Neural responses to observed eye blinks in normal and slow motion: an MEG study

Siiri Helokunnas
Master's Thesis

Cognitive Science
Institute of Behavioural Sciences
University of Helsinki

Brain Research Unit
O.V. Lounasmaa Laboratory
Aalto University School of Science

Instructors: Elina Pihko & Anne Mandel

November, 2012

CONTENTS

Acknowledgements

This work was done in the Brain Research Unit of the O.V. Lounasmaa Laboratory, Aalto University School of Science. I am grateful to Acad. Prof. Riitta Hari for providing directions for the project with her outstanding experience and contagious enthusiasm, for clearly pointing out the important things to learn about MEG, and for detailed comments on manuscripts. She has the talent to raise questions that incite others to think thoroughly. I am also thankful to my instructor, Doc. Elina Pihko, for her time, warm encouragement and careful advice on MEG analysis, as well as for her thoughtful comments on various drafts of this thesis. I thank Prof. Minna Huotilainen for guiding our seminar group at the Helsinki University and for providing expert comments and suggestions on the thesis.

I express my gratitude to M.Sc. Anne Mandel for the warm and joyful moments in the lab; she has the ability to find the humoristic point of view even in challenging situations. Further, she has invaluably helped me with the analyses, which would not have been that accurate without her rigorous attitude and skill. I thank nurse in clinical neurophysiology Mia Illman and M.Sc. (Tech.) Eerik Puska for their help in the MEG measurements and Eerik also for his contributions to the analysis. I am also thankful to all other people who have helped me with technical issues—especially Priv.-Doz. Sebastian Pannasch, Prof. Lauri Parkkonen, M.Sc. (Tech.) Kranthi Kumar Nallamothu, and Mr. Petteri Räisänen. I am happy for the encouraging atmosphere in the lab and the pleasant company I have had during lunch and coffee breaks, as well as in outside-the-lab events.

The project was funded by the ERC Advanced Grant Brain2Brain (to R. Hari). I remain thankful for the company Infradex (Vantaa, Finland), which provided the high-speed camera for our use.

I would like to thank my friends for always being there for me. With some of you we shared the experience of writing a Master's thesis—with some of you we have shared much deeper things in life. I cannot find the right words to express how important my boyfriend Touko has been to me. Thank you for listening to me when I have poured out my work-related frustration or bursts of enthusiasm, and thank you for accepting me as I

am. I owe my deepest thanks to my family; my parents have always positively encouraged me to keep on studying, and, believing in my abilities, they have continuously supported me.

Contributions of the author

I joined in an ongoing project, but I participated in the planning of the experiment together with our research team. I designed and filmed the stimulus videos with Anne Mandel. I edited the stimuli and made the script for displaying the stimuli. I recruited the participants. I performed the MEG measurements with Eerik Puska and Mia Illman. I analyzed the data with the help of my instructor and team members, except for the results for the self-performed blink timing which I received from Anne and Eerik. I made the figures and wrote the thesis.

Abbreviations

ASD	autism spectrum disorders
ECD	equivalent current dipole
EEG	electroencephalography, eletroencephalogram
EMG	electromyography, electromyogram
EOG	electro-oculography, electro-oculogram
ERP	event-related potential
fMRI	functional magnetic resonance imaging
HPI	head position indicator
MEG	magnetoencephalography, magnetoencephalogram
MRI	magnetic resonance imaging
PCA	principal component analysis
SEM	standard error of mean
STS	superior temporal sulcus

1 Introduction

When we say that something happens "in the blink of an eye", we mean it is over very quickly—so quickly we barely notice it. It is true that a single blink is short in duration, only about two tens of a second, but we certainly would notice if the lights went out for the same time. However, when we blink, the world seems continuous to us as if our sight had not been obscured. What is more, we remain happily unaware of losing about 5% of all visual information coming to our eyes because of blinking: blinks, each lasting for about 0.2 s, occur on average 15 times per minute (Doughty, 2001), meaning about 3 s of lost input each minute. Perhaps clever tricks performed by our brains make the eye blink appear even shorter than it is, because we actually fail to detect the event that went past while we blinked.

Considering that we do not usually pay attention to our own blinks, what about our friend's blinks? A person who does not blink at all but just stares at us appears strange or even hostile. In the same way very frequent blinking may give a sign to the interacting partner that the blinker is nervous or that something is wrong. Blink rate can indeed serve as an indicator of the cognitive or emotional state of the blinker (e.g., Ousler et al., 2008). Blinking might also contribute to social interaction by strengthening mutual synchronization in movements and gestures (Cummins, 2012). Therefore it is intriguing to study what happens in the brain when we see someone blinking.

In a wider perspective, motivation for this study arises from the pursuit of two-person-neuroscience with magnetoencephalography (MEG)(Baess et al., 2012; Hari & Kujala, 2009). In ongoing and future experiments, MEG signals are recorded from two participants simultaneously while they are interacting via video connection. In those experimental settings simulating face-to-face encounters, small conversational expressions and gestures, potentially blinks as well, enhance mutual understanding and even affect the smoothness and pleasantness of the interaction. However, the brain mechanisms of non-verbal communication are not well-known, for instance, how the small expressions or eye blinks are registered in the brain.

When MEG signals are recorded during a conversation, many features of the stimulus may elicit responses. Thus, the brain responses to small expressions are not feasibly

distinguishable from the data, and therefore those small factors should be first studied in separate experiments. Neural correlates of blink viewing have been studied with electroencephalography (EEG) by Brefczynski-Lewis and co-workers (2011), but the topic has not been addressed using MEG, which provides a better spatial resolution for source localization.

The purpose of this thesis is to investigate with MEG how the brain reacts to viewed blinks, presented with normal speed and in slow motion.

2 Background

This chapter will review literature concerning blinking first from a physiological and behavioral perspective. Then some methodological issues are considered, especially the basics of electro-oculography (EOG) and MEG. It is also examined how visual and moving stimuli, in general, affect MEG responses. The third chapter states the research questions and hypotheses.

This thesis will examine eye blinks from two viewpoints: one is the viewer's and the other is the blinker's. It is thus important to distinguish between these two and keep in mind which blink we are talking about. From here on, *viewed blink* refers to the blink of another individual, shown for example in a stimulus video, whereas the term *self-performed blink* is used for blinks that people make themselves.

2.1 Behavioral aspects of eye blinks

2.1.1 Definition and classification of eye blinks

The following section on blink classification concerns self-performed blinks. First of all, what is an eye blink? A blink is simply performed by closing and opening the eyelids. The primary, physiological function of blinking is to moisten the cornea, thereby cleaning and protecting it with a thin tear film (e.g., Ousler et al., 2008). Despite the apparent simplicity, all blinks are not the same. Different kinds of blink taxonomies have been suggested, among which a common one distinguishes between three types of blinks: reflexive, spontaneous, and voluntary (proposed by Stern & Dunham, 1990). Reflexive blinks usually occur as an automatic reaction to an external stimulus, e.g., to an air puff to the cornea, to a speck in the eye, or to an object closely approaching the eye. They can also be part of the startle reflex. Spontaneous blinks, also referred to as

endogenous or involuntary, are unconscious but may be cortically inhibited according to a given ongoing task; they may thus have social importance. Voluntary blinks might have a conscious social function. Measured with EOG, the mean amplitude and duration of spontaneous blinks are shorter than those of voluntary or reflex blinks (Kaneko & Sakamoto, 1999).

Ousler and co-workers (2008) also divided eye blinks into three categories, but now into incomplete blinks, complete blinks, and twitch blinks. "Twitch" seems to correspond to the reflex blink of Stern and Dunham (1990). Herrmann (2010), on the other hand, investigated the prosodic use of eye blinks in German Sign Language, classifying the blinks in seven groups according to their placement with respect to the grammatical structure of the utterances: Prosodic blinks comprise blinks marking intonational phrase (IP) boundaries, blinks marking phonological phase (PP) boundaries, and sentence initial blinks, whereas non-prosodic blinks include lexical blinks, reflexive blinks, cognitive triggers (blinks during slips of the hand, pondering, fingerspelling etc.), and blinks to moisten the eyes. Cummins (2012) criticized the idea of defining blinks as voluntary or conscious; he argues that it is not feasible to decide objectively whether a blink is conscious or not. For the purposes of his study, he proposed a classification which uses two parameters: gaze direction and blink duration. The gaze, before and after the blink, can be directed away or towards the partner, and blinks are either short (less than 240 ms) or long (240–400 ms). In his taxonomy, an eye closure longer than 400 ms does not count as a blink.

In Cummins's study, the recording of blink duration started when the eyelid covered the major portion of the cornea. This view differs slightly from that of Herrmann (2010), who considered a blink to begin when the upper lid starts to fall down and to end when the eye is completely open again.

2.1.2 Implications of blink rate

Humans usually blink 8–21 times per minute (Doughty, 2001). The reported averages vary greatly among studies and obviously depend on the subjects, on the circumstances, and on what is counted as a blink in the measurement. Blink rate is affected by external physical conditions, such as humidity, temperature, lighting, and air flow (Ousler et al., 2008). More importantly, blink rate depends on the mental state and activity of the individual: blink rate decreases during a task that implies increased cognitive load, for

instance reading (Bentivoglio et al., 1997), lipreading (Lesner & Hardick, 1982), memorizing series of digits (Holland & Tarlow, 1972) or internal counting (Holland & Tarlow, 1975). In addition, lying in an authentic situation is associated with suppressed blinking, which has been attributed to increased cognitive demand (Leal & Vrij, 2010; Mann et al., 2002). Blink rate rises immediately after telling the lie, whereas after truth telling the blink rate does not change (Leal & Vrij, 2008). A stimulus discrimination task also affects blink frequency; when more attention is required, blink rate is attenuated before the stimulus, and higher processing load results in higher blink peaks after the stimulus (Fukuda & Matsunaga, 1983). A possible explanation for the varying blink rates is that blinking interrupts cognitive processes and therefore reduced blinking could be beneficial during cognitive tasks (Holland & Tarlow, 1972).

On the other hand, more frequent blinking occurs during emotional excitement, for instance when one is angry (Ponder & Kennedy, 1927). Harrigan and O'Connell (1996) monitored facial movements of participants who were describing an anxious event from their past. When the participants experienced more anxiety, they blinked more often. Hirokawa and co-workers (2000) compared blink rates in three conditions varying in stressfulness: a telephone conversation either in Japanese, English, or French. The participants were native Japanese speakers with intermediate skills in English, but they were not able to speak French. They reported the highest nervousness levels during the conversation in English; the conversation in French was considered the least stressful. Accordingly, blink frequency was at its highest when the subjects were discussing in English.

However, conversation is in any situation accompanied by more frequent blinks than a relaxed resting state (Karson et al., 1981; Bentivoglio et al., 1997; see Doughty, 2001 for a review). Even the blind have blink rates similar to those of the normal-sighted when they are having a conversation with a stranger (Hall, 1945).

In addition to cognitive and emotional factors, mental diseases and neurological disorders can affect the blink rate. Mackintosh and colleagues (1983) found that depressed patients blinked more frequently than healthy control subjects; however, the patients' blink rates returned to normal when they recovered from depression. Blink rates are also augmented in schizophrenia (Chan & Chen, 2004; Karson et al., 1990; Swarztrauber & Fujikawa, 1998). In Tourette's syndrome, blink rates are higher than

usual during resting or watching videos, but during conversation the blink rate does not increase in Tourette patients in contrast to healthy control subjects (Tulen et al., 1999).

It has been widely suggested that the blink rate is related to the dopaminergic system—higher blink rate predicts higher dopaminergic activity (Dreisbach et al., 2005; Karson, 1983). Even recreational cocaine use, reducing dopaminergic function, can manifest itself in reduced blink rates (Colzato et al., 2008b). The blink rate can predict dopaminergic activation in more complex settings. For instance, higher blink rate has been associated with a longer "attentional blink", i.e., the difficulty to recognize a rapidly succeeding stimulus among distractors after the preceding target (Colzato et al., 2008a). In other words, those who blink more fail to detect the second visually presented target after detecting the first one. This association is thought to be mediated by dopaminergic function and its influences on working memory systems.

In another study, subjects with higher blink rate—indicating higher dopaminergic function—were more influenced by positive priming stimuli when they were supposed to think what kind of outcomes would result from their actions; baseline blink rate thus indicated how much positive priming would affect the sense of agency of the subject (Aarts et al., 2012). Nevertheless, van der Post and colleagues (2004) obtained conflicting results on the relationship of blink rate and dopaminergic function, showing that drugs affecting the dopaminergic system had no impact on the blink rates of the participants.

The findings cited above indicate that several cognitive processes and mental states influence the frequency of *self-performed blinks.* On the other hand, *viewed blinks* can have an impact on certain kinds of mental processes, namely, how the viewer evaluates the characteristics of the blinker. When the viewed person blinked more frequently, she was rated more nervous and careless (Omori & Miyata, 2001). For ratings of unfriendliness, the curve followed an inverted U-shaped pattern, i.e., normal blink frequencies resulted in positive evaluations, but abnormal—too low or too high—blink rates conveyed a negative impression of the person. Throughout the different blink rate conditions, the viewed person maintained a neutral expression without other movements than blinks, which excluded other possible factors affecting the evaluations. The authors suggested that by experience it is possible to learn to associate high blink rates with nervousness and anxiousness, but that these associations are unconscious. Therefore a

person who blinks more is perceived as more nervous, especially when complementary information is lacking.

All in all, blinking is easily observable in daily interaction, and when the blink rate is augmented or reduced, it can be a sign of a certain mental state. Consequently, blink rate might be utilized as a cue in assessing a person. This kind of assessment would most probably be unconscious, since people are usually unaware of someone else's blinks, except when blinking is strikingly abnormal. Obviously, one cannot determine the mental state of the other solely on the basis of blinks, because high or low blink rate can have various reasons. Nevertheless, because blink rate can convey some information about the mental state of an individual and because it influences the evaluations of a person, blinks are likely to be relevant in social interaction.

2.1.3 Timing and synchronization of blinks

Spontaneous eye blinks are more likely to occur with certain events. As mentioned above, increased visual attention reduces the blink rate of readers, and interestingly, readers blink more likely at page turns and at punctuation marks (Hall, 1945). Nakano and colleagues (2009) found that blinks were synchronized between participants who were watching video stories without sound: the participants tended to blink more during scenes that were less informative, for instance at the conclusion of an action or when the main character disappeared. Control conditions—a video without a story and an auditorily presented story without any visual stimuli—did not elicit blink synchronization. On the basis of the results, the authors suggested that humans unconsciously control their blink timing to lose only the minimum amount of visual information.

In accordance with the results of Nakano and colleagues (2009), Shultz and co-workers (2011) demonstrated that the viewers of a video blink less when they see important content. When viewing a video of children's play, children with autism spectrum disorders (ASD) showed different blinking patterns compared with the healthy children. The blink rates were compared between two conditions: during affective events in the video (e.g., when a child became angry), and during non-affective events (e.g., when a wagon door was moving). The blink rate of the healthy children decreased more when they saw affective content, whereas the blink rate of the ASD children decreased more when they saw non-affective content. Thus, Shultz and co-workers concluded that the

affective content was more important to the healthy children than to the children with ASD.

During a blink, vision is suppressed physically by the eyelid closure, although some light, about 5% of red and 0.3% of blue and green wavelengths, can still enter through the eyelid (Ando & Kripke, 1996). Moreover, vision is suppressed also at the neuronal level even prior to the blink; the suppression is at its strongest around 30–40 ms before the eye begins to close (Volkmann et al., 1980; Volkmann, 1986) [1]. Because of the suppression, blinks go unnoticed for the performer and an apparently continuous visual awareness is maintained. Despite of the perceived continuity of vision, some visual input is lost during blinking, and therefore the timing of blinks requires regulation.

Nakano and Kitazawa (2010) found that when participants view a video showing the face of a speaker, they spontaneously blink in synchrony with the speaker. The authors concluded that the synchrony did not equal to a mere imitation of an action, because the extent of the synchronization was related to the content of the video: blinks were more strongly synchronized during the pauses in speech. Blink synchrony was absent when only the sound was present, and the authors thus concluded that the cognitive demand as such did not cause the variation in the blink rate.

The synchronization of blinks that was present in healthy subjects when they were viewing the face of the speaker was absent in subjects with ASD, although both the ASD and control groups spent the same amount of time looking at the eyes of the speaker (Nakano et al., 2011). Therefore the absence of entrainment of blinks in individuals with ASD cannot be explained by different gaze patterns. In ASD, social communication is impaired, including difficulties in face perception (Schultz, 2005). Considering that the subjects with ASD did not show synchronization of blinks, Nakano and co-workers (2011) suggest that blinking contributes to face-to-face interaction together with other facial gestures. Temporal adjustment of movements, including blinks, with the interacting partner would thus enhance communication. People with

[1] Note the distinction between *blink suppression* (neural insensitivity to visual input during blinking) and *suppressed blinking* (reduced blink rate during reading, for instance).

ASD seem to fail in the temporal attuning, which in turn may be one reason for their impaired interaction.

Cummins (2012) investigated the blinking and gaze patterns in real dyadic conversations. The behavior of each individual was consistent across dyads with respect to certain aspects of the conversation: blink rate depended on speaking turn and the direction of gaze, i.e., whether the gaze was directed towards or away from the partner. Moreover, blinks were rather consistently associated with turn onsets. However, the behavioral patterns differed between the participants.

2.2 General methods in studying blinking

2.2.1 Blink-rate measurement

Several methods have been used for recording blink rates, blink parameters, and brain responses to blinks. At the time when electrical measurement devices were unavailable, the blink rate was recorded mechanically, for example by attaching a silk thread to the eyelid of the subject (Ponder & Kennedy, 1927). Later on, an infrared sensor clipped to the frame of eye glasses has been used for blink rate tracking, since the eyelids and the eyeball reflect infrared light in different ways (Caffier et al., 2003). A micro-camera, used together with an infrared illuminator, can also track the diameter of the pupil and detect blinks in that way (Ousler et al., 2008).

A common method for monitoring eye movements has been EOG (Denney & Denney, 1984; for a review, see Marg, 1951). The EOG electrodes for blink detection are normally placed above and below the eye, and one vertical pair of electrodes usually suffices, because in most cases the two eyes blink in synchrony. The cornea is positively charged in relation to the retina, and the resulting current distribution in the eye can be modeled with a single current dipole directed from the retina to the cornea (Antervo et al., 1985). When the eyelid closes, it changes the shape of the volume conductor: positive ions are conducted upwards resulting in a difference in the potential between the two electrodes (Barry & Jones, 1965; Matsuo et al., 1975).[2] When the eyelid reopens, the potential returns back to the original. In consequence, a blink is

[2] For the same reason, blinks cause fluctuations also in MEG signal (see section 2.3.4).

visible in the EOG signal as a deflection with an average duration of 200 ms. The peak-to-peak amplitude of an EOG blink is of the order of 1 mV, but the amplitudes are affected by lighting conditions among other factors (François et al., 1955; Miles, 1940). Skotte and colleagues (2007) confirmed that EOG is a reliable method for determining blink rates of the participants doing active computer work and moving their eyes freely: with EOG the researchers were able to detect 95.4% of the blinks that they had counted manually from a videotape.

2.2.2 Blink viewing studied by EEG

EEG correlates of blink viewing have been studied only recently by Brefczynski-Lewis and co-workers (2011). Their blink stimulus consisted of three images of a face looking directly at the viewer: eyes open, eyes closed, and eyes open. Those frames were presented at a fast pace yielding an impression of a natural blink (*apparent motion;* see section 2.4). The other stimuli they used were an eye closure—the eyes were closed for 100 ms in contrast to the blink condition, where the eyes were closed for 33 ms—and gaze aversion. The frame showing the direct gaze was constantly present, yielding an impression of a continuous video of a face making occasional eye movements and always returning back to looking at the observer.

Scalp EEG showed robust P100 and N170 responses to all eye movements in the temporo-occipital areas, with right-hemisphere dominance. Later deflections (P240, P450, and P600) had smaller amplitudes to blinks than to the eye movements. Brefczynski-Lewis and colleagues suggested that these late evoked potentials to blinks and other eye movements could be related to processing of socially significant features. Consequently, blinks together with other eye movements would be possible sources of useful information in making inferences about other people's mental states.

2.3 Magnetoencephalography

2.3.1 Generation of MEG signals

The following discussion on MEG is mainly based on the publications of Hämäläinen and colleagues (1993), Hari and colleagues (2000), Hari (2005), Okada and colleagues (1999), Salmelin and Parkkonen (2010), and Baillet (2010). MEG, as well as EEG, has a millisecond-scale temporal accuracy, which is beneficial for probing quickly changing brain activation. Both MEG and EEG signals mainly reflect neural currents caused by

synchronous postsynaptic potentials of cortical pyramidal neurons. Consequently, results from EEG and MEG should not contradict, although the sensitivity patterns differ between the two methods. The differences arise from the recording technique: EEG measures the potential differences on the scalp, whereas MEG detects the magnetic fields induced by the electrical currents. The electrical conductances of the skull, skin, and brain affect the flow of the current, which makes the analysis of EEG data more complicated. On the contrary, these extracerebral tissues can be considered practically transparent for the magnetic field. Therefore the different properties of tissues do not have to be taken into account in the analysis of MEG data and only the shape of the used head model is essential. The lesser distortion of MEG signals also results in a higher spatial resolution of MEG compared with EEG—the sources of MEG signals can be localized more reliably.

Importantly, the direction of the intracellular current flow can be directly deduced from the magnetic field patterns by applying the right-hand rule. This is often very useful for trying to understand the physiological events underlying the responses.

The major difference of MEG with respect to EEG is that in a spherical volume conductor it is sensitive to tangential components of the currents, whereas EEG also captures the radial components. Thus, the cortical sources detectable by MEG are typically located in the sulci, which is useful to know in practical work. The radial currents are not generally detected by MEG, whereas tilted sources can be observed because of their tangential component, especially if they are close to the sensors. The signal from them is weaker than a signal from a tangential current of the same strength and depth. In addition, MEG mostly neglects deep sources, contrary to EEG. This is why EEG and MEG can be regarded as complementary techniques. Figure 1 illustrates the field patterns of MEG and EEG. Both fields are dipolar, but the magnetic flux is oriented at 90° with respect to the electric potential and it is more narrowly distributed. Therefore the inaccuracies in localization also differ: the shadowed areas illustrate the uncertainty for inferring the source location on the basis of the electric or the magnetic field.

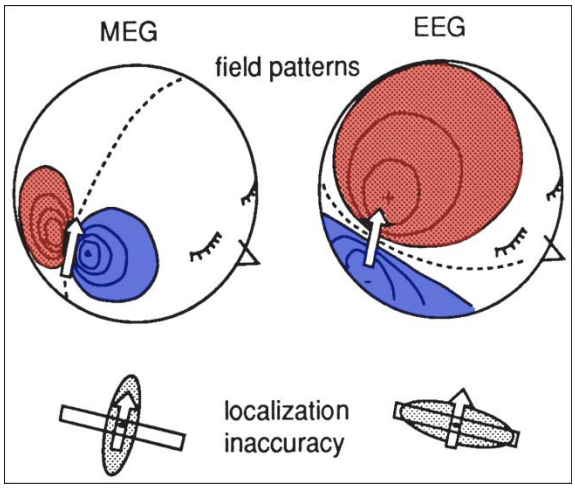

Figure 1. Differences of MEG and EEG field patterns, and localization inaccuracies. The white arrow represents the dipolar current. In the magnetic field, the magnetic flow comes out in the red area and goes into the head in the blue area. In the electric field, the red area is positively charged and blue area negative. (Adapted from Hari, R. 2005. Magnetoencephalography in Clinical Neurophysiological Assessment of Human Cortical Functions. In E. Niedermeyer, & F. Lopes da Silva (Eds.), *Electroencephalography: basic principles, clinical applications, and related fields*, 5th ed. USA: Lippincott Williams & Wilkins.)

2.3.2 Evoked responses versus rhythmic activity

Magnetic fields arising from the brain are extremely weak. A SQUID (superconducting quantum interference device) sensor is usually employed to detect the changes in the field, and yet a synchronous activation of a large population of parallel dendrites is needed for a reliable signal. A brain response to a single stimulus, such as an image or a sound, is usually too weak to be distinguished from other brain activity, "noise", occurring at the same time with the stimulus. Two alternative methods are available to increase the signal-to-noise ratio: time-locked averaging (comparable to evoked potential analysis) and processing the rhythmic activity of the brain, e.g., calculating spectra (comparable to the study of brain oscillations in EEG). Averaging is a powerful means to render the stimulus-related activity visible if the activity and noise are more or less constant across trials. The inconvenience of this method is the necessity to repeat the same stimulus over and over again. As a rule of thumb, each experimental condition should generally have 100 accepted trials, but the appropriate number of trials depends on the nature of the stimuli and tasks. Even 16 trials have sufficed for averaging responses to painful, olfactory stimuli (Hari et al., 1997). If the experiment is too long and monotonous, the subject may get less alert and even drowsy, which impairs the quality of the data.

The changes in the rhythmic activity of certain brain areas can be associated with specific events. For instance, alpha rhythm in the occipital cortex strengthens when the eyes are closed, but opening the eyes or even visual imagery can suppress the rhythm (Cohen, 1968; Kaufman et al., 1990; Salmelin & Hari, 1994a). In a similar manner, the magnetic mu rhythm—20 Hz in the anterior sensorimotor cortex and 10 Hz in the

posterior sensorimotor cortex—is suppressed by movements (Salmelin & Hari, 1994b), movement observation (Hari et al., 1998), and motor imagery (Schnitzler et al., 1997). In the present study, the evoked-responses technique is employed.

2.3.3 Source modeling

A common method for further analysis of averaged MEG responses is dipole modeling. Strictly speaking, the generators of MEG signals are never ideal current dipoles (that is, pointlike currents with a specified direction), but an equivalent current dipole (ECD) is often an adequate model. The ECD represents the electrical current resulting from the simultaneous activation of neurons in a certain area. Usually the activation is distributed to several distinct brain areas resulting in complicated field patterns. The location of the source can also vary as a function of time. Therefore a multi-dipole model is required to identify the sources separately. First, a subset of channels is selected for estimating the location of an ECD. One ECD thus accounts for the activation only on the selected channels at a given time. Other time points or subsets of channels are then selected to find additional sources. Besides location, the dipole parameters include direction and magnitude as a function of time.

Finally, the waveforms that should emerge if the modeled dipoles really existed in the brain are compared with the measured waveforms to see the explanatory power of the created model. In addition to this kind of visual evaluation, dipoles can be ranked by various parameters, such as goodness-of-fit value (g), a percentage indicating how much of the variance of the measured signals on the selected channels the dipole accounts for. Another important parameter is *confidence volume*, the size of the volume which contains the source with a likelihood of, e.g., 95%.

Inferring the source locations on the basis of the measured MEG data is an attempt to solve the inverse problem. From the mathematical point of view, this inverse problem always has several solutions, and therefore one has to set constraints according to the known brain anatomy and physiology. Converging evidence from other brain studies can also be helpful. A trivial constraint is that the sources need to reside inside the head. The head is usually modeled as a sphere, because the spherical head model is sufficiently accurate for rather superficial currents. A more realistic head model is possible, as well, although it can be more laborious to implement. Additionally, the allowed locations for the sources can be limited for instance to cortical tissue, if it is

generally known that the brain function in question recruits mainly the cortical areas. In identifying the locations for the ECDs, the participant's magnetic resonance (MR) images are very useful. Namely, the ECDs can be superimposed on the structural MR images, revealing the precise anatomical positions of the ECDs (see Figures 10 and 11).

2.3.4 Magnetic field patterns related to self-performed blinks

Although MEG responses to observed blinks have not been previously investigated, the effects of self-performed blinking on the brain activation have been examined. The focus has been on the artifacts that blinking causes in the MEG recordings, because those artifacts may distort the results if blinks occur in a systematic relation with the stimuli. Hughes and colleagues (1977) reported eye blink artifacts in MEG signals over the frontal areas. Antervo and colleagues (1985) modeled the sources of the MEG artifacts, observing that voluntary blinking causes changes in the magnetic field pattern over the posterior parts of the orbits. Using current dipole and current quadrupole (current loop) modeling they concluded that eyelid closure alters the form of the volume conductor. The closed eyelid conducts the corneal positive charge upwards and alters the magnetic field pattern so that the magnetic flux enters the head on the left side and emerges from the scalp on the right side. In addition to the strong and short-latency artifact (around 80 ms after the blink) close to the eyes, Hari and colleagues (1994) observed another response to voluntary blinks in the parieto-occipital sulcus 220–285 ms after the blink. This blink-related parietal response did not emerge when the lights of the measurement room were turned off. Therefore the authors proposed that the response is associated with spatial working memory and reflects the tendency to perceive continuity in the visual environment although the eye closure transiently prevents visual input from entering the eye.

Other imaging techniques and MEG analysis methods provide complementing evidence for the conclusion of Hari and colleagues (1994): In a study using functional magnetic resonance imaging (fMRI), visual continuity was similarly associated with activation of the parieto-occipital fissure (Bristow et al., 2005). Bristow and co-workers also extended these results by showing that *blink suppression* (i.e., reduced sensitivity to visual input during blinking) corresponds to decreased activation of the lateral occipital visual areas.

2.4 MEG responses to visual stimuli

Visual stimulation elicits clear MEG responses, as were first observed by Cohen (1975) and Brenner and co-workers (1975). Responses to visual stimuli appear mainly in the occipital cortex, but also in other brain areas depending on the features of the particular stimulus. Visual cortical areas are hierarchically organized, but the hierarchy does not necessarily imply serial processing. Response latencies in higher areas can be as short as in lower areas, as demonstrated by EEG and MEG (Ffytche et al., 1995; Vanni et al., 2001) and with computer simulation (Petroni et al., 2001). The lower areas (V1, V2, and V3) in the hierarchy are retinotopically organized, which has also been demonstrated using MEG (e.g., Maclin et al., 1983).

2.4.1 Visual motion

Visual motion principally activates the human visual motion area V5/MT that was discovered with PET recordings by Zeki and collaborators (1991). With MEG and MEG–fMRI combination this area V5/MT has been found in the occipito-temporal cortex, inferior to the superior temporal sulcus (STS)(Ahlfors et al., 1999; Bundo et al., 2000; Uusitalo et al., 1997). Besides V5/MT, several other cortical areas also react to visual motion. Motion-responsive areas include for instance the primary visual cortex V1, and other early projection cortices V2, V3, and V3A, lingual gyrus, fusiform gyrus, the STS, the parieto-occipital cortex and the medial posterior parietal cortex (Bartels et al., 2008; see Culham et al., 2001 for a review). The characteristics of the moving stimulus and the task determine which particular brain area is involved in the processing. The V5/MT complex itself has several parts that are specialized for certain kinds of motion (Howard et al., 1996; Watanabe et al., 2001).

Biological motion, that is, natural movements of living creatures in contrast to artificial motion, is generally associated with activation of the STS (for a review, see Blake & Shiffrar, 2007). Especially the posterior part of the STS (pSTS) responds to human motion displayed for example with light dots (Bonda et al., 1996). When the recognition of human motion was made harder by embedding the light dots in noise, the pSTS response was stronger if the viewer was able to recognize the biological motion (Grossman et al., 2004). Accordingly, the pSTS responses are weaker for inverted point-light displays, which are presumably harder to recognize as biological (Grossman

& Blake, 2001). In contrast, if the light dots move in a scrambled order, the STS is not activated—instead, V5/MT responds to the incoherent, non-biological motion.

An impression of motion can be produced beyond real motion, e.g., by flashing two adjacent lights one after another. The phenomenon is called *apparent motion.* As one would expect on the basis of subjective experience, apparent motion and real motion create similar activation patterns covering the same brain region (V5/MT)(MEG study by Kaneoke et al., 1997). Probably this similarity is due to the human mechanism of motion detection: we perceive an object at different positions, and if the time interval fits to the position change, we interpret it as motion. Therefore results from studies that use apparent motion as stimulus (such as the study on viewing blinks by Brefczynski-Lewis et al., 2011, cited in section 2.2.2) are comparable with the results concerning smoother motion. Obviously, videos always present apparent motion, and the smoothness depends on frame rate, which is 25–30 frames per second in movies, for example. Real motion is encountered in real life only.

The effect of movement speed on brain responses has been examined with simple light dots and sinusoidal gratings. The latencies of the MEG responses are longer when the visual motion is slower, and the amplitudes are higher for fast than slow motion (Kawakami et al., 2002; Maruyama et al., 2002; Wang et al., 2003).

2.4.2 Perception of faces

Faces surround us from the beginning of our lives, providing us with crucial information regarding social interaction. Nearly all of us become experts in identifying individual faces, and not in vain, since recognizing familiar people among strangers is difficult without discerning facial features correctly. Moreover, facial expressions convey information about the person's emotional state in a fast and vivid way. This section reviews the brain mechanisms contributing to face perception.

Haxby and colleagues (2000) proposed a model (updated by Haxby & Gobbini, 2011) for separate face-sensitive brain areas and their distinctive functions. According to this model, mainly built on the basis of fMRI data from different studies, the *core system* comprises the fusiform gyrus which deals mainly with the permanent features of faces, such as identity, and the STS which reacts to temporal aspects of faces, such as expressions, eye gaze, and facial motion. Moreover, the inferior occipital gyri

participate in the early processing of facial forms. In addition to the core system, the model includes an *extended system*, which recruits other brain areas useful in processing further information retrieved from the faces, for instance emotion-related information or semantic knowledge about the person in question.

Consistently with fMRI (Puce et al., 1995) and PET results (Sergent et al., 1992), face-sensitive MEG responses appear mainly in the fusiform face area (FFA) of the fusiform gyrus (Halgren et al., 2000; Sams et al., 1997). Among others, Gauthier and colleagues (1999; 2000) and McGugin and colleagues (2012) have argued that the FFA would participate in identification at expert level rather than in recognition of faces *per se*, but the existing evidence is controversial (Grill-Spector et al., 2004; Rhodes et al., 2004; Tong et al., 2008). The review by Kanwisher and Yovel (2006), for instance, defends the face-specificity of the FFA. However, the main conclusion is that faces activate the fusiform gyrus. MEG studies have also shown that other brain areas involved in face processing include the occipitotemporal junction, the inferior parietal lobe and the middle temporal lobe (Lu et al., 1991), as well as the posterior extrastriate cortex (peak at 120 ms) and the inferior temporal gyrus (peak at 170 ms) (Liu et al., 2002).

As it comes to the timing of the face-sensitive brain activations, MEG recordings have shown—in accordance with previous EEG literature (e.g., Jeffreys, 1989)—that responses to observed faces usually peak around 140–170 ms after the stimulus onset (Halgren et al., 2000; Linkenkaer-Hansen et al., 1998; Liu et al., 2002; Lu et al., 1991). However, face-sensitive deflections may peak around 100 ms at the earliest, and around 700 ms at the latest (Allison et al., 1999). More specifically, the different deflections may reflect different degrees of face recognition: a peak at 100 ms (M100) is higher if a stimulus is recognized as a face among non-face stimuli, whereas a response at 170 ms is related to the correct recognition of the identity of a face (Liu et al., 2002). This finding implies that faces are processed at different stages. The robust face-sensitive response found across studies occurs at 140–170 ms.

Many factors modulate the amplitudes and latencies of the face-sensitive responses, for instance the luminance, contrast and other features of the face stimulus. For an inverted face, the deflections in MEG signals have larger amplitudes (37% at 120 ms and 42% at 170 ms) and latencies (120 vs. 124 ms and 170 vs. 180 ms) than for upright faces (Linkenkaer-Hansen et al., 1998), possibly indicating that more effort is required for the

processing of inverted than upright faces. Interestingly, the N160 evoked response is stronger to faces that the participants rate more pleasant (Pizzagalli et al., 2002). Moreover, familiarity of a face increases the N170 response, and the influence of familiarity can extend to deflections with a latency of 250 ms (Caharel et al., 2002).

N170 and later face-sensitive deflections are affected by spatial attention, as was demonstrated in a setting where the subject was guided to attend a certain location and to ignore stimuli at other locations (Holmes et al., 2003). On the other hand, when the location of the stimuli is the same across conditions, the early deflections are unaffected by the task: the N170 response is similar, whether the face stimulus is a target or not (Carmel & Bentin, 2002; Cauquil et al., 2000). Thus, in this case the face stimulus is probably further processed to determine if it is a target and should be reacted to, whereas in the spatial attention task, the location conveys the necessary information to ignore the face.

2.4.3 Viewing eye gaze

When faces are observed, the eye region attracts the attention of the viewer more than other facial features (Janik et al., 1978). Static images of eyes evoke N170 responses comparable with the responses to faces. Nevertheless, the N170 responses to eyes presented alone peak about 16 ms later and are stronger (−5.9 vs. −3.6 μV; Bentin et al., 1996) than responses to whole faces, but other facial features shown in isolation do not elicit such N170 response. Accordingly, the neuromagnetic M170 response peaks later to eyes than to faces (200 ± 5 vs. 183 ± 2 ms), but the amplitudes are of the same magnitude in both situations (Taylor et al., 2001a).

With static stimuli, it has remained controversial whether the N170 response is affected by gaze direction (Conty et al., 2007; Taylor et al., 2001b; Watanabe et al., 2002). Also MEG responses to faces with different eye gaze directions differ only slightly (Taylor et al., 2001a). The response amplitudes in the study by Taylor and colleagues were lower to faces with eyes closed (247.5 ± 20 fT) compared with faces with eyes open (263.9 ± 17 fT).

In two MEG studies, the participants viewed eyes shifting from direct to averted gaze (“*away”*) or from averted to direct gaze (*“back”*) (Watanabe et al., 2001; 2006). Both gaze shifts—*away* and *back*—evoked responses in V5/MT, peaking on average at 160

ms. The response to the gaze shifts was located posterior and inferior to the response in the control condition, namely, to motion that was displayed in the background of the face stimulus (Watanabe et al., 2001). The locations also varied between the gaze shift conditions: the ECDs for *away* were more posterior than the ECDs for *back* (Watanabe et al., 2006). On the basis of these data, Watanabe and colleagues suggest that V5/MT has specialized sub-areas, although it generally responds to several types of motion. Further, the responses in V5/MT were stronger for *back* compared with *away* (Watanabe et al., 2006).

Puce and colleagues (1998), using in an fMRI study stimuli similar to those by Watanabe and colleagues (2001), observed activation also in the STS in addition to V5/MT. The STS activation during viewed eye gaze motion is consistent with the model of Haxby and colleagues (2000, reviewed in the previous section). The failure to detect responses to eye gaze motion in the STS with EEG and MEG might be explained by the differences in the sensitivity of the imaging techniques. However, in MEG studies the STS has been found to respond to still images of implied biological motion, for example to facial expressions of pain (Kujala et al., 2009).

The general differences in the processing of direct versus averted gaze can be interpreted by means of the behavioral implications: seeing an averted gaze can guide the viewer's attention to the direction of the gaze, whereas direct gaze creates social contact between the persons. When mutual gaze is established, gaze aversions, as well as blinks, disrupt the eye contact. If the gaze is averted, it can still remain visible, but during a blink the gaze totally disappears. Usually the disappearance is very brief, lasting about 200 ms, but in the present study also slow blinks (950 ms) are presented. Because of this slowness, the reopening might be interpreted as re-establishing of mutual gaze.

2.5 Influence of the dynamic aspects on the interpretation of facial movements and expressions

Relatively little research exists on how the perception of facial expressions changes if the expressions are presented in motion rather than in static images. Neuroimaging studies with fMRI and PET have shown that dynamical faces expressing emotions elicit stronger activation in several brain areas compared with stationary faces with the same emotional expressions (Kessler et al., 2011; Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004; Trautmann et al., 2009); these areas include V5/MT, the amygdala, the fusiform gyrus, and the STS.

Behavioral studies agree with neuroimaging studies on the importance of dynamics for the perception of facial expressions. Kamachi and collaborators (2001) investigated the effect of presentation speed on the recognition of emotional expressions from videos showing faces. The expression of sadness was better recognized from slow videos (duration 3367 ms), whereas happiness was better recognized from the videos presented at fast speed (duration 200 ms). Thus, dynamic properties are important in emotion recognition, and presentation speed can influence the interpretation of the expressions. Moreover, presentation speed has an impact on the perceived intensity of an emotional expression (Yoshikawa & Sato, 2008). When participants were shown videos of unfolding emotional expressions and they had to choose the image they thought to be the last frame of the video they had seen, they picked up images with more emotional intensity than the image that they had seen as the last one in reality. The effect was stronger at the higher presentation speed, speeds ranging from 12.5 to 100 frames per second.

Besides recognition accuracy and perceived intensity, presentation speed influences the perceived naturalness of an emotional expression (Sato & Yoshikawa, 2004). More precisely, when the videos of unfolding basic expressions were presented at the fastest speed of the four speeds, with duration of 255 ms, surprise was judged the most natural among the expressions, whereas sadness was evaluated the most natural in the slowest condition, where the duration of the expression was 2040 ms.

Krumhuber and Kappas (2005) argue that “natural” expressions do not necessarily look authentic if people are not actually feeling the emotions they are expressing. They asked

the participants rate the genuineness of different smiles, and those smiles with longer onset and offset durations but a shorter apex duration, i.e., the time the expression stays at its strongest, were judged the most genuine. This finding supported the earlier conclusions of Ekman and Friesen (1982) about the characteristics of felt smiles. In a similar study, the viewed persons were considered more attractive, reliable, and less dominant when the onset duration of their smiles was longer (Krumhuber et al., 2007). These results indicate that an authentic smile has an optimal onset, offset, and apex duration. Hence, the dynamic aspects of a facial expression are crucial for the perceived genuineness of the expression.

In the previously mentioned experiments, the dynamic aspects of the expressions had been artificially manipulated. Hess and Kleck (1990) demonstrated that the temporal characters differ also in real life depending on how the expressions are evoked. When the subjects were asked to pose an expression, its onset, offset, and total duration were of different length than in the condition that required the participants actually feel the emotion they were expressing.

Eye blink closure duration is usually related to the degree of fatigue (Stern et al., 1994), although blinks can also be slowed down voluntarily. Caffier and colleagues (2003) proposed that blinks could be monitored to measure drowsiness, because in their data sleepiness was associated with longer closing time (i.e., how long it takes to close the eyelid; 71 ± 2 vs. 63 ± 2 ms) and reopening time (187 ± 7 vs. 138 ± 6 ms). Consequently, the blinks lasted longer in drowsy versus alert participants (259 ± 7 vs. 202 ± 6 ms). Thus, it could be possible that people also perceive someone being drowsy when seeing that their blinks become slower.

3 Objectives

The aim of this thesis is to explore the following questions:

1. Do viewed eye blinks elicit measurable MEG responses?
2. If they do, which brain regions are involved?
3. How does the response to the slowly presented blink differ from the response to the normal blink?
4. Are the self-produced blinks synchronized with the viewed blinks?

An MEG response to a viewed eye blink is expected to emerge, because responses to other kinds of small visual movement have been demonstrated earlier. However, as responses to the small and quick normal blinks might elicit quite tiny responses, the blink video is presented also in slow motion to see whether the responses would then be more pronounced and clear. Since previous studies have suggested synchronization in blink timing when the subject is viewing a speaking face, the viewers are expected to blink more after seeing a blink in the video.

4 Methods

4.1 Participants

Twelve healthy volunteers with no record of neurological disorders participated in the study. However, three of them had to be excluded from the analyses because of too noisy data. Four of the included subjects were men, five women. Their ages ranged from 20 to 42 years (mean 28 years). One participant reported to be left-handed and the others right-handed. The participants signed an informed consent and they were compensated for their lost working hours and travel expenses. The experiment had a prior approval by the Ethics Committee of Hospital District of Helsinki and Uusimaa.

4.2 Stimuli

A short video of a female face with no obvious movements other than eye blink was used as the stimulus (see Figure 2). The video was presented at normal speed and slowed down by 2.6—the durations of the videos were 2720 ms for the normal-speed video and 7140 ms for the slow-speed video with blink durations[3] of 351 ms and 950 ms. The pair of normal and slow-speed videos was shown 102 times, and the presentation order within each pair of videos was randomized. After pilot measurements, the subjects reported that the viewing of the 204 blink videos had been tedious. Therefore five other videos of facial expressions were added to keep the subject less bored. Those expressions were "thinking", "agreeing", "confused", "smiling", and "disgusted". Each of them was shown only once, one expression after every 17th pair of the normal and slow blink videos. ("Thinking" was repeated once at the end of the session.) For the blink videos, the onset of the subsequent stimulus was immediately at the offset of the preceding stimulus. Only when other facial expressions (such as "thinking") were shown, a blank, gray screen appeared for 1 s before and after the expression. Due to the continuous presentation of the face and the late blink onset time—the blink started 1017 ms and 2651 ms after the video onset—any response related to the appearance of the face had most likely degraded before the blink (see

[3] A blink was considered to start when the eyelids began to move downwards and to end when the eyes were open again.

section 2.4). Thus, the responses to blinks could be examined without disturbances from the face-related brain activity.

The stimuli were acquired with a high-speed camera "Fastec InLine 1000" borrowed from the company Infradex (Vantaa, Finland). The videos were filmed in grayscale, 500 frames per second, in front of a white background. The author of this thesis performed a voluntary blink and other facial expressions while she was being filmed. Her head did not move during the filming. In the experiment, the videos were presented with the Experiment builder software version 1.10.1 (from SR Research). The frame rate was 500 frames per second in the normal-speed video and 160 frames per second in the slow-speed video.[4] The background color and luminance of the screen were adjusted to be similar to the background of the video.

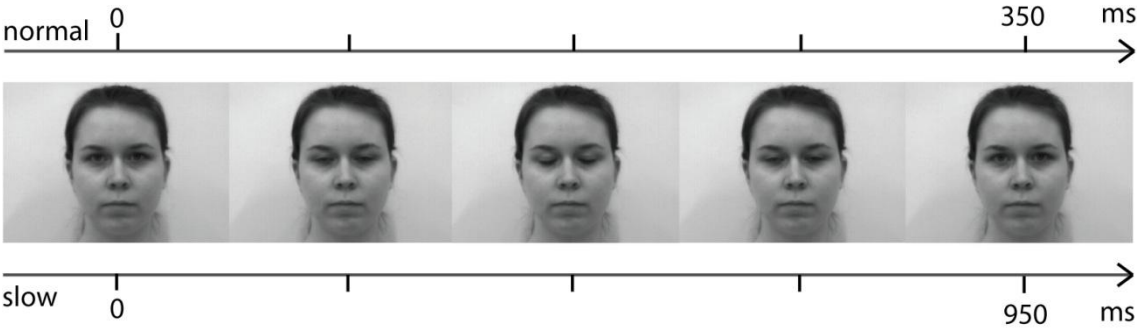

Figure 2. Example frames of the stimulus video. The timelines illustrate the durations of the normal and slow blinks.

4.3 Data acquisition

MEG signals were recorded with a whole-scalp neuromagnetometer (Elekta Neuromag Oy, Helsinki, Finland). The system contains 306 sensors: a magnetometer and two orthogonal planar gradiometers within each of the 102 elements. The signals were bandpass-filtered to 0.03–200 Hz, digitized at 600 Hz, and averaged online time-locked to the blinks in the videos. The analyzed period extended from –500 ms to 1000 ms (normal) or to 2400 ms (slow), the blink starting at 0 ms. All trials were included in the online averages.

[4] Nevertheless, showing 500 frames per second was not feasible due to the software and video projector restrictions, and all the frames were not shown. Despite that, the speed of the video was as fast as intended and it looked smooth and natural.

Before the MEG measurement, EOG electrodes were placed above and below the left eye to record vertical eye movements, and on both sides of the eyes to record horizontal eye movements. Four head position indicator (HPI) coils were attached to the scalp of the subject, and personal head coordinates were registered with a 3D digitizer by identifying the locations of the HPI coils together with the locations of three anatomical points (nasion and bilateral preauricular points) and some additional points on the scalp. In the beginning of the recording, small currents were led through the HPI coils, and the head position with respect to the sensors was determined from the produced field patterns.

It was ensured that the subject did not wear anything magnetic. The subject was seated in the magnetically shielded room (Euroshield Ltd., Eura, Finland) of the MEG Core, Brain Research Unit, Aalto University, with the head inside the helmet containing the sensors. The screen (width 72 cm, height 54 cm) displaying the projected stimuli was placed 1 m in front of the subject's eyes, and the size of the face in the video was approximately 14 x 20 cm (visual angle 11.5° x 8.0°). The subject was instructed to sit still and relaxed and to observe the facial expressions attentively, keeping in mind what kind of expressions were shown. Nothing was mentioned about eye blinking. The presentation lasted 20 min in total.

After the experiment, the participants were asked to tell which expressions they were able to recall. However, the free recalling task turned out too frustrating. Therefore all except the first three subjects were provided with a list of ten possible expressions among which they had to pick the ones they had seen. They marked the remembered order of the videos with numbers. The instructions and the information before the measurement were the same for all the twelve subjects, and thus the additional memory task after the measurement was not supposed to affect the recorded brain responses.

4.4 Data preprocessing

The MEG data were preprocessed with the temporal signal-space separation method (tSSS)(Taulu & Simola, 2006; Taulu & Hari, 2009) using MaxFilter^{TM} software (version 2.2). The procedure enhanced the signal-to-noise ratio of the data by suppressing the effects of artifacts. It also reduced the effects of malfunctioning channels (2 or 3 per measurement) by replacing their signals with a signal estimated on

the basis of the other channels. Additionally, the signals were lowpass-filtered at 10 Hz for the sensor-level analysis and at 30 Hz for source modeling.

Baseline period was defined as 500 ms before the blink onset in the video so that the face without movement was visible during the baseline period. Other baseline periods (from 200 to 1000 ms) were also tested, but changing the baseline did not visibly affect the results.

The intrasubject reliability was tested visually for each subject: the averaged waveforms of the first half of the recording were superimposed (with Elekta Neuromag Xplotter software, version 4.8) with the waveforms of the second half of the recording. The idea was that if the subject's responses gathered in the beginning were similar to those gathered in the end, the data would be reliable.

For three subjects who had more than 45 blink-free epochs in both conditions, the analysis was also performed without the trials during which the subject had blinked (defined as trials in which the vertical EOG exceeded 250 μV). However, the results were not visibly changed after the rejection. After this, it was decided that not to lose any data, no trials should be rejected because of self-performed blinks.

4.5 Analysis

4.5.1 Sensor-level analysis

Sensor-level waveforms were analyzed from the planar gradiometers. The apparent change in the magnetic field that is visible in a single gradiometer varies according to the orientation of the source current; for a current of a given magnitude, the planar gradiometer can detect a large deflection or no deflection at all depending on the orientation of the current. For the purpose of covering all possible orientations, the applied MEG device has two orthogonal gradiometers at each sensor position.

To minimize the effect of current orientation on the analyzed waveforms, vector sums were calculated for each pair of gradiometers: the signals of each gradiometer pair were squared and summed together, and a square root was computed out of the sum. The vector sums with the strongest peaks at about 300 ms for the normal-speed blinks and at 400 ms for the slow blinks were included in the analysis. The selected locations were mainly over the occipito-temporal areas of the right hemisphere (see Figure 7). Two

subjects in the normal-speed condition and three subjects in the slow-speed condition had stronger responses over the left hemisphere and therefore their channels were chosen on the left side. The strongest peak amplitude for each waveform and its latency with respect to the blink onset in the video were measured. A paired, two-tailed t-test was used to test the statistical significance of the differences between the normal-blink and slow-blink conditions.

Additionally, the durations of the statistically significant responses, here called *return-to-baseline durations* (Figure 3), were measured. The return-to-baseline duration expresses the amount of time that the activation stays stronger than two standard deviations from the baseline. Standard deviation was calculated on the basis of the values within the 500-ms baseline prior to the blink in each video. Also the mean amplitudes of the return-to-baseline durations were examined.

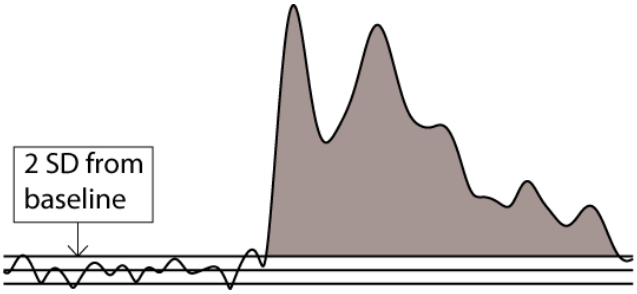

Figure 3. The gray area marks the return-to-baseline duration, i.e., the duration of the response more than 2 SD above the baseline.

The same analyses were also performed for single channels without vector sums. Again, the channels showing the most prominent responses were selected, but these channel locations slightly differed from those obtained in vector sum analysis.

4.5.2 Source modeling

The current sources of the evoked responses were modeled as ECDs in a spherical head model. Only planar gradiometers were used, and 40–50 channels were selected at a time; the resulting goodness-of-fit values (*g*) expressed how well the ECD explained the data (100% would mean a perfect fit). Anatomical MR images were available for 6 subjects. The estimated ECDs were superimposed on the MR images of these subjects so that the anatomical locations of the ECDs could be identified.

4.5.3 Self-performed blinks

To examine whether the timing of the self-performed blinks varied in accordance with the viewed blinks, each subject's self-performed blinks were counted from the EOG recordings. A blink was defined to occur when the vertical EOG exceeded the threshold value for the period of at least 10 and at most 300 data points (from 17 to 500 ms with the 600 Hz sampling rate). The threshold value was set as 150 μV. We checked visually that the noise level of the EOG never exceeded the threshold value but that all peaks resulting from complete eye closure were included in the calculation. A new data set was created, where a square wave of 100 ms in duration was drawn at each time point of a self-performed blink onset. For each subject individually, the square waves indicating blinks were summed according to the stimulus onset, in a similar way than in time-locked averaging. The resulting figure showed how many times the subject had blinked when viewing a particular epoch of the stimulus video.

Since the general blink rate varied considerably between subjects, the number of blinks at each time point was normalized for each subject by dividing it by the total number of times the participant had blinked during the whole experiment, which resulted in a curve of blink *proportions.* The normalized blink proportion curves were then averaged across subjects. After normalization, it was more plausible to compare the subjects with each other, and the data of a single subject did not affect the group sum excessively. However, the data of one subject had to be left out from the sum, because the subject had blinked so rarely that the relative impact of a single blink was disproportionate.

The mean proportions of self-performed blinks within time windows were compared with the baseline. The baseline was set as the mean during 100 ms (normal) or 200 ms (slow) from the viewed blink onset. The normal-speed condition had 13 time windows of 100 ms, beginning at the end of the viewed blink, whereas the slow-speed condition had 6 time windows of 200 ms. The altogether 19 t-test results were corrected with the Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995).

Moreover, the MEG signals related to self-performed blinks were analyzed. First, the self-performed blinks were obtained from the EOG with the same threshold values as in the blink-rate analysis. The MEG signals were then averaged time-locked to the blinks. The resulting waveforms were inspected and the sources modeled with ECDs.

5 Results

5.1 Behavioral recall of facial expressions

The seven participants who completed the questionnaire remembered on average 4.3 expressions (out of the six right ones with five false alternatives) that were really shown, but they also reported to have seen on average 0.9 expressions that were not actually shown. All participants recognized a smiling, a disgusted, and a thinking face. The confused expression was chosen by five, and the agreeing one by two participants.

5.2 Overview of MEG data

Both normal- and slow-speed viewed blinks elicited clear brain responses. The intrasubject reliability plots indicated that the reliability was good for the channels with the most prominent responses. Figure 4 shows channels from subject S1. The three subjects whose data were noisy had also poor intrasubject reliability, which supported the exclusion of their data.

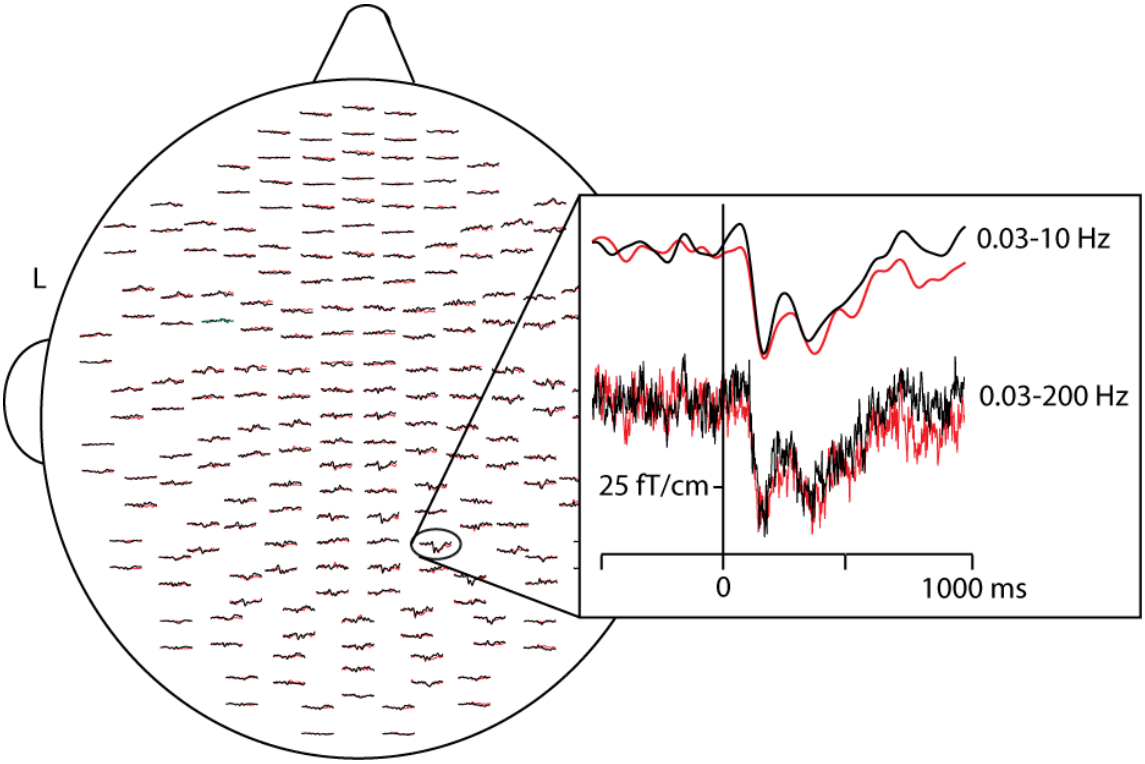

Figure 4. Intrasubject reliability of MEG responses in Subject S1 to the viewed normal-speed blink. A flattened view of the sensor helmet with pairs of planar gradiometers is seen from above; L stands for left. The first half (black waveform) and the second half (red waveform) of the averaged responses are superimposed. The blink in the video started at 0 ms. On the selected channel the response was the most prominent.

Figure 5 shows averaged responses from subject S4. This subject had salient responses with one clear peak on the occipito-temporal channels in both hemispheres and smaller deflections also on parietal channels. In contrast, some of the subjects (as S1, see Figure 4) had two subsequent peaks in their strongest responses. Although the responses varied largely between the individuals, prominent responses were observed in all subjects in the occipito-temporal cortex of either hemisphere.

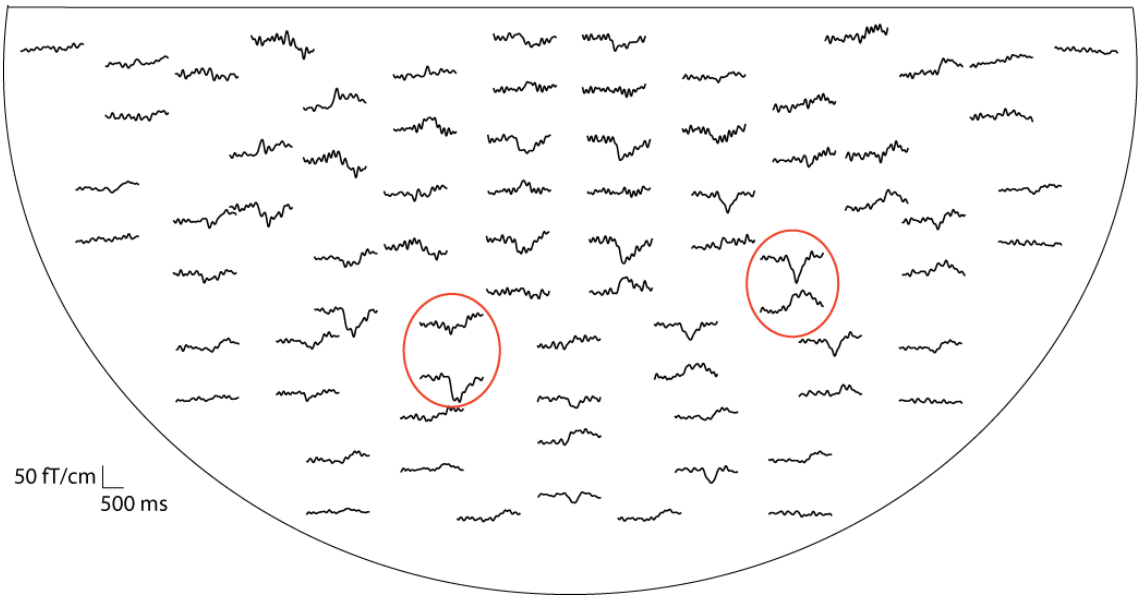

Figure 5. Planar gradiometers showing the averaged responses to the viewed normal-speed blinks in subject S4. The posterior part of the head is viewed from above of the head. The red circles indicate the gradiometer pairs showing the most prominent responses.

5.3 Sensor-level analysis

Figure 6 shows the chosen vector sum waveforms, and the helmet-shaped sensor array in Figure 7 illustrates the locations of the chosen sensors, which were mainly in the occipito-temporal areas. The response amplitudes rise rather steeply after the viewed blink onset and return to baseline shortly after the viewed blink offset.

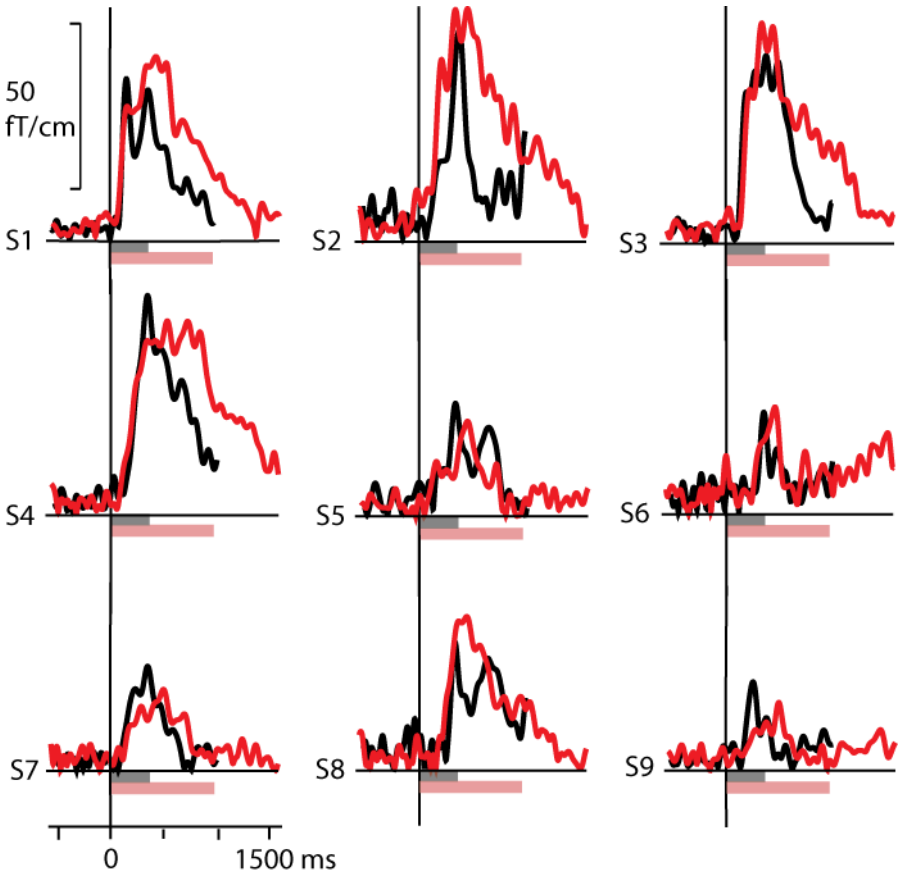

Figure 6. Waveforms from the individually selected vector sums of planar gradiometers for each subject (S1–S9). The responses were averaged with respect to the beginning of the viewed blink indicated by the vertical line. Black curves are for the normal-speed blink, red curves for the slow-speed blink. The horizontal lines mark the zero level. The gray bars indicate the duration of the viewed normal-speed blink, and the red bars stand for the duration of the slow blink.

Figure 7. The sensor locations on the helmet-shaped arrays viewed from the back of the head. The numbers indicate how many subjects had the selected vector sum (of a gradiometer pair) at a given location. The locations differ between normal-speed and slow-speed conditions, because the most clear and prominent responses were chosen individually.

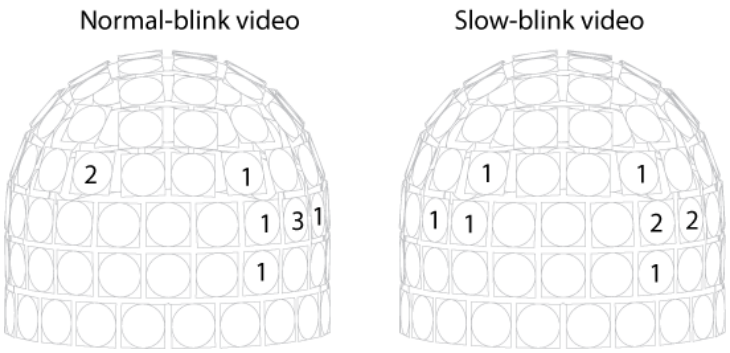

Figure 8 illustrates the peak latencies and amplitudes. The vector sum waveforms in response to the blink in the normal-speed video peaked at 317 ± 22 ms (mean ± SEM), thus earlier than those to the blink in the slow video [445 ± 19 ms; paired t-test, $t(8) = 4.55$, $p = 0.002$]. Peak amplitudes did not differ significantly between the normal (44 ± 5 fT/cm) and the slow (45 ± 6 fT/cm) blinks [$t(8) = 0.32$, $p = 0.76$].

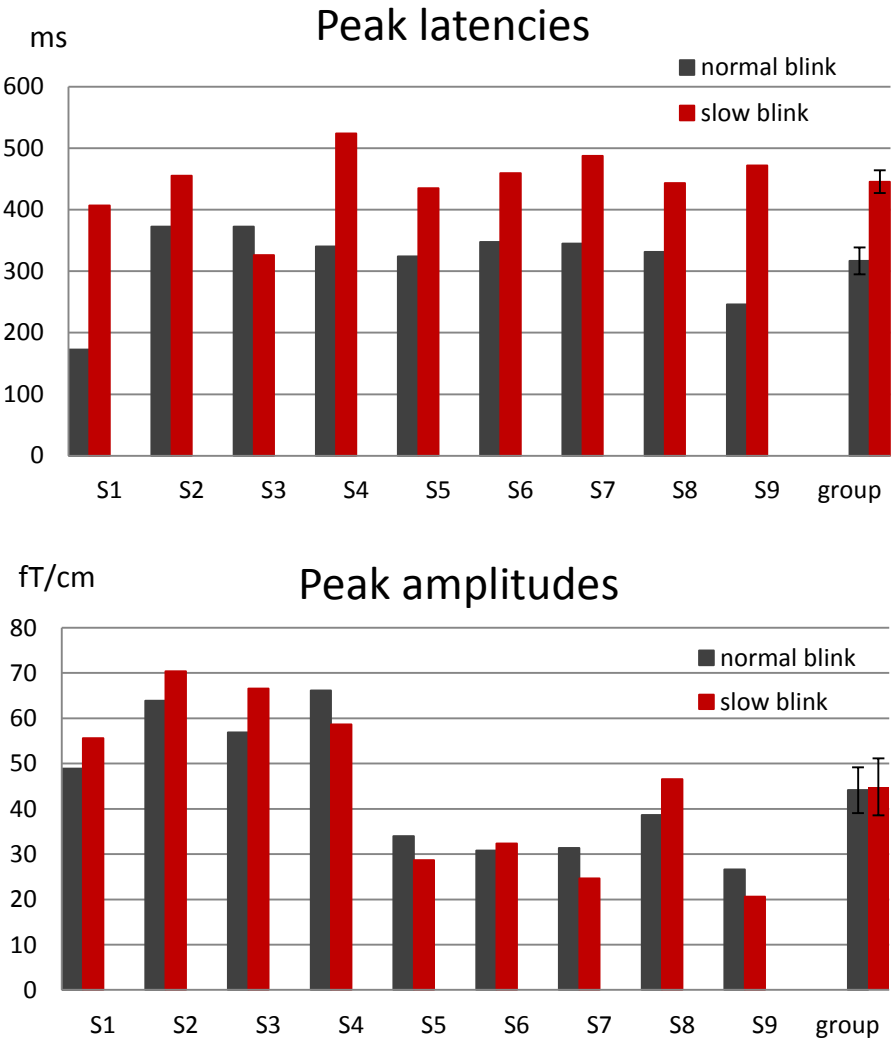

Figure 8. Peak latencies (above) and amplitudes (below) in the selected vector sums for all subjects (S1–S9) for normal-speed and slow-speed conditions. The ”group” bars show the mean (± SEM) over subjects.

Figure 9 shows the return-to-baseline durations for the responses to normal and slow blinks. The activation returned to the baseline earlier for normal blinks (537 ± 83 ms) than for slow blinks [921 ± 155 ms; $t(8) = 3.52$, $p = 0.008$]. However, the mean amplitudes of the return-to-baseline periods (normal: 21.4 ± 2.4 fT/cm; slow 21.6 ± 3.1 fT/cm) did not significantly differ [$t(8) = 0.23$, $p = 0.82$]. The response onset times (i.e.,

the time points where the waveform exceeds two SDs) did not significantly differ between the conditions, either: the onset of the response to normal blinks was on average at 165 ± 24 ms and to slow blinks at 136 ± 24 ms [$t(8) = 1.73$, $p = 0.12$].

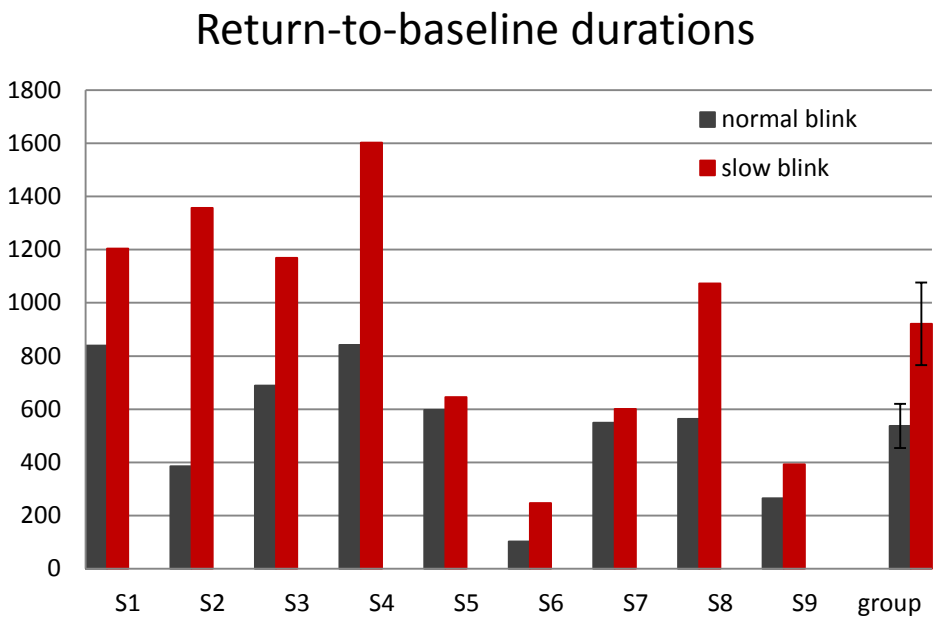

Figure 9. Return-to-baseline durations for the selected vector sum of each subject in normal-speed and slow-speed conditions. ”Group” bars show the mean (± SEM) over the subjects.

The single channel analysis without creating vector sums yielded substantially similar results concerning response latencies, amplitudes, and return-to-baseline durations. Only the latency difference between normal and slow speed was slightly smaller (110 ms) than with vector sums (128 ms), but the difference was still significant.

5.4 Source modeling

Figures 10 and 11 show the locations of the ECDs in two subjects. Despite the substantial variability across subjects, the most common locations for a dipole in the normal-speed condition were the middle occipital lobe (six out of nine subjects) and the right temporal lobe (five subjects). Some of the dipoles fitted for the data in the normal-speed condition were also able to explain the field patterns in the slow-speed condition. However, the slow-speed condition also yielded field patterns that an ECD could not explain, particularly in subjects S4, S5, and S7. Table 1 shows the *g*-values and confidence volumes of the best fitting dipoles for each subject in both conditions.

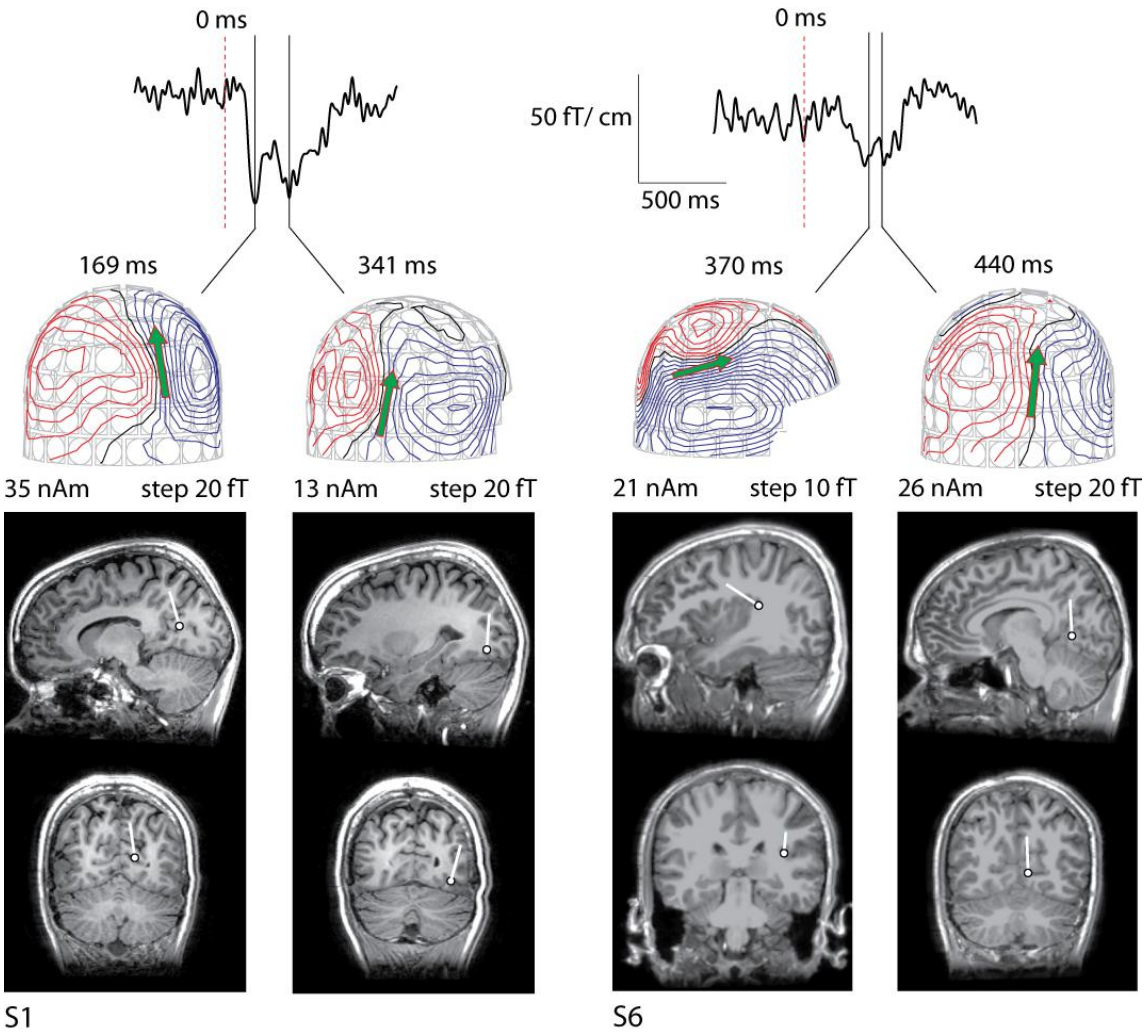

Figure 10. The ECDs for two subjects (S1 and S6) in the normal-speed condition. The waveforms were taken from those single gradiometer channels that had the most prominent responses. The black vertical lines indicate the time points at which the dipoles were fitted (for instance, the first dipole of S6 is at its strongest 370 ms after the onset of the viewed blink). The field patterns are shown on the helmet-shaped sensor array, where the green arrow represents the ECD, and the isocontours indicate the magnetic field (red: out, blue: in). The dipoles were superimposed on the subject's own 3D MR images (sagittal and coronal view shown here). The circle is at the location of the source and the white bar points to the direction of the estimated ECD.

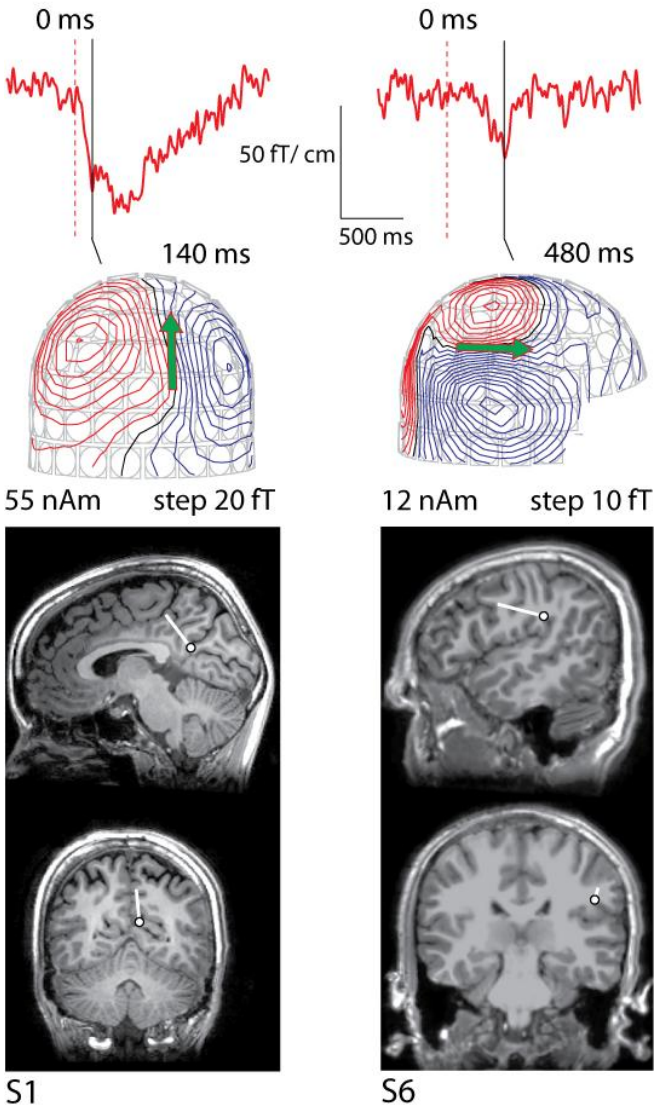

Figure 11. Dipole models for subjects S1 and S6 in the slow-speed condition. Contrary to the normal-speed condition, only one plausible source (instead of two) for each subject could be estimated.

Table 1

Goodness of fit - values (%) and confidence volumes (mm^3) for the best fitting dipoles

	condition			
Subject	normal		slow	
	g-value	volume	*g*-value	volume
1	94.1	239.7	92.9	723.0
2	91.7	227.6	97.6	161.4
3	97.6	286.3	97.5	567.0
4	69.6	174.7	87.8	113.0
5	72.6	2357.7	82.6	1116.3
6	93.7	824.7	91.8	3206.7
7	88.8	1961.8	80.7	4826.3
8	88.6	590.9	94.8	344.6
9	88.7	4918.5	89.9	9849.2

40–50 channels were selected at a time, and the dipoles which best explained the variation within those channels are reported here. In the normal condition, four ECDs have a g-value higher than 90%, whereas in the slow condition, five ECDs are with g-values over 90%. The confidence volume values show the size of the volume where the dipole is located with a probability of 95%.

5.5 Timing of the self-performed blinking

Figure 12 presents the proportions of self-performed blinks (i.e., what percentage of the total number of blinks occurred at each time point with respect to the viewed blink). The average blink rate is presented as proportions, because blink rates varied considerably across subjects. The baseline in the normal-speed condition was 3.3% and in the slow condition 1.1%[5]. For the normal speed, the mean blink proportion was 2.2 percentage points higher than the baseline during the time window 651–750 ms after viewed blink onset ($p < 0.05$). For the slow speed, the mean blink proportion was 0.8 percentage points higher than baseline during the time window 1350–1550 ms, but the difference (for the slow speed) was not statistically significant when the p-values were adjusted for multiple comparisons. Moreover, the Figure 12 shows that the blink proportions in normal and slow conditions seemed to peak also before the viewed blink onset.

[5] The baselines did not significantly differ from the means during the whole viewed blink (3.1% for normal and 1.1% for slow).

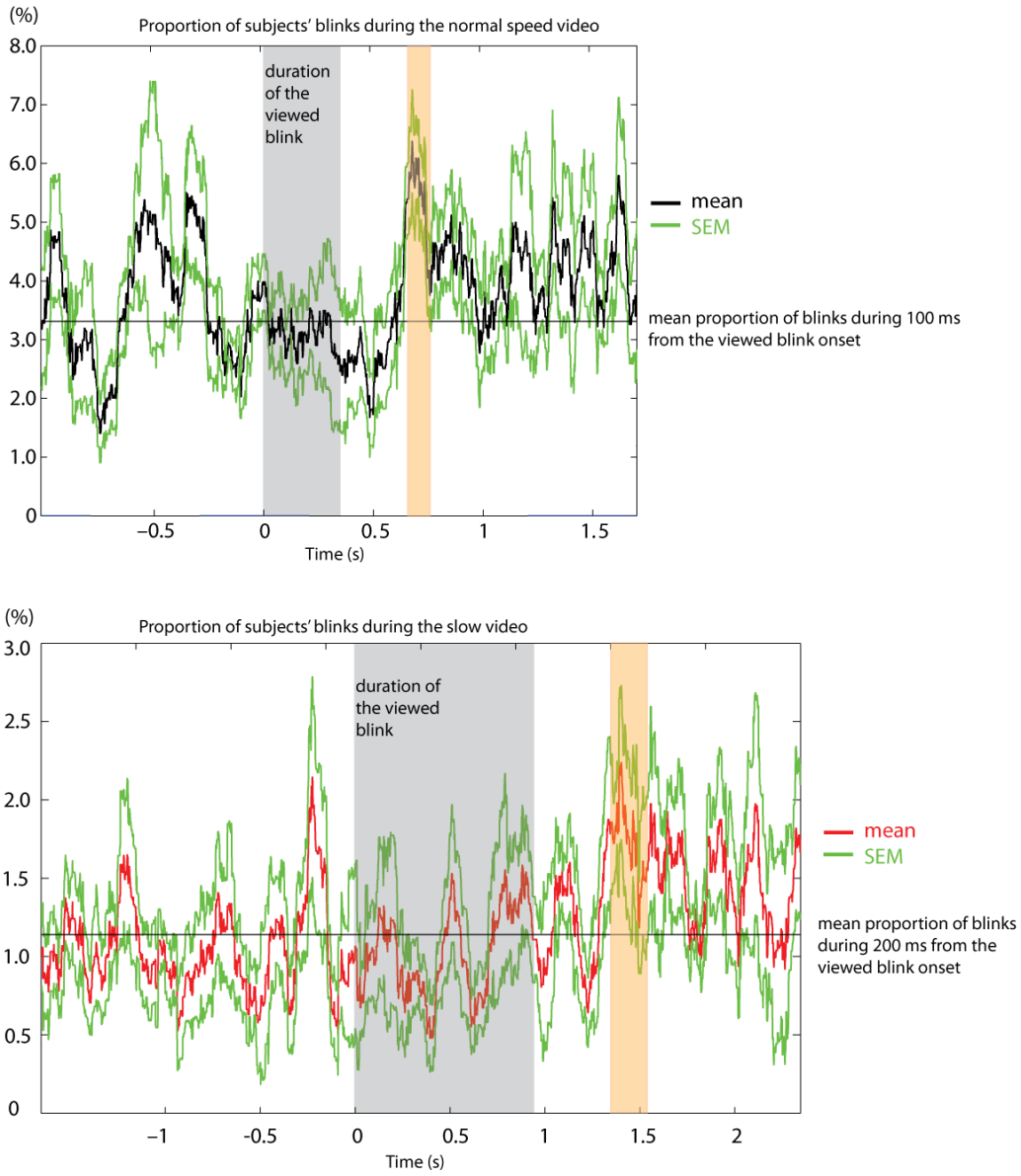

Figure 12. The proportion of self-performed blinks for the normal-speed video (above; black curve) and the slow video (below; red curve). The green curves show SEM above and below the mean. The gray band extends over the time period between the onset and offset of the viewed blink. The horizontal line indicates the baseline. The light red band indicates the time window where the difference from the baseline was the greatest.

5.6 MEG responses to self-performed blinks

Since the timing of self-performed blinks was significantly affected by the blink in the video, the question arose whether the eye-movement-related artifacts in the MEG signal could have confounded the actual results. First of all, self-performed blinks caused no changes in the signal before the onset of the self-performed blink. Source modeling yielded a three-dipole model: the first two dipoles appeared very shortly (around 40 ms) after the blink onset at the orbits and the third with a latency of 200–300 ms in the posterior parietal cortex.

For each subject, the averaged MEG responses to the *viewed blinks* were also visually compared with the vertical EOG waveforms averaged by the viewed-blink onset. The peaks in the MEG waveforms had no systematic relationship with the peaks in the EOG data, which suggested that the self-performed blinks (peak in the EOG averages) did not substantially affect the MEG signals of interest.

6 Discussion

The aim of this study was to investigate using MEG how the brain reacts to seeing eye blinks. The responses to viewed blinks were prominent. Contrary to the expectations, the strength of the response did not differ between the two stimulus conditions (the normal-speed blink video vs. the same video in slow motion). However, the peak latencies and return-to-baseline durations were significantly longer when viewing the slow blink. Although the source locations varied between individuals, the sources were mainly located in the occipito-temporal cortical areas. As expected, the participants tended to blink more after seeing a blink when compared with the average blink rate during the blink in the video. The results will now be discussed in more detail.

6.1 Behavioral recall of facial expressions

The purpose of the behavioral task was to increase the subject's attention towards the face stimuli and to check whether they had been focusing on the videos. Some subjects still reported boredom and fatigue after the measurement, but with the additional expressions the experiment was less monotonous. The recall rates are challenging to interpret, because the subjects might have verbalized the "confused" and "agreeing" expressions in a manner differing from the verbalization in the questionnaire. Namely, the "surprised" option was chosen by three participants, which may indicate that they

had perceived either the intended ”confused” or the intended ”agreeing” as surprised. Anyhow, the participants seemed to have looked at the videos throughout the measurement, since all participants had recalled at least three expressions out of five.

6.2 Brain responses to viewed blinks

Considering that an eye blink is such a small event, it was uncertain before the current study whether a brain response to it would be detectable with MEG. No previous data on the topic were available while planning and conducting the present experiment, because at the time of our MEG measurements, Brefczynski-Lewis and colleagues (2011) had not yet published their study about EEG responses to viewed eye blinks. Nevertheless, responses to simple light dot motion (slowest speed 0.4°/sec) had been observed with a stimulus duration of 10 ms only (e.g., Kawakami et al., 2002) and therefore eye blinks, lasting around 350 ms at normal speed, were assumed to elicit observable responses. Since the visible peaks in the waveforms result from averaging of about a hundred responses to the same blink video, the neural process that is captured is probably an automatic mechanism of observing a blink rather than more demanding, higher-order cognitive processing.

Contrary to the earlier evidence showing that the response amplitude increases with the speed of the moving stimulus (Kawakami et al., 2002), the response amplitudes for the slow blink were of the same magnitude as the amplitudes for the fast blink. However, the experiment of Kawakami and colleagues was done with simple dots as stimuli, whereas in the current experiment the stimuli were blinks. This suggests that blinks might be more important than just simple motion. On the other hand, the peak latencies were longer when seeing slow blinks, which was consistent with previous MEG studies where simpler stimuli, such as moving dots (Kawakami et al., 2002; Maruyama et al., 2002) or sinusoidal gratings (Wang et al., 2003) were presented with varying speeds. It had not been previously studied how slowing down blinks or other facial motion affects the neural responses of the viewer. From a subjective point of view, slowing down the blink results in an impression of “suspension”; the viewer wonders why it is taking such a long time for the viewed person to close and open her eyes.

Not only the peak amplitudes occurred considerably later in the slow-speed condition, but also the activation returned to baseline slower. Possibly, the responses to single trials have followed the stimulus pattern in duration. An alternative explanation for the

longer averaged responses is that the single trial responses to the slow blink were more widely scattered, resulting in an average waveform without a steep peak. Therefore slowing down the stimulus does not necessarily render the data analysis more straightforward. On the other hand, this finding about longer responses can be useful when studying brain responses that might be too fast to be reliably discerned. This can be the case for instance with small conversational expressions, which contribute to the discussion but might stay in a tiny scale compared with other factors influencing the brain signals. Slowing down the stimuli might then facilitate the detection of the brain activation.

In some cases the response to blinks peaked twice (e.g., at 170 ms and 340 ms for S1). However, only the peak with the strongest amplitude was selected for the analysis of latencies and amplitudes, because this criterion made the selection unambiguous. The present data did not allow the comparison of separate deflections in the waveforms (as in Brefczynski-Lewis et al., 2011). Namely, saying that a small peak in the waveform of a given subject is an "M450", for instance, would have been rather arbitrary labeling.

The vector sum analysis was the principal method used here. Although the results did not change substantially when analyzed with single channels only, vector sum analysis yielded more robust and reliable results. This robustness is understandable also on theoretical basis: creating vector sums is a means to remove the orientation information that might otherwise cause ambiguity in the responses.

6.3. Source locations

The most prominent responses to viewed blinks were observed in the occipito-temporal cortical areas, mainly in the right hemisphere. This finding is consistent with the recent EEG study by Brefczynski-Lewis and colleagues (2011). Although the source locations varied substantially between the subjects, the sources were typically situated within the occipital, visual areas and the sulci of the right temporal lobe.

When the normal blink was shown, the earliest source—with a latency of approximately 350 ms— was often located in the temporo-parietal area, close to V5/MT (e.g., in subject S6, see Figure 10). This is in accordance with the earlier finding that the responses to rapid visual motion may peak earlier in V5/MT than in V1, whereas slower motion elicits activation first in V1 (Ffytche et al., 1995). However, in addition to the

responses at 350 ms, one would have expected to find also an earlier response at 170 ms (Brefczynski-Lewis et al., 2011). The question remains open why it emerged only in one subject (S1).

According to Brefczynski-Lewis and colleagues (2011), many kinds of eye movements, including blinks, elicit similar N170 responses, but later ERP deflections are smaller for blinks than eye gaze diversions. Thus, those later deflections would better distinguish blinks from other eye movements. Most subjects in the present data demonstrated only one clear peak (around 350 ms), and for this reason the analysis did not distinguish between separate response deflections. In dipole fitting, the most prominent source was modeled first and other sources after this when possible. Figure 10 shows the dipole models for two subjects who actually had two clearly distinct sources at different time points.

As a disadvantage, ECDs were not able to explain all of the current data. Although many *g*-values in the Table 1 appear high, they do not prove the dipole model valid. Especially in three subjects in the slow condition the field pattern did not look dipolar at all—therefore it was questionable to try to model the responses as ECDs. Additionally, the estimated sources had in some cases rather deep locations. Since MEG and especially planar gradiometers are not very sensitive to deep sources, these estimates appear quite unreliable. Besides, dipole fitting can produce too deep and strong estimates if two sources lie side by side (Okada, 1985). The relatively large confidence volumes (> 1000 mm^3) in Table 1 also show that many of the dipoles are unreliable. Due to these difficulties and the intersubject variation, comparing the dipoles statistically was not plausible (otherwise a test comparing the strengths, locations or latencies of the dipoles in the normal and slow condition could have been made).

Those complicated field patterns possibly reflected activation originating from several sources which were difficult to differentiate because they were simultaneously activated. Thus, analyzing vector sums turned out to be more reliable than dipole fitting in this study—when analyzing vector sums, all activations within a certain area are assumed to be summed together, whereas ECDs are supposed to model single, uniform sources. In conclusion, since dipole fitting was not very suitable for analyzing the present data, the vector sum results are more emphasized in this study.

6.4 Self-performed blinks

As expected, the subjects blinked more after seeing the blink than during the blink in the video. They might have "responded" to the observed blink by blinking themselves; namely, in a listening situation, the listeners' blinks are somewhat synchronized with the speakers blinks (Nakano & Kitazawa, 2010). Alternatively, they might just have suppressed their blinks during the viewed blink, because it was the only event in the whole video and they sought not to miss it. The latter explanation can be supported in the light of studies where blink rate decreased when something important was happening (e.g., Nakano et al., 2009). Since the same video was repeated about 100 times in the current experiment, the participants may have learned to anticipate the upcoming blink. This learning effect could explain why the subjects' blink rate peaked also before the viewed blink. In the slow-video condition the blinking pattern was not so clear, probably because it would have been difficult to suppress blinks during the whole event and because the timing of the slow blink was more difficult to predict.

As most of the subjects did not seem to have a distinctive increase in blinking after the viewed blink in their individual data, the peak in blinking in the average curve might result from synchronized blinking between the subjects at the particular moment. The average curve thus showed that the subjects were more likely to blink approximately 700 ms after seeing a blink.

Self-performed blinks were related to activation in the posterior parietal cortex. Hari and colleagues (1994) had observed a similar effect, although they had measured voluntary blinks whereas in the current study the participants blinked spontaneously. Consequently, one has to be aware of the problem about the inclusion of the trials during which the subject has blinked. Namely, sometimes the change in the magnetic field caused by the subject's blinking can be of a greater magnitude than the response of interest.

Regardless of the risks, all the trials were included in the analysis for the following reasons: In the current study the subjects were not instructed to avoid blinking during stimuli, because we also sought to examine the natural timing of self-produced blinks with respect to the viewed blink. As a result, some of the subjects blinked so frequently—about 60 times per minute—during the periods included in the averages

that an excessive number of data should have been excluded if the trials containing blinks had been rejected.

The inclusion of all trials is also motivated by the finding that the activation related to the possibly systematic blinking always occurred later than the actual response to the viewed blinks. Namely, the peak of self-performed blinks occurred around 700 ms, whereas the MEG responses to the viewed normal-speed blinks peaked always within 400 ms after the viewed blink. What is more, the number of trials summed up in one average was considered sufficient in the sense that those blinks that occurred randomly should not have distorted the results. In fact, the rejection of the blink-contaminated trials for the subjects who did not blink excessively did not affect the averaged waveforms substantially.

6.5 Caveats

The current study adopted an explorative approach towards a novel topic. Therefore the experimental procedure would require some improvement before reliable conclusions can be made. First, the number of subjects was limited, especially because the data of some of the subjects had to be excluded from the analysis. Second, the experimental setup could have been enhanced by a control stimulus. Lacking other types of motion for comparison, one cannot directly conclude that the elicited responses were selectively typical of blink viewing processes. It remains unclear whether other eye movements, facial movements or any motion with corresponding velocity and duration could have caused similar brain activation. Moreover, the presentation speed was not implemented exactly as it should have been, because the projector was not able to display 500 frames per second. On the other hand, the high frame rate allowed smooth slow motion presentation. The normal speed blink turned out rather long—350 ms—compared with the average blink duration of 200 ms, but that might have also been due to the voluntary nature of the videotaped blink (Kaneko & Sakamoto, 1999).

Since the responses varied substantially between the subjects, average waveforms or general dipole models would not have been plausible. The lack of consistent response patterns across subjects also makes it difficult to draw precise conclusions concerning general reactions to viewed blinks. Nevertheless, people are not similar in other respects, either, and other studies on brain responses to facial stimuli have also demonstrated individual variation (Susac et al., 2010).

The intersubject variation could be partly explained by differences in attention. Namely, attention influences the perception of visual motion (Raymond, 2000), and the amplitudes of neural responses increase when a stimulus is attended whereas the latencies or spatial distribution of the responses should not be affected by attention (Luck et al., 1994; Luck & Hillyard, 2000). Besides, the task assigned to the subject can guide their attention. In the current study, the task was perhaps too loosely defined; the subjects were instructed only to view the videos and to keep in mind the presented expressions. Nothing was mentioned about blinking or the nature of the videos (except that the videos would show faces with expressions). Thus, the subjects might have interpreted blinking as an expression, or they might have ignored the blinks because the blink video did not contain any "expression" and the task was to memorize facial expressions in particular. Additionally, the attention of the subject obviously decreased when they saw the same blink video a hundred times. [6]

Concerning the reliability of the sensor-level analysis, it might have been a risk to choose different channels for different subjects. For several subjects the selected channel was different also for normal and slow blinks. On the other hand, in this way it was possible to find something comparable in each subject despite the variation. It would not have been reasonable to select the same channel for each subject, because one subject could have no response on a channel where another subject had the most prominent response. Additionally, in some subjects the right hemisphere was more active, whereas in other subjects the activation was mainly in the left hemisphere. Nevertheless, head position normalization was not done, and head position differences among subjects might account for varying response amplitudes in certain sensors or vector sums. But after all, responses to normal and slow blinks were compared within individuals, not between individuals, and therefore normalization between subjects was less important. In the experimental setting normal and slow blinks were always shown in pairs; consequently, the head position of a given subject should have been adequately similar when viewing normal versus slow blinks.

[6] However, according to the intrasubject reliability check (section 3.4), the responses were sufficiently constant also during the latter half of the experiment.

6.6 Suggestions for further research

Now that we have demonstrated a response to a viewed blink in a simple, reduced setting, it would be interesting to see if the effect is robust also in more natural and ecologically valid conditions. In the current study, the video appeared stagnant and monotonous because it contained no other motion than the blink and because it was filmed in grayscale. In contrast, in our daily lives we usually interact with more lively persons. A step forward would be to show a video of a natural discourse of an actor with blinks occurring unintentionally. The story of the speaker would involve the listener and the video would be more interesting to follow than the previous one. The blinks would not be isolated as in the current video, because other motion would also be present.

To precise the current results, it would be important to create control stimuli. A suggested control stimulus could be the same face with other kind of motion than blink in the eye region, e.g., eye gaze shifts or moving dots replacing the eyes or even a moving background (examples of control eye movement in Watanabe et al., 2001). However, the face in the stimulus might give too strong an implication of eyes and blinks even if no eyes were visible. For that reason, simple eye-sized bars moving down and up could form a better control video. If a freely talking face is shown, blink timing could be artificially changed to see if the blinks of the listener follow the blinks of the speaker, or whether they are paced by something else, say, the course of the speech.

To expand the current knowledge on social interaction, it would be useful to investigate the responses to other small expressions. Quite many studies have addressed basic emotions, but conversational expressions have not received much attention. Cunningham and Wallraven (2009) demonstrated that dynamic conversational expressions are easier to classify than static, but the question remains how those expressions are processed in the brain. Other presentation speeds for the expressions—quicker or slower—could also be tested to explore the impact of dynamics.

When using visual stimuli, it would be fruitful to measure gaze direction with an eye-tracker together with MEG signals. Gaze direction can affect MEG responses, depending on whether the subject gazed the eyes when a blink occurred or whether the subject looked at the smiling mouth of the viewed person, for example. Nevertheless, eye tracking does not tell everything about the subject's attention, since attention can be

directed covertly, which can in turn affect the neural responses to a given stimulus (Luck et al., 1994).

Direct gaze is a rather strong signal, and even the face-sensitive N170 response is stronger when the eyes are staring directly at the viewer (Conty et al., 2007). In the current study, the viewed person was looking straight at the camera. A blink or gaze shift thus disrupts the mutual gaze between the blinker and the viewer. It remains open whether the brain response would change if the other person was looking in another direction while blinking. Further, Hietanen and collaborators (2008) found that direct gaze has a more powerful effect if the subject is viewing a real person rather than a photograph or a video. Also Pönkänen and colleagues (2008) compared live faces and photographs and suggest that the early processing of a live face differs from the processing of a face in a picture. It is an interesting question whether blinks, as well, would evoke different reactions if observed in a live person. A live person is potentially an interacting partner unlike a photograph or a video, and this distinction is relevant when seeking to address real social interaction.

The current experimental setting was not primarily designed for measuring the timing of self-performed blinks or synchronization between the viewed blinks and self-performed blinks. Since the reported preliminary results are promising, the possible synchronization of blinks would be worth investigating more thoroughly. If synchronization exists, it evokes the question of who is following whom. If the acts of the viewed person are fixed as in the current stimuli, the direction of the relationship cannot be examined. But a study with two participants interacting could reveal the leader of the blink timing, should there be one.

6.7 Conclusion

Viewed blinks elicited clear brain responses in the occipito-temporal cortex, which has not been previously reported with MEG. The peak latencies were longer for the blinks presented in slow motion, whereas the amplitudes did not differ between the slow-speed and normal-speed conditions, although slower movement has previously been associated with lower peak amplitudes. The viewers also increased their blinking right after the blink had occurred in the video. Combining these results with the earlier findings showing that blink rate may convey information about the person's mental state and that blink timing relates to certain events, one could suggest that the fleeting

blink be more meaningful than generally thought; its potential social significance remains to be further studied.

References

Aarts, H., Bijleveld, E., Custers, R., Dogge, M., Deelder, M., Schutter, D., & Haren, N. E. (2012) Positive priming and intentional binding: Eye-blink rate predicts reward information effects on the sense of agency. *Social Neuroscience, 7*(1), 105–112.

Ahlfors, S. P., Simpson, G. V., Dale, A. M., Belliveau, J. W., Liu, A. K., Korvenoja, A., . . . Ilmoniemi, R. J. (1999) Spatiotemporal activity of a cortical network for processing visual motion revealed by MEG and fMRI. *Journal of Neurophysiology, 82*(5), 2545–2555.

Allison, T., Puce, A., Spencer, D. D., & McCarthy, G. (1999) Electrophysiological studies of human face perception. I: Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cerebral Cortex, 9*(5), 415–430.

Ando, K., & Kripke, D. F. (1996) Light attenuation by the human eyelid. *Biological Psychiatry, 39*(1), 22–25.

Antervo, A., Hari, R., Katila, T., Ryhänen, T., & Seppänen, M. (1985) Magnetic fields produced by eye blinking. *Electroencephalography and Clinical Neurophysiology, 61*(4), 247–253.

Baess, P., Zhdanov, A., Mandel, A., Parkkonen, L., Hirvenkari, L., Mäkelä, J. P., . . . Hari, R. (2012) MEG dual scanning: A procedure to study real-time auditory interaction between two persons. *Frontiers in Human Neuroscience, 6*, 83.

Baillet, S. (2010) The dowser in the fields: Searching for MEG sources. In P. C. Hansen, M. L. Kringelbach & R. Salmelin (Eds.), *MEG: An Introduction to Methods* (pp. 83–123). New York: Oxford University Press.

Barry, W., & Jones, G. M. (1965) Influence of eyelid movement upon electro-oculographic recording of vertical eye movement. *Aerospace Medicine, 36*, 855–858.

Bartels, A., Zeki, S., & Logothetis, N. K. (2008) Natural vision reveals regional specialization to local motion and to contrast-invariant, global flow in the human brain. *Cerebral Cortex, 18*(3), 705–717.

Benjamini, Y., & Hochberg, Y. (1995) Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society.Series B (Methodological), 57*(1), 289–300.

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996) Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8*(6), 551–565.

Bentivoglio, A. R., Bressman, S. B., Cassetta, E., Carretta, D., Tonali, P., & Albanese, A. (1997) Analysis of blink rate patterns in normal subjects. *Movement Disorders, 12*(6), 1028–1034.

Blake, R., & Shiffrar, M. (2007) Perception of human motion. *Annual Review of Psychology, 58*(1), 47–73.

Bonda, E., Petrides, M., Ostry, D., & Evans, A. (1996) Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *The Journal of Neuroscience, 16*(11), 3737–3744.

Brefczynski-Lewis, J. A., Berrebi, M. E., McNeely, M. E., Prostko, A. L., & Puce, A. (2011) In the blink of an eye: Neural responses elicited to viewing the eye blinks of another individual. *Frontiers in Human Neuroscience, 5*, 68.

Brenner, D., Williamson, S. J., & Kaufman, L. (1975) Visually evoked magnetic fields of the human brain. *Science, 190*(4213), 480–482.

Bristow, D., Frith, C., & Rees, G. (2005) Two distinct neural effects of blinking on human visual processing. *NeuroImage, 27*(1), 136–145.

Bundo, M., Kaneoke, Y., Inao, S., Yoshida, J., Nakamura, A., & Kakigi, R. (2000) Human visual motion areas determined individually by magnetoencephalography and 3D magnetic resonance imaging. *Human Brain Mapping, 11*(1), 33–45.

Caffier, P. P., Erdmann, U., & Ullsperger, P. (2003). Experimental evaluation of eye-blink parameters as a drowsiness measure. *European Journal of Applied Physiology, 89*(3), 319–325.

Caharel, S., Poiroux, S., Bernard, C., Thibaut, F., Lalonde, R., & Rebai, M. (2002) ERPs associated with familiarity and degree of familiarity during face recognition. *The International Journal of Neuroscience, 112*(12), 1499–1512.

Carmel, D., & Bentin, S. (2002) Domain specificity versus expertise: Factors influencing distinct processing of faces. *Cognition, 83*(1), 1–29.

Cauquil, A. S., Edmonds, G. E., & Taylor, M. J. (2000) Is the face-sensitive N170 the only ERP not affected by selective attention? *Neuroreport, 11*(10), 2167–2171.

Chan, R. C., & Chen, E. Y. (2004) Blink rate does matter: A study of blink rate, sustained attention, and neurological signs in schizophrenia. *The Journal of Nervous and Mental Disease, 192*(11), 781–783.

Cohen, D. (1968) Magnetoencephalography: Evidence of magnetic fields produced by alpha-rhythm currents. *Science, 161*(3843), 784–786.

Cohen, D. (1975) Measurements of the magnetic fields produced by the human heart, brain, and lungs. *IEEE Transactions on Magnetics, 11*(2), 694–700.

Colzato, L. S., van den Wildenberg, W. P. M., & Hommel, B. (2008b) Reduced spontaneous eye blink rates in recreational cocaine users: Evidence for dopaminergic hypoactivity. *PLoS One, 3*(10), e3461.

Colzato, L. S., Slagter, H. A., Spapé, M. M. A., & Hommel, B. (2008a) Blinks of the eye predict blinks of the mind. *Neuropsychologia, 46*(13), 3179–3183.

Conty, L., N'Diaye, K., Tijus, C., & George, N. (2007) When eye creates the contact! ERP evidence for early dissociation between direct and averted gaze motion processing. *Neuropsychologia, 45*(13), 3024–3037.

Culham, J., He, S., Dukelow, S., & Verstraten, F. A. J. (2001) Visual motion and the human brain: What has neuroimaging told us? *Acta Psychologica, 107*(1–3), 69–94.

Cummins, F. (2012) Gaze and blinking in dyadic conversation: A study in coordinated behaviour among individuals. *Language and Cognitive Processes, 27*(10), 1525–1549.

Cunningham, D. W., & Wallraven, C. (2009) Dynamic information for the recognition of conversational expressions. *Journal of Vision, 9*(13), 1–17.

Denney, D., & Denney, C. (1984) The eye blink electro-oculogram. *The British Journal of Ophthalmology, 68*(4), 225–228.

Doughty, M. J. (2001) Consideration of three types of spontaneous eyeblink activity in normal humans: During reading and video display terminal use, in primary gaze, and while in conversation. *Optometry & Vision Science, 78*(10), 712–725.

Dreisbach, G., Müller, J., Goschke, T., Strobel, A., Schulze, K., Lesch, K. P., & Brocke, B. (2005) Dopamine and cognitive control: The influence of spontaneous eyeblink rate and dopamine gene polymorphisms on perseveration and distractibility. *Behavioral Neuroscience, 119*(2), 483–490.

Ekman, P., & Friesen, W. V. (1982). Felt, false, and miserable smiles. *Journal of Nonverbal Behavior, 6*(4), 238–252.

Ffytche, D. H., Guy, C. N., & Zeki, S. (1995) The parallel visual motion inputs into areas V1 and V5 of human cerebral cortex. *Brain: A Journal of Neurology, 118*(Pt 6), 1375–1394.

François, J., Verriest, G., & De Rouck, A. (1955) Modification of the amplitude of the human electro-oculogram by light and dark adaptation. *The British Journal of Ophthalmology, 39*(7), 398–408.

Fukuda, K., & Matsunaga, K. (1983) Changes in blink rate during signal discrimination tasks. *Japanese Psychological Research, 25*(3), 140–146.

Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999) Activation of the middle fusiform 'face area' increases with expertise in recognizing novel objects. *Nature Neuroscience, 2*(6), 568–73.

Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000) Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience, 3*(2), 191–197.

Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004) The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience, 7*(5), 555–562.

Grossman, E. D., & Blake, R. (2001) Brain activity evoked by inverted and imagined biological motion. *Vision Research, 41*(10–11), 1475–1482.

Grossman, E. D., Blake, R., & Kim, C. (2004) Learning to see biological motion: Brain activity parallels behavior. *Journal of Cognitive Neuroscience, 16*(9), 1669–1679.

Halgren, E., Raij, T., Marinkovic, K., Jousmäki, V., & Hari, R. (2000) Cognitive response profile of the human fusiform face area as determined by MEG. *Cerebral Cortex, 10*(1), 69–81.

Hall, A. (1945) The origin and purposes of blinking. *The British Journal of Ophthalmology, 29*(9), 445–467.

Hämäläinen, M., Hari, R., Ilmoniemi, R. J., Knuutila, J., & Lounasmaa, O. V. (1993) Magnetoencephalography—theory, instrumentation, and applications to noninvasive studies of the working human brain. *Reviews of Modern Physics, 65*(2), 413–497.

Hari, R. (2005) Magnetoencephalography in clinical neurophysiological assessment of human cortical functions. In E. Niedermeyer, & F. Lopes da Silva (Eds.), *Electroencephalography: Basic Principles, Clinical Applications, and Related Fields* (5th ed.). New York: Lippincott Williams & Wilkins.

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998) Activation of human primary motor cortex during action observation: A neuromagnetic study. *Proceedings of the National Academy of Sciences, 95*(25), 15061–15065.

Hari, R., Salmelin, R., Tissari, S. O., Kajola, M., & Virsu, V. (1994) Visual stability during eyeblinks. *Nature, 367*(6459), 121–122.

Hari, R., & Kujala, M. V. (2009) Brain basis of human social interaction: From concepts to brain imaging. *Physiological Reviews, 89*(2), 453–479.

Hari, R., Levänen, S., & Raij, T. (2000) Timing of human cortical functions during cognition: Role of MEG. *Trends in Cognitive Sciences, 4*(12), 455–462.

Hari, R., Portin, K., Kettenmann, B., Jousmäki, V., & Kobal, G. (1997) Right-hemisphere preponderance of responses to painful CO2 stimulation of the human nasal mucosa. *Pain, 72*(1–2), 145–151.

Harrigan, J. A., & O'Connell, D. M. (1996) How do you look when feeling anxious? Facial displays of anxiety. *Personality and Individual Differences, 21*(2), 205–212.

Haxby, J. V., & Gobbini, M. I. (2011) Distributed neural systems for face perception. In A. Calder, G. Rhodes, M. Johnson & J. Haxby (Eds.), *Oxford handbook of face perception* (pp. 93–110). New York: Oxford University Press.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000) The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4*(6), 223–233.

Herrmann, A. (2010) The interaction of eye blinks and other prosodic cues in German Sign Language. *Sign Language & Linguistics, 13*(1), 3–39.

Hess, U., & Kleck, R. E. (1990) Differentiating emotion elicited and deliberate emotional facial expressions. *European Journal of Social Psychology, 20*(5), 369–385.

Hietanen, J. K., Leppänen, J. M., Peltola, M. J., Linna-aho, K., & Ruuhiala, H. J. (2008) Seeing direct and averted gaze activates the approach–avoidance motivational brain systems. *Neuropsychologia, 46*(9), 2423–2430.

Hirokawa, K., Yagi, A., & Miyata, Y. (2000) An examination of the effects of linguistic abilities on communication stress, measured by blinking and heart rate, during a telephone situation. *Social Behavior and Personality, 28*(4), 343–353.

Holland, M. K., & Tarlow, G. (1972) Blinking and mental load. *Psychological Reports, 31*(1), 119–127.

Holland, M. K., & Tarlow, G. (1975) Blinking and thinking. *Perceptual and Motor Skills, 41*(2), 503–506.

Holmes, A., Vuilleumier, P., & Eimer, M. (2003) The processing of emotional facial expression is gated by spatial attention: Evidence from event-related brain potentials. *Cognitive Brain Research, 16*(2), 174–184.

Howard, R. J., Brammer, M., Wright, I., Woodruff, P. W., Bullmore, E. T., & Zeki, S. (1996) A direct demonstration of functional specialization within motion-related visual and auditory cortex of the human brain. *Current Biology, 6*(8), 1015–1019.

Hughes, J. R., Cohen, J., Mayman, C. I., Scholl, M. L., & Hendrix, D. E. (1977). Relationship of the magnetoencephalogram to abnormal activity in the electroencephalogram. *Journal of Neurology, 217*(2), 79–93.

Janik, S. W., Wellens, A. R., Goldberg, M. L., & Dell'Osso, L. F. (1978) Eyes as the center of focus in the visual examination of human faces. *Perceptual and Motor Skills, 47*(3 Pt 1), 857–858.

Jeffreys, D. A. (1989) A face-responsive potential recorded from the human scalp. *Experimental Brain Research, 78*(1), 193–202.

Kamachi, M., Bruce, V., Mukaida, S., Gyoba, J., Yoshikawa, S., & Akamatsu, S. (2001) Dynamic properties influence the perception of facial expressions. *Perception, 30*(7), 875–887.

Kaneko, K., & Sakamoto, K. (1999) Evaluation of three types of blinks with the use of electro-oculogram and electromyogram. *Perceptual and Motor Skills, 88*(3 Pt 1), 1037–1052.

Kaneoke, Y., Bundou, M., Koyama, S., Suzuki, H., & Kakigi, R. (1997) Human cortical area responding to stimuli in apparent motion. *Neuroreport, 8*(3), 677–682.

Kanwisher, N., & Yovel, G. (2006) The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society B: Biological Sciences, 361*(1476), 2109–2128.

Karson, C. N. (1983) Spontaneous eye-blink rates and dopaminergic systems. *Brain: A Journal of Neurology, 106*(Pt 3), 643–653.

Karson, C. N., Berman, K. F., Donnelly, E. F., Mendelson, W. B., Kleinman, J. E., & Wyatt, R. J. (1981) Speaking, thinking, and blinking. *Psychiatry Research, 5*(3), 243–246.

Karson, C. N., Dykman, R. A., & Paige, S. R. (1990) Blink rates in schizophrenia. *Schizophrenia Bulletin, 16*(2), 345–354.

Kaufman, L., Schwartz, B., Salustri, C., & Williamson, S. J. (1990) Modulation of spontaneous brain activity during mental imagery. *Journal of Cognitive Neuroscience, 2*(2), 124–132.

Kawakami, O., Kaneoke, Y., Maruyama, K., Kakigi, R., Okada, T., Sadato, N., & Yonekura, Y. (2002) Visual detection of motion speed in humans: Spatiotemporal analysis by fMRI and MEG. *Human Brain Mapping, 16*(2), 104–118.

Kessler, H., Doyen-Waldecker, C., Hofer, C., Hoffmann, H., Traue, H. C., & Abler, B. (2011) Neural correlates of the perception of dynamic versus static facial expressions of emotion. *Psycho-Social Medicine, 8*, Doc03.

Kilts, C. D., Egan, G., Gideon, D. A., Ely, T. D., & Hoffman, J. M. (2003) Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions. *NeuroImage, 18*(1), 156–168.

Krumhuber, E., & Kappas, A. (2005) Moving smiles: The role of dynamic components for the perception of the genuineness of smiles. *Journal of Nonverbal Behavior, 29*(1), 3–24.

Krumhuber, E., Manstead, A., & Kappas, A. (2007) Temporal aspects of facial displays in person and expression perception: The effects of smile dynamics, head-tilt, and gender. *Journal of Nonverbal Behavior, 31*(1), 39–56.

Kujala, M. V., Tanskanen, T., Parkkonen, L., & Hari, R. (2009) Facial expressions of pain modulate observer's long-latency responses in superior temporal sulcus. *Human Brain Mapping, 30*(12), 3910–3923.

LaBar, K. S., Crupain, M. J., Voyvodic, J. T., & McCarthy, G. (2003) Dynamic perception of facial affect and identity in the human brain. *Cerebral Cortex, 13*(10), 1023–1033.

Leal, S., & Vrij, A. (2008) Blinking during and after lying. *Journal of Nonverbal Behavior, 32*(4), 187–194.

Leal, S., & Vrij, A. (2010) The occurrence of eye blinks during a guilty knowledge test. *Psychology, Crime & Law, 16*(4), 349–357.

Lesner, S. A., & Hardick, E. J. (1982) An investigation of spontaneous eye blinks during lipreading. *Journal of Speech and Hearing Research, 25*(4), 517–520.

Linkenkaer-Hansen, K., Palva, J. M., Sams, M., Hietanen, J. K., Aronen, H. J., & Ilmoniemi, R. J. (1998) Face-selective processing in human extrastriate cortex around 120 ms after stimulus onset revealed by magneto- and electroencephalography. *Neuroscience Letters, 253*(3), 147–150.

Liu, J., Harris, A., & Kanwisher, N. (2002) Stages of processing in face perception: An MEG study. *Nature Neuroscience, 5*(9), 910–916.

Lu, S. T., Hämäläinen, M. S., Hari, R., Ilmoniemi, R. J., Lounasmaa, O. V., Sams, M., & Vilkman, V. (1991) Seeing faces activates three separate areas outside the occipital visual cortex in man. *Neuroscience, 43*(2–3), 287–290.

Luck, S. J., & Hillyard, S. A. (2000) The operation of selective attention at multiple stages of processing: Evidence from human and monkey electrophysiology. In M. S. Gazzaniga (Ed.), *The New Cognitive Neurosciences* (2nd ed.). Cambridge, MA: MIT Press.

Luck, S. J., Hillyard, S. A., Mouloua, M., Woldorff, M. G., Clark, V. P., & Hawkins, H. L. (1994) Effects of spatial cuing on luminance detectability: Psychophysical and electrophysiological evidence for early selection. *Journal of Experimental Psychology: Human Perception and Performance, 20*(4), 887–904.

Mackintosh, J. H., Kumar, R., & Kitamura, T. (1983) Blink rate in psychiatric illness. *The British Journal of Psychiatry: The Journal of Mental Science, 143*, 55–57.

Maclin, E., Okada, Y., Kaufman, L., & Williamson, S. (1983) Retinotopic map on the visual cortex for eccentrically placed patterns: First noninvasive measurement. *Il Nuovo Cimento D, 2*(2), 410–419.

Mann, S., Vrij, A., & Bull, R. (2002) Suspects, lies, and videotape: An analysis of authentic high-stake liars. *Law and Human Behavior, 26*(3), 365–376.

Marg, E. (1951) Development of electro-oculography; standing potential of the eye in registration of eye movement. *A.M.A.Archives of Ophthalmology, 45*(2), 169–185.

Maruyama, K., Kaneoke, Y., Watanabe, K., & Kakigi, R. (2002) Human cortical responses to coherent and incoherent motion as measured by magnetoencephalography. *Neuroscience Research, 44*(2), 195–205.

Matsuo, F., Peters, J. F., & Reilly, E. L. (1975) Electrical phenomena associated with movements of the eyelid. *Electroencephalography and Clinical Neurophysiology, 38*(5), 507–511.

McGugin, R. W., Gatenby, J. C., Gore, J. C., & Gauthier, I. (2012) High-resolution imaging of expertise reveals reliable object selectivity in the fusiform face area related to perceptual performance. *Proceedings of the National Academy of Sciences, 109*(42), 17063–17068.

Miles, W. R. (1940) Modification of the human-eye potential by dark and light adaptation. *Science, 91*(2367), 456.

Nakano, T., Kato, N., & Kitazawa, S. (2011) Lack of eyeblink entrainments in autism spectrum disorders. *Neuropsychologia, 49*(9), 2784–2790.

Nakano, T., & Kitazawa, S. (2010) Eyeblink entrainment at breakpoints of speech. *Experimental Brain Research, 205*(4), 577–581.

Nakano, T., Yamamoto, Y., Kitajo, K., Takahashi, T., & Kitazawa, S. (2009) Synchronization of spontaneous eyeblinks while viewing video stories. *Proceedings of the Royal Society B: Biological Sciences, 276*, 3635–3644.

Okada, Y. (1985) Discrimination of localized and distributed current dipole sources and localized single and multiple sources. In H. Weinberg, G. Stroink & T. Katila (Eds.), *Biomagnetism: Applications & Theory* (pp. 266–272). New York: Pergamon.

Okada, Y. C., Lähteenmäki, A., & Xu, C. (1999) Experimental analysis of distortion of magnetoencephalography signals by the skull. *Clinical Neurophysiology, 110*(2), 230–238.

Omori, Y., & Miyata, Y. (2001) Estimates of impressions based on frequency of blinking. *Social Behavior and Personality: An International Journal, 29*(2), 159–167.

Ousler, G. W., Hagberg, K. W., Schindelar, M., Welch, D., & Abelson, M. B. (2008) The ocular protection index. *Cornea, 27*(5), 509–513.

Petroni, F., Panzeri, S., Hilgetag, C., Kotter, R., & Young, M. (2001) Simultaneity of responses in a hierarchical visual network. *Neuroreport, 12*(12), 2753–2759.

Pizzagalli, D. A., Lehmann, D., Hendrick, A. M., Regard, M., Pascual-Marqui, R. D., & Davidson, R. J. (2002) Affective judgments of faces modulate early activity (~160 ms) within the fusiform gyri. *NeuroImage, 16*(3, Part A), 663–677.

Ponder, E., & Kennedy, W. P. (1927) On the act of blinking. *Experimental Physiology, 18*(2), 89–110.

Pönkänen, L.,M., Hietanen, J. K., Peltola, M. J., Kauppinen, P. K., Haapalainen, A., & Leppänen, J. M. (2008) Facing a real person: An event-related potential study. *Neuroreport, 19*(4), 497–501.

Puce, A., Allison, T., Gore, J. C., & McCarthy, G. (1995) Face-sensitive regions in human extrastriate cortex studied by functional MRI. *Journal of Neurophysiology, 74*(3), 1192–1199.

Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998) Temporal cortex activation in humans viewing eye and mouth movements. *The Journal of Neuroscience, 18*(6), 2188–2199.

Raymond, J. E. (2000) Attentional modulation of visual motion perception. *Trends in Cognitive Sciences, 4*(2), 42–50.

Rhodes, G., Byatt, G., Michie, P. T., & Puce, A. (2004) Is the fusiform face area specialized for faces, individuation, or expert individuation? *Journal of Cognitive Neuroscience, 16*(2), 189–203.

Salmelin, R., & Parkkonen, L. (2010) Experimental design. In P. C. Hansen, M. L. Kringelbach & R. Salmelin (Eds.), *MEG: An Introduction to Methods* (pp. 75–82). New York: Oxford University Press.

Salmelin, R., & Hari, R. (1994a) Characterization of spontaneous MEG rhythms in healthy adults. *Electroencephalography and Clinical Neurophysiology, 91*(4), 237–248.

Salmelin, R., & Hari, R. (1994b) Spatiotemporal characteristics of sensorimotor neuromagnetic rhythms related to thumb movement. *Neuroscience, 60*(2), 537–550.

Sams, M., Hietanen, J. K., Hari, R., Ilmoniemi, R. J., & Lounasmaa, O. V. (1997) Face-specific responses from the human inferior occipito-temporal cortex. *Neuroscience, 77*(1), 49–55.

Sato, W., Kochiyama, T., Yoshikawa, S., Naito, E., & Matsumura, M. (2004) Enhanced neural activity in response to dynamic facial expressions of emotion: An fMRI study. *Cognitive Brain Research, 20*(1), 81–91.

Sato, W., & Yoshikawa, S. (2004) The dynamic aspects of emotional facial expressions. *Cognition & Emotion, 18*(5), 701–710.

Schnitzler, A., Salenius, S., Salmelin, R., Jousmäki, V., & Hari, R. (1997) Involvement of primary motor cortex in motor imagery: A neuromagnetic study. *NeuroImage, 6*(3), 201–208.

Schultz, R. T. (2005) Developmental deficits in social perception in autism: The role of the amygdala and fusiform face area. *International Journal of Developmental Neuroscience,*
23(2–3), 125–141.

Sergent, J., Ohta, S., & MacDonald, B. (1992) Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain: A Journal of Neurology, 115 Pt 1*, 15–36.

Shultz, S., Klin, A., & Jones, W. (2011) Inhibition of eye blinking reveals subjective perceptions of stimulus salience. *Proceedings of the National Academy of Sciences, 108*(52), 21270–21275.

Skotte, J., Nøjgaard, J., Jørgensen, L., Christensen, K., & Sjøgaard, G. (2007) Eye blink frequency during different computer tasks quantified by electrooculography. *European Journal of Applied Physiology, 99*(2), 113–119.

Stern, J. A., & Dunham, D. N. (1990) The ocular system. In J. T. Cacioppo, & L. G. Tassinary (Eds.), *Principles of Psychophysiology: Physical, Social, and Inferential Elements* (pp. 513–553). Berkeley, CA: University of California Press.

Stern, J. A., Boyer, D., & Schroeder, D. (1994) Blink rate: A possible measure of fatigue. *Human Factors, 36*(2), 285–297.

Susac, A., Ilmoniemi, R. J., Pihko, E., Ranken, D., & Supek, S. (2010) Early cortical responses are sensitive to changes in face stimuli. *Brain Research, 1346*(0), 155–164.

Swarztrauber, K., & Fujikawa, D. G. (1998) An electroencephalographic study comparing maximum blink rates in schizophrenic and nonschizophrenic psychiatric patients and nonpsychiatric control subjects. *Biological Psychiatry, 43*(4), 282–287.

Taylor, M. J., George, N., & Ducorps, A. (2001a) Magnetoencephalographic evidence of early processing of direction of gaze in humans. *Neuroscience Letters, 316*(3), 173–177.

Taylor, M. J., Itier, R. J., Allison, T., & Edmonds, G. E. (2001b) Direction of gaze effects on early face processing: Eyes-only versus full faces. *Cognitive Brain Research, 10*(3), 333–340.

Tong, M. H., Joyce, C. A., & Cottrell, G. W. (2008) Why is the fusiform face area recruited for novel categories of expertise? A neurocomputational investigation. *Brain Research, 1202*(0), 14–24.

Trautmann, S. A., Fehr, T., & Herrmann, M. (2009) Emotions in motion: Dynamic compared to static facial expressions of disgust and happiness reveal more widespread emotion-specific activations. *Brain Research, 1284*(0), 100–115.

Tulen, J. H., Azzolini, M., de Vries, J. A., Groeneveld, W. H., Passchier, J., & van De Wetering, B. J. (1999) Quantitative study of spontaneous eye blinks and eye tics in Gilles de la Tourette's syndrome. *Journal of Neurology, Neurosurgery, and Psychiatry, 67*(6), 800–802.

Uusitalo, M. A., Virsu, V., Salenius, S., Näsänen, R., & Hari, R. (1997) Activation of human V5 complex and rolandic regions in association with moving visual stimuli. *NeuroImage, 5*(4), 241–250.

van der Post, J., de Waal, P. P., de Kam, M. L., Cohen, A. F., & van Gerven, J. M. (2004) No evidence of the usefulness of eye blinking as a marker for central dopaminergic activity. *Journal of Psychopharmacology, 18*(1), 109–114.

Vanni, S., Tanskanen, T., Seppä, M., Uutela, K., & Hari, R. (2001) Coinciding early activation of the human primary visual cortex and anteromedial cuneus. *Proceedings of the National Academy of Sciences, 98*(5), 2776–2780.

Volkmann, F. C. (1986) Human visual suppression. *Vision Research, 26*(9), 1401–1416.

Volkmann, F. C., Riggs, L. A., & Moore, R. K. (1980) Eyeblinks and visual suppression. *Science, 207*(4433), 900–902.

Wang, L., Kaneoke, Y., & Kakigi, R. (2003) Spatiotemporal separability in the human cortical response to visual motion speed: A magnetoencephalography study. *Neuroscience Research, 47*(1), 109–116.

Watanabe, S., Kakigi, R., Miki, K., & Puce, A. (2006) Human MT/V5 activity on viewing eye gaze changes in others: A magnetoencephalographic study. *Brain Research, 1092*(1), 152–160.

Watanabe, S., Kakigi, R., & Puce, A. (2001) Occipitotemporal activity elicited by viewing eye movements: A magnetoencephalographic study. *NeuroImage, 13*(2), 351–363.

Watanabe, S., Miki, K., & Kakigi, R. (2002) Gaze direction affects face perception in humans. *Neuroscience Letters, 325*(3), 163–166.

Yoshikawa, S., & Sato, W. (2008) Dynamic facial expressions of emotion induce representational momentum. *Cognitive, Affective, & Behavioral Neuroscience, 8*(1), 25–31.

Zeki, S., Watson, J. D., Lueck, C. J., Friston, K. J., Kennard, C., & Frackowiak, R. S. (1991) A direct demonstration of functional specialization in human visual cortex. *The Journal of Neuroscience, 11*(3), 641–649.