

In addition, anatomical MRIs of the subjects' brains were acquired using a 1.5-T Siemens Magnetom Sonata System (Erlangen, Germany). During MRI acquisition, similar ear-plugs, now with a drop of vitamin E in place of the coils, were used to allow coregistration of the MRI and MEG data for source analysis.

Data Analysis

Behavioral performance on the task was computed in terms of discrimination rate (percentage correct responses) and RT on correct trials. To assess the effect of conditions on performance, a repeated measures ANOVA with factor Distracter (no, weak, strong, and no*) was applied.

For the MEG data analysis, we used custom-built Matlab code and the Matlab-based FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011; <http://www.ru.nl/neuroimaging/fieldtrip>). For each subject, all trials were first cleaned from artifacts (this was done on all conditions combined). We used independent component analysis (Jung et al., 2000) to identify eye artifacts, which were then projected out of the data. Furthermore, trials with extremely high variance (containing, e.g., MEG sensor jumps or muscle artifacts) were removed from the data upon visual inspection (on average 6% of trials).

Sensor-level Analysis

Planar gradients of the MEG field distribution were calculated using a nearest-neighbor method (comparable with the method described by Bastiaansen & Knösche, 2000), which makes interpretation of the sensor-level data easier, as sensors showing maximal activity are typically located above the actual sources.

From each trial, the 1-sec prestimulus window ($t = 0.5$ – 1.5 sec) was extracted and multiplied with a Hanning taper, after which power spectra (4–36 Hz) were computed using a fast Fourier transform (FFT) approach. For the baseline contrasts (see below), power spectra were computed using the same approach, for a baseline ($t = -0.5$ to 0 sec) and prestimulus window ($t = 1$ – 1.5 sec). Note that here we used 0.5-sec long windows, as baseline length was limited to avoid bleeding in of effects of the previous trial (the intertrial interval was 1 sec).

Furthermore, time-frequency representations (TFRs) of power were computed to inspect the temporo-spectral pattern of power changes. We used an adaptive sliding time window of four cycles length ($\Delta t = 4/f$) for each frequency of interest, multiplied with a Hanning taper before estimating the power using an FFT approach.

Source Analysis

To disentangle contributions of somatosensory and posterior alpha sources, we applied a beamformer adaptive spatial filtering technique (Schoffelen, Oostenveld, & Fries, 2008; Gross et al., 2001). Using the individual ana-

tomical MRI, we constructed a realistically shaped single-shell description of the brain for each subject. The brain volume was divided into a grid with a 1-cm resolution and normalized toward the template Montreal Neurological Institute (MNI) brain (International Consortium for Brain Mapping, Montreal Neurological Institute, Canada) using SPM8 (www.fil.ion.ucl.ac.uk/spm). Lead fields were calculated for all grid points (Nolte, 2003).

Fourier spectra (11 Hz) were obtained by applying a multitaper FFT approach to the 1-sec prestimulus segments, with five orthogonal Slepian tapers resulting in ± 3 Hz smoothing (Percival & Walden, 1993), that is, a band of 8–14 Hz. With the lead fields and the Fourier spectra (of all conditions combined), a common spatial filter was constructed for each grid point, for each subject. Using this common filter, the spatial distribution of power was estimated for each trial separately. These power estimates were used for all reported analyses other than the baseline contrasts. For the baseline contrasts, source power estimates were computed using a similar common filter approach, now applied to the 0.5-sec baseline and prestimulus windows (note that the 0.5-sec window length was too short to use the same multitaper settings as described above, instead a Hanning taper, centered at 10 Hz, was applied).

The grid points ("voxels") included in the ROIs were selected on the basis of an anatomical atlas (Talairach & Tournoux, 1988). We used the following ROIs: left primary somatosensory cortex (centered at MNI coordinates $[-50 -20 50]$, BA 3), right primary somatosensory cortex (MNI coordinates $[50 -20 50]$) and occipital cortex (MNI coordinates $[-20 -80 30]$, including BA 7 and BA 17 and equivalent for the right hemisphere). A sphere of 30 grid points was placed centered at the coordinates provided by the atlas, and for each subject, power was averaged over grid points within each ROI.

Statistical Analysis

Statistical analysis was performed on the whole-brain source level alpha power. For each subject, trials were averaged for attention left and right separately and then contrasted the following way: (attention-left – attention-right)/(attention-left + attention-right). To establish whether the difference between attention left and right was significantly different from 0, a cluster-based nonparametric randomization test was applied within subjects (Maris & Oostenveld, 2007). By clustering neighboring grid points that show the same effect, this test deals with the multiple comparisons problem while taking into account the dependency of the data. For each grid point, a dependent samples t value was computed. All samples for which this t value exceeded an a priori threshold (uncorrected $p < .05$) were subsequently clustered on the basis of spatial adjacency. The sum of the t values within a cluster was used as cluster-level statistic, and the cluster with the maximum sum was used as test statistic. By randomizing the data across the two conditions (i.e., the normalized contrast and 0) and recalculating the

test statistic 2000 times, we obtained a reference distribution of maximum cluster t values to evaluate the statistic of the actual data.

Alpha Normalization

To assess the direction of the ipsilateral and contralateral effects, that is, to see if there was indeed an ipsilateral increase and contralateral decrease, we contrasted the prestimulus power ($t = 1\text{--}1.5$ sec) with precue baseline activity ($t = -0.5$ to 0 sec). For each subject, we baseline-normalized the single trial prestimulus alpha power in the following way: $(\text{prestimulus} - \text{avg-baseline})/\text{avg-baseline}$, wherein avg-baseline is the mean baseline power over all trials and conditions in that subject (this was computed per sensor/grid point). This procedure reduces intersubject variability in the power estimates, thus providing a convenient normalization.

Next, to capture the modulation of ipsilateral and contralateral alpha power over conditions and its effect on behavioral performance, we normalized each single-trial prestimulus window ($t = 0.5\text{--}1.5$ sec) using the average prestimulus power over all trials and conditions in that subject. Hereby, we could separately address the contributions of ipsilateral and contralateral sides in a normalized measure (to exclude that subjects with particularly strong power values drive the result), while avoiding baseline effects to contribute to the observed effects. For each subject, we used the following normalization per trial: $(\text{prestimulus} - \text{avg-power})/\text{avg-power}$, where avg-power is the average prestimulus alpha power for all trials combined, per subject.

RESULTS

MEG data were acquired while subjects performed a tactile stimulus discrimination task (Figure 1A), in which a visual cue directed attention either to their left or right hand. We manipulated the strength of distracters presented to the unattended hand.

Behavioral Performance

The average performance over all conditions in 24 subjects was $87.1 \pm 8.8\%$ correct responses and the mean RT was 526.4 ± 88.6 msec (computed on correct trials only). Figure 1B shows the average performance per condition. To assess the effect of the different conditions, a repeated measures ANOVA with factor Condition (no, weak, strong, and no* distracter) was performed. There was a significant effect of Condition both on discrimination rate ($F(3, 69) = 9.487, p < .001$) and RT ($F(3, 69) = 3.235, p < .05$). Post hoc pairwise comparisons showed that discrimination rate differed significantly between the no and weak distracter conditions (uncorrected $p < .01$), no versus strong ($p < .001$), no versus no* ($p < .001$) and weak versus strong ($p < .05$), and there was a trend for weak versus no* ($p = .1$). For RT, there was a significant difference between

the no and no* conditions (uncorrected $p < .05$), weak versus no* ($p < .05$), and a trend for strong versus no* ($p = .1$). To summarize, discrimination rate decreased as distracter strength increased, and in addition, performance decreased for the weak target condition.

Ipsilateral Increase and Contralateral Decrease of Alpha

Contrasting the prestimulus ($t = 0.5\text{--}1.5$ sec) alpha band power for attention to the left hand versus attention to the right hand, we confirmed our previous findings (Haegens, Händel, et al., 2011) and showed that the direction of attention is reflected in somatosensory alpha lateralization (Figure 2A; all conditions combined). Source reconstruction using a beamformer approach localized the bulk of the activity to the left and right primary somatosensory cortices (cluster-based randomization test $p < .01$; BA 3; Figure 2B).

Next, we asked whether the observed lateralization was caused by a contralateral decrease and/or ipsilateral increase versus baseline activity. It is crucial to do this analysis at the source level to disentangle somatosensory from posterior contributions (compare Figure 2A and B). The source reconstructions revealed an ipsilateral increase and a contralateral decrease versus baseline over somatosensory cortex (Figure 2B). Additionally, an increase of posterior alpha activity versus baseline can be observed. The differences between attention left and right were significant for both the left ($t(23) = 4.957, p < .001$) and right primary somatosensory cortex ($t(23) = -4.132, p < .001$), that is, somatosensory alpha activity was significantly lateralized (Figure 2C). A one-tailed t test of baseline-corrected contralateral alpha activity versus 0 was significant ($t(23) = -2.750, p < .01$), whereas ipsilateral alpha activity versus 0 showed only a trend ($t(23) = 1.104, p = .14$). Note that all trials (also incorrect responses) were included in this analysis and that the inter trial window was only 1 sec and thus rather short for return to a “stable” or “neutral” baseline. The crucial contrast to assess the relevance of the (ipsilateral) alpha modulation is correct versus incorrect trials (see below).

Furthermore, the TFR of power (Figure 2D) showed that the ipsilateral increase was limited to the alpha band and sustained throughout the prestimulus interval. While ipsilateral alpha increased, beta band activity (15–25 Hz) decreased, indicating a clear dissociation between the two rhythms. On the contralateral side, both alpha and beta band activity decreased versus baseline (not shown).

Thus, we report lateralization of alpha band activity, driven by both a contralateral decrease and, importantly, an ipsilateral increase of power. The sources of the lateralized alpha activity were localized to primary somatosensory cortex.

Alpha Power Influences Task Performance

To assess the influence of alpha power on task performance, we contrasted correct with incorrect response trials

To directly compare the two studies, we computed a two-way mixed ANOVA with factors Study (current vs. previous; between-subject factor) and Hemisphere (ipsilateral vs. contralateral; repeated measures factor). There was a significant main effect of Hemisphere, confirming a difference between ipsi- and contralateral alpha levels ($F(1, 39) = 24.071, p < .001$), that is, alpha lateralization. The between-group factor Study was near significance ($F(1, 39) = 3.809, p = .058$). Importantly, there was a significant interaction effect between Hemisphere and Study ($F(1, 39) = 6.643, p < .05$). Although in both studies we report a significant difference between ipsilateral and contralateral modulation (current: $t(23) = 4.862, p < .001$; previous: $t(16) = 2.456, p < .05$), different strategies were adopted. Clearly, the introduction of distracters in the current study led to a pattern of ipsilateral alpha increase (vs. baseline), even in the no-distracter conditions, whereas in the previous study a decrease was reported.

DISCUSSION

In the current study, we tested the hypothesis that an increase of alpha band activity serves to suppress task-irrelevant, distracting input. We used a somatosensory spatial attention task where subjects had to discriminate stimuli presented to the cued hand while distracters were presented to the nonattended side. We show that the anticipation of distracters indeed leads to an ipsilateral alpha increase, in addition to a contralateral decrease and a general posterior alpha increase. Using source level analysis—crucial to disentangle the primary somatosensory and posterior contributions—we were able to show that these three alpha components all contributed to optimal task performance. Importantly, not only contralateral decrease but also ipsilateral increase of alpha activity plays a key role in predicting discrimination performance.

The current findings are in line with our previous work showing that somatosensory alpha influences discrimination performance (Haegens, Händel, et al., 2011; Haegens, Osipova, Oostenveld, & Jensen, 2010), and with the visuospatial attention literature (Rihs et al., 2009; Kelly et al., 2006; Thut et al., 2006; Fu et al., 2001; Worden et al., 2000; Foxe et al., 1998). Altogether, this provides further evidence that rolandic/somatosensory alpha and posterior/visual alpha activity play similar roles for the respective sensory systems (Ritter, Moosmann, & Villringer, 2009), thereby strengthening the case that alpha activity reflects a general mechanism for functional engagement and disengagement (Jensen & Mazaheri, 2010; Klimesch et al., 2007; Cooper et al., 2003). Here, we show that alpha activity is crucial not only for facilitation of processing on the attended side but also in the blocking of potentially distracting input on the nonattended side.

Alpha Modulation Depends on Task Context

Interestingly, whereas in our previous spatial attention study alpha lateralization seemed to be mainly driven by

a decrease contralateral to the attended side (Haegens, Händel, et al., 2011), we now report an additional ipsilateral increase, even in the blocks with no distracter present. Although we did hypothesize alpha increase to be dependent on task requirements, it is striking that the increase is observed even in the conditions where there is seemingly no requirement for suppression. A possible explanation is that the persistent ipsilateral increase reflects a context effect. Subjects were trained on all conditions before the experimental recordings, and conditions were presented in a random order. Hence, it is possible that subjects adopt a strategy which includes both facilitation of the attended side and suppression of the unattended side and use this same strategy throughout the experiment, rather than just on the distracter blocks. Our finding is in line with previous work on selective visuospatial attention also reporting alpha increase in the absence of distracters, which the authors ascribe to task demand and context (Rihs et al., 2007, 2009).

Vigilance Reflected by Alpha Decrease?

Manipulating the distracter strength in four experimental conditions (no, weak, and strong distracter, and a fourth condition with no distracter but weaker stimulus to control for task difficulty independent of distracter presence) led to some unexpected results. Although we predicted a further increase of ipsilateral alpha with increasing distracter load, potentially accompanied by a contralateral decrease, we observed a general decrease of alpha activity in both the contralateral and ipsilateral hemispheres with increasing task difficulty (statistical trend only; note that with “decrease,” we here refer to relative decreases comparing conditions, for all conditions ipsilateral alpha activity increased relative to the baseline). Upon further inspection, it turned out that already baseline levels of alpha showed a weak negative modulation.

These findings are in contrast with a study on visual working memory by Sauseng et al. (2009), showing an increase of ipsilateral posterior alpha with increase of distracter load, which predicted individual memory capacity. The global decrease of alpha level with increasing distracter level we find here might be reflecting an increase in vigilance or arousal because of increasing task demands (Bollimunta, Mo, Schroeder, & Ding, 2011; Klimesch et al., 2007; Pfurtscheller & Lopes da Silva, 1999; Ray & Cole, 1985). This interpretation would be in line with previous work showing that spontaneous fluctuations in ongoing alpha activity reflect changes in detection ability of near-threshold stimuli, with lower alpha levels related to better perceptual performance (Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Zhang & Ding, 2010; Hanslmayr et al., 2007; Ergenoglu et al., 2004; Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004).

Given the spatial resolution of the currently used methods, it is hard to tell whether on top of this global alpha decrease there was still a modulation of ipsilateral

alpha. Previous studies have suggested a “center-surround” pattern of alpha modulation for directing focal attention (Suffczynski, Kalitzin, Pfurtscheller, & Lopes da Silva, 2001; Pfurtscheller & Lopes da Silva, 1999). We might be tapping into a similar mechanism here, and perhaps the MEG/beamformer approach is not spatially sensitive enough to detect such a focal effect. Alternatively, it could be that the alpha increase plateaus at a certain level and further increases do not lead to any additional benefits.

Alpha versus Beta Activity

Previous work on somatosensory attention has reported that—in addition to alpha—beta band activity predicts detection performance (Schubert, Haufe, Blankenburg, Villringer, & Curio, 2009) and is modulated by expectation (Van Ede et al., 2011; Van Ede, Jensen, & Maris, 2010), suggesting that somatosensory alpha and beta activity reflect similar or related mechanisms (although there is an ongoing debate as to whether these rhythms originate from the same sources, see, e.g., Van Ede et al., 2010; Cheyne et al., 2003; Hari & Salmelin, 1997). However, here we report a dissociation between alpha and beta band responses, as the ipsilateral alpha increase was accompanied by a beta band decrease (Figure 2D). Furthermore, beta band oscillations have been implicated in somatosensory working memory maintenance and decision-making (Haegens, Nacher, et al., 2011; Spitzer & Blankenburg, 2011; Spitzer, Wacker, & Blankenburg, 2010). It seems that alpha is generally reflective of the state of the sensory system, whereas beta plays a more versatile role and is perhaps also involved in active processing.

Conclusion

Our findings demonstrate that alpha power is modulated depending on task demands: Contralateral alpha activity decreases when the main requirement is stimulus detection, whereas ipsilateral alpha activity increases when active suppression of distracters is important. Both contralateral and ipsilateral alpha modulations are required for optimal task performance. This study further extends the notion that alpha band activity is involved in shaping the functional architecture of the working brain by determining the engagement and disengagement of specific regions.

Our study prompts the following questions to be addressed in the future: Clearly the alpha activity in somatosensory and visual regions is under strong top-down control; which regions and mechanisms control the alpha activity? The alpha activity is likely to exercise gain control by modulating the spikes encoding the sensory representations; what is the underlying mechanism by which alpha oscillations modulate the spike activity? Further research, including intracranial (spike) recordings, is required to address these issues.

Acknowledgments

This work was supported by the Division for the Earth and Life Sciences (ALW) Open Competition Grant (817.02.010) and a Vici grant (453.09.002) from the Netherlands Organization for Scientific Research (NWO).

Reprint requests should be sent to Saskia Haegens, Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, P.O. Box 9101, 6500HB Nijmegen, Netherlands, or via e-mail: shaegens@gmail.com.

REFERENCES

- Anderson, K. L., & Ding, M. (2011). Attentional modulation of the somatosensory mu rhythm. *Neuroscience*, *180*, 165–180.
- Bastiaansen, M. C. M., & Knösche, T. R. (2000). Tangential derivative mapping of axial MEG applied to event-related desynchronization research. *Clinical Neurophysiology*, *111*, 1300–1305.
- Bollimunta, A., Mo, J., Schroeder, C. E., & Ding, M. (2011). Neuronal mechanisms and attentional modulation of corticothalamic alpha oscillations. *Journal of Neuroscience*, *31*, 4935–4943.
- Cheyne, D., Gaetz, W., Garnero, L., Lachaux, J.-P., Ducorps, A., Schwartz, D., et al. (2003). Neuromagnetic imaging of cortical oscillations accompanying tactile stimulation. *Cognitive Brain Research*, *17*, 599–611.
- Cooper, N. R., Croft, R. J., Dominey, S. J. J., Burgess, A. P., & Gruzelić, J. H. (2003). Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses. *International Journal of Psychophysiology*, *47*, 65–74.
- Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., & Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Cognitive Brain Research*, *20*, 376–383.
- Foxe, J. J., Simpson, G. V., & Ahlfors, S. P. (1998). Parieto-occipital ~10Hz activity reflects anticipatory state of visual attention mechanisms. *NeuroReport*, *9*, 3929–3933.
- Fu, K. M. G., Foxe, J. J., Murray, M. M., Higgins, B. A., Javitt, D. C., & Schroeder, C. E. (2001). Attention-dependent suppression of distracter visual input can be cross-modally cued as indexed by anticipatory parieto-occipital alpha-band oscillations. *Cognitive Brain Research*, *12*, 145–152.
- Gould, I. C., Rushworth, M. F., & Nobre, A. C. (2011). Indexing the graded allocation of visuospatial attention using anticipatory alpha oscillations. *Journal of Neurophysiology*, *105*, 1318–1326.
- Gross, J., Kujala, J., Hämäläinen, M., Timmermann, L., Schnitzler, A., & Salmelin, R. (2001). Dynamic imaging of coherent sources: Studying neural interactions in the human brain. *Proceedings of the National Academy of Sciences, U.S.A.*, *98*, 694–699.
- Haegens, S., Händel, B. F., & Jensen, O. (2011). Top-down controlled alpha band activity in somatosensory areas determines behavioral performance in a discrimination task. *Journal of Neuroscience*, *31*, 5197–5204.
- Haegens, S., Nacher, V., Hernández, A., Luna, R., Jensen, O., & Romo, R. (2011). Beta oscillations in the monkey sensorimotor network reflect somatosensory decision-making. *Proceedings of the National Academy of Sciences, U.S.A.*, *108*, 10708–10713.
- Haegens, S., Osipova, D., Oostenveld, R., & Jensen, O. (2010). Somatosensory working memory performance in humans depends on both engagement and disengagement of regions in a distributed network. *Human Brain Mapping*, *31*, 26–35.

- Händel, B. F., Haarmeier, T., & Jensen, O. (2011). Alpha oscillations correlate with the successful inhibition of unattended stimuli. *Journal of Cognitive Neuroscience*, *23*, 2494–2502.
- Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C. S., & Bäuml, K. H. (2007). Prestimulus oscillations predict visual perception performance between and within subjects. *Neuroimage*, *37*, 1465–1473.
- Hanslmayr, S., Gross, J., Klimesch, W., & Shapiro, K. L. (2011). The role of alpha oscillations in temporal attention. *Brain Research Reviews*, *67*, 331–343.
- Hari, R., & Salmelin, R. (1997). Human cortical oscillations: A neuromagnetic view through the skull. *Trends in Neurosciences*, *20*, 44–49.
- Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: Gating by inhibition. *Frontiers in Human Neuroscience*, *4*, 186.
- Jones, S. R., Kerr, C. E., Wan, Q., Pritchett, D. L., Hamalainen, M., & Moore, C. I. (2010). Cued spatial attention drives functionally relevant modulation of the mu rhythm in primary somatosensory cortex. *Journal of Neuroscience*, *30*, 13760–13765.
- Jung, T. P., Makeig, S., Humphries, C., Lee, T. W., McKeown, M. J., Iragui, V., et al. (2000). Removing electroencephalographic artifacts by blind source separation. *Psychophysiology*, *37*, 163–178.
- Kelly, S. P., Lalor, E. C., Reilly, R. B., & Foxe, J. J. (2006). Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *Journal of Neurophysiology*, *95*, 3844–3851.
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews*, *53*, 63–88.
- Linkenkaer-Hansen, K., Nikulin, V. V., Palva, S., Ilmoniemi, R. J., & Palva, J. M. (2004). Prestimulus oscillations enhance psychophysical performance in humans. *Journal of Neuroscience*, *24*, 10186–10190.
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*, 177–190.
- Nolte, G. (2003). The magnetic lead field theorem in the quasi-static approximation and its use for magnetoencephalography forward calculation in realistic volume conductors. *Physics in Medicine and Biology*, *48*, 3637–3652.
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*(156869), 1–9.
- Percival, D. B., & Walden, A. T. (1993). *Spectral analysis for physical applications: Multitaper and conventional univariate techniques*. Cambridge, U.K.: Cambridge University Press.
- Pfurtscheller, G., & Lopes da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology*, *110*, 1842–1857.
- Ray, W., & Cole, H. (1985). EEG alpha activity reflects attentional demands, and beta activity reflects emotional and cognitive processes. *Science*, *228*, 750–752.
- Rihs, T. A., Michel, C. M., & Thut, G. (2007). Mechanisms of selective inhibition in visual spatial attention are indexed by α -band EEG synchronization. *European Journal of Neuroscience*, *25*, 603–610.
- Rihs, T. A., Michel, C. M., & Thut, G. (2009). A bias for posterior alpha-band power suppression versus enhancement during shifting versus maintenance of spatial attention. *Neuroimage*, *44*, 190–199.
- Ritter, P., Moosmann, M., & Villringer, A. (2009). Rolandic alpha and beta EEG rhythms' strengths are inversely related to fMRI-BOLD signal in primary somatosensory and motor cortex. *Human Brain Mapping*, *30*, 1168–1187.
- Sauseng, P., Klimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, A. A., et al. (2009). Brain oscillatory substrates of visual short-term memory capacity. *Current Biology*, *19*, 1846–1852.
- Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., et al. (2005). A shift of visual spatial attention is selectively associated with human EEG alpha activity. *European Journal of Neuroscience*, *22*, 2917–2926.
- Schoffelen, J.-M., Oostenveld, R., & Fries, P. (2008). Imaging the human motor system's beta-band synchronization during isometric contraction. *Neuroimage*, *41*, 437–447.
- Schubert, R., Haufe, S., Blankenburg, F., Villringer, A., & Curio, G. (2009). Now you'll feel it, now you won't: EEG rhythms predict the effectiveness of perceptual masking. *Journal of Cognitive Neuroscience*, *21*, 2407–2419.
- Spitzer, B., & Blankenburg, F. (2011). Stimulus-dependent EEG activity reflects internal updating of tactile working memory in humans. *Proceedings of the National Academy of Sciences, U.S.A.*, *108*, 8444–8449.
- Spitzer, B., Wacker, E., & Blankenburg, F. (2010). Oscillatory correlates of vibrotactile frequency processing in human working memory. *Journal of Neuroscience*, *30*, 4496–4502.
- Suffczynski, P., Kalitzin, S., Pfurtscheller, G., & Lopes da Silva, F. H. (2001). Computational model of thalamo-cortical networks: Dynamical control of alpha rhythms in relation to focal attention. *International Journal of Psychophysiology*, *43*, 25–40.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.
- Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience*, *26*, 9494–9502.
- Van Ede, F., de Lange, F., Jensen, O., & Maris, E. (2011). Orienting attention to an upcoming tactile event involves a spatially and temporally specific modulation of sensorimotor alpha- and beta-band oscillations. *Journal of Neuroscience*, *31*, 2016–2024.
- Van Ede, F., Jensen, O., & Maris, E. (2010). Tactile expectation modulates prestimulus beta-band oscillations in human sensorimotor cortex. *Neuroimage*, *51*, 867–876.
- Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *Journal of Neuroscience*, *20*, RC63.
- Zhang, Y., & Ding, M. (2010). Detection of a weak somatosensory stimulus: Role of the prestimulus mu rhythm and its top-down modulation. *Journal of Cognitive Neuroscience*, *22*, 307–322.