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The N2 event-related potential component indicates
differential target representations for
eye and hand movements

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1 General introduction

In most of our daily activities we are in need of a very precise eye-hand-coordination. It is necessary to efficiently integrate the temporal and spatial aspects of a movement in order to enable fine motor skills. The question arises whether a combined eye and hand movement to the same target can be performed with one target representation, or if separate processing for eye and hand is required. This study focuses on the possible differences in target representation while performing eye- or pointing movements at a stimulus. If these motor systems are indeed based on separate representations, an effect on the corresponding event related potentials (ERP) should be measurable. The ERP in question is investigated using the N2 component which is most suited to this approach because it has been linked to target processing (Holguín, Doallo, Vizoso and Cadaveira, 2009).

1.1 Eye-hand-coordination

Eye-hand-coordination in humans and animals gets investigated regarding its spatial and temporal aspects. Furthermore, the mechanisms of attention are an important point regarding the interpretation of experiments on eye-hand-coordination. Depending on the context, attention can be seen as being under goal-driven control, based on the current search for a relevant target, or under stimulus-driven control which implies an influence of salient distractors in the environment (Hickey, McDonald, and Theeuwes, 2006).

Generally, studies about the nature and the degree of coupling between eye- and hand movement lead to inconsistent results, depending on the task in the experiment. This is partly due to different systems being activated. For example eye movement can be classified into two subcategories: Intentional (voluntarily) or reflexive (reactive). A sudden external stimulus can trigger reflexive saccades. In contrast to that, intentional saccades are willful and derive from memorized or imagined stimuli. In this regard, Sailer, Eggert, Ditterich and Straube (2000) performed an experiment using a number of tasks in order to differentiate between their influence on ocular and manual movements. They observed on the one hand changes in the directional and variable errors of eye and hand according to the task which were not correlated, and on the other hand mean

latencies which were organized in the same pattern for eye and hand movements. This correlation of latencies suggested common initiation of both motor systems. In addition, the temporal coupling appeared to be stronger for intentional tasks compared to reflexive tasks.

1.1.1 Coupling, cross-coupling or dissociation?

Eye movements are yoked to hand movements. This coupling has been shown in various experiments which demonstrated that hand movements are more accurate when eye movements are flexible and not locked to a fixation point. Three different kinds of feedback could be responsible for this connection: A feedback loop which guides the hand to the target, using visual feedback, a feedback-feedforward which generates ocular-proprioceptive feedback in order to update the hand movements or a feedforward model, where the copy of the eye movement efference can modulate hand movements. The most important aspect in the feedback loop hypothesis is that the limb movement could use foveal information (Wilmot, Wann and Brown, 2006). Otherwise, the feedback would rely on peripheral vision which is less accurate. This could be compensated by a gap-closure computation (Lee, Georgopoulos, Clark, Craig, Port, 2001). In contrast to that, the ocular-proprioceptive feedback is based on information about head and eye position from extra-retinal signals. Wilmot et al. (2006) summarize findings which demonstrate that ocular-proprioception serves to generate a target representation in space. The authors name this model feedback-feedforward loop because through feedback information, an estimate of the target in egocentric coordinates from eye and head signals is send forward to update the hand's trajectory. Lastly, as has been mentioned before, the third approach is solely feedforward and suggests an efference copy of the eye movements for the coding of the hand movements. Here, errors could occur more frequently because the accuracy depends on an internal model based on egocentric coordinates. Wilmot et al. (2006) argue for a complex system with a major contribution of the feedforward model, due to the fact that during their experiments subjects moved their gaze so well ahead of the hand target that a foveal contribution seems unlikely.

In addition, the final eye position seems to be pre-programmed before the hand movement initiation. This was observed during an experiment where participants had to

point at a stimulus and could either win a reward or gain a penalty. The visual saliency of the target determined the end point of the initial saccade, but all subsequent saccades were driven by the goal of the hand movement (Stritzke and Trommershäuser, 2007). In contrast to the observation of eye movements ahead of the hand movements (Wilmot et al., 2006), other experiments found that humans could not initiate saccades to a second target until the hand had reached the first target (Neggers and Bekkering, 2000). However, it has to be noted, that it is not necessary to see the whole movement in questions of precision: According to Blouin, Teasdale, Bard and Fleury (1993) the control of direction depends primarily on the visual feedback during the first distance-covering phase. At that time error detection and correction is important – this is reflected by the observation of no improvement in precision when the entire movement is visible compared to vision only during the initial phase of a pointing movement (Blouin et al., 1993). On the other hand, some experiments found initial kinematics being a poor predictor for final accuracy. These studies focused on different ways to implement feedback in hand movements. In this context, target capture does not seem to be the only critical time point for feedback. This is reflected by the inability to predict the variability of the amplitude of hand movements using the initial variability of movement acceleration – thus, a modification after the target capture has to take place. Additionally, the final variability of hand and eye is unrelated – indicating that gaze direction is not a target signal for arm control (Desmurget, Turner, Prablanc, Russo, Alexander and Grafton, 2005).

It is important to note that eye movements seem to be strongly influenced by hand movements: Thura, Hadj-Bouziane, Meunier and Boussaoud (2008) found a modulation of frontal eye field saccadic activity by visual and proprioceptive signals, depending on hand position relative to the end point of the eye saccade. Tipper, Howard and Paul (2001) published another experiment, where the eye saccade to a target was influenced by performing a reach. The authors interpreted this effect as a shift of the spatial frame of reference for the saccade to a hand-centered frame.

Many eye-hand-coordination studies have used a paradigm where participants had to look at a fixation point and then turned their gaze to point at a target as quickly as possible. The corresponding reactions appeared sequential: The hand moved 70-120 ms after the eye. As the whole movement of the eye takes about that time, the hand usually starts around the completion of the first response (Desmurget et al., 2005).

The hand's trajectory is determined by the spatial-temporal coupling of eye and hand movements. It has been demonstrated that at the time when the eyes acquired target position and the initial saccade ended, the hand achieved its highest acceleration and velocity. After the peak velocity the hand movements show decreased variability before they reach the target. This has been explained as a temporal and spatial coupling, where the relative position of eye, hand and target can be predicted based on retinal and extra-retinal information (Binsted, Chua, Helsen and Elliott, 2001). Regarding the question of velocity, Snyder, Calton, Dickinson and Lawrence (2002) investigated the sequence relationship of saccades and coordinated movements in rhesus monkeys. Firstly, they assessed the so called main sequence which consists in a strong coupling of the amplitude and peak velocity of isolate eye movements. This sequence changes during coordinated eye and hand movements – the peak eye velocity becomes approximately 4% faster and the saccade duration was reduced by the equivalent amount of time. The observed effect did not appear when the arm moves in the opposite direction, suggesting the necessity of tight coordination.

1.1.2 Brain areas

Regarding the question to what degree saccades and limb movements are coupled, Gorbet and Sergio (2009) investigated the effect of dissociation in the spatial coupling of eye and hand movements. Their participants were supposed to look in one direction and to perform a reaching movement in another direction at the same time. This manipulation led to changes in eye reaction time, peak eye velocity, hand-path curvature and arm movement time. These observations hint at the disruption of a brain system which is responsible for the coupling of eye and hand movements (maybe in order to make reaching movements as efficient as possible). Gorbet and Sergio (2009) summarize findings about possible cortical and subcortical networks for this coordination mechanism: Brain sources may lie in the superior colliculus which plays a role in orientating gaze and also shows activity correlating with electromyographic recordings from muscles. Further, the superior parietal lobule (SPL) and its reciprocal connections with the dorsal premotor area in the frontal lobe are mentioned as important structures for visually guided reaching movements. The possibility of dissociating eye and hand movements could be based on reach-specific neurons

encoding movements in eye centered frames which are contained in the SPL, the medial intraparietal area and the dorsal part of the parietal occipital area. These cells are not used for the organization of an eye movement, but firing has been recorded during the time of a saccade. Gorbet and Sergio (2009) interpret this finding as a sign of cross-coupling between reach and eye movement systems which could allow the described dissociation.

Planning and execution of eye and hand movements are achieved by a variety of signals which are generated by superior and inferior parietal lobules. The corresponding activation has been demonstrated during fMRI studies where participants performed grasping and pointing movements as well as saccades (Simon, Mangin, Cohen, Le Bihan and Dehaene, 2002). The parietal neurons can be regarded as an intermediate stage between vision and movement. According to Battaglia-Mayer, Archambault and Caminiti (2006), the corresponding network includes visual information input from the extrastriate occipital lobe and cortico-cortical connections to the premotor and motor areas in the frontal lobe. In further detail, the functional properties are organized in a gradient like system with different parts being dominated by hand- or eye-signals. The areas which are named in the following description can be seen in figure 1. Eye-signals are more pronounced in the parietal cortex (areas V6A, 7m) and in the dorso-rostral premotor cortex (area PMdr or F7). In contrast to that, hand information is dominant over eye information in the rostralmost part of the parietal cortex (areas PE) and caudalmost part in the frontal cortex (PMdc or F2, MI). The coexistence of eye and hand signals has been found in the parietal lobes (areas MIP, PEc and PEa) as well as in the frontal lobes (F2/M1 border). So far the explanations referred to a functional structure. In a second partitioning, regarding the type of information being treated, the processing can be subdivided into a part which transits from preparatory to movement signals (from caudal to rostral in the superior parietal lobules) and a second one with the opposite development (frontal cortex). Another gradient concerning eye properties (pre- or postsaccadic activity) has been found in the areas 7a (with mostly post-saccadic neural activity) and the lateral intraparietal area (pre-saccadic). The observed linkage between frontal and parietal areas with similar neural activities can be interpreted as a progressive matching of information through intracortical ipsilateral connections. Regarding the dynamics of matching operations the preferred direction of neurons in the superior parietal lobules (PEc, V6A and 7m) has been shown to align to each other during different eye-hand tasks. These parts were named 'global tuning fields' and

interpreted as a coexistence of matching procedures in one cortical region (Battaglia-Mayer et al., 2006).

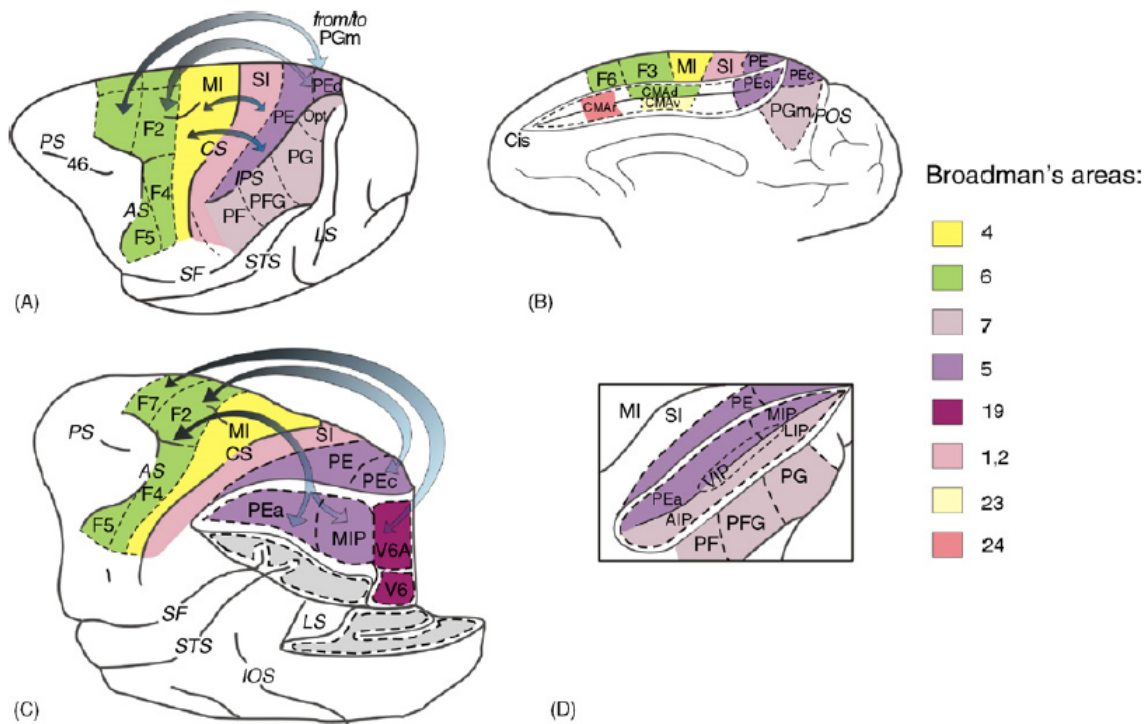


Figure 1. Areas in the parieto-frontal network for reaching movements in a macaque monkey. A: Lateral view on the hemisphere. B: Medial view on the hemisphere. C: Lateral view on the hemisphere with certain parts of the parietal and occipital cortex having been removed, showing areas in the medial bank of the intraparietal sulcus and in the rostral bank of the parieto-occipital sulcus. D: Parietal region around the intraparietal sulcus. The arrows represent the ipsilateral connections between parietal and frontal regions (Battaglia-Mayer et al., 2006).

An important role of the parietal cortex for hand and eye movement related activity has also been investigated in other studies with macaque monkeys. Single-unit activity identified two specialized areas for saccadic eye movements (lateral intraparietal area) and for the control of arm movements (parietal reach region) (Carey, 2000). Studies using transcranial magnetic stimulation further claimed that the coding of a reach plan is based on eye-centered coordinates in posterior parietal cortex and limb-centered coordinates in premotor cortex (Van Donkelaar, Lee and Drew, 2002).

Buneo and Andersen (2006) focused on the role of the posterior parietal cortex (PPC) as a sensorimotor interface between eye and hand movements, in form of a mapping from representations of target and hand position in eye coordinates to representations of motor error in hand-centered coordinates. This mapping does not

use a transformation into intermediate head- and body-centered reference frames, but works directly in a way of the functional properties of the cells along the ventro-dorsal axis of the superior parietal lobule (from inside the sulcus to the surface) being gradually changed. This change takes shape as a different specification among cells for various movements which can be observed as a variation in activation. The corresponding activation shows a characteristic pattern in distinct regions, see figure 2.

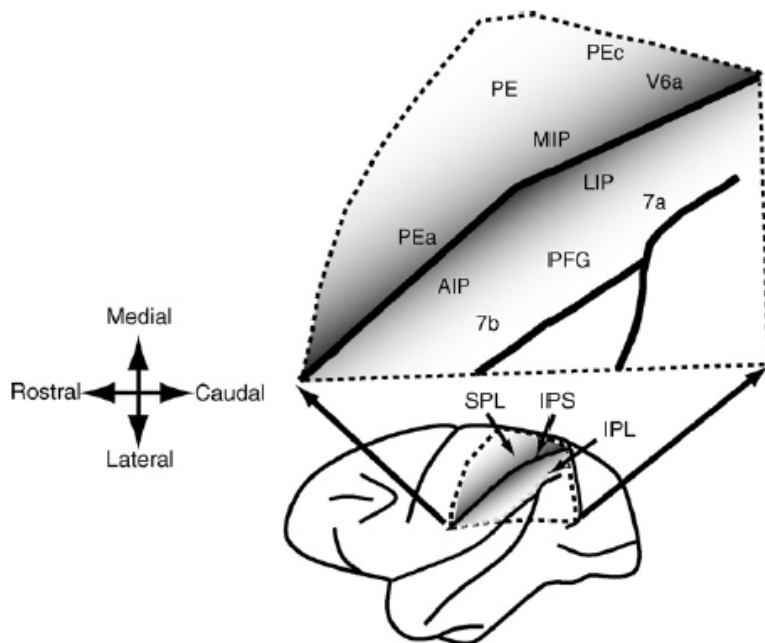


Figure 2. PPC highlighted from a lateral view in the macaque monkey brain. The intraparietal sulcus (IPS) is indicated through the shaded regions. Abbreviations: Superior parietal lobule (SPL); inferior parietal lobule (IPL); dorsal area 5 (PE); medial intraparietal area (MIP and V6a); lateral intraparietal area (LIP) (Buneo and Andersen, 2006).

Regarding specific structures in the PPC, research has disclosed some distinctive functions: The LIP is characterized through a large overlap of eye movement activation and sensory attention in the context of saccades – in other words, the function of the LIP can be interpreted as a sensorimotor interface during the production of saccades. Even in the early stages of movement planning, evidence has been found that the PPC may not have the same influence during the planning and control of arm movements such as in corresponding eye movements. Neural circuitries within the PPC differ with regard to these actions. The IPL (containing 7a and LIP) is responsible for eye movement, whereby arm movement is related to activation in both IPL (7a) and subdivisions of the SPL (including dorsal area 5 (PE), PEc, Pea, MIP and 6a (the last two comprising the parietal reach region)). Area 5 and PRR are thought to build a sensorimotor interface for reaching movements, on the one hand in the inverse

transformation from sensory information to motor command and on the other hand in the reverse (forward) way in integrating sensory information with motor commands in order to maintain awareness about the arm state (Buneo and Andersen, 2006).

Tziridis, Dicke and Their (2009) summarize different concepts about the networks of cortical areas. These include parieto-occipital parts which are responsible for the integration of information on the location of the hand and the eye and parts of the frontal cortex which serve to develop the subsequent movement plans. Tziridis et al. (2009) focused on the involvement of the pontine nuclei in rhesus monkeys, in order to investigate an alternative theory of eye-hand-coordination. This idea is based on a cerebropontocerebellar projection for the sensory guidance. During their experiments, a specific region in the dorsorostral pontine nuclei was activated while the monkeys prepared and executed hand reaches. The saccade-related neurons were located in a close, but distinct area. In addition, their activity started later than in the movement-related neurons. Tziridis et al. (2009) suggest a connection between the delay in the onset of discharge and the onset of movement. They cite studies which observed a time window of only 2-11 ms from the onset of discharge in an oculomotor neuron to an eye movement (Fuchs and Luschei, 1970) compared to 120 ms in the case of hand movements (Flanders, 1991). Generally, the discharge in the dorsal pontine nuclei is not sensitive to aspects of coordination. It shows very similar patterns in tasks where eye- or hand movements or both are required. Therefore, the necessary neuronal adjustments for eye-hand-coordination could take place in the context of cerebrocortical input – possibly through modifications in the temporal fine structure. Tziridis et al. (2009) conclude that their findings suggest anatomically and functionally separate precerebellar, pontine visuomotor channels for hand reaches and eye movements.

Regarding the context of target representation, this delay in the activity in saccade-related neurons could also reflect the necessity of higher efficiency in the processing of movement-related information compared to saccade-related information. In other words, the earlier onset of discharge in movement related neurons could be connected to a more complex processing of information. This aspect will be discussed in further detail in chapter 1.3.

Gottlieb (2002) suggests another mechanism of target representation in the parietal lobe. She proposes that movement and perception are based on a common target selection mechanism in this area. She focuses on the high selectivity of parietal

neurons with regard to behavioral needs and their participation in the selection of potential targets. These parietal representations could reflect an attentional mechanism which is capable to simultaneously specify targets for perception and movements. In particular, the inferior parietal lobule has been demonstrated to form highly selective salience representations of objects with relevance for behavior. For example, the neurons in the lateral intraparietal area (LIP) respond more strongly to stimuli which are related to a reward. The role of the neurons in the LIP is reflected by the increase of activity during saccades which is inversely proportional to the difficulty of the selection process. Regarding saccadic movements, it has to be noted that the LIP-neurons can respond before the saccade, but they do not always predict the following oculomotor behavior. Gottlieb (2002) suggest that the LIP could serve the initial target selection, but the specification of these movements could rather happen in downstream structures, such as the frontal eye field and the superior colliculus. Concerning the further characterization of the role of the LIP, a correlation between activity in neurons in LIP and area 7a could be found during shifts in spatial attention. Furthermore, it is linked to attentional load and can predict the detection of peripheral visual cues. Interestingly, parietal neurons have been found to encode arm movement targets in retinotopic coordinates (see 1.2). In addition, they carry information about variables such as position and movement of eyes, head and arms (explicitly or in the form of modulations in retinotopic receptive fields) (Gottlieb, 2002).

Another approach used a task where saccades and pointing movements had to be performed in the context of an investigation about decision-making processes (Tosoni, Galati, Romani and Gorbetta, 2008). The corresponding study demonstrated that even in more complex decision-making tasks, intraparietal neurons accumulate information over time. In addition, the impact of the sensory evidence is reflected by the posterior parietal cortex. During the experiment by Tosoni et al. (2008), participants had to point at specific stimuli and perform saccades toward others. As stimuli served pictures of places and faces which are normally related to different specific brain areas. The pictures were blended with a certain amount of noise, in order to investigate the role of the strength of sensory evidence. The stimuli which triggered a pointing movement lead to a pattern of activity that correlated with the provided sensory evidence within two regions in the medial parietal cortex. A more complex situation which was also related to perceptual difficulty was found in the saccade-sensitive posterior intraparietal region. The particular regions of interest were identified with fMRI-

scan during memory-guided saccade or pointing tasks. The authors identified two pointing-specific regions which were labeled anterior and posterior parietal reach region. They are both situated in the precuneus which is on the medial surface of the parietal lobe. The lateral side of the parietal lobe contained a saccade-specific region, localized in the medial bank of the posterior intraparietal sulcus (pIPS). The action-related areas in the frontal lobe could also be distinguished into two pointing- and one saccade-specific regions. The first two lay in the left central sulcus at the sensory-motor cortex and also dorsal in the precentral sulcus in the posterior end of the superior frontal sulcus (frontal eye fields, FEF). Tosoni et al. (2009) hypothesized that these pointing-selective regions in the posterior parietal cortex could be linked to the medial intraparietal area and V6A in the macaque monkey. The same could apply to the saccade-selective region and pIPS and FEF in relation to LIP and FEF.

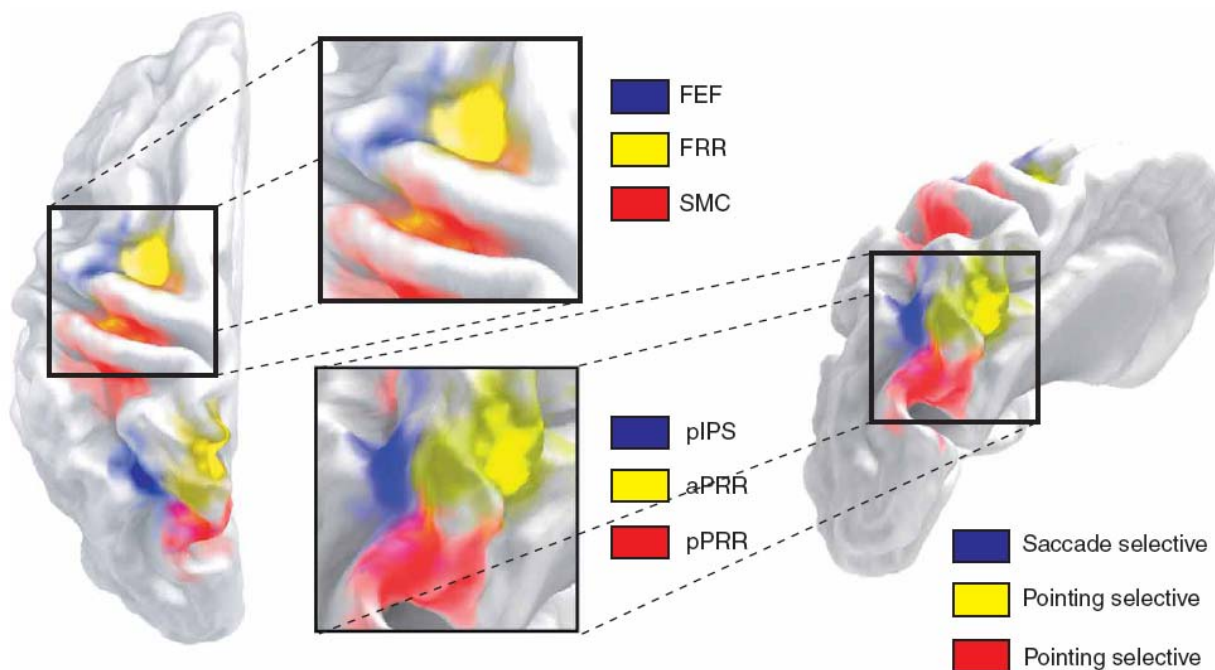


Figure 3. Regions in the posterior parietal and frontal cortex which were selective for saccades or pointing movements. Frontal eye fields (FEF); frontal reach region (FRR); sensory-motor cortex (SMC); posterior intraparietal sulcus (pIPS); anterior parietal reach region (aPRR); posterior parietal reach region (pPRR) (Tosoni et al., 2009).

During the pointing condition, several regions in the posterior parietal cortex responded more strongly to a higher load of sensory evidence. Tosoni et al. (2009) interpret their findings as evidence for a sensory-motor mechanism for arbitrary visual decisions within the posterior parietal cortex. They understand the observed changes in

activity as an accumulation of sensory relevant input toward a behavioral outcome of a decision. In this regard, visual decisions would not rely on high-level representations, but instead be included in direct transformations between sensory- and motor representations. Here, the premotor circuitries could judge sensory evidence in relation to learned behavioral choices. Tosoni et al. (2009) explain this as 'embodied cognition', where cognitive functions are not based on specialized modalities, but are integrated in sensory-motor processing mechanisms.

Regarding the role of the posterior parietal cortex (PPC) it has to be noted that some studies suggested a distinct function of the left and right hemisphere in this context. Mevorach, Humphreys and Shalev (2006) observed a different effect of transcranial magnetic stimulation (TMS) on both sides. On the right PPC, it interrupted the appointment of attention to a stimulus, whereby, on the left PPC, TMS led to an inability to guide attention away from a stimulus. The authors suggest that this effect could be easily overlooked in some paradigms, because a salient and irrelevant target could activate the right PPC, and being followed by activity in the left PPC which is supposed to keep the stimulus from being selected (Mevorach, Humphreys and Shalev, 2006).

In the context of clinical implications, Milner and Goodale (1995) describe a possible condition which is related to eye-hand-coordination: The optic ataxia. Affected patients suffer from damage in the posterior parietal cortex (which is connected to the dorsal pathway, see 1.2.1). They are no longer capable of generating eye- or reach movements toward a target. In this context, it would be interesting to further differentiate between pointing and saccades.

1.1.2.1 Cerebellum

Another part of the brain which serves sensorimotor integration is the cerebellum. It is important in matters of adjusting motor commands to temporal and spatial parameters (Liu, Ingram, Palace and Miall, 1999). Furthermore, there is evidence that the cerebellum plays an important role in motor learning and control (Wolpert, Miall and Kawato, 1998). Miall, Reckess and Imamizu (2001) investigated the activity of the cerebellum during a number of tasks which demanded different degrees of eye-hand-coordination using fMRI. They found a complex pattern of reactions with increased activation both in coordinated and in independent movements. These results were explained based on the role the cerebellum plays in learning of motor coordination: In tasks where new control modules became necessary, the cerebellum could not immediately select an existing control module – and therefore appeared relatively inactive (Miall et al., 2001).

Wolpert et al. (1998) discuss the possibility that the cerebellum contains an internal model of the motor apparatus. This could either provide a motor command for a planned trajectory or be used to predict consequences of actions and in this way limit delays from feedback control. This idea of an internal model which produces predictive signals for motor coordination is further explored by Miall and Jenkinson (2005). They observed effects of learning a coordination task using fMRI and demonstrated increased activity in the cerebellum independently of performance error. They interpreted their findings as two factors being involved in the change of activation after learning: One is probably directly related to performance error and declined during training. The other could refer to gaining experience and increased during the task. Miall and Jenkinson (2005) state that improved performance is due to selective modifications of the processing of ocular and manual control signals in the cerebellum. According to Miall and Jenkinson (2005) these results support the theory of an internal model in the cerebellum as a basis for eye-hand-coordination.

Sailer, Eggert and Straube (2005) investigated eye-hand-coordination, specifically temporal prediction in this regard, in patients with cerebellar lesions. The authors observed that the cerebellar patients were affected concerning their ability to generate eye movements. These difficulties mainly derived from disturbed eye movements and synchronization with hand movements. Coming to a conclusion, the

function of the cerebellum was interpreted as a basis for the synchronization of saccades. Opposed to that, the primary representation seemed not to be affected. The patients did not have problems with suppressing early inappropriate saccades or performing anticipatory saccades and did not differ in regard to the error of visually triggered saccades. Another study by van Donkelaar and Lee (1994) also worked with cerebellar patients. The authors investigated the influence of cerebellar dysfunctions on the interaction between eye and hand movements. The cerebellar patients and control subjects showed a different degree of coupling between hand movements and saccades. For example, during a task where a moving target had to be tracked with the hand, the hand movement resulted in a higher accuracy of the eye movements in normal controls (compared to eye movements in isolation) and in contrast to that, to decreased accuracy in the cerebellar patients. Van Donkelaar and Lee (1994) interpret their findings as a reciprocal interaction between hand and motor systems or a common influence from another hierarchically higher structure.

1.2 Target representation

One important question concerning target representation is, whether the degree of coupling between eye and hand movements is influenced by different task characteristics. If this coupling changes depending on the importance of target attributes for the hand or the eye, then a separate target representation based on different target features seems likely. Sailer, Eggert, Ditterich, Hassenzahl and Straube (2002) investigated the effects of haptic textures on the kinematics of eye and hand movements. The haptic texture is important for hand movements, but not for eye movements – thus, the hypothesis of two different ways of information processing would predict variation between haptic textures for the hand, but not for the eye. During the experiment, participants were asked to perform pointing movements or saccades toward fur (slippery target) or sandpaper (rougher target). Due to a longer deceleration phase, the pointing movement took longer in the case of a slippery target. In contrast to that, the eye was not affected by the texture. This experiment demonstrated that information about target texture is used differently by the hand and the eye, and provides evidence for a separate target representation during eye-hand-coordination.

This interpretation is further supported by another behavioral experiment. Sailer, Eggert, Ditterich and Straube (2002) used different tasks to investigate the effects of a distractor in various positions relative to the target. The experiments were based on the global effect paradigm in eye movements which results in a certain tendency of the eye to land in between a distractor and the target if they are presented at the same time. This effect is typically observed for eye movements. Generally, this study found a global effect being present for hand movements as well. However, a number of arguments which derived from observations during different tasks speak against one shared target representation for hand and eye. First of all, the global effect influenced latencies only in regard of eye movements. The measured amplitudes for eye and hand movements changed in two cases in different directions. Furthermore, the effect in question differed for hand and eye concerning magnitude and stability. These results suggest parallel processes during selection which influence separate target representations for the hand and the eye. The observation of a common global effect, differing between task conditions, could be interpreted as an interaction, or an exchange of information, between the target representations. Another interesting aspect in this context is a stronger influence of eye movements on hand movements than the other way around. The authors argue that this could be either due to an asymmetry in the reciprocal interaction or a continuous modification of the hand target representation (Sailer et al., 2002).

During experiments with a variation in background information, a systematic underestimation of the pursuit distance, concerning the magnitude of the eyes' trajectories, has been observed when a reach to remembered targets had to be performed. Apart from the size of the background, reasons which derive from the organization of the target representation could be responsible for this misinterpretation. As the target and the hand need to be represented in a common coordinate frame in order to be able to perform a reaching movement, a coordinate transformation is required. This framework is thought to be eye-centered. The transformation leads to time delays – for example, the eye continues to move while the representation of the hand gets transformed to eye-centered coordinates. This could explain the underestimation of the distance between gaze position and the target. Altogether, these findings would suggest a time lag of the hand representation compared to the target representation (Whitney and Goodale, 2005).

Another approach states the existence of multiple target representations for movement planning and explains gaze-dependent errors with a bias in the transformation between those representations (McGuire and Sabes, 2009). (According to McGuire et al. (2009), an example for a gaze-dependent error is the retinal eccentricity effect where the distance between the gaze location and a peripheral target gets overestimated during a reaching movement. The authors claim that the use of sensory signals depends on their statistical properties as a consequence of different reference frames). McGuire et al. (2009) used Gaussian likelihood to refer to the probability of a true target location compared to sensory input. During the experiments different tasks were provided for eye and pointing movements. McGuire et al. (2009) assume that visual signals start with a retinotopic representation and proprioceptive signals are based on body-centered reference frames. If the brain can rely on both modalities, the signals can be integrated in both reference frames' representations. The transformation processes add to the variability. Consequentially, the gaze-dependent error is interpreted as a product of the relative weighting of the sensory signals. The authors tried to predict the gaze-dependent error with a direct readout of either the retinotopic- or body-centered representations. Additionally, the resulting movement vector could in itself be an integration of contributions from both representations. The integration model proved to be best at predicting the results of different trials. Furthermore, McGuire et al. (2009) argue that the two representations could either be found in different subsets of the cortical areas, or the described computation could derive from a heterogeneous population of neurons which contains retinotopic and body-centered components in a mixed representation. The neurophysiological literature hints at all relevant areas making use of mixed representations, according to McGuire et al. (2009), whereby the parietal cortex is more retinotopically organized and the frontal cortex is rather hand- and body centered. This interpretation is also supported by investigations of the ventral intraparietal area (VIP) of macaque monkeys by Avillac, Denève, Olivier, Pouget and Duhamel (2005). They argue for a model based on multisensory integration. This is supported by their findings in the VIP, where tactile representations were encoded in a single head-centered reference frame. In contrast to that, the visual receptive fields were distributed between eye- and head-centered coordinates.

1.2.1 Information stream during signal processing in target representation

The processing of information through to the formation of a target representation and target selection differs highly within the hierarchy of the brain systems. Hopf, Vogel, Woodman, Heinze and Luck (2002) describe the stream of information as follows: The initial processing seems to happen automatically. The neural activity in the retina is not sensitive to the direction of attention. The influence of arousal and attention manifests when the information reaches the primary visual cortex (V1). Here, the effects of top-down processes are still smaller than in extrastriate visual areas. At this time point, and within inferotemporal visual areas, a modulation of feedforward sensory activity can take place. Generally, the top-down factors play a larger role for visual information on higher levels, regarding time and cortical region.

Maunsell (1995) also provided a detailed model of the flow of information during the processing of visual input. He states that the encoded information varies greatly in different cortical brain areas. At the beginning, neurons in V1 react to light or edges. In contrast, neurons at hierarchical higher stages react to complex features and depend on a variety of conditions. One possible interpretation of these multiple levels in the brain is that they are a precondition for a range of sensory representations. The influence of attention leads to suppression of unimportant information and the interpretation of the meaning of relevant features. Maunsell (1995) demonstrated in his experiment state-dependent modulations of the representations which derive from the retina during the processing of visual information. The representation is edited through filtering of details and adding information from memory.

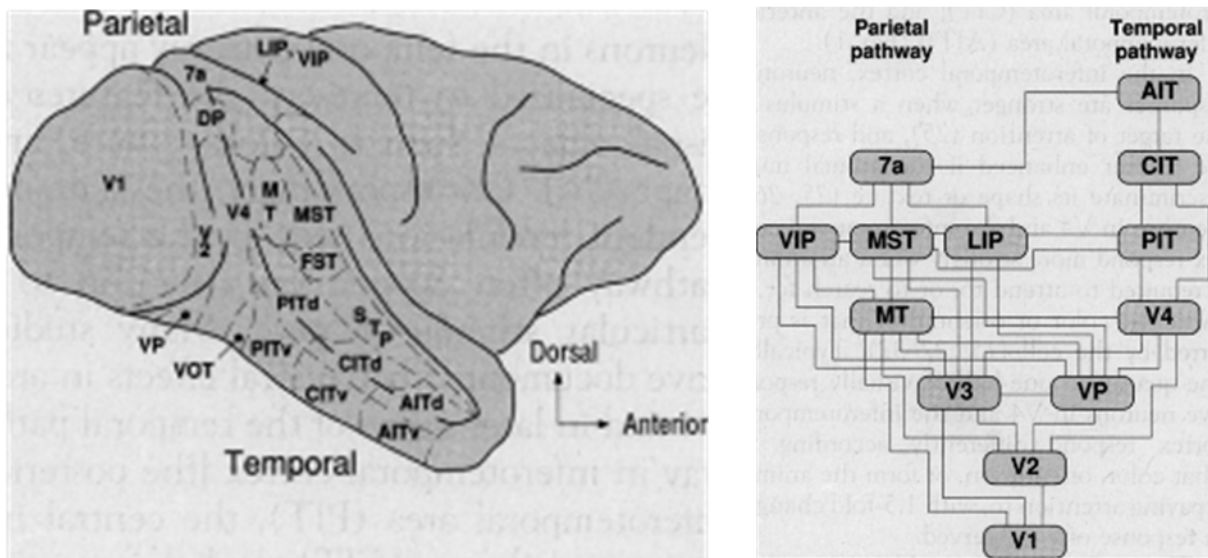


Figure 4. Left: Lateral view on the right hemisphere in macaque monkeys. Superior temporal sulcus appears open. Right: Hierarchical organization of visual areas. Earlier stages are at the bottom and are linked with others through axonal projections. Two different streams of processing are subdivided, the parietal and temporal pathway. Brodmann's area (7a); anterior inferotemporal area (AIT); central inferotemporal area (CIT); dorsal parietal area (DP); fundus of the superior (FST); lateral intraparietal area (LIP); medial superior temporal area (MST); middle temporal (MT); posterior inferotemporal area (PIT), visual area 2 (V2); visual area 4 (V4); ventral intraparietal area (VIP); ventral occipitotemporal (VOT); ventral posterior area (VP) (Maunsell, 1995).

Maunsell (1995) summarizes that state-dependent modulations derive from sources other than the retina. Different types of extraretinal signals which influence neurons in the parietal cortex are vestibular signals, proprioceptive signals (possibly from the neck), or the position of the eyes. As can be seen in figure 4, the extrastriate cortex can be subdivided into two streams of information processing: The parietal areas which are responsible for analysis of motion and spatial relations and the temporal stream which mostly deals with visual recognition and identification. The parietal pathway is sensitive to state-dependent modifications, especially in, or close to, area 7a. This has been demonstrated in different studies, where attention had to be fixed on different targets for eye movements or hand movements. Modifications of this kind can also play a role when the stimulus is not visible and a representation has to be developed – for example LIP and area 7a are activated when animals have to remember a location (Maunsell, 1995).

However, it should be noted that an influence of beliefs and expectations could probably happen even during the earliest stages of visual processing, even in the striate

cortex. Kosslyn, Ganis and Thompson (2001) summarize findings where areas 17 and 18 could be altered by imagery and conclude that modulations through expectancies can change what we actually see during perception.

A wide range of possible interpretations of the two separate parietal and temporal pathways exist. Bruce, Green and Georgeson (2003) give an overview about some approaches to understand visual processing. They describe possible interconnections in the visual system. First, visual input can bypass the striate area, through the lateral geniculate nuclei and the pulvinar nucleus which receives signals from the retina and the superior colliculus. As has also been stated by Maunsell (1995), Bruce, Green and Georgeson (2003) explain how two main pathways segregate after V2. The dorsal pathway moves from V3 and V3A over the middle temporal area (MT) and the medial superior temporal area (MST) to area 7a in the parietal lobe. The ventral pathway is located in between V4 and the posterior and anterior inferotemporal areas (PIT and AIT) in the temporal lobe. Milner and Goodale (1995) stated that these two pathways differ in the way they analyze visual information. According to them, the ventral pathway forms a basis for a conscious awareness of visual surroundings, through building representations using identities, properties and spatial layout. On the other hand, the dorsal pathway controls movements in interactions with visual input. However, Bruce, Green and Georgeson (2003) emphasize that the two pathways and the visual areas in general, are interconnected by various feedback loops. Therefore, timing is a very important point regarding the interpretation of activation in different locations. This has important implications for the application of EEG-studies. As a good temporal resolution is an advantage of ERPs, these feedback loops could be investigated. The combination with other methods, such as MRI, can provide information about the source of the components (for example, Woldorff, Liotti, Seabolt, Busse, Lancaster and Fox (2002)). If a certain ERP appears at a defined time point, it is important to know, whether it could be a re-entrant activation which derives from a hierarchically higher structure. Therefore, especially when modifications of target representations are taken into account, information about the interconnections between different pathways is crucial.

Regarding the fact that visual information is not processed in a direct forward manner, the question arises which influence different movements have: Astafiev, Stanley, Shulman and Corbetta (2004) report activity in the human lateral occipital cortex being modulated by limb movements. This effect was even observable when no

visual feedback of the movement was provided. The study focused on the so called extrastriate body area which has been linked to the perception of body parts. The authors suggest that this area could be modulated by planning, executing or even imaging of limb movements. During the experiment, Astafiev (2004) compared the BOLD reaction (measured with fMRI) in the lateral occipital cortex during tasks requiring changes of the locus of attention (with fixed eye position), saccadic or pointing movements. They found a significantly stronger reaction in the pointing condition. These findings were interpreted as evidence for action-related activations within the visual cortex at an early stage.

1.3 Pointing studies

Several theories have tried to explain the control over pointing movements. Vindras and Viviani (1998) sum up three different approaches: The final position control hypothesis (Bizzi, Hogan, Mussa-Ivaldi and Giszter, 1992, cited by Vindras et al. 1998) states that the target position provides a setting which leads to a spontaneous tendency in the muscles synergies to adapt to the corresponding new configuration. This idea implies that the final position is independent of the starting position. In another model an extrinsic representation with a shoulder-centered coordination system is generated based on retinal information and head and eye position signals. During the next step a conversion to arm and forearm movements toward the target takes place. The complete motor plan derives from the vectoral differences of the joint angles in the initial and final positions (Flanders, Helms Tillery and Soechting, 1992, cited by Vindras et al. 1998). Another approach, the vector coding hypothesis, includes the coding and storing of the extrinsic coordinates, the identification of intrinsic coordinates which code the target location in the postural orientation and finally the delivery of motor commands. Between the first and the second step the extrinsic coordinates are transformed to a vector, for example by amplitude and direction which takes the starting position into account. Vindras et al. (1998) summarize an experiment which systematically modified the starting position of the hand and found a corresponding pattern at the end of the reaching movements. The results were interpreted as contradicting the final position control hypothesis. Regarding the hypothesis about a shoulder-centered coordination system, they are compatible with a motor plan based on the initial and final joint angles

of the arm articulations. However, an explanation based on comparing initial and desired postures could not fully explain the variability in different aspects concerning pointing movements. Coming to a conclusion, the vector coding hypothesis provided the best explanation of the results (Vindras et al., 1998).

The computation of coordinates for the representation of the target could be head- or eye-centered, hand-centered or making use of allocentric representations. Thaler and Todd (2008) investigated different frameworks and found the highest accuracy and reliability in visually guided hand movements in settings which allowed an egocentric hand- or eye-centered representation. Another approach did not focus on the question of different coordinates, but on correlation structures between the two-effector movements in eye-head or eye-arm, and, with eye-head-arm, a three-effector condition (Suzuki, Izawa, Takahashi and Yamazaki, 2008). The coupling of the motor systems varied among different tasks. The eye-arm coupling was higher in the three-effector condition compared to movements that included only eye and arm. The same was not true for the eye-head coupling. Generally, head movements appeared to be quite flexible: Sometimes they were more closely linked to arm movements than to eye movements. According to the authors, these results indicate that motor commands for different motor effectors are linked in a way which can be adapted to different tasks. Another way of investigating the coordinates which are used during reaching movement is single-cell recording. Stuphorn, Bauswein and Hoffmann (2000) recorded the discharge of neurons in the superior colliculus (an oculomotor structure) in rhesus monkeys. The reach-related neurons were measured while the monkeys reached at the same target location during different gaze orientations. The results revealed that 60% were neither influenced by the target representation on the retina nor by the eye position. The gaze-independent neurons operated in a shoulder- or arm-centered reference frame. In contrast to that, only 40% of the neurons were significantly influenced by the gaze and appeared to be activated when the target had specific coordinates in relation to the gaze axis.

1.3.1 Contextual information

On a more general level, the value of different models for the planning and execution of pointing studies is discussed. According to Mendoza, Elliott, Meegan, Lyons and Timothy (2006), visual processing is often analyzed in context of the ventral and the dorsal stream (see 1.2.1). Different models have been developed in order to understand the functional differences between these two pathways. In contrast to the subdivision into 'where' (dorsal stream) and 'what' (ventral stream) (Ungerleider and Mishkin, 1982), the perception-action model claims that the ventral stream serves perception, whereby the dorsal stream allows the control of action (Milner and Goodale, 1995). However, some experiments failed in demonstrating an independence of the perceptual estimate and the visuomotor control of action – therefore, Franz, Fahle, Bühlhoff and Gegenfurther (2001) suggested that one common target representation underlies both functions. As this model also has shortcomings in explaining the differences between perception and action, another approach has been presented: The planning-control model (Glover, 2002). Here the difference is seen between planning (a movement in advance) and online control. The effects of illusions depend on the relative contributions of these two processes. The perception suffers from the surroundings, but during the movement adaptations through visual or proprioceptive feedback or efference copies can take place. In contradiction to the planning-control model, some experiment using different configurations of visual feedback provided evidence against its predictions, as has been summarized by Mendoza et al. (2006). Another important point is that a strong influence of contextual information and different ways of interaction seem to have an impact on pointing movements. This suggests rather a flexible model, which can use multiple visual cues to adapt to a changing environment, instead of a simple single representation model or the former dichotomous approaches such as the perception-action model or the planning-control model (Mendoza et al., 2006).

Visual illusions are a feasible way to investigate the differences in processing streams or during various functions, because under certain circumstances, they influence only particular aspects of processing and actions. This way they can elucidate characteristics of information handling during eye-hand-coordination. The well known experiment using the Titchener circle illusion by Aglioti, DeSouza and Goodale (1995) might also be of interest: It shows that the grasping movement at a circle is not affected by an optical illusion which makes most people think that the size of a circle changes

depending on its surroundings (which would be in line with the perception-action model by Milner and Goodale (1995)).

A more differentiated result was presented by Binsted, Chua, Helsen and Elliott (2001): They used the Müller-Lyer illusion to demonstrate that it does have an effect on hand movements, but only if the target figures disappeared during movement initiation. The Duncker illusion provided a third way to investigate the effect of visual illusions. Here, a moving background influences the perception of the direction of a target motion: Soechting, Engel and Flanders (2001) used the Duncker illusion in an experiment with pointing movements. They found a higher correlation of the error in pointing with the gaze position shortly before the hand reached the target, compared to the end of the saccade. The authors concluded that the target signal for the arm seems to derive from a gaze position signal – this signal, in turn, could be provided by extraretinal signals such as efference copies from motoneurons (Soechting et al., 2001).

1.4 EEG components related to eye-hand-coordination mechanisms

A range of ERP components can be used to investigate the neural processing of attentional capture and the manipulation of target characteristics. A large variety of search paradigms has been invented to isolate the important features during the flow of neural information. The following text gives an overview about selected components which are important for visual processing.

1.4.1 P1

During experiments, the P1-component proved to be sensitive to stimulus parameters – due to its origin in the extrastriate cortex - , the direction of spatial attention or to the state of arousal (Luck, 2005). Furthermore, the P1 has been interpreted as a marker of perceptual difficulties during visual search (Akyürek, Dinkelbach and Schubö, 2010).

The first positive peak appears approximately 100 to 130 ms after stimulus onset. Studies suggested that the early part of the component could derive from the dorsal extrastriate cortex (middle occipital gyrus) and a later part from the fusiform gyrus. Regarding the fact that during the first 100 ms after stimulus onset, already thirty or more visual areas are activated, the recorded component could include multiple contributions (Luck, 2005).

1.4.2 N1

The N1 component reflects discrimination processes. It appears to be larger in discrimination tasks compared to detection tasks. In addition it is influenced by attention. Furthermore, the N1 includes different subcomponents. The earliest ones appear 100 to 150 ms after stimulus onset at the anterior side. Between 150 to 200 ms poststimulus, at least two posterior subcomponents appear, one deriving from parietal cortex and the other one from lateral occipital cortex (Luck, 2005).

1.4.3 P2

The P2 is interpreted as visual feature discrimination (Akyürek et al., 2010). This component appears at anterior and central scalp sites, but only in reaction to fairly simple stimulus attributes. In this aspect it differs from the P3 which is also sensitive to complex targets (Luck, 1995).

1.4.4 N2

Studies on attentional capture or selection processes which are based on the analysis of ERPs often include the N2. This component can be further subdivided regarding the time range in question and its source. Deriving from frontocentral regions, it is labeled as anterior N2 and has been linked to various aspects of cognitive control, including response inhibition, conflict or error monitoring. In this context, the N2 is usually investigated using Go/NoGo-tasks and is recorded at the Fz-electrode. Here, it is often interpreted in connection with the later P3 which has been linked to inhibition mechanisms (Oddy, Barry, Johnstone and Clarke, 2005). In other words, in approaches based on applying Go/Nogo-trials, the N2 is interpreted as detecting or inhibiting an inappropriate tendency to respond (Kopp, Mattler, Goertz and Rist, 1996).

However, the posterior N2 or N2p (with a posterior scalp distribution) reflects mechanisms of target processing. In this regard, enhanced N2p components have been detected during target detection or classification, visual discrimination and oddball paradigms (Holguín et al., 2009). Holguín et al. (2009) demonstrated that the N2p correlated with the reaction needed and was larger in conditions where more attentional processing was necessary. These findings suggest that the N2 represents selection and classification of target characteristics. Kamitani and Kuroiwa (2009) summarize the N2 components as belonging to an attention related family of ERPs. Folstein and Van Petten (2008) review the N2-related research as firstly focusing on 'cognitive control', including strategic monitoring or regulation of motor responses and secondly based on attention, novelty or mismatch detection. The authors also emphasize the difference between the anterior N2 which should be divided into control or mismatch related subcomponents and the attention-dependent posterior N2. They even specify further and define one frontocentral N2 that refers to detection of novelty or mismatch, another

frontocentral subcomponent that is related to cognitive control and two different posterior parts, being related to aspects of visual attention. The oddball paradigm has also been used to investigate the N2. Here, rare visual stimuli elicit a larger N2, followed by a larger posterior P3 (Folstein and Van Petten, 2008). The posterior N2 has also been observed to show an enhanced negativity during the presentation of pop-out targets compared to homogenous arrays (Luck and Hillyard, 1994). Senkowski and Herrmann (2002) report a maximum activation of the N2b in a hard discrimination task compared to an easier discrimination task.

A broad overview is presented by Patel and Azzam (2005): They subdivide into involuntary and active processing. The anterior N2a is evoked by conscious attention or ignoring a stimulus. The N2b is distributed posteriorly and is evoked only by attention to a stimulus. The N2c can be found centrally and frontally and refers to classification processes. A deviation from expectations or a general mismatch in a search task, have been suggested as possible connections to the N2b. In this context, it is thought to be generated in the frontal and superior temporal cortex. Regarding the locus of generation, the anterior cingulate cortex has also been discussed in relation to general detection during tasks using color selection. Patel and Azzam (2005) mentioned the posterior ERPs, N2p and N2pc, as characteristic for pop-out paradigms. According to them, the N2pc appears during discrimination tasks and disappears again when the number of stimuli increases above a certain level. In contrast to that, the N2p is more negative in relation to increased set size: Patel and Azzam (2005) offer an alternative interpretation of this component as a part of texture segmentation. Luck and Hillyard (1994) suggest a further differentiation between the N2pc and the N2pb – the latter consists in the difference wave from the subtraction of waveforms in homogenous arrays from waveforms in ipsilateral pop-out conditions. The N2pb was sensitive to pop-out dimensions and was larger when a colored pop-outs was presented.

Regarding the question of source localization, the specifications differ between the studies – probably due to a more or less profound distinction between the subcomponents. Woldorff et al. (2002) name the dorsal occipital region which was investigated in combination with PET studies. However, it has to be noted that in this study, the N2 was not clearly differentiated from the N2pc which Woldorff et al. (2002) describe as arising from contralateral ventral occipital cortex (fusiform gyrus).

Potts and Tucker (2001) used the N2 and the P2a to investigate the interaction between the executive function of the prefrontal cortex and the representative functions in the posterior cortex through a target detection task. They used a paradigm, where participants had to respond to a stimulus, depending on its spatial location or its target features. This way, the authors tried to elucidate the difference between the dorsal pathway ('where' stream) which leads to the posterior parietal cortex and the ventral pathway ('what' stream), projecting to the inferior temporal cortex (see 1.2.1.). Potts and Tucker (2001) summarize the characteristics of the N2 as being linked to activation in neurons which represent visual features defining the target – including spatial location and frequency, orientation, color and size. According to the authors, the posterior negativity in general has been linked to activity in inferior temporal neurons during detection tasks. Additionally a connection has been assumed between P2a and N2b and the interaction between the inferior temporal cortex and the prefrontal cortex. This has been demonstrated in studies where responsiveness to features, timing and distribution of the N2b and the P2a are in accordance with responses in the prefrontal cortex and the inferior temporal cortex in monkeys during visual detection tasks. These responses have also been recorded in the posterior parietal cortex (Potts and Tucker, 2001). However, Potts and Tucker (2001) emphasize that these linkages remain assumptions, because the scalp distribution of an ERP-component does not necessarily refer to its neuronal origin. Consistent with their hypothesis, the experiment yielded a more ventral distribution in the target-feature task and a rather dorsal distribution in the target-location task during the peak of the frontal P2a. The authors understood their findings as an interaction with prefrontal cortex of the ventral pathway in the object task and of the dorsal pathway in the spatial task.

The N2-component is usually recorded at the Cz electrode (Kamitani and Kuroiwa, 2009). The regarded time range differs partly between the studies. Kopp et al. (1996) calculated the mean latency between 250 to 350 ms post-stimulus, because the N2 did not show a specific peak. Folstein and Van Petten (2008) define the time range broader as 200 to 350 ms after stimulus onset. Kamitani and Kuroiwa (2009) measured the N2 from 200 to 400 ms after stimulus onset. On the other hand, Woldorff et al. (2002) focus on a lateralized N2 effect in between 230 and 280 ms.

1.4.5 N2pc

The N2-posterior-contralateral (N2pc) component correlates with visual target selection and reflects the allocation of attention to the location of a target (Hopf, Boehelman, Schoenfeld, Luck und Heinze, 2004). Additionally, the N2pc appears during search depending on motion, color and orientation which suggests a common attentional mechanism (Girelli and Luck, 1997). An influence of task difficulty on the N2pc could not be detected (Robitaille and Jolicoeur, 2006).

1.4.6 P3

The P3-family can be subdivided into various subcomponents. Most importantly, a frontally maximal component has been observed (P3a) and a parietally one (P3b). Generally, it has been investigated in the context of unexpected, unusual, surprising or infrequent stimuli. In addition, it has been observed that the P3 increases whenever target probability gets smaller. It is also sensitive to the effort which is devoted to a task, forming a possible connection to resource allocation (Luck, 1995).

1.4.7 Possible interconnections between ERPs and brain activity

A very promising approach for investigating brain activity lays in the combination of different methods. Woldorff et al. (2002) worked with a combination of results from separate sessions with PET and MRI (which are good tools for mapping brain areas, but suffer from poor temporal resolution), and EEG recordings for better information about timing and sequence during basal visual-spatial attention (for details on EEG recordings, see 1.4). The authors name as the first observable component during a task in the visual ERP the P1 attention effect. It appears as an increased positivity in the occipital cortex contralateral to the direction of attention, in a time window from 80 to 130 ms after stimulus onset. The PET results showed increased activity in the dorsal occipital cortex contralateral to the direction of attention. The source analysis of the P1-effect confirmed activity in the same region during the time period of interest. In further detail, the authors concluded that the attentional manipulation included dorsal V2, V3

and V3a (the lower visual field), but not the primary visual cortex V1. The analysis of the P1 effect suggested an organization in a series of subcomponents, representing the sequential activation in the named lower-field visual areas, beginning at V2. Another important aspect concerning visual-spatial attention is the re-entrant of activity in the same retinotopically organized region during the time window of the N2 (240 – 280 ms). This was observed through early activation in V2 which later moved to higher-level areas and then returned to V2 again. This effect is interpreted by Woldorff et al. (2002) as a top-down attentional control, resulting in re-entrant activation. Regarding the component N2, a further differentiation is suggested concerning the N2 attention effect as a reaction to non-targets and the N2b which appeared a bit later and only in the presence of target stimuli. The N2 attention effect seems to derive exclusively from the dorsal occipital cortex, whereby the N2b includes a contribution from the ventral occipital cortex as well. This N2b could be related to the N2pc component (see 1.4). Interestingly, an MEG analogue of the N2pc has been linked to the fusiform gyrus in the contralateral ventral occipital cortex (Hopf, Luck, Girelli, Hagner, Mangun, Scheich and Heinze, 2002).

Hayakawa, Miyauchi, Fujimaki, Kato and Yagi (2003) used magnetoencephalography in a visual search task to investigate the sequence of neural activation. They identified four components at different mean latencies: The calcarine sulcus and the posterior fusiform gyrus in the occipital cortex contralateral to the stimuli (110 and 146 ms), the intraparietal sulcus and the posterior superior temporal sulcus in both hemispheres (196 ms) and again the calcarine sulcus at 250 ms. They concluded that the early feature processing takes place in the two areas in the occipital cortex. After that, the information gets further processed in the named areas at 196 ms poststimulus which belong to parietal and temporal regions – a part of that information is then send back to the occipital cortex. (Similar results have been discussed in connection with the results of Woldorff et al. (2002), see 1.1.2.). The authors argue that their findings support the 'guided search model'. This model assumes two stages within a single search mechanism: The early parallel feature processing is based on a feature map and the second (late) phase consists in a serial search with attentional shifts in relation to an attention map. Both components can be modulated by top-down-processes. Furthermore, the authors link their results to previous findings, where the two ERP components P1 and N2pc were modulated by top-down-processes. They suggest a correspondence between the P1 and the early activity in the occipital cortex.

The N2pc could be related to the activity in the regions of the superior temporal sulcus and the intraparietal sulcus. However, Hayakawa et al. (2003) note as well a certain difference which could be due to the experimental procedure: The N2pc was enhanced by attentional demands and, in contrast to that; the areas in question were activated during an efficient search which did not require a lot of attention.

2 Aim of the study

Target representation is a crucial point in the planning and execution of eye and hand movements. Therefore, this study aims at investigating its neuronal basis and to explore a part of the eye-hand-coordination mechanism. Since the N2 has been suggested to indicate target processing in the context of detection, classification and visual discrimination (Holguín et al., 2009; Potts and Tucker, 2001), this component is suitable to investigate target representation or target selection for eye and hand movements. It also has been linked to monitoring or regulation of motor responses and is modulated by attention (Folstein and Van Petten, 2008). Potential differences in the N2 for both effectors would provide further information for understanding the processing of target information in motor control. The main hypothesis is that due to the higher need of efficiency in the attentional selection of visual information for hand movements, the amplitude of the generated N2 should be more negative in the pointing condition than in the saccade condition. This is based on the necessity of more information for hand movements, concerning for example size or material of the target, compared to eye movements.

Regarding the time of the maximal amplitude of N2 the higher efficiency in the pointing condition could either speed up its generation or cause a delay due to more intensive data processing.

3 Method

3.1 Procedure

Subjects

24 subjects (10 women), who were students or former students from Vienna University participated in the study. They were all right-handed (handiness was assessed with Edinburgh Handiness Inventory (Oldfield, 1971)) and gave written informed consent before the experiment. The age of the participants ranged between 22 and 36 years, with an average of 26.4 years and a standard deviation of ± 3.7 years. All of them were naïve with regard to the hypotheses of the experiment. None had a previous history of neurological or psychiatric disorders and all were medication free. They all had normal or corrected to normal vision.

Apparatus

The subjects were seated in a separate room for the experiment and the stimuli were presented on a CRT monitor (Sony, Triniton, Multiscan G520 with a refreshing rate of 85 Hz). The subjects were seated in front of the table with the monitor in a distance of approximately 42 cm. Their chin and forehead were stabilized by an adaptable rest. Their right elbow was placed on a padded support on the table and the resting position of the right hand was marked with stripes on the table. The stimuli were presented using an E-prime script (Psychology software tools).

Stimuli and procedure

640 trials were presented. They were organized in four equal blocks with breaks in between. The subjects could decide how long they wanted to rest during the breaks. Each condition (saccade and pointing movement) contained 320 trials. All stimuli were presented in randomized order.

The search array appeared against a white background and was designed as follows:

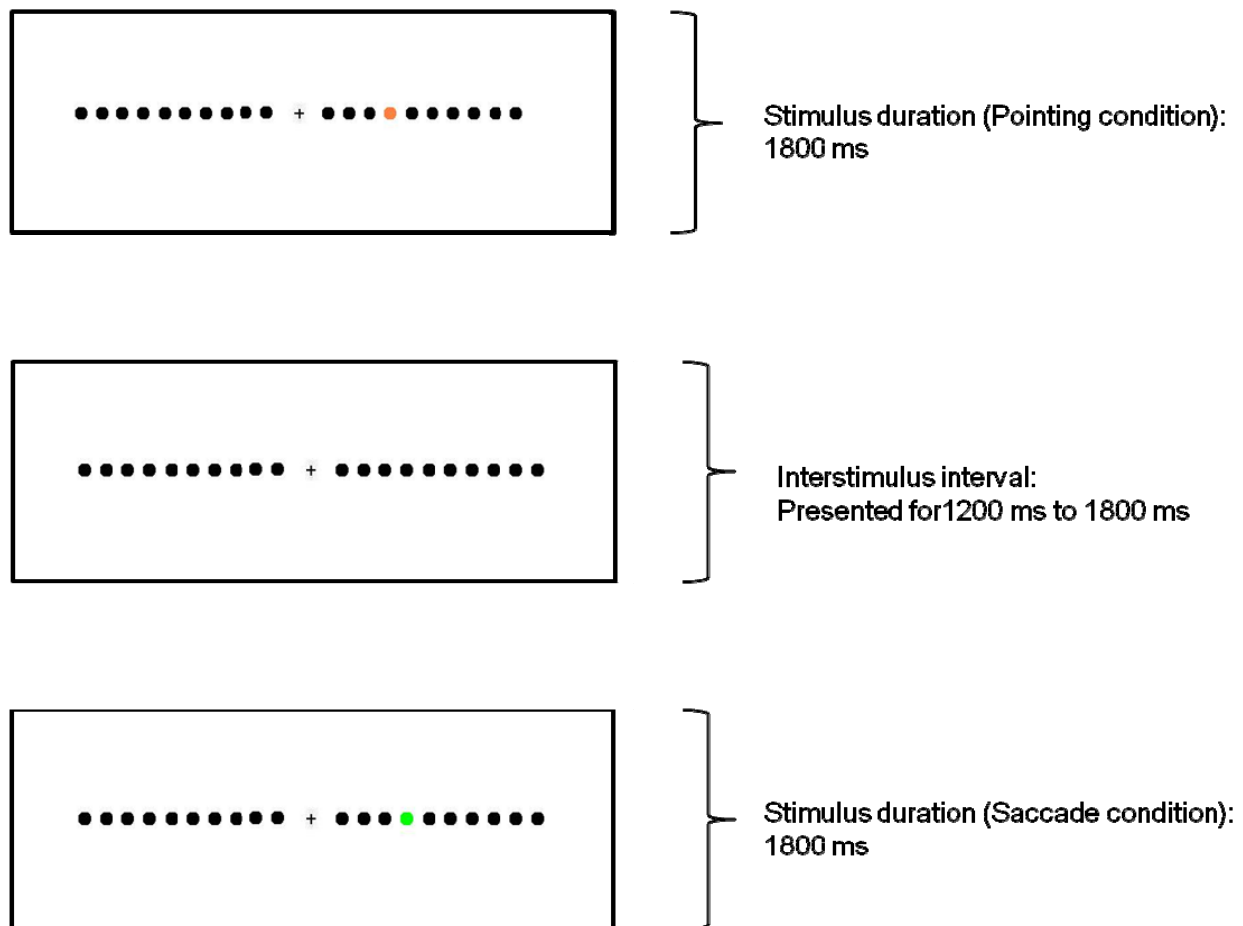


Figure 5. Design of the visual search arrays. The search arrays consisted in 20 circles. The targets appeared in orange in the pointing condition and in green in the saccade condition. Distractors are black circles. All singletons are placed on a horizontal line left or right to a fixation cross. The stimulus lasted for 1800 ms and was followed by a variable Interstimulus interval (1200 to 1800 ms). The colored circles appeared in a randomized order with equal frequency at all twenty possible positions.

The subjects were instructed to fixate the fixation cross in the middle of the screen. Whenever a green circle appeared, they were supposed to saccade towards the target as long as it lasted and then return their gaze to the fixation cross. When an orange circle became visible, subjects were asked to point at it with their right index finger. They were told to touch the screen in the pointing condition, to provide better

comparability of the hand movements of all participants. During the pointing condition, subjects were allowed to move their gaze freely. In addition, they were reminded not to follow their hand with their eyes when returning to the resting position, but to look at the fixation cross. All participants were also instructed that they could perform the movements with normal speed and should not concentrate on reacting very fast or perfectly accurate. Before the data recording, the participants performed 20 practice trials and had another opportunity to ask questions about the task after that.

3.2 EEG and EMG recording

The EEG was recorded at seven scalp electrodes in an equidistant system with the positions 8, 16, 26, 24, 28, 30, 27. This was done using a cap from EasyCap Montage No.10, see figure 6. In the 10/20 system those are equal to Fz, Cz, Pz, 24 and 28 were averaged over the whole channel for PO7 and the same was done with 30 and 27 to generate a measure equal to PO8.

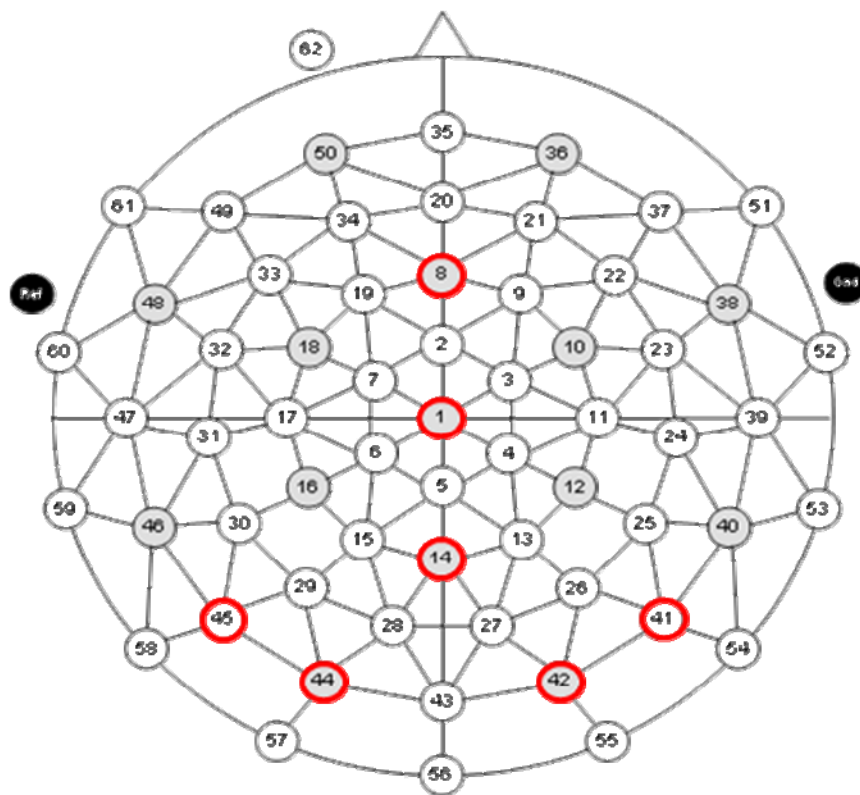


Figure 6. EasyCap Montage No. 10. Red circles refer to the 7 applied scalp electrodes. (EasyCap, 2010).

The arm movements were controlled with four electrodes on the right arm to measure EMG at musculus biceps brachii and musculus extensor digitorum. They were applied with regard to the instructions provided by Zipp (1982).

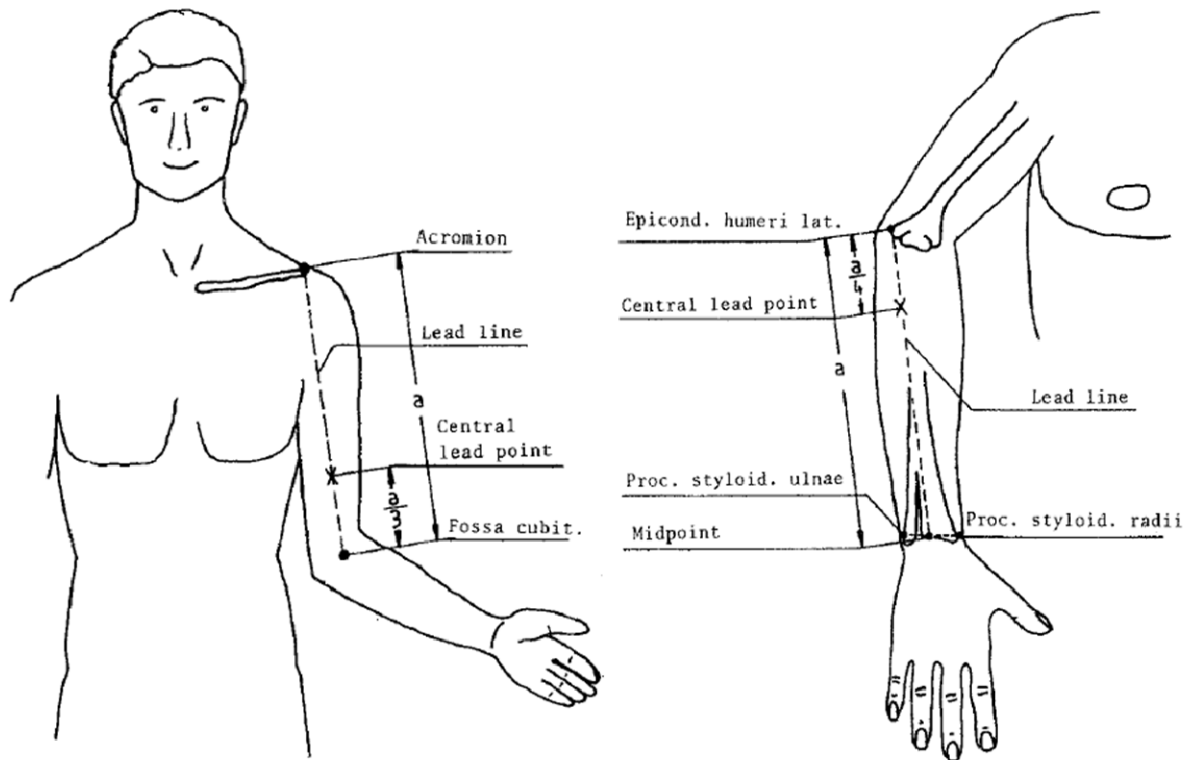


Figure 7. Application positions for EMG electrodes. On the left side: Lead placement musculus biceps brachii. On the right side: Lead placement musculus extensor digitorum (Zipp, 1982).

The sizes of the heads of the participants were measured around forehead and back of the head and caps adjusted with the position of the central electrode (Cz). To decrease the impedance of the skin, the hair was put aside and the skin softly scratched with a sterile needle. All impedances were kept below 3 kΩ. For recording eye movements and blinks, four electrodes were placed left and right of both eyes and above and below the left eye, in a line with the subject's pupil. The first reference was recorded with an electrode close to the *Extremitas sternalis*. A second reference electrode was placed at the *Vertebra prominens*. The ground electrode was applied to the forehead.

3.3 EEG and EMG analysis

A correction factor for eye movement was automatically estimated, based on the formulas (Bauer and Lauber, 1979):

$$\text{EEG}_{\text{corr}} = \text{EEG} - r\text{EOG}$$

$$\text{EOG} = \text{EOG} - r\text{EOG}$$

$$C = \text{Cov}(\text{EEG}_k, \text{EOG}) / \text{Var}(\text{EOG})$$

C...correction factor

EEG_k...EEG of channel k

EOG...electrooculogram

Cov(EEG_k, EOG)...covariance of EEG_k/EOG

Var(EOG)...variance of EOG

Another correction factor was estimated for the correction of blinks. The data were sampled with 1000Hz (DC). The main data analysis was performed using the Matlab tool Eeglab. The data were epoched from 200 ms prior to stimulus onset to 700 ms after the targets appeared (the last 200 ms were not included in artifact correction). The 200 ms before the stimulus onset were used for the baseline correction. The data which derived from scalp electrodes was low pass filtered with 30 Hz. Artifact correction was applied automatically in Eeglab for abnormal values below +/- 50 µV and for abnormal trends over 40 µV. In addition, trials were visually inspected and manually eliminated. The saccades and arm movements were also visually monitored. Trials in the pointing condition with no arm and hand movements recorded in the EMG were rejected, as well as trials in the saccade condition where an arm or hand movement was falsely initiated. The same applies to trials in the saccade condition, where no saccade took place. Three participants were completely excluded due to high abundance of artifacts. Generally, an average of 22% of all trials per subject was excluded.

The N2 was recorded at the Cz-electrode, as has been suggested by other studies (Czigler and Balázs (2005); Bartholow, Pearson, Dickter, Sher, Fabiani and Gratton, (2005); Nieuwenhuis, Yeung and Cohen, (2004); Kopp et al., (1996)). It was calculated based on mean amplitude in a time range from 160 to 350 ms post-stimulus, due to examination of the variance in the waveforms and based on analysis units stated

in the literature (Folstein and Van Petten (2008); Kopp et al. (1996); Kamitani and Kuroweia (2009)). Beforehand, the amplitude values for each condition per subject and condition over all trials were calculated in Eeglab.

From the time range in question, the mean value of the amplitude was extracted in Matlab. In addition to the mean amplitudes, the peak amplitudes of the N2 in all participants were determined. This was done by selecting the largest or most pronounced local negative peak in the same time range. This selection procedure yielded the average of each participant per condition as well as the latencies of the N2-component. Additionally, to further explore the difference between the conditions, the difference wave between the pointing and the saccade condition was calculated by subtracting the grand average waveform from the saccade condition from the grand average waveform from the pointing condition. The corresponding scalp topography was plotted with standard EasyCap coordinates. The data was analyzed with two separate 2x2 repeated-measures ANOVAs for the peak and the mean amplitude, using the factors stimulus position in the right or left visual field (right/left) and the two conditions (pointing/saccade). Another 2x2 repeated-measures ANOVA based on the factors (pointing/saccade) and (left/right) was calculated for the latencies of the N2-component.

4 Results

N2

Figure 8 shows the waveforms which were elicited during the pointing and the saccade condition. They were calculated from the means of all participants. The peak of the N2 in both tasks appears approximately between 200 and 300 ms post-stimulus. Obviously, the N2 reached a higher negativity during the pointing condition.

Regarding the question which subcomponents of the N2 are especially manipulated by the experimental conditions, the waveforms at the parietal and the frontal electrodes are also of interest, see figures 10 and 11.

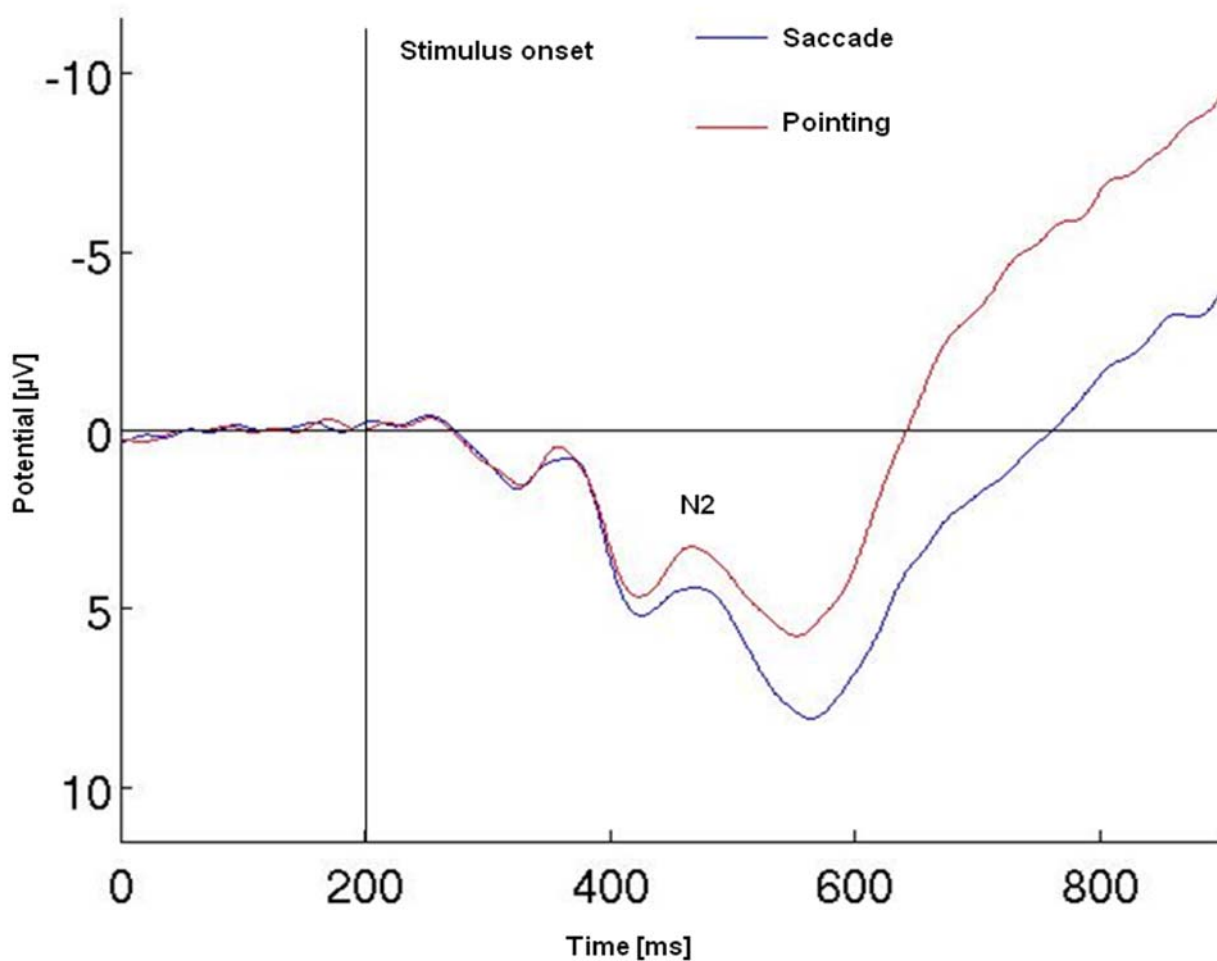


Figure 8. Grand average waveforms for all participants in the saccade and the pointing condition from electrode Cz (N = 21).

Another aspect of the calculation of the amplitudes was a certain difference between the means which derived from mean amplitude or peak amplitude (see table 1).

Table 1. Descriptive statistics; mean +/- standard deviation; in [μ V] for mean amplitudes and peak amplitudes of the N2-component, recorded at the Cz-electrode in the time range between 160 ms to 350 ms.

Mean amplitudes	Visual field	Left	Right
	Saccade	4.56 +/- 3.31	4.84 +/- 3.36
	Pointing	3.36 +/- 3.84	3.90 +/- 3.87
Peak amplitudes	Visual field	Left	Right
	Saccade	2.63 +/- 5.34	2.43 +/- 3.86
	Pointing	1.42 +/- 4.78	1.27 +/- 3.86

Due to the fact that peak amplitude (see table 1) does not take the surrounding time points into account, the peak amplitude values are more negative than the mean amplitude values. These differences resulting from the way of calculation did not result in a difference in the results of the statistical analysis regarding the saccade and the pointing condition (see results of the ANOVAs point 4).

The bar chart in figure 9 shows the mean amplitudes for the two conditions.

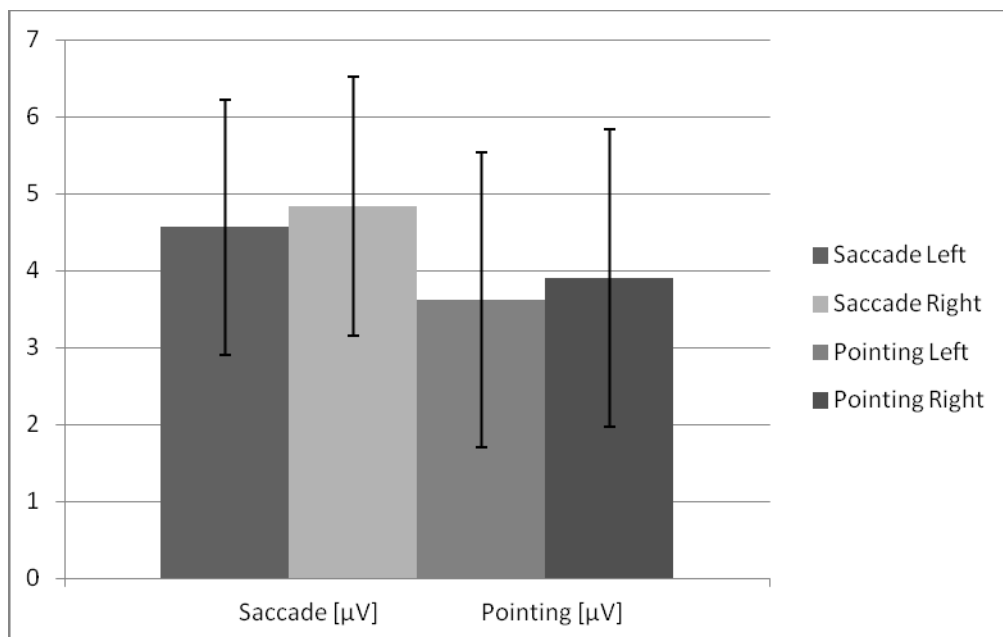


Figure 9. Mean amplitudes for the two conditions in the time range between 160 ms to 350 ms, recorded at electrode Cz, with stimuli being presented on the right and the left visual field.

The ANOVAs showed that the N2-component was more negative during the pointing than during the saccade condition (see also Table 1). This was evident from a main effect for peak amplitude when peak amplitude was the dependent variable ($F(1,20) = 9,17, p < 0.05$), and for mean amplitude when mean amplitude was the dependent variable ($F(1,20) = 8,73, p < 0.05$). As expected, there was no effect of the stimulus being presented on the right or the left visual field.

No differences in N2 latencies were observed.

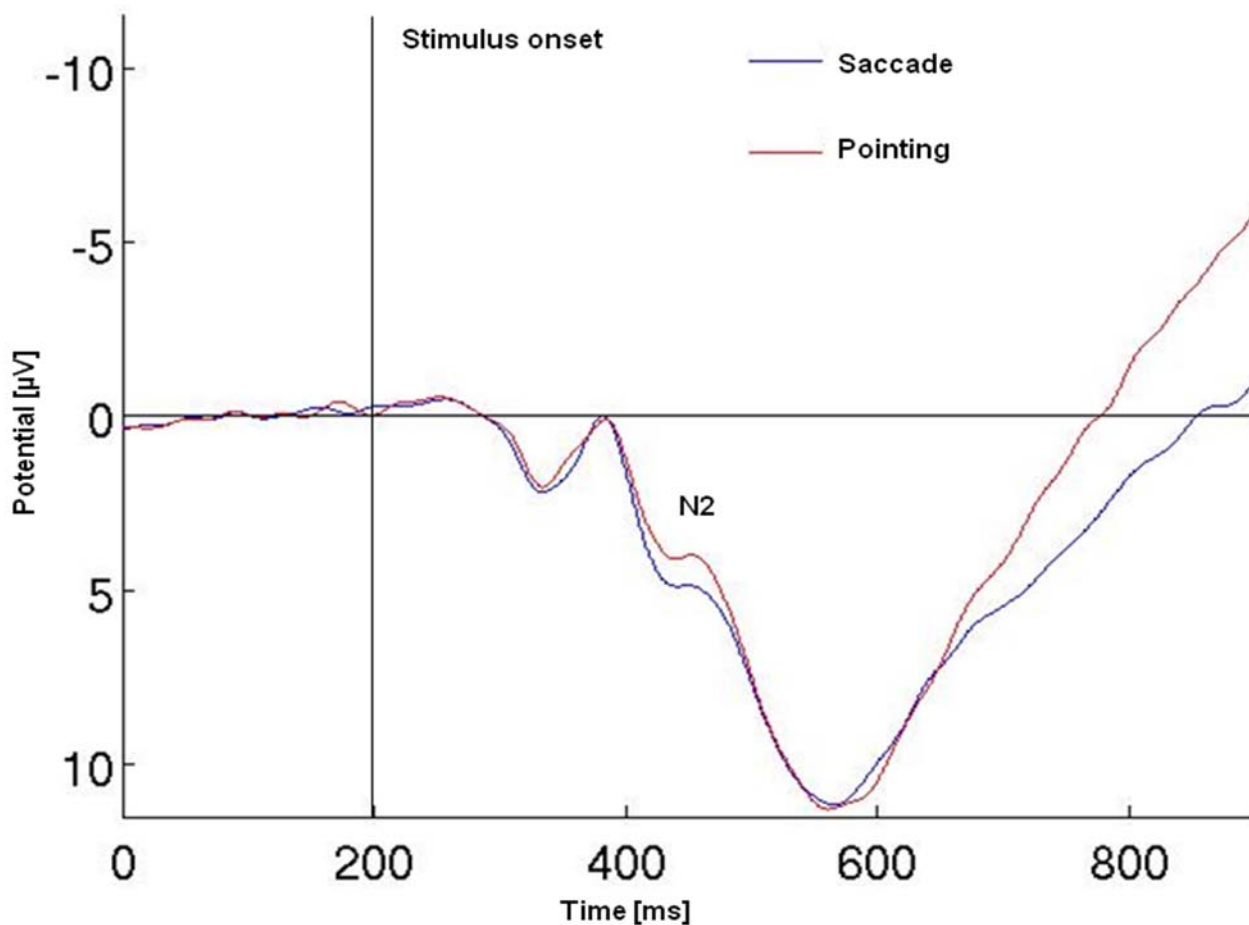


Figure 10. Grand average waveforms for all participants in the saccade and the pointing condition from electrode Pz (N = 21).

In figure 10 these results can be compared to the data which derived from the Pz-electrode. The difference in the N2 is still visible. This suggests that it was rather the posterior subcomponent, the N2p which was affected by the different tasks, not the anterior subcomponent (N2a). In line with this observation, the recordings at the frontal

electrode Fz (see figure 11) suggest no differences in the time range of the N2 when subjects fixated or pointed at the stimulus.

Figure 10 also shows that the P3-component is almost identical in both conditions. This fits the expectations, as no unusual or surprising stimuli occurred in the experiment. Also the P1 and the N1 seem to be unaffected by the two conditions. As this study focuses on target representation and no differences in the grand averages could be observed, the two earliest components were not further analyzed.

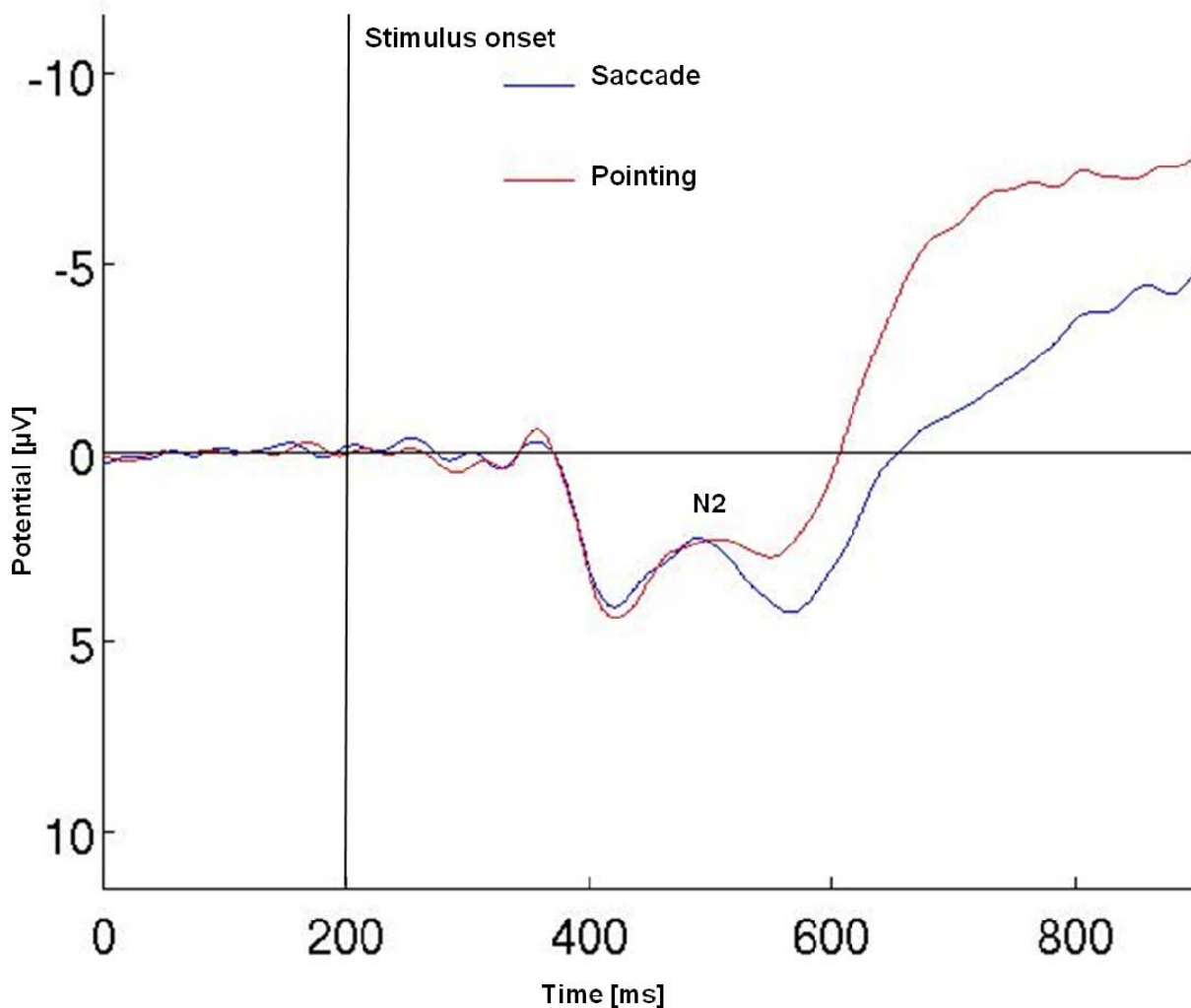


Figure 11. Grand average waveforms for all participants in the saccade and the pointing condition from electrode Fz (N = 21).

Furthermore, the standard coordinates from EasyCap were used to plot the scalp topographies across all tasks for all subjects. Figure 12 shows the development of the largest activity throughout the time course of the experiment. At 200 ms the stimulus

was presented. As expected, the activity is rather low in all areas at this time point. The time frame of the N2, estimated from the plot of the mean waveforms, appears between 400 and 500 ms (because the 200 ms baseline is still included). Accordingly, this refers to 360 to 550 ms in figure 12. The largest activity during this period can be seen at the central electrodes, especially pronounced at 440 ms (which is equal to 220 ms post-stimulus). Later, the activity moves further to the posterior side of the scalp. This agrees with the observation of a pronounced P3 component at the electrodes Cz and Pz.

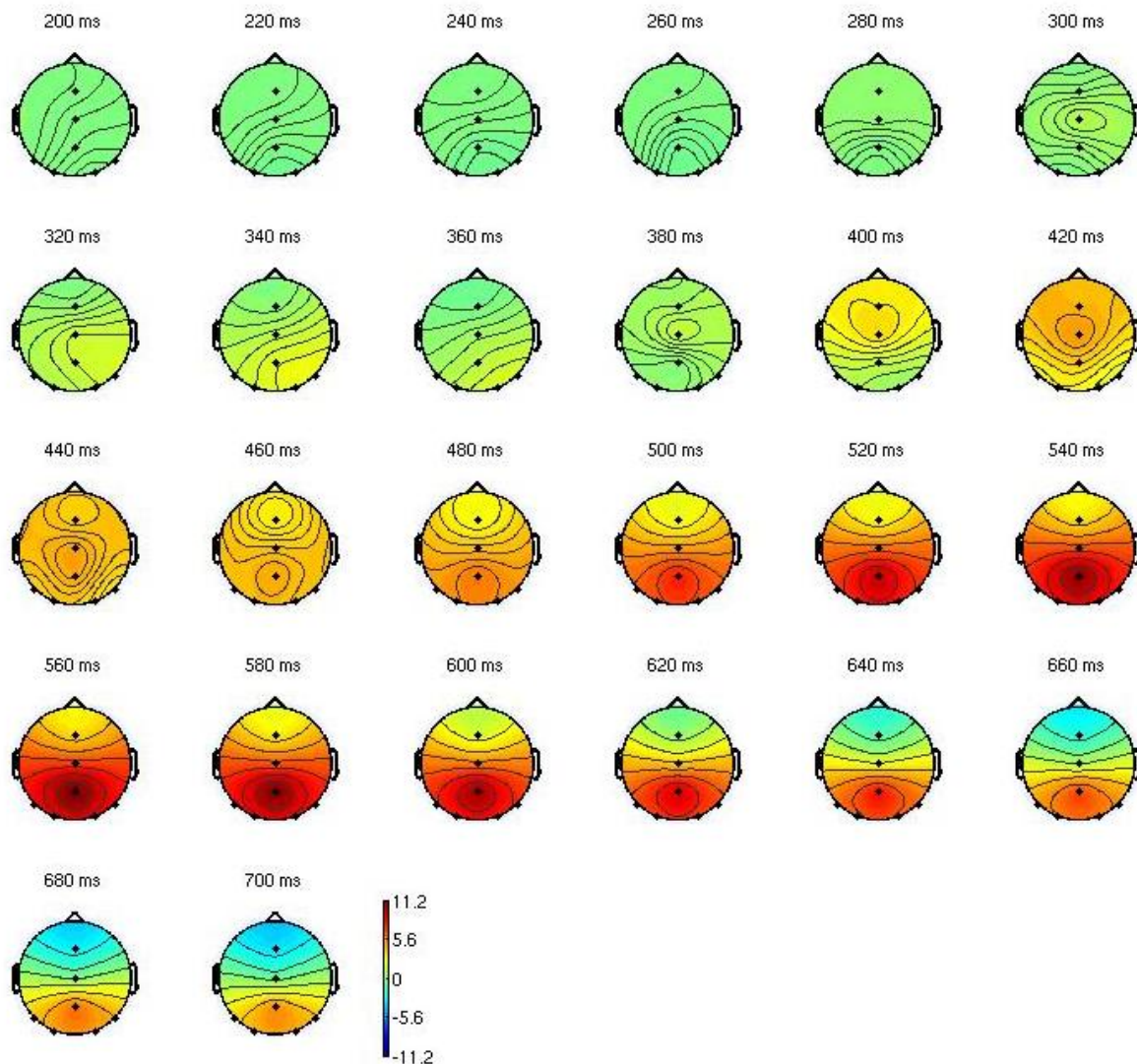


Figure 12. Plots for the scalp topography at different times during the experiment. 200 ms marks the time point of stimulus onset. The calculation was done using standard coordinates from EasyCap and the mean waveforms for all subjects over both conditions.

Difference wave

For a better understanding of the differences between the pointing and the saccade condition, a difference wave was calculated (from the same data sets as in figure 12), see figure 13. This way, the activation according to the scalp topography shown in figure 13 refers to the largest difference between the conditions.

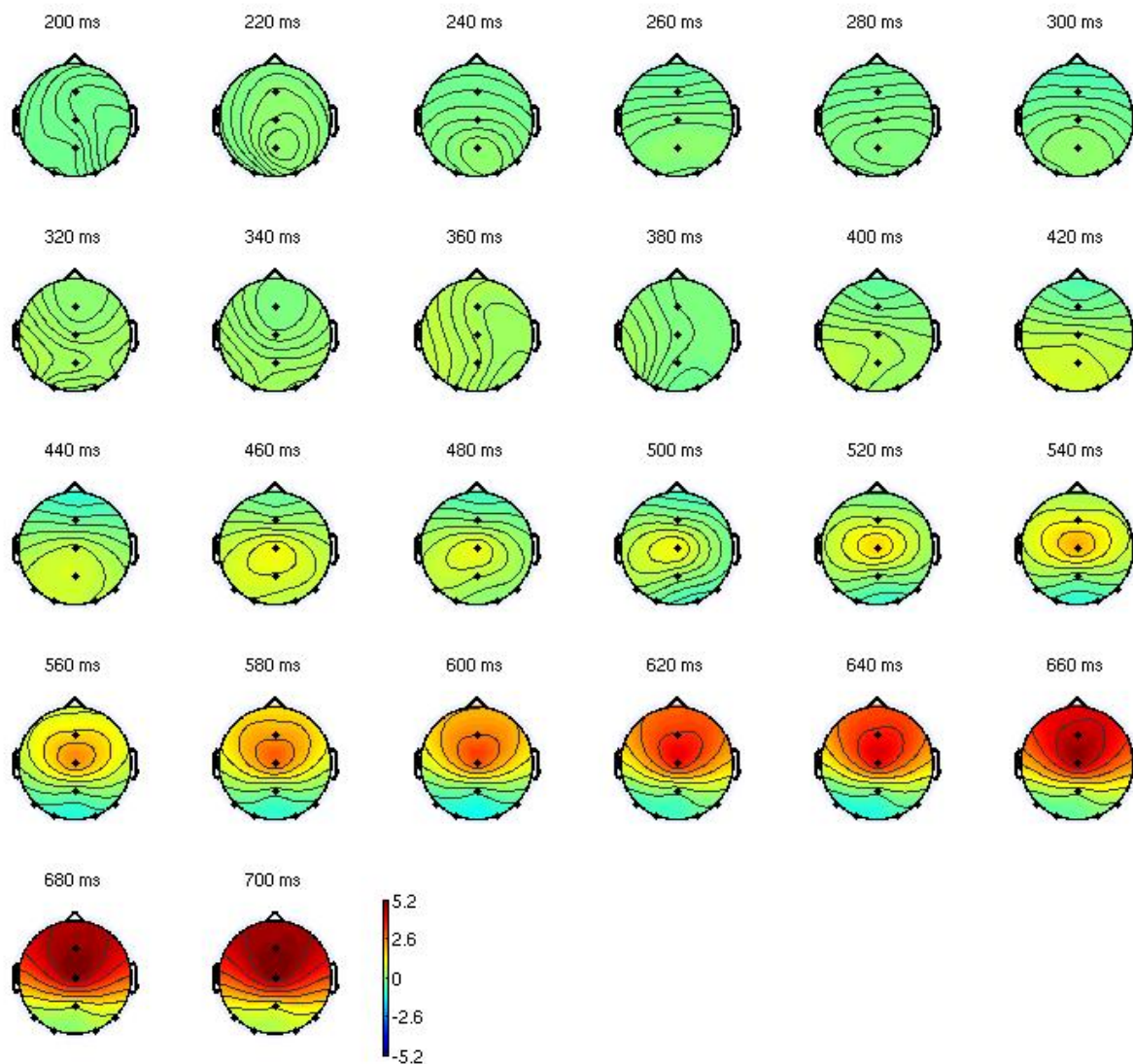


Figure 13. Plots for the scalp topographies at different times during the experiment. The plots derived from the difference wave from the grand average waveform of the saccade condition being subtracted from the grand average waveform of the pointing condition. 200 ms marks the time point of stimulus onset. The calculation was done using standard coordinates from EasyCap and the mean waveforms for all subjects over both conditions.

The difference wave shows an even more pronounced central activity during the time range of the N2 (in figures 12 and 13 equal to 360 to 550 ms, including the baseline of 200 ms) than the mere plot of mean activation during both tasks. The large differences on the anterior side at the end of the investigated time frame, starting approximately at 400 ms post-stimulus (at 600 ms in figure A) are probably due to a larger activation in the motor cortex during the pointing condition.

5 Discussion

The aim of this study was to investigate the differences in target representation depending on the question whether the target was relevant for a further limb movement. This was done by recording the EEG-component N2 which has been linked to matters of target representation (Holguín et al., 2009) while subjects had to either fixate or point at a stimulus. The N2-component was significantly more negative during the pointing condition than in the saccade condition. Regarding possible interpretations of these findings, the classification of the N2 in different subcomponents has to be taken into account. The scalp distribution of the N2 demonstrates that the activity, and the difference in the activities between the two conditions, derives from the posterior N2. Accordingly, apart from the central electrode Cz, where the N2 was measured, the waveforms of the Pz-electrode still show the differential patterns of this component for pointing and saccade condition. In contrast, there was no difference at all between the two conditions at the frontal electrode Fz. This suggests that the recorded difference refers to variation in target processing (Holguín et al., 2009) rather than aspects of control and response inhibition (Oddy et al., 2005) (which would be possible, as the participants had to suppress a pointing movement in the saccade condition). An effect of movement inhibition also seems unlikely, not just because there was no difference between the conditions at the frontal scalp sides, but also because the P3-component at the electrode Pz was not sensitive to the two tasks. This would have been expected if inhibition were an important aspect, because the P3, or an N2-P3-complex, are linked to inhibition mechanisms (Oddy et al., 2005).

Regarding the difference in target processing which is reflected by the difference in the N2-component (Holguín et al., 2009), various models can be considered for the implementations on target representation. Maunsell (1995) stated that attention plays an important role for the weighting of visual information during the formation of cortical representations. In this context, the higher negativity of the N2 for pointing as compared to saccading could be a result of a larger need of attention in the pointing condition. The subjects had to find the target – as in the saccade condition – and additionally perform a movement. Therefore, the participants probably experienced the pointing as the more ‘taking’ condition and concentrated more on this task. As Maunsell (1995) demonstrated the influence of attention already in the early stages in the visual cortex.

Correspondingly, Bruce et al. (2003) summarize findings which provide evidence for an effect of attention under certain circumstances already in V1 (compare Kosslyn et al. (2001)). Increased attention from the start of the task could have led to a different weighting in the target representation which was further processed. However, in this context it has to be noted that the description of the possible origin of the N2-component has varied in different studies. Additionally, many of the named structures are largely interconnected. Potts and Tucker (2001) describe linkages between the N2b and the P2a and activity in the prefrontal cortex, inferotemporal cortex and posterior parietal cortex. The parietal pathway is especially sensitive to state-dependent modifications (Maunsell, 1995). Patel and Assam (2005) suggested another N2 subcomponent, the N2b, to derive from the centrality of the frontal and the superior temporal cortex. Woldorff et al. (2002) name the dorsal occipital region which was investigated in combination with PET studies. Regarding the multiple interconnections between the dorsal and the ventral stream (Bruce et al., 2003) and possible re-entrant activations at earlier stages of processing (Woldorff et al., 2002) an influence of attention could (directly or indirectly) affect the N2 at different time points. As has been described before, the recordings at the Pz-electrode suggest a parietal distribution of the N2-component, but the scalp distribution of an ERP-component does not necessarily refer to its neuronal origin (Potts and Tucker, 2001).

The study of Astafiev et al. (2004) also compared saccade and pointing movements, although based on fMRI measurements. They found a significantly stronger BOLD reaction during the pointing condition in the human lateral occipital cortex. These observations were interpreted as a modulation of the visual cortex through limb movements. In other words, already at an early stage an action-related activation seemed to take place within the visual system. The authors included a control condition, where subjects directed their attention to a location and detected the target while remaining with their gaze at a fixation point and without performing a movement. While Astafiev et al. (2004) found a significantly higher activation during the preparation of the pointing movement compared to the preparation of the saccade, no effect was detected comparing the preparation of an attentional shift to both the preparation of a limb or an eye movement. This is interesting, because it could be used as an argument against an explanation of the effect in the present study which is merely based on attention modulation or different attentional load. The difference in the processing of visual information in saccade or pointing movements is probably more complex. Another

important aspect in the context of the findings presented by Astafiev et al. (2004) is that fMRI has – in contrast to EEG – a rather poor temporal resolution. Therefore it is not quite clear whether the activation in the early visual cortex was different from the start, or whether there was some kind of ‘loop’ in the pathway and the activation returned during a later stage of processing. Hayakawa et al. (2003) reported a pathway of visual information, where early feature processing takes place in the occipital cortex, then the information is sent to the intraparietal sulcus and the posterior temporal sulcus in both hemispheres and a part is later send back to the occipital cortex. Hayakawa et al. (2003) explained this as two stages within one visual search mechanism: At the beginning parallel feature search, based on a feature map, takes place, and later converges to a serial search with attention shifts. Another important study in this context has been published by Woldorff et al. (2002). They reported a re-entrant of activation in V2 during the time window of the N2 (240 – 280 ms). This effect was interpreted as a result of top-down attentional control, whereby the N2-component derives from the dorsal occipital cortex (with the later N2b being a contribution from the ventral occipital cortex as well) and refers to an attention effect. These findings show that the observed N2 differences could relate to a difference at a very early stage of processing, or a re-entrant of activation in the visual cortex which is modulated by movement planning. Also, it seems to be important to interpret the posterior N2 not solely as representing an attention effect, but also as a component in the context of target processing (Holguín et al., 2009). This would better agree with the findings of Astafiev et al. (2004), who argue against a mere shift in attention. A possible interpretation could lay in the deployment of different reference frames at early stages of visual information processing during the two conditions which is related to shifts in activation to the parietal- and back to the visual cortex and could be modulated by attention. A model about the generation of a movement vector from various reference frames is discussed in the following paragraph.

Based on another approach, the observed larger negativity in the N2 could be a result of the development of a movement vector from different reference frames. McGuire and Sabes (2009) demonstrated that the gaze-dependent error could best be predicted from a model which integrated contributions from retinotopic and body-centered reference frames. Studies about the neurophysiological organization of the neural population in a cortical area hint at a rather retinotopic structure in the parietal cortex and a major influence of a body-centered reference frame in the frontal cortex,

whereby in both cases a heterogeneous population of neurons exists, according to McGuire and Sabes (2009). In this context, the more pronounced N2 in the pointing condition could reflect a more complex computation between the different reference frames. Especially due to the retinotopic organization of the parietal cortex, a larger shift in the relative contributions of the two reference frames would be necessary in the pointing condition. This could explain the difference between the two conditions.

However, the behavioral studies by Sailer et al. (2002) added another aspect: They investigated the effects of haptic textures on the kinematics of eye and hand movements. Their subjects had to perform saccades or pointing movements either to a slippery or a rougher target. The pointing movement proved to take longer in the case of the slippery target, due to a longer deceleration phase. This demonstrates that information about target texture is used differently by the hand and the eye. Here, a variation in feature processing takes place which could not be completely explained by a shift in reference frames. Rather it seems likely that the ranges of representations from different cortical levels, as has been suggested by Maunsell (1995), differ qualitatively in their attributes. In the context of a shift in reference frames, this could be linked to a need of higher efficiency in the computation of a differently weighted representation in the pointing condition, because the main target characteristics have to be processed as well. Up to here, the best explanation of the difference behind the N2-effect could be multiple target representations which vary regarding their relative contribution from different reference frames and the weighting of relatively important target features. Of course, shifts in attention could modulate the processing of this information from the start.

Especially interesting in this context would be to investigate at which time points and in which areas the differentiation in target processing starts. This could be done with further EEG-measurements in combination with fMRI studies. These could elucidate the role of re-entering information in certain areas in contrast to differences at very early stages. In the present study, the components N1 and P1 seemed to be slightly more negative in the first case and accordingly slightly more positive in the second case at the frontal electrode during the pointing condition, but weren't further investigated due to the marginal differences. These could probably be done with a search paradigm which lays more emphasis on discrimination processes in the two conditions.

Another way to observe the differences between target representations, or changing reference frames, could be an EEG-experiment, where subjects have to perform saccades and pointing movements in opposite directions. Gorbet and Sergio (2009) worked with a paradigm like this and observed changes in eye reaction time, peak eye velocity, hand-path curvature and arm movement time. They suggested that specific areas could be responsible for the dissociation of hand and eye movements: Within the superior parietal lobule, the medial intraparietal area and the dorsal aspect of the parietal occipital area. Here, reach-specific neurons have been suggested to contain movement information in an eye-centered frame. Although the cells are not directly involved in the planning of saccadic movements, firing neurons in the time course of a saccade have been observed. This was interpreted as a cross-coupling between the systems for reach- and eye movements. In this context, this aspect would be an interesting add-on to further experiments based on the N2 or different components related to eye-hand-coordination. If the areas in question are indeed specialized on decoupling eye and hand movements, a difference in the ERPs should be measurable. This could hint at another kind of target processing, for situations when the two modalities cannot rely on common sensory feedback. Generally, if the more negative N2-component in the pointing condition is linked to a more complex shift in reference frames, an even more pronounced signal would be expected when eye and hand movements are decoupled.

Apart from the amplitudes of the ERP-component which are discussed above, the latencies of the N2-component recorded at the Cz-electrode were also investigated. The fact that there was no effect regarding latency could be due to a mutual compensation of two tendencies. If a necessity of higher efficiency for target processing which is followed by pointing movements exists and a larger amount of information has to be processed, then these two factors could compensate and result in different amplitudes rather than having an effect on the latencies.

Regarding possible limitations of the study it has to be noted that although the subjects reported that they had enough time for the pointing movement, the reach condition was probably experienced as the more taking or more difficult task. This could have had an influence on the corresponding ERPs. However, it has to be noted that task difficulty is usually investigated in the context of visual discrimination (Senkowski and Herrmann, 2002). Therefore, it is questionable whether this aspect has an influence

in the present study, as the possible difficulty in the pointing movement depended on the generation of a later movement and not discrimination processes. Another possible objection is the choice of target stimuli. On the one hand, the different colors could have led to different reactions. On the other hand, this variation should have become obvious during the earliest components – like P1 or N1 – rather than producing a difference in the later stages of target processing.

6 Conclusion

The present study investigated whether a difference in target processing for eye and hand movements manifests in the N2-component. The experiment consisted in a task where subjects had to either fixate or point at a target. It was hypothesized that reaching could elicit a larger N2 than saccades; because a more efficient target processing is necessary if a target has to be used for a limb movement. The two tasks indeed resulted in a more negative N2 during the pointing condition. Regarding the possible processing of target representation, the question arises how and in which way the saccadic and the pointing movement are processed or prepared differently. Various models for the development of target representations in eye-hand-coordination have been suggested. Therefore, the N2, or the differences during the time frame of the N2, could be interpreted as a link to a shift in reference frame, a different weighting in important target features or in connection to multiple sensory representations which are built along interconnected pathways in the brain. The observed effect could also be related to shifts in attention. This would be supported by findings which provide evidence for a modulation through attention at very early stages of visual processing (Kosslyn et al., 2001). However, later imaging studies included control conditions for mere attention effects and their results speak for a more complex picture (Astafiev et al., 2004). As has been mentioned before, a shift in reference frames – probably in the case of movement preparation from a rather retinotopic organization in the parietal cortex to a more body-centered frame in the frontal cortex - could account for differences in the pointing and the saccade condition (McGuire and Sabes, 2009). Clearly, these results could not explain differences between pointing movements toward different targets. A study by Sailer et al. (2002) demonstrated that specific target features play a role during the generation of pointing movements. Therefore, the necessity of higher efficiency during the reaching task could also be due to a more complex processing of important target characteristics. According to Maunsell (1995), the multiple levels in the cortical areas which are related to the processing of visual information, could serve the purpose of implementing a range of sensory representations, where information is already interpreted and weighted according to its relative importance.

In this context, further studies on this topic could concentrate on differences during the target processing in regard to the degree of coupling between eye-hand-

coordination. In the present study, the two movements were very closely coupled. Therefore, it would be of interest to investigate how the differences in the relevant ERPs develop when target representations have to include not only different, but opposing features.

Another important aspect would be the question at what time point segregation between the two target representations takes place. As has been reported by Bruce et al. (2003) some studies could show an influence of attention even in V1. Accordingly, (Astafiev et al., 2004) demonstrated an action-related modulation at the early stages of target processing. Thus, the good temporal resolution of the EEG could provide a basis for the interpretation of target representation during the early stages.

Coming to a conclusion, the early ERP-components – such as the N2 – seem to be a suitable tool to investigate characteristics of target representation. This is due to the information they provide about temporal development and also, because the different components have been found to reflect important aspects during target processing at different stages.

Appendix

Abstract

During multiple tasks, we are in need of a very precise eye-hand-coordination. Taking into account the variable factors of influence, like attentional demands, changing context or limited information, the question arises, how the brain is able to develop a target representation which is best suited to all kinds of situations in everyday-life. Generally, studies reached different results regarding possible reference frames or the processing of different target features. Whether movements' trajectories or corresponding errors are correlated, depends largely on the paradigm which is used in a certain experiment. In consequence, some researchers rather focused on the relative contribution of different informative frame works on multiple target representation than on comparing the probabilities of concurrent models. Behavioral and functional studies provide evidence that not solely an implementation of different reference frames for a movement vector is necessary, but also the relative weighting of target features in relation to the required eye- or hand movement (McGuire and Sabes (2009); Sailer et al. (2002)). In addition, shifts of attention have been suggested to modulate nearly all steps of eye-hand-coordination (Maunsell, 1995). In this context, the present study tries to further investigate the underlying principles for generating coupled saccades and pointing movements. The method of choice is the comparison of an ERP-component, the N2, during a task, where participants had to either fixate or perform a reaching movement at a target. The N2 is of interest in this behalf, because it has been linked to target processing, classification of stimuli and is influenced by attention (Holguín et al., 2009). During the experiment, the N2 showed a significantly more pronounced negativity during the pointing condition. This can be interpreted as a need for higher efficiency during target processing that leads to a limb movement, because additional and more complex information has to be taken into account. Accordingly, the results fit a model based on multiple rather than one common target representation. The specific differences could result either from a more complex computation concerning reference frames for the pointing movement or a weighting procedure of relatively important target features.

Zusammenfassung

In diversen alltäglichen Situationen benötigen Menschen eine präzise Auge-Hand-Koordination. Diese gewährleistet, dass wir sinnvoll mit unserer Umwelt interagieren können und beispielsweise die Fähigkeit zu geplanten, genaueren Greif- oder Zeigebewegungen haben. Aufgrund der Vielfalt von Situationen und Anforderungen, beziehungsweise der großen Masse an Information, welche schon während des Vorgangs der Wahrnehmung bewältigt werden muss, stellt sich die Frage, in welchen Schritten das menschliche Gehirn diese Verarbeitung vornehmen kann.

Die vorliegende Studie setzt sich mit dieser Frage auseinander, indem die ERP-Komponente N2 im Vergleich bei Sakkaden zu einem Ziel oder einer entsprechenden Zeigebewegung untersucht wird. Die N2-Komponente erscheint hier besonders geeignet, da sie einen Zusammenhang mit Zielverarbeitung oder Stimulusklassifikation zeigt und durch Aufmerksamkeit moduliert werden kann (Holguín et al., 2009). Aufgrund dessen wurde angenommen, dass die Notwendigkeit einer effizienteren Zielverarbeitung in der Zeige-Bedingung zu einer stärker negativ ausgeprägten N2 führen würde. Während des Experiments führten die Teilnehmer Zeigebewegungen und Sakkaden zu einem Stimulus aus und lediglich Sakkaden zu einem anderen. Anhand dieser Aufgabe konnte der erwartete Unterschied in der Amplitude der N2-Komponente gezeigt werden, welche in der Zeigebewegung stärker negativ ausgeprägt war. Bezüglich der Latenzen stellten sich die beiden Bedingungen als gleichwertig heraus. Dies könnte an zwei einander ausgleichenden Einflüssen liegen: Zum einen muss das Ziel für die Zeige-Bedingung effizienter verarbeitet werden, zum anderen ist eine größere Menge an Information zu bewältigen.

Im Hinblick auf eine mögliche Interpretation der Ergebnisse muss genauer zwischen den Subkomponenten der N2 unterschieden werden. Die Tatsache, dass der beobachtete Effekt an der zentralen Elektrode am größten war, an der parietalen Seite noch zu sehen war, aber in Richtung frontal verschwand, spricht für einen Einfluss der Bedingung auf die posteriore N2p. Hierbei ist zu sagen, dass keine eindeutige Unterscheidung von der N2b getroffen werden kann, welche im Zusammenhang mit abweichenden Stimuli untersucht wurde (Patel und Assam, 2005). Allerdings wurde die N2b mit dem superioren Temporalcortex in Verbindung gebracht, welcher, sowie Teile

des Parietalcortex, zum dorsalen Pfad der Verarbeitung der visuellen Wahrnehmung gehört (Bruce et al., 2003). Aus diesem Grund wären beide Subkomponenten mit der Bildung von Augen- und Handbewegungen verbunden.

Wesentlich ist bei der vorgegeben Aufgabe der Einfluss der Aufmerksamkeit. Studien haben gezeigt, dass bereits während der ersten Verarbeitungsschritte Modulationen durch Ausrichtung der Aufmerksamkeit wirksam werden können (Maunsell, 1995). In diesem Sinne könnte der N2-Effekt durch ungleiche Verteilung von Aufmerksamkeit zustande gekommen sein, da die Zeige-Bedingung wahrscheinlich als die anstrengendere von beiden wahrgenommen wurde. Dazu ist zu sagen, dass andere Untersuchungen, welche Augen- und gerichtete Handbewegungen nutzten, keinen ausschlaggebenden Einfluss von Aufmerksamkeit durch eine zusätzliche Kontrollbedingung zeigen konnten (Astafiev et al., 2004). Diese Beobachtungen sprechen für eine komplexere Ursache des N2-Effektes.

Eine weitere entscheidende Grundlage bezüglich der Auge-Hand-Koordination ist, welche Koordinatensysteme für die Berechnung des Bewegungsvektors verwendet werden. McGuire und Sabes (2009) präsentieren eine Studie, bei der Fehler in den Augenbewegungen am besten durch ein Model vorausgesagt werden konnten, bei dem Beiträge von retinotopen und körperzentrierten Koordinatensystemen mit einbezogen wurden. Aufgrund der posterioren Verteilung der N2-Komponente könnte die retinotop Organisation des parietalen Cortex dazu führen, dass für die Überleitung zum stärker körperzentriert strukturierten frontalen Cortex (McGuire und Sabes, 2009) eine effizientere Verarbeitung im Falle der Zeige-Bedingung von Nöten ist. Dadurch könnte eine stärker negative N2-Komponente entstehen.

Die Untersuchung von Sailer et al. (2002) weist auf einen weiteren Aspekt hin. In einem Verhaltensexperiment hatten Versuchspersonen Augen- und Zeigebewegungen zu Zielen mit unterschiedlichen Charakteristika durchzuführen. Hierbei kam es zu Unterschieden bei der Zeigebewegung. Dies kann als Hinweis auf die Bedeutung von Zielcharakteristika bei der Bildung einer Zielrepräsentation gewertet werden. Da diese offenbar nur im Falle der Zeige-Bedingung relevant waren, kommt es anscheinend zur Bildung von unterschiedlichen Zielrepräsentationen, je nach Relevanz für spätere Bewegungen. Im Sinne von Maunsell (1995) könnte man auch von multiplen Zielrepräsentationen sprechen, welche in den unterschiedlich organisierten Schichten

der Verarbeitungsbahnen gebildet werden, um relevante Information für das Individuum sinnvoll zu gewichten.

Im Zusammenhang mit dem beobachteten Effekt bei der N2-Komponente könnte die unterschiedliche Gewichtung einen Einfluss haben, da in der Zeige-Bedingung andere Zielcharakteristika analysiert und gewichtet werden müssen.

So gesehen könnte eine möglichst komplette Erklärung des N2-Effektes lauten, dass verschiedene Zielrepräsentationen ausgebildet werden, welche sich unterscheiden im Hinblick des Beitrages von Koordinatensystemen und außerdem bezüglich der relativen Gewichtung von Zielcharakteristika. Natürlich könnte auf allen Stufen dieses Verarbeitungsprozesses Aufmerksamkeit eine wesentliche Rolle spielen.

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