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Functional correlate and delineated connectivity pattern of human motion aftereffect responses substantiate a subjacent visual-vestibular interaction

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ABSTRACT

The visual motion aftereffect (MAE) is the most prominent aftereffect in the visual system. Regarding its function, psychophysical studies suggest its function to be a form of sensory error correction, possibly also triggered by incongruent visual-vestibular stimulation. Several observational imaging experiments have deducted an essential role for region MT+ in the perception of a visual MAE but not provided conclusive evidence. Potential confounders with the MAE such as ocular motor performance, attention, and vection sensations have also never been controlled for. Aim of this neuroimaging study was to delineate the neural correlates of MAE and its subjacent functional connectivity pattern.

A rotational MAE ($n = 22$) was induced using differing visual stimuli whilst modulating ocular motor parameters in a 3T scanner. Data was analyzed with SPM12. Eye movements as a response to the same stimuli were studied by means of high-resolution videooculography.

Analysis for all stimuli gave bilateral activations along the dorsal visual stream with an emphasis on area MT. The onset of a visual MAE revealed an additional response in the right medial superior temporal area (MST) and a concurrent deactivation of vestibular hub region OP2. There was no correlation for the BOLD effects during the MAE with either ocular motor or attention parameters.

The functional correlate of a visual MAE in humans may be represented in the interaction between region MT and area MST. This MAE representation is independent of a potential afternystagmus, attention and the presence of egomotion sensations. Connectivity analyses showed that in the event of conflicting visual-vestibular motion information (here MAE) area MST and area OP2 may act as the relevant mediating network hubs.

Introduction

The motion aftereffect (MAE) is one of several known visual aftereffects (Mather et al., 2008; Thompson and Burr, 2009). It can be experienced by almost everyone after exposure to an optic flow pattern for a prolonged period of time (Anstis et al., 1998). Recent research about MAEs even indicates a reference-frame dependent motion aftereffect for observed voluntary movements of ones own body parts (Mancini and Haggard, 2014; Matsumiya and Shioiri, 2014).

The MAE itself has traditionally been a subject of psychophysical studies investigating visual motion perception in the extrastriate cortex. High- and low-level MAEs have been described, allowing inferences on different levels of visual motion processing depending on the properties of the adaptor and the test pattern (Anstis et al., 1998; Culham et al., 2000). With respect to the cognitive function of the MAE, one theory proposes that the MAE is a form of sensory error correction when subjects are exposed to incongruent visual and vestibular stimulation. The effect hereby appears to adjust the sensitivity of motion detectors and thus might improve internal motion representation (Anstis et al., 1998). It is presumed that the MAE reflects a recalibration of the visual motion-processing network after adaptation to gain a higher sensitivity in an optimal range (Tolias et al., 2001; Watamaniuk and Heinen, 2007). This predicts storage of the MAE, as for recalibration an alternate visual input is needed (Anstis et al., 1998; Wiesenfelder and Blake, 1992). Another idea holds that the MAE serves as a recalibration mechanism when visual and vestibular stimulation are not congruent (Crane, 2013;

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Harris et al., 1981). Indeed, psychophysical studies reported an inhibition of the MAE when combining forward self-motion with a congruent visual stimulus, whereas incongruent visual and vestibular stimuli evoked a MAE which was similar to the stationary measured one (Harris et al., 1981; Wallach and Flaherty, 1975). Recent psychophysical data extended these findings, suggesting a role of the MAE in differentiation of self-motion versus external visual motion (Crane, 2013). However, functional imaging data concerning the underlying networks during the MAE is limited and imaging correlates for the presumed visual-vestibular interaction have not been reported yet. To further pinpoint the neural correlates of MAE we therefore aimed to exclude vection effects by using a visual adaptor with an incoherent and inhomogeneous flow pattern and a stimulus presentation field of view that did not induce an egomotion perception.

The ocular motor response to stimuli inducing MAE is the optokinetic nystagmus (OKN) (Farooq et al., 2004). Mediated by the velocity storage mechanism, this response persists even after termination of the visual motion stimulation, resulting in what is called the optokinetic after-nystagmus (OKAN) (Leigh and Zee, 2006). Only a few studies outside the context of neuroimaging have investigated optokinetic eye movements during visual stimulation at all and even fewer in the context of a subsequent MAE (Ibbotson et al., 2005; Seidman et al., 1992). OKN and OKAN have been examined during circular vection, an illusionary egomotion perception during horizontal large-field optokinetic stimulation (Brandt et al., 1973, 1974; Cheung and Howard, 1991). Although there appeared to be no evidence for a direct connection between the properties of circular vection and the OKN, it was shown that OKAN and circular vection are dependent on the duration and field size of visual stimulation (Brandt et al., 1973). To the best of our knowledge, no data has been published yet concerning a link between the optokinetic response and the duration of the MAE within functional imaging.

The last decades have seen an increasing interest in the cortical networks underlying the MAE though. One of the first fMRI studies reported a correlation of the response time course in MT+ with the time course of the MAE (Tootell et al., 1995). The ensuing studies allowed a more detailed view on the cortical networks underlying the MAE, confining an anterior and posterior network (Taylor et al., 2000). The anterior network comprises the anterior cingulate cortex as well as Brodmann areas 37, 40, 44, 46, and 47. Its functional importance might be to control and mediate awareness during the perception of the MAE, while the posterior network responses could be mainly related to visual motion-analysis, including motion sensitive area MT+ as well as visual regions V1-V3. A PET-study extended these findings by demonstrating additionally increased regional cerebral blood flow (rCBF) in the right dorsolateral prefrontal cortex (DLPFC) and the left cerebellum during MAE (Hautzel et al., 2001). Both studies used a horizontally orientated bar adaptor pattern eliciting a linear MAE in single-digit group samples. Psychophysical experiments examining the properties of linear and rotational MAE suggest a close connection between the neuronal networks of both effects (Hershenson, 1993). We aimed to find further cues for this hypothesis by investigating a rotational MAE with fMRI.

With respect to a hierarchical relevance of the areas mentioned above, especially the functional role of MT+ has been discussed controversially. Earlier fMRI studies emphasized an involvement of motion-sensitive area MT+ during perception of the MAE (Culham et al., 1999; He et al., 1998; Theoret et al., 2002; Tootell et al., 1995). On the other hand, the response of MT+ could be just an effect of attention to the MAE (Huk et al., 2001). Using a 2-alternative forced-choice speed discrimination task to equalize attention resulted in equally large responses in MT+ during the control and the MAE condition. Nonetheless, it was argued that an interference of a concurrent motion task with the MAE-related response in MT+ might account for these findings (Castelo-Branco et al., 2009). Indeed, replicating Huk's experiments but including a nonmotion-feature to direct attention led to an enhanced response in MT+. Another recent fMRI study presented further evidence for the implication of MT+ in the MAE (Hogendoorn and Verstraten, 2013). In this study, neural activity was compared in real motion and during MAE using multivariate pattern classification with a focus on visual areas V1-V4 and MT+. A shift in activation patterns during MAE was only seen in MT+. These studies were unfortunately not able to further localize their findings within the subregions of the MT+ complex.

Against the background of all of the aforementioned findings on MAE the aim of our study was multifold: First, to explore the use of a torsional stimulus (clockwise/counter-clockwise) at a small field of view, which would allow a rotational MAE to be elicited. The combination of torsion two factors (torsion/limited field of view) should avoid a potential self-motion perception and the interfering effects of visual motion coherence due to homogenous flow patterns in area MT at the same time (Handel et al., 2007, 2008). Secondly, we wanted to control for the occurring ocular motor parameters (OKN/OKAN) as well as the level of attention in our subjects by means of a combined neuroimaging and videooculography (VOG) setup and look for possible interferences from those parameters. Thirdly, we intended to work with a cohort size (>20) which would first and foremost allow for a general inference on the population that the participants were drawn from in contrast to all previously published imaging studies (Guo et al., 2014a, 2014b; Thirion et al., 2007). Finally; to identify and differentiate the cortical and subcortical networks subjacent to the MAE, we also aimed to investigate the functional connectivity patterns of the core cortical regions involved.

Material and methods

Participants

Twenty-two healthy volunteers (12 female) with a mean age of 23.4 years (range: 19–25 years) participated in the experiments after giving their informed written consent. The modified laterality quotient of handedness and footedness according to the 14-item inventory of the Edinburgh test (Chapman and Chapman, 1987) was determined, since differential effects within the vestibular system due to hemispheric dominance had to be considered (Dieterich et al., 2003). All subjects had to be right-handed, with normal uncorrected vision and had to exhibit binocular parity. The participants were not on any medication. Only subjects without a previous history of neurotological or ocular disease or a CNS disorder were included in the study. All volunteers underwent a diagnostic procedure consisting of neurological, neuro-ophthalmolocigal and neuro-otological examinations including the head-impulse test, positioning maneuvers, the Unterberger stepping test, examination with Frenzel's glasses, and the head-shaking test. This study was carried out in accordance with the Declaration of Helsinki (2004) and was approved by the local Ethics Committee. Subjects were paid for participation. The guidelines and principles for reporting fMRI studies laid down by Poldrack and colleagues were followed (Poldrack et al., 2008).

Videooculography experiment

By determining the perceived length of MAE and concurrently recording of the eye movements during and after the circular motion stimulation with VOG we aimed to investigate a potential correlation between ocular motor performance and the duration of the MAE. In addition, we intended to delineate the influence of the adaptor and different test patterns as well as of the duration, direction and speed of rotatory visual motion stimulation. Further aim was to later enter our eye movement findings as relevant subject covariates of individual ocular motor performance with the neuroimaging findings. All of this was done prior to the neuroimaging experiment.

A high-contrast vector-drawn windmill pattern of 12 equal-sized black and white sectors with a central fixation area and a lower-contrast circular sphere pattern of 64 globes without a central fixation zone were used as visual stimuli rotating at a velocity of 20°/s or 30°/s for 20 s or 30 s in clockwise (cw) or counterclockwise (ccw) direction. These patterns unlike a spiral or flow pattern composed of a translating