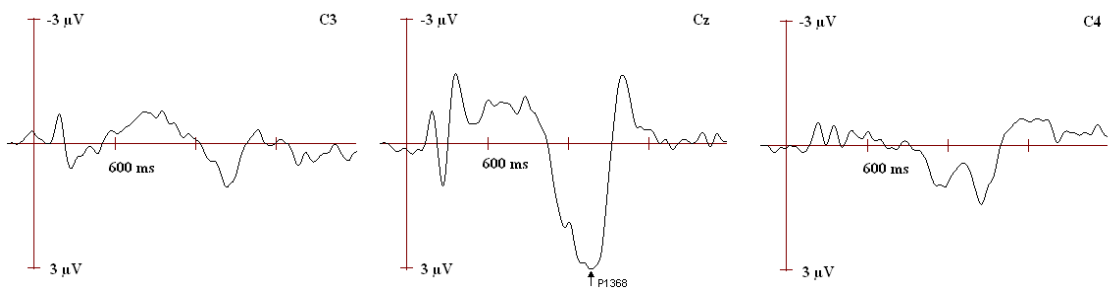
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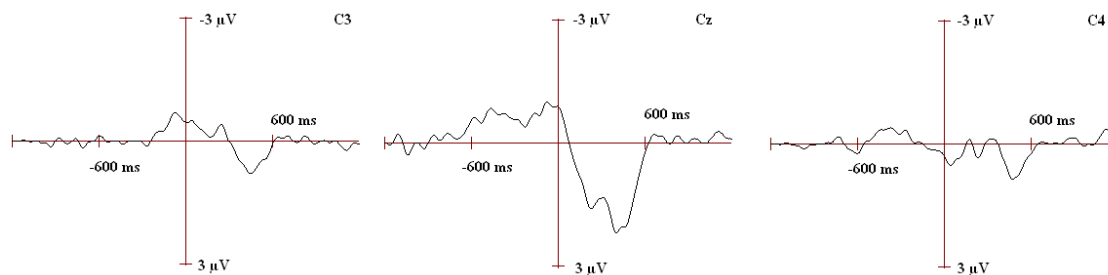
B

Figure 5. Grand average waveforms for the fast velocity displaying brain electrical activity in channel C3, Cz and C4. For both figures the vertical axes mark the experimental triggers at y = 0 and provide a measurement of the voltage level. In **A** the trigger is response-locked to the joystick movement and in **B** the trigger is time-locked to stimulus onset. There is a positive electrical charge evolving immediately after joystick onset and the effect is stronger in Cz compared to C3 and C4 (**A**). The same tendency is also present at about 1000 ms in the time-locked waveform (B) where the amplitude at the positive peak is even higher (3.04 µV compared to 2.19 µV in the response locked grand average). Further the polarity changes in Cz (**B**) starting at about 130 ms are not present in the other channels.

3. Results

3.1. Identifying movement-related potentials.

The response-locked grand average waveform display show that the beginning of the joystick movement was accompanied with a positive movement-related potential (MRP) in Cz starting at about 70 ms and ending at 600 ms (figure 5a). The activity in C3 and C4 was less pronounced in the same period of time peaking at 0.81 µV and 0.87 µV compared to 2.19 µV in Cz. Similar activity is evident in the grand average that is time-locked to stimulus onset in which the MRP in Cz started at 1046 ms, ended at 1522 ms and peaked at 3.04 µV compared to 1.07 µV in C3 and 1.44 µV in C4 (figure 5b). Furthermore both Cz waveforms are distinguished with a negative build up which abruptly ends when the movement begins. In addition the time-locked Cz is characterized with polarity changes starting at about 130 ms after stimulus onset which are not evident in the other channels for either waveform.
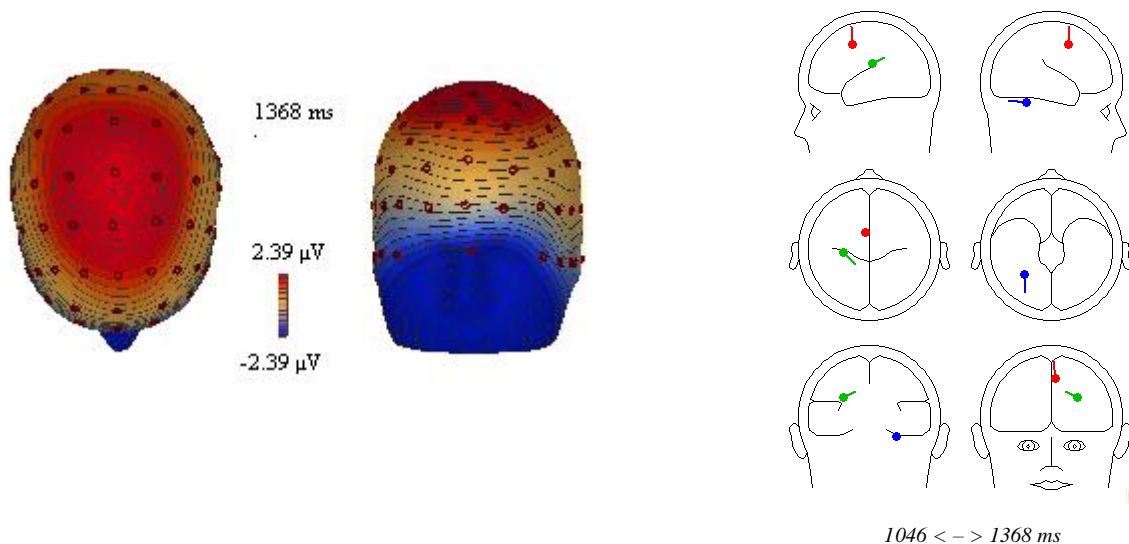

1046 < – > 1368 ms

Figure 6. The 3D map on the left displays the voltage distribution at 1368 ms for the time-locked grand average waveform. The source model shows the location of the three main dipoles that can explain most of the voltage distribution in the time frame 1046 – 1368 ms post trial onset. The red dipole located in the medial frontal lobe accounts for 74.5 % of the variance while the blue dipole in the right occipital lobe accounts for 18.9 % of the variance. 4.1 % of the variance can be explained by the green dipole positioned in contralateral parietal lobe. The residual variance of the source model is 8.3 %.
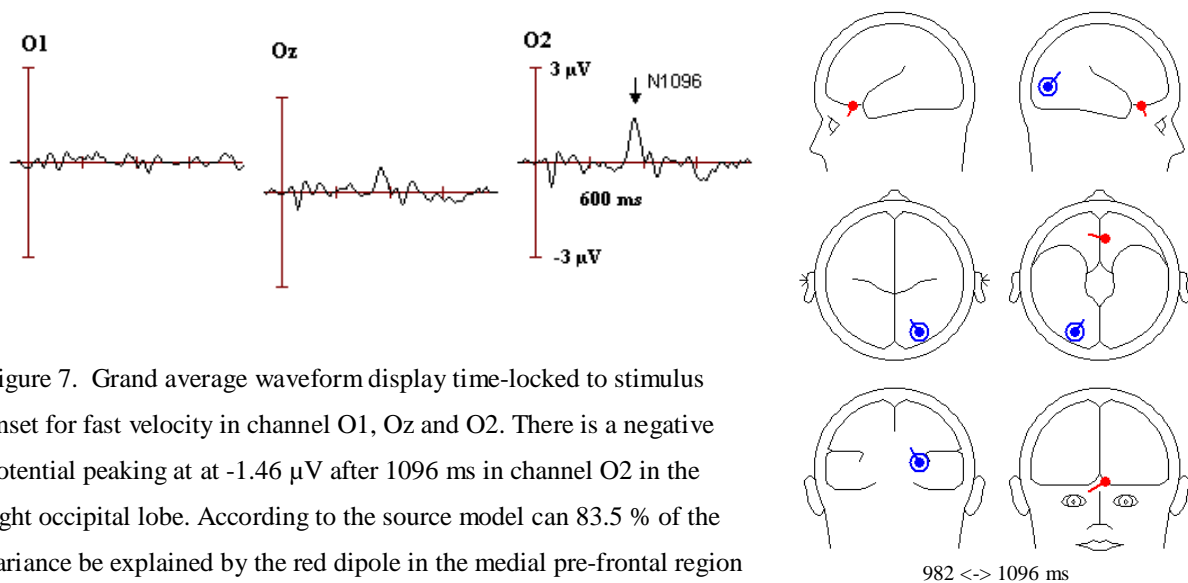
Figure 7. Grand average waveform display time-locked to stimulus onset for fast velocity in channel O1, Oz and O2. There is a negative potential peaking at at -1.46 µV after 1096 ms in channel O2 in the right occipital lobe. According to the source model can 83.5 % of the variance be explained by the red dipole in the medial pre-frontal region while the blue dipole in the right occipital lobe accounts for 13.7 %.

982 <-> 1096 ms

In order to establish a stronger connection between the MRP in Cz and specific brain areas a source analysis was performed for the fast condition starting the epoch at the onset of the positive waveform (y = 0 µV) at 1046 ms and ending at the peak of the waveform at 1368 ms. The 3d image (figure 6) shows the positive voltage distribution extending across the frontal - parietal areas and the negative facial voltage spread at the peak of the MRP. According to the source analysis can 93.4 % of the variance be explained by the red dipole (74.5 %) found in the medial frontal lobe and the blue dipole (18.9 %) located in the right occipital lobe.

Associated with the activity in the right occipital lobe is a negative MRP succeeding immediately after the joystick movement, peaking at -1.46 µV after 1096 ms in the grand average (figure 7). The activity is predominantly in channel O2 and the source model stipulated that 97.2 % of the activity is related to a dipole (83.5 %) in the medial pre-frontal areas and a second dipole (13.7 %) located in the right occipital lobe.
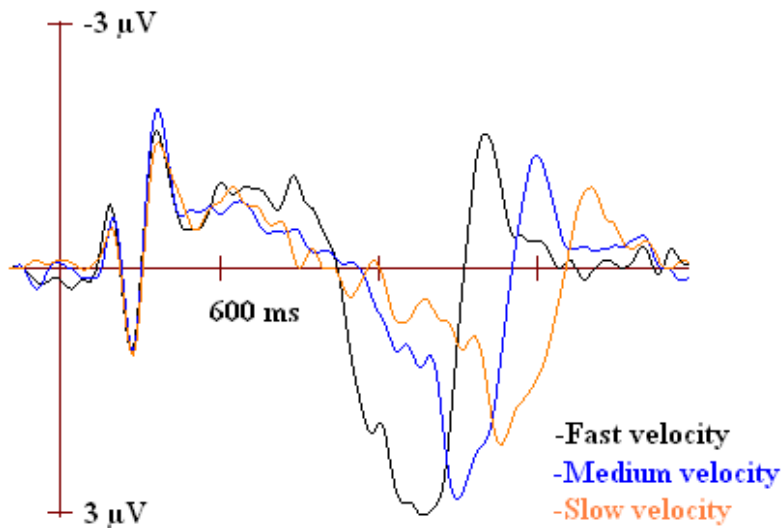
Figure 8. Grand average waveform display of channel Cz for fast, medium and slow velocity. Trial onset is at x = 0, fast velocity is colored black, medium is blue while slow is yellow. The amplitude of the positive potential starting at about 1000 ms is larger for fast velocity than medium and slow respectively and, as expected, the earliest peak amplitude is for fast followed by medium and slow.

3.2 Velocity related potentials

The grand average waveform displaying velocity show little if any difference between the three conditions in the early activity in the timeframe 130 – 350 ms (figure 8). However, it is evident by visual inspection alone that the amplitude of the positive potential appearing at about 1000 ms after stimulus onset is larger for fast than medium and slow velocity respectively.

Based on the individual files an average for peak amplitude, mean amplitude and mean area (µV*ms) were calculated for the MRPs in channel Cz (figure 9). Peak amplitude was larger for fast (4.3 µV, SD = 1.7) than medium (3.6 µV, SD = 1.2) and slow (2.9 µV, SD = 1.2) respectively. A repeated measures ANOVA was performed on peak amplitude with velocity (fast, medium and slow) as within subject factor. This revealed a main effect of velocity, $F(2, 9) = 10.336$, $p < .05$. However a pairwise comparison adjusted for multiple comparisons with Bonferoni didn`t show any significant effect between fast and medium velocity.
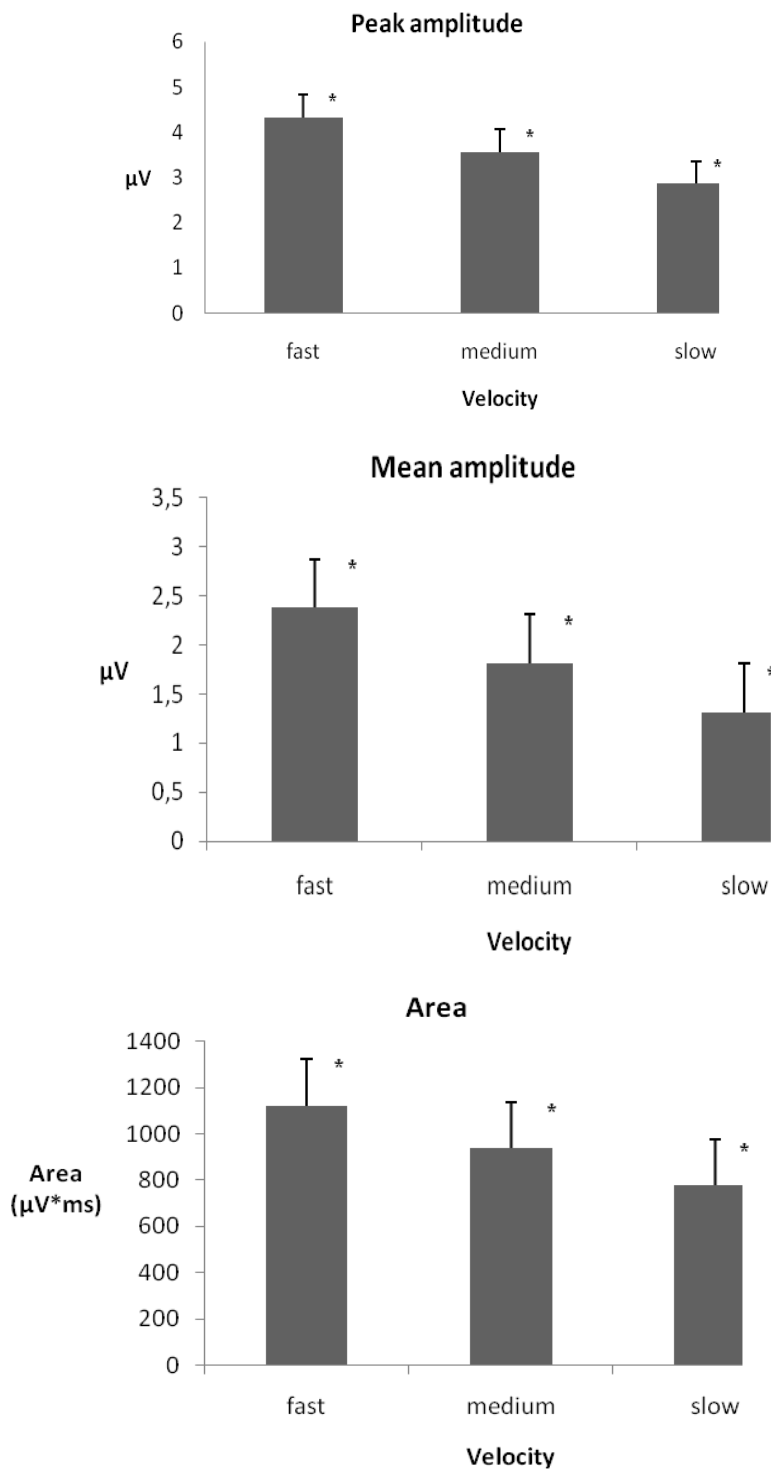
Figure 9. Graphic representation of average scores (including SD bars) for fast, medium and slow velocity according to peak amplitude, mean amplitude and area (µV*ms) in channel Cz. The fast condition yields higher scores in all three measurement categories compared to medium and slow velocity respectively. *A repeated measures ANOVA showed a significant effect of velocity.

Mean amplitude for the MRP followed the same pattern and was larger for fast (2.4 µV, SD = 0.9), then medium (1.8 µV, SD = 0.8) and slow (1.3 µV, 0.6). A repeated measures ANOVA showed a main effect for velocity, $F (2, 9) = 39.455$, $p < .05$.

In the final category area (µV * ms), fast velocity also generated the larger area (1123.4, SD = 440), followed by medium (939.8, SD = 408.2) and slow (779.1, SD = 363.5). The repeated measures ANOVA showed that the area generated by the fast velocity is significantly larger than medium and slow velocity respectively, $F(2, 9) = 25.375$, $p < .05$.

The same procedure was repeated for the MRP in channel O2 (figure 7, table 1). Fast velocity was associated with the larger brain electrical activity for both peak amplitude and mean amplitude however a repeated measures ANOVA showed that there wasn`t any main effect of velocity for either peak amplitude, $F (2, 9) = 1,703$, $p > .05$, mean amplitude, $F (2, 9) = 2,807$, $p > .05$, or area, $F (2, 9) = 0,683$, $p > .05$

	Peak amplitude	Mean amplitude	Area
Fast	3.5 (5.2)*	1.7 (2.6)	528,2 (743.1)
Medium	2.8 (5.0)	1.1 (1.5)	590,4 (1051.8)
Slow	2.2 (2.2)	1.4 (1.4)	483,3 (874.6)

Table 1. Averages for peak amplitude, mean amplitude and area in channel O2.
*(SD)

4.1 Discussion

In this study high density EEG recording was used to investigate the brain electrical activity accompanying a visually guided joystick movement intercepting with a target decelerating in one of three different velocities. The task requires motor cortex to process visual information that is propagated from the primary visual cortex and the sensorimotor area in order to execute the movement.

4.1 Movement related potentials

We identified a positive brain electric activity, spreading across the medial frontal-posterior region, accompanying the joystick movement. The evoked potential was evident in all subjects and the activity was most pronounced in channel Cz in which it peaked at 3.04 µV in the grand average for fast velocity (figure 5b).

The source analysis showed that 93.4 % of that brain electrical activity could be explained by two dipoles, in which 74.5 % was accounted for by one dipole located medial in the sensorimotor areas. Together, the larger frontal dipole and the MRPs in Cz connect the EEG activity accompanying the joystick movement to the medial sensorimotor area in the brain. The other dipole was positioned in the occipital lobe (18.9 %), in the brain areas corresponding to the right hemisphere of the primary visual cortex (figure 6). As the subjects in our experiment fixed their gaze on the opening between the two occlusions on the right side of the screen and the stimulus car arrived from the left, the subsequent activation of right primary visual cortex is in concordance with the generally accepted theory stating that the left visual field is processed in the contralateral V1.

Numerous studies have been conducted displaying the link between voluntary movements and activation in M1-S1 and research on internally paced finger movements point out to several pre-MRPs as well as post-MRPs (Vaughn et. al., 1967; Shibasaki et al., 1980; Kim et al., 1993; Urbano et al., 1996). The negative build up in C3 and Cz (figure 3b) starting about 400 ms before the movement begins evolved in a time frame corresponding to the late part of the RP, however the slope of the potential was not as steep and the amplitude was considerable lower. The activity was also stronger in the medial areas (Cz) compared to the predominantly contralateral activity in M1-S1 that has been described by others (Babiloni, Carducci, Cincotti, Rossini, Neuper, Pfurtscheller & Babiloni, 1999; Shibasaki et al, 2006).

We didn`t identify the readiness potential as previously reported but that is more likely due to the differences between the experimental designs as the movements in our study were externally paced to the stimulus onset and the inter-trial latency was short compared to the established procedure in research on internally paced movements that often use inter-movement intervals lasting from 3 to 20 seconds (Shibasaki et al., 1980 & Urbano et al., 1996). In addition the task in our experiment was more complex than the regular self-paced finger movement as a successful performance depended on the brain to integrate information from the visual system with the sensorimotor system, and it is plausible that the readiness potential was concealed in the overall evoked EEG activity.

Shibasaki et al. (1980) described a widely distributed positive potential across the sensorimotor area accompanying the finger extensions/flexions with the larger activity contralateral to the movement in channel C3. This activity resembles the MRPs in our study, spreading across the M1-S1, predominantly in channel Cz (figure 5). The distribution of the activation is not as widespread as Shibasaki et al. (1980) report and the activity is stronger in the medial M1-S1. In Shibasakis` experiment the subjects performed voluntary brisk extensions and flexions of the middle finger which put less strain on the nervous system compared to the more complex visually guided joystick movement in our study. We propose that the confined brain electrical activity could reflect more specific sensorimotor processes involved in processing the visual information and coordinating it with motor cortex in order to execute the movements.

4.2 Velocity related potentials

By comparing the MRPs in fast, medium and slow velocity, significant differences between all groups were observed for area, mean amplitude and peak amplitude with one exception, there wasn`t any significant difference between fast and medium velocity for peak amplitude. Peak amplitude reflects the maximum voltage build up in a selected interval but it neglects the preceding and succeeding activity inside the block. Both area and mean amplitude reflect the overall activity in a certain period of time and it is therefore possible that they give a more precise measurement of the brain electric activity participating in a visually guided movement which is not restricted to an instantaneous moment of time but on the contrary depends on continuous interaction between sensory-motor and visual areas in the brain. In addition to provide a measure for the overall voltage activity, mean amplitude also corrects for any sudden random fluctuations of alternating polarity.

The fast condition is associated with the larger brain electrical activity as it yields the larger score for peak amplitude ((4.3 µV), mean amplitude (2.4 µV) and area (1123.4) followed by medium and then slow velocity (see figure 9). The corresponding relationship between the MRP and the velocity of the stimulus car indicates that the medial sensorimotor area is involved in processing velocity, which can apply to both visual motion and the execution of the motor response. However, figure 5a shows that the positive potential does not evolve until the actual joystick movement begins, suggesting that the potential reflects neural activity participating in the motor response. This is supported by Hill (2009) who conducted an ERP experiment in which the subjects performed a joystick controlled tracking

pursuit. He showed that a positive ERP with a maximum in CZ was time-locked to directional corrections executed with the joystick but not to the mere visual input of directional changes, proposing that the ERP could be assigned to the planning and execution of the required response. The topography of the component was also strongly restricted to the central cites, corresponding with the results of our study as opposed to the widespread positive complex reported by Vaughn et al. (1967) and Shibasaki et al. (1980).

Ashe (2005) proposes that the motor cortex is involved in spatial encoding of motor output and the direct specific muscle control, and he further states that the direct motor commands and spatial encoding are coordinated in a neural network where the gain fields of the neurons account for the bimodal processing. Georgopoulos et al. (1988) showed that the single cell would discharge to movements in many directions but at different rates and the direction of the arm movement was close to the direction of the neuronal population vector. Further, it was demonstrated that the single cell responded to different visual motion characteristics such as direction and velocity (Ashe et al., 1994, Moran et al. 1999), suggesting that the single cell could be involved in a neuronal ensemble encoding for multiple motion parameters. The concurrence of larger brain electrical activity with increased velocity can reflect the involvement of a neuronal ensemble encoding for visual motion and the subsequent motor output, thereby providing visuomotor control when executing the movement. In our study, there was with one exception a significant effect of velocity for peak amplitude, mean amplitude and area in channel Cz and the main part of that activity was according to the source model caused by one dipole located in M1-S1. The differentiated activity in M1-S1 can be explained by a neural network responding to increased velocity by gradually increasing the discharge rate, however this doesn`t necessarily imply a neuronal ensemble dedicated to velocity only, as the neuronal population code may account for multiple parameters such as velocity and direction.

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