Ongoing activity fluctuations in hMT+ bias the perception of coherent visual motion

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Abstract

We have recently shown that intrinsic fluctuations of ongoing activity during baseline impact on perceptual decisions reported for an ambiguous visual stimulus (G. Hesselmann, Kell, C.A., Eger, E., Kleinschmidt, A., 2008). To test whether this result generalizes from the visual object domain to other perceptual and neural systems, the current study investigated the effect of ongoing signal fluctuations in motion-sensitive brain regions on the perception of coherent visual motion. We determined motion coherence thresholds individually for each subject using a dynamic random dot display. During functional magnetic resonance imaging (fMRI), brief events of sub-, supra- and periliminal coherent motion were presented with long and variable inter-stimulus intervals between them. On each trial, subjects reported whether they had perceived 'coherent' or 'random' motion, and fMRI signal time courses were analyzed separately as a function of stimulus and percept type. In the right motion-sensitive occipito-temporal cortex (hMT+), 'coherent' percepts of periliminal stimuli yielded a larger stimulus-evoked response than 'random' percepts. Pre-stimulus baseline activity in this region was also significantly higher in these 'coherent' trials than in 'random' trials. As in our previous study, however, the relation between ongoing and evoked activity was not additive but interacted with perceptual outcome. Our data thus suggest that endogenous fluctuations in baseline activity have a generic effect on subsequent perceptual decisions. While mainstream analytical techniques used in functional neuroimaging do not capture this non-additive effect of baseline on evoked response, it is in accord with postulates from theoretical frameworks as, for instance, predictive coding.

Introduction

Fluctuating spontaneous brain activity is a prominent but persistently puzzling feature in any type of neurophysiological recording. It can be thought of as unexplained variance in relation to the experimental paradigm under investigation and has been observed with a wide range of methods on different temporal and spatial scales (B. Biswal et al., 1995; T. Kenet et al., 2004; D. Holcman and

M. Tsodyks, 2006; M. D. Fox and M. E. Raichle, 2007). In fMRI studies, spatially distributed fluctuations of the blood oxygenation level dependent (BOLD) signal have been linked to variability in action (motor output, (M. D. Fox et al., 2007)) and perception (in the somatosensory and nociceptive domain (M. Boly et al., 2007)). We have shown that even local intrinsic activity variations, occurring over and above those that manifest in distributed patterns, play an important role in visual perception. We found that the variability in ongoing BOLD activity of fusiform face-sensitive visual areas (FFA) biases the way in which subjects perceive Rubin's classic 'face-vase' ambiguity. Right FFA activity levels during pre-stimulus baseline and at the evoked response peak were significantly correlated with subjects' reports of face percepts (G. Hesselmann, Kell, C.A., Eger, E., Kleinschmidt, A., 2008). In line with different theoretical accounts of perceptual decisions (P. L. Smith and R. Ratcliff, 2004; K. J. Friston, 2005), however, response peak variability did not originate from a passive propagation of variability prior to stimulation over time. This latter observation speaks against a simple additive mechanism, by which evoked activity superimposes onto ongoing activity (A. Arieli et al., 1996).

Here, we sought to investigate whether these effects of ongoing activity fluctuations would also be observed in another domain of vision and thus other cortical substrates. We targeted the perception of coherent visual motion and motion-sensitive human brain areas. In the macaque brain, a medial temporal (MT) area is crucial for integrating local motion vectors and thus perceiving coherent motion (R. T. Born, Bradley, D.C., 2005). Direct electrical stimulation of MT biases motion direction judgements (C. D. Salzman et al., 1990). A variety of functional neuroimaging studies have related subjects' perceptual experience of motion to activity of hMT+, the assumed human homologue of MT (R. Goebel et al., 1998; G. Rees, Friston, K., Koch, C., 2000; J. T. Serences and G. M. Boynton, 2007)..

We framed our experiment as a perceptual decision task on an ambiguous stimulus. In a sparse event-related fMRI design with long and variable rest intervals, subjects were intermittently

exposed to motion stimuli with a coherence level at their previously determined detection thresholds as well as to occasional sub- or supraliminal stimuli. They reported for each trial whether they perceived 'coherent' or 'random' motion. We tested whether higher pre-stimulus BOLD activity levels in hMT+ biased perception towards reporting coherent visual motion. Furthermore, we analyzed the effect of pre-stimulus activity on the peak BOLD response in order to corroborate – or not - our earlier finding of a non-additive relation between evoked and ongoing activity.

Materials and methods

Subjects and experimental protocol

Twelve right-handed subjects with normal or corrected-to-normal visual acuity (6 female, average age: 21 years, range: 19–30 years) gave written informed consent. We had ethics committee approval for this study. Stimuli were video-projected at a 120cm viewing distance using a VSG2/5 stimulus generator card (CRS, Rochester, UK). Stimuli were dynamic dot displays of 500 white squares (size 0.2°) randomly distributed on a dark grey annulus (23°) (Fig. 1A). Subjects were instructed to maintain gaze within a central blue rectangle (1°) surrounded by a light grey circular patch (3°) throughout the experimental sessions. Eye-tracking during fMRI was not available, but off-line recordings ensured that subjects could well comply with this instruction. For 355ms intervals, stimuli moved up- or downwards, at 14°/s and with variable coherence. Noise dots moved in a 'random walk'. Signal dots had a limited lifetime of one frame (17ms). Subjects were asked to report as quickly and accurately as possible by hand key presses after each stimulus whether they had perceived coherent or random motion.

Prior to scanning we used the method of constant stimuli (30 trials each with motion coherence of 2, 6, 10, 14, 18, 22, and 26%, order randomized, no feedback) to determine individual motion coherence thresholds (50% level of a cumulative normal distribution fit, average motion coherence threshold across subjects 13%, range 8 to 20%). During fMRI, three motion coherence levels were

used: subliminal (1% coherence, 20 trials), periliminal (individually estimated theshold, 60 trials), and supraliminal (30% coherence, 20 trials). Stimuli were presented in two 25 minute sessions with 50 trials each. Between stimuli, the display was static for inter-stimulus intervals (ISI) of 20 to 40s that were randomly selected from a uniform distribution.

Acquisition and processing of fMRI data

Functional images for two 1000 volume experimental sessions and a 208 volume localizer session were acquired on a 3T MRI scanner (Tim Trio, Siemens, Erlangen) by T2*-weighted gradient-echo echo-planar imaging (25 slices, TR = 1500ms, TE = 30ms, voxel size 3x3x3mm, inter-slice gap 20%). Anatomical images were acquired with a T1-weighted MPRAGE sequence (160 slices, TR = 2300ms, TE = 2.98ms, FOV 256, voxel size 1.0x1.0x1.1mm). We used SPM5 (http://www.fil.ion.ucl.ac.uk, Wellcome Trust Centre for Neuroimaging, London, UK) for image pre-processing (realignment, coregistration, normalization to MNI stereotactic space, spatial smoothing with an isotropic Gaussian kernel of 6 and 12mm full-width-half-maximum for single subject and group analyses, respectively) and estimation of the statistical maps.

Definition of regions of interest (ROIs)

Localizer fMRI sessions identified cortical regions sensitive to two types of coherent visual motion, up- or downwards motion and an expanding 'starfield'. Continuous 16s motion blocks were separated by 10s stationary periods, and each condition was repeated over 6 blocks in counter-balanced order. Motion-sensitive areas were identified by mapping for each subject the contrast 'motion > stationary' at $p<0.001$, uncorrected. A local maximum near the ascending limb of the inferior temporal sulcus, was defined as hMT+, a second posterior, superior and medial maximum putatively labeled as hV3/V3A ((R. B. H. Tootell, Mendola, J.D., Hadjikhani, N.K., Ledden, P.J., Liu, A.K., Reppas, J.B., Sereno, M.I., Dale, A.M., 1997) see supplementary table T1 for coordinates of all ROIs).

Analysis of fMRI data

After removing session effects and linear trends from the BOLD signal time series, we extracted for each ROI the percent signal change time courses of all periliminal trials from 4 scans (6s) before to 12 scans (18s) after target onset and sorted them according to 'coherent' and 'random' percepts. Based on our previous findings (G. Hesselmann, Kell, C.A., Eger, E., Kleinschmidt, A., 2008), three time points were chosen for statistical analysis: time points -1.5 and 0s in the immediate pre-stimulus baseline as well as the peak hemodynamic response at 6s. Data were submitted to a repeated-measures 2x3 ANOVA ('percept' x 'time point') and post-hoc testing with paired t-tests.

Results

Behavioral data

Periliminal motion stimuli yielded across subjects 57% 'coherent' and 43% 'random' percepts (t_{11} = 2.06, n.s.; range for 'coherent' 43–77%). This ratio was consistent across the two sessions. Subliminal stimuli were more often seen as 'random' than periliminal stimuli (74%, $t_{11} = 5.64$, $p < 0.001$) and supraliminal stimuli more often as 'coherent' (94%, $t_{11} = 17.97$, $p < 0.001$). We found no carry-over of percepts reported in successive trials, with average incidence of percept repetitions (across trials and coherence levels) well approximated by a binomial distribution indicating stochastic behavioral reports (Fig. 1B). Subjects responded faster in supraliminal (1119ms) than subliminal (1259ms) and periliminal trials (1241ms). In periliminal trials, subjects responded approximately 160ms faster for 'coherent' (1160ms) than for 'random' percepts (1324ms, $t_{11} = 4.03$, $p < 0.01$).

Functional imaging data

All motion-sensitive ROIs showed a clear hemodynamic response in the periliminal experimental trials of interest. A significantly larger response for 'coherent' than for 'random' perception of

periliminal stimuli was found only in right hMT+ (main effect 'percept', $F_{1,11} = 8.91$, $p = 0.012$, posthoc $t_{11} = 2.26$, $p = 0.045$) but not in left hMT+ and both hV3/V3A (Fig. 2). Significant percept-dependent signal differences in pre-stimulus activity during these trials were also restricted to right hMT+. In 'coherent' trials, activity starting at about 1.5s before stimulus onset was higher than in 'random' trials. Planned post-hoc tests revealed an effect at the immediate pre-stimulus time point 0s ($t_{11} = 3.61$, $p < 0.005$). The activity difference at -1.5s did not reach significance, whereas exploratory analysis of the peri-stimulus time point 1.5s did ($t_{11} = 2.25$, $p = 0.046$) but this time segment was not targeted a priori and the effect did not survive Bonferroni correction for testing at multiple time points. Overall, the effect could neither be related to a significant activity increase over time in one nor a decrease within another of the two conditions.

To explore the spatial specificity of the pre-stimulus signal for perceptual performance, we analyzed time courses in a set of control regions that significantly activated or deactivated during perceptual decisions (Fig. S1). These regions included areas involved in early visual motion processing (V1/V2), as well as attention and perceptual decision making (right IPL, right and left FEF, right IFG, and ACC). No region showed percept-dependent signal differences in the pre-stimulus baseline epoch, and additional voxel-based whole brain analyses were also negative. Early visual cortex showed a significantly larger evoked response in 'random' than in 'coherent' trials when testing for the effect of condition in an ANOVA ($F_{1,11} = 7.391$, $p = 0.020$). Although this difference appears to arise at time points that cannot yet carry stimulus-driven signal, this observation of opposite sign as in hMT+ remained non-significant for individual time points including baseline.

To further probe the relationship between right hMT+ activity and perception, we analyzed choice probabilities for the immediate pre-stimulus baseline (0s) and the peak response (6s). Across subjects, a 'coherent' percept could be predicted significantly better than chance from the pre-stimulus baseline level (mean area under the curve (AUC) = 0.57, $t_{11} = 3.89$, $p < 0.005$) as well as from the response peak (mean AUC = 0.55, $t_{11} = 2.02$, $p = 0.035$). An earlier 'reference' time point at -6s was of no predictive power (mean AUC = 0.50), underlining the temporal specificity of the

pre-stimulus effect in right hMT+ and hence activity fluctuations as its origin (Fig. S2). Interestingly, however, the intermediate time points between the pre-stimulus baseline segment and the response peak also failed to show significant prediction. This observation suggests that the fMRI signal carries two different types of information that are both related to perception but in a different way. One source of information can be captured prior to the effects of sensory stimulation, the other in their presence, but at time points mixing the two, these effects cancel out. In line with this interpretation, we observed that classification either from the pre-stimulus period or from the response peak was preserved when testing signal at each time point after its covariance with signal at the other time point had been removed by regression.

Next, we analyzed behavioral correlations with activity levels at baseline and response peak in periliminal trials. Although on average RTs differed between the two percepts, they did not within or across conditions correlate trial-by-trial with activity levels in right hMT+, neither at the prestimulus baseline, nor at the peak response (for findings in other regions see Fig. S1). This lack of reaction time correlation is compatible with a task-unrelated origin of pre-stimulus signal variations and is often considered a characteristic of 'stimulus-independent' as opposed to 'stimulus-oriented' neural activity (S. J. Gilbert et al., 2007). RT shortening is generally considered a hallmark of deploying attention, and the variability in baseline therefore cannot be linked to attentional mechanisms in a straightforward way.

Finally, we assessed the trial-by-trial variability in ongoing and evoked activity and their relation to perceptual outcome of periliminal trials. If the fundamental mechanism that links evoked responses to ongoing activity was additive, as suggested by earlier work in anesthetized animals (A. Arieli et al., 1996), then there should be a positive correlation across trials between activity levels at the response peak with those during the preceding baseline. In other words, the higher activity prior to stimulation, the higher the peak of the response amplitude. We hence calculated the linear regression of the peak response at 6s on the prestimulus activity at -1.5s for each subject (Fig. 3A). We then submitted the resulting beta values to a paired test. In 'random' trials, there was indeed a

weak positive correlation between ongoing and evoked activity levels but not in 'coherent' trials (Fig. 3B). Accordingly, statistical testing showed a significant interaction of these correlations with perceptual outcome. This interaction expresses that hMT+ response peaks were significantly less correlated with ongoing activity when subjects perceived coherent motion than when they failed to do so. This observation is not trivial because on average both ongoing and evoked hMT+ activity were correlated with coherence perception in the identical stimulus. Yet notwithstanding this average result, the pre-stimulus and the stimulus-driven activity were not on a trial-by-trial basis correlated with each other, which in turn suggests that variability in both time segments contributes independently to whether coherent motion is perceived on individual periliminal trials (P. L. Smith and R. Ratcliff, 2004).

Discussion

In the present study, we extend our earlier observation (G. Hesselmann, Kell, C.A., Eger, E., Kleinschmidt, A., 2008) to a different domain of visual perception and thus corroborate an effect that we propose to be a general principle. We show that local ongoing activity in motion-sensitive area hMT+ significantly predicted whether for a periliminal random dot motion stimulus coherence was perceived or not. We expected this region to be the most suitable candidate for detecting an effect from ongoing activity on perception because a wide functional neuroimaging literature has shown responses in this area to correlate with visual motion perception. Recent multi-voxel response pattern analyses, for instance, have shown that fMRI activation in hMT+ matches the observer's perception, whereas responses in other visual areas do not (J. T. Serences and G. M. Boynton, 2007).

We did not observe effects from ongoing activity in any other brain regions responding to the task, which probably reflects the fact that our paradigm was optimized to target functional properties of hMT+ (M. N. Shadlen and W. T. Newsome, 2001). An important difference of our previous and

current findings from spontaneous activity fluctuations compared to artificial activity manipulation by microstimulation of specialized cortical areas is that microstimulation *before* stimulus onset has to our knowledge not yet been shown to influence perceptual outcome (C. D. Salzman et al., 1990). We propose that this difference between experimental methods can be explained by the non-physiological structure of microstimulation-induced activity changes as opposed to the physiological nature of spontaneous BOLD fluctuations.

That our effect was confined to right hMT+ is internally consistent within our data set in that this region was also the only one to demonstrate a significant response difference to the periliminal stimulus as a function of how it was perceived. In other words, this region seems to be the most sensitive one in relation to task-relevant stimulus features. This interpretation is congruent with a larger literature which has shown a right hemisphere lateralization of hMT+ activity when wide-field optic flow stimuli are used, as was the case here including our masking of the central field portion (H. Peuskens et al., 2001).

Previous experiments in anesthetized animals described that the stimulus-evoked response simply adds to the level of ongoing activity present during stimulus onset (A. Arieli et al., 1996). This additive mechanism could nonetheless be functionally relevant, for instance by determining whether a neural response on a given trial passes a threshold. We found that in awake humans the impact of local spontaneous ongoing activity variations on stimulus-evoked activity is not simply additive but interacts with perceptual outcome. Our findings, including lower evoked response in V1 for 'coherent' trials, are compatible with theoretical perspectives that emphasize the constructive nature of perceptual processes, e.g., predictive coding and related conceptual frameworks (K. J. Friston, 2005); (L. M. Harrison et al., 2007). Seen from this perspective, it could be argued that spontaneous activity fluctuations carry 'dynamic predictions', as suggested recently (M. D. Fox and M. E. Raichle, 2007).

Dynamic predictions could manifest in pre-stimulus activity as a prior against which the incoming

sensory input is matched. With independent variability in both parameters, the prior and the input representation (M. G. Philiastides et al., 2006), one can sketch four illustrative situations. High prior activity and congruent sensory input processing generate little mismatch or prediction error and thus a weak evoked response in a 'coherent' perception. Low prior activity but strongly represented coherence in the input signal generates a mismatch with a strong evoked response and the perception of coherence. This would explain why response peak activity levels in coherent percepts do not increase with baseline activity. Conversely, if the prior is high but the trial is perceived as random, there has been a fair amount of prediction error, and thus a greater signal increment than in trials where the prior was low and that were reported as random and thus congruent with the prior. The latter two cases would then explain why in the case of 'random' percepts there is a weak but significant positive relation between ongoing and evoked activity levels. Importantly, the pre-stimulus prior in itself also represents a prediction error, namely between the top-down prediction of a specific sensory signal and the pre-stimulus instance when such input is still lacking.

Beyond such a speculative account, however, the key point is that the relation between ongoing and evoked activity depends on perceptual outcome. This observation in itself cannot be explained in a simple mechanistic model where responses add onto ongoing activity levels and where this relation should be the same across trials whatever the perceptual outcome As in our previous experiment, the functionally significant effect was apparently restricted to a focal brain region that is crucial for the task at hand. Our findings characterize the consequences of such spontaneous variations in ongoing activity for visual motion perception and thus inform models of perceptual decision-making (H. R. Heekeren et al., 2008).

The physiological origin or cognitive meaning of spontaneous fluctuations in the awake brain, is not yet fully understood and cannot be clarified by our or any related results because studies that address functional significance inevitably require an overarching task context so as to probe the perceptual or behavioral consequences of baseline signal fluctuations. In current views on the nature of spontaneous brain activity (M. D. Fox and M. E. Raichle, 2007), signal fluctuations observed in

fMRI may span processes at several different levels of neural activity, ranging all the way from intrinsic noise over low-level physiological processes to uncontrolled mental activity with varying degrees of contribution from the actual experimental context. One of several important unresolved issues is the relation of baseline fluctuations to attention (M. Boly et al., 2008). Across a distributed system of areas underpinning selective attention, variability in cued pre-stimulus fMRI signal changes has been found to predict perceptual performance (A. Sapir et al., 2005). Allocation of attention raises baseline fMRI signal even in the absence of sensory input (S. Kastner et al., 1999) but also leads to RT shortening and an often linear increase in evoked sensory responses (D. Chawla et al., 1999; S. A. McMains et al., 2008). That the effects in our study did not show these but in part opposite properties cannot formally rule out a contribution from attentional mechanisms but renders them unlikely. In the absence of a full account of origin and connotation of spontaneous activity, however, our findings are important because they show that this unexplained variance, whatever its origin, contributes significantly to the way in which the brain and the observer respond to external sensory stimuli (G. Deco and R. Romo, 2008).

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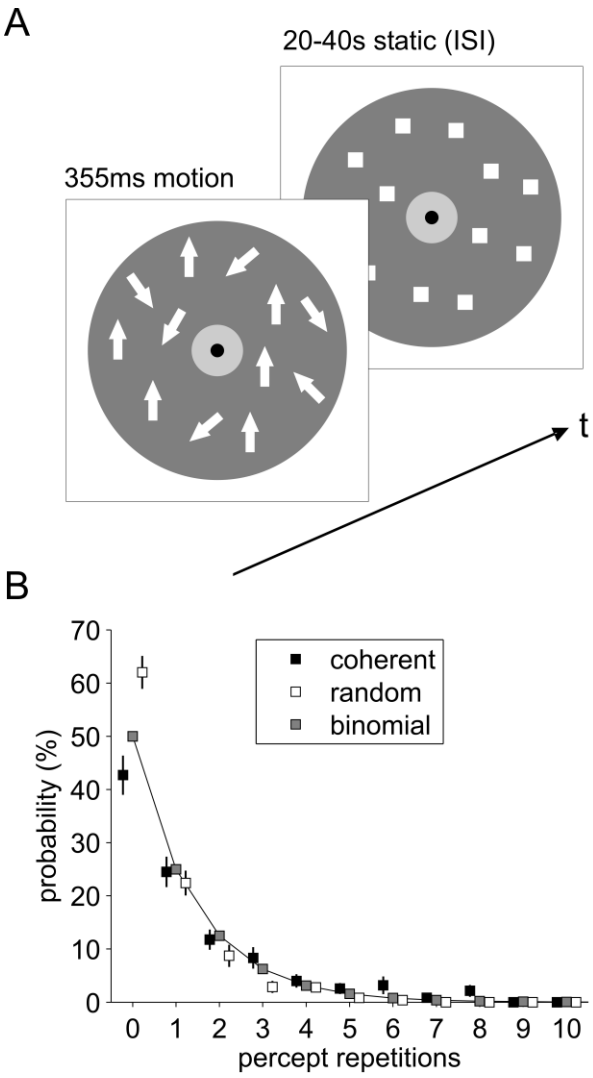
Figure legends

Figure 1. (A) On every trial, a motion stimulus (either up- or downwards) of variable coherence (sub-, peri-, or supra-threshold) was presented for 355ms in a dynamic random dot display. Subjects reported whether they had perceived 'coherent' or 'random' motion. Inter-stimulus intervals (ISI) with stationary display ranged from 20 to 40s. White arrows represent the motion vectors of dynamic dots. (B) The incidence of repetitions for either percept averaged across all ISIs can very well be approximated by a binomial distribution (goodness-of-fit $R^2 = 0.98$, for 'coherent' percepts, $R^2 = 0.91$, for 'random' percepts).

Figure 2. Peristimulus fMRI signal time courses from motion-sensitive brain regions, hMT+ (upper panels) and putative hV3/V3A (lower panels). Data averaged across all subjects with error bars representing standard error and filtered with a [1 2 1] kernel for display purposes. Statistical parametric maps from an individual subject localize motion areas as identified by the contrast 'motion > stationary' ($p < 5*10^{-5}$, uncorrected, axial slices overlaid on the average anatomy).

Figure 3. Single subject and mean percept-dependent regressions between trial-by-trial pre-stimulus activity at -1.5s and peak activity at 6s in right hMT+. (A) Illustrated for a single subject, linear regressions ($y = a + bx + c$) were fitted to the data from periliminal trials (upper panel for trials with 'random' percepts, lower panel for 'coherent' percepts). (B) Plot of the linear regression coefficients b for all subjects as a function of percept. As indicated by asterisks, coefficients were significantly larger than 0 in 'random' trials (0.28, $t_{11} = 3.55$, $p < 0.01$) but not in 'coherent' trials (0.09, $t_{11} = 1.7$, n.s.), and significantly different between the two perceptual outcomes ($t_{11} = 3.24$, $p < 0.01$, two-sided paired t-test).

Figures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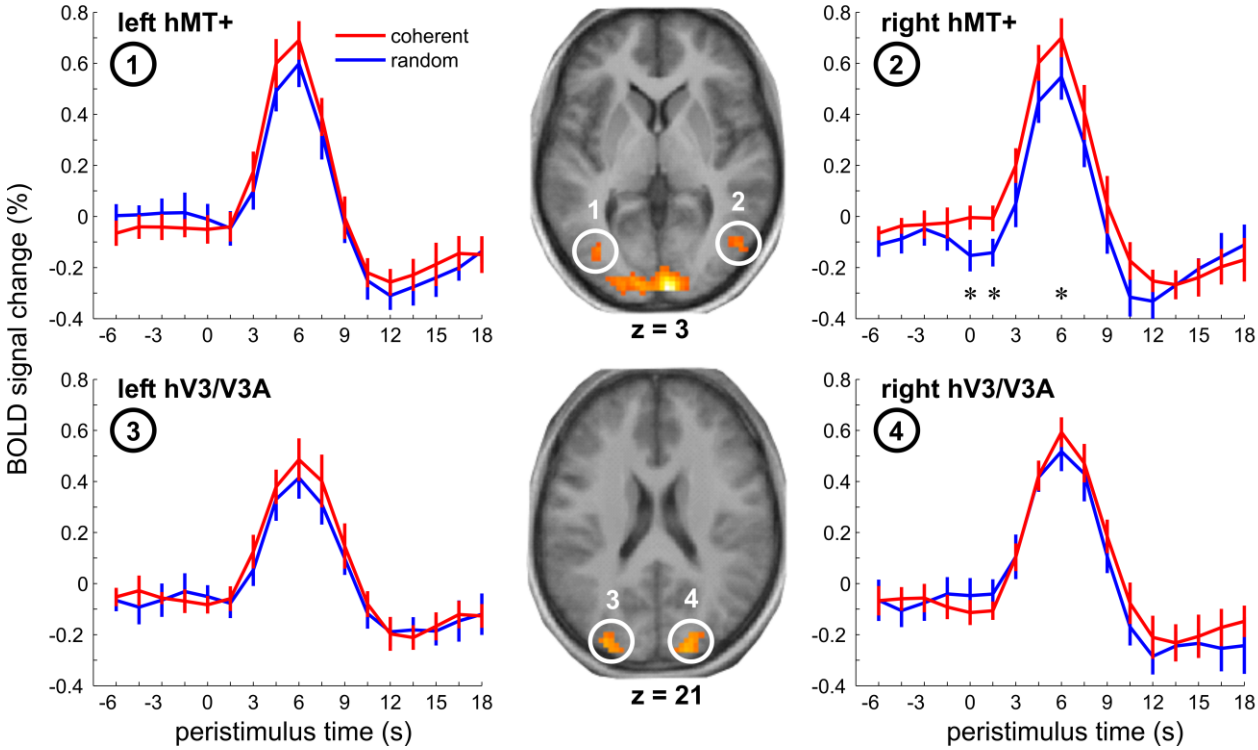
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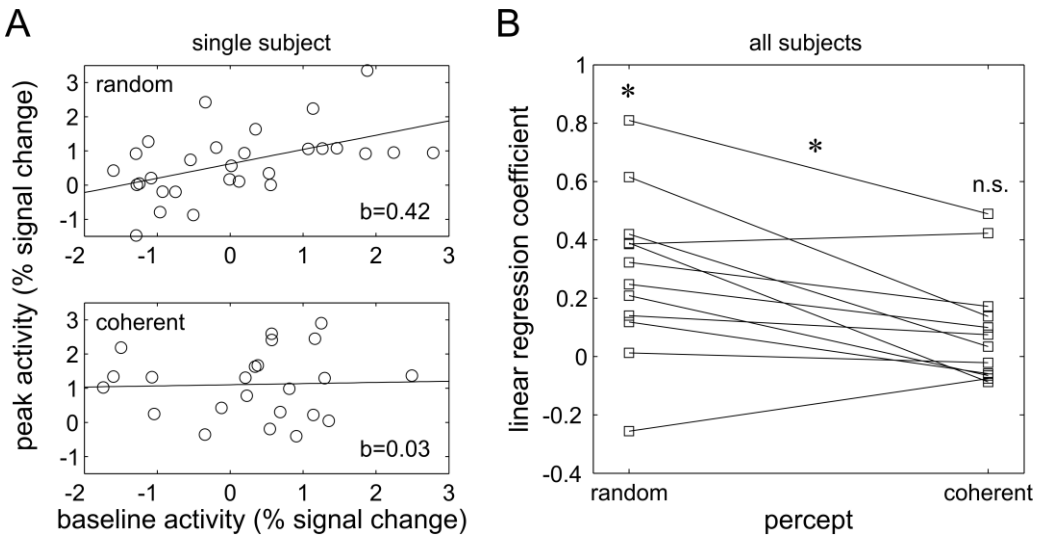
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