Synchronization between the end-stages of the dorsal and the ventral visual stream

Bram-Ernst Verhoef, Rufin Vogels and Peter Janssen*

Laboratorium voor Neuro- en Psychofysiologie
Campus Gasthuisberg, O&N2,
Herestraat 49, Bus 1021,
BE 3000 Leuven,
Belgium.

*Address correspondence to: Peter Janssen
Peter.Janssen@med.kuleuven.be

Running title: Functional connectivity between IT and AIP

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Abstract

The end-stage areas of the ventral (IT) and the dorsal (AIP) visual streams encode the shape of disparity-defined three-dimensional (3D) surfaces. Recent anatomical tracer studies have found direct reciprocal connections between the 3D-shape selective areas in IT and AIP. Whether these anatomical connections are used in order to facilitate 3D-shape perception is still unknown. We simultaneously recorded multi-unit activity (MUA) and local field potentials in IT and AIP while monkeys discriminated between concave and convex 3D shapes, and measured the degree to which the activity in IT and AIP synchronized during the task. We observed strong beta-band synchronization between IT and AIP preceding stimulus onset that decreased shortly after stimulus onset and became modulated by stereo-signal strength and stimulus contrast during the later portion of the stimulus period. The beta-coherence modulation was unrelated to task-difficulty, regionally-specific and dependent on the MUA-selectivity of the pairs of sites under study. The beta-spike-field coherence in AIP predicted the upcoming choice of the monkey. Several convergent lines of evidence suggested AIP as the primary source of the AIP-IT synchronized activity. The synchronized beta activity seemed to occur during perceptual anticipation and when the system has stabilized to a particular perceptual state but not during active visual processing. Our findings demonstrate for the first time that synchronized activity exists between the end-stages of the dorsal and ventral stream during 3D-shape discrimination.
Keywords: dorsal-ventral stream, 3D-shape perception, functional connectivity, IT-AIP, synchronization
Introduction

To understand the functioning of brain networks, one must know the properties of its constituting elements and the interconnections between them. Traditional neuroscience has mainly focused on the functional properties of brain elements (e.g. feature tuning of neurons or the functional role of brain regions). However, recently there has been an increased interest in the brain’s “connectome” (Sporns et al. 2005), i.e. the neural connections at the micro-, meso- and macroscale. The study of neural connections is important since it can be argued that the function of a network is critically dependent on the pattern of its interconnections (Bullmore and Sporns 2009; Bressler and Menon 2010). Although considerable attention has been given to the study of anatomical connections, so far relatively few studies have concentrated on the “functional” connectivity between brain areas, especially at the macroscale (Krienen and Buckner 2009; Rodriguez et al. 1999; Schatpour et al. 2008; Uhlhaas et al. 2006).

Functional connectivity has been defined as a statistical dependency between the activity of the elements of a system (Bullmore and Sporns, 2009). Functional connectivity between two brain areas is often assessed by measuring the degree of synchronization between the simultaneously recorded neural activities of these areas (Buschman and Miller 2007; Fries 2005; Gregoriou et al. 2009; Kayser and Logothetis 2009; Pesaran et al. 2008). Such synchronization has been related to task manipulations and behavioral measures (Buschman and Miller 2007; Fries et al. 2001; Pesaran et al. 2008; Schoffelen et al. 2005).
The primate visual system consists of (at least) two distinct processing streams: a ventral visual stream for object recognition and a dorsal visual stream for visuo-motor transformations and spatial vision (Goodale and Milner 1992; Ungerleider and Mishkin 1982). Previous studies have demonstrated that neurons in the inferior temporal cortex (IT, area TEs), part of the ventral visual stream, are selective for three-dimensional (3D) shapes in which depth is defined by binocular disparity (Janssen et al. 2000a, 2000b). In addition, neurons in the anterior intraparietal area AIP, the end-stage of the dorsal visual stream, also exhibit selectivity for disparity-defined 3D shapes (Srivastava et al. 2009; Verhoef et al. 2010). Furthermore recent anatomical tracer studies have found direct reciprocal connections between 3D-shape selective areas IT (area TEs) and AIP (Borra et al. 2008, 2010). Accordingly, several authors have hypothesized that these anatomical connections are used in order to facilitate 3D-shape perception (Chinellato and Del Pobil 2009; Orban et al. 2006). To test this possibility, we trained two rhesus monkeys to discriminate between disparity-defined concave and convex 3D shapes, and recorded simultaneously in IT (TEs) and AIP during 3D-shape discrimination. We then assessed the functional connectivity between both areas by measuring the degree to which the activity in IT and AIP synchronized during the performance of the task.
Materials and Methods

Subjects and surgery

Two male rhesus monkeys (*Macaca mulatta*) served as subjects. Under isoflurane anesthesia and aseptic conditions a recording cylinder (32 mm diameter; Thomas Recording Ltd, Marburg, Germany) was implanted oriented vertically above the Intraparietal Sulcus (IPS) and anterior IT in the same hemisphere (left hemisphere for monkey B1, right hemisphere for monkey B2). All surgical procedures and animal care were approved by the K.U. Leuven Ethical Committee and in accordance with the European Communities Council Directive 86/609/EEC. Monkey B1 also received an ultrasound cylinder implanted below and orthogonal to the recording cylinder in the coronal plane (left hemisphere). This extra cylinder allowed real-time imaging of the IPS and the electrode tip before and after the recording sessions by means of high-resolution ultrasound imaging (Philips HDI 9 5000 SonoCT: scan frequency 17 Mhz, resolution 0.5 mm. Philips, Eindhoven, The Netherlands). Structural MRI (0.6 mm slice thickness) using glass capillaries filled with a 1% copper sulphate solution inserted into several grid positions and the pattern of grey- to white matter transitions confirmed that the recordings were made in the anterior part of the lateral bank of the IPS and in the anterior part of the lower bank of the Superior Temporal Sulcus (STS; IT: Horsley-Clark coordinates: 16-17.5mm anterior, 22-24mm lateral; AIP: 3.5-4.5mm anterior, 13-14mm lateral).
The stimulus set has been described in detail in Verhoef et al. (2010). Briefly, the stimulus set consisted of static random-dot stereograms with 8 different circumference-shapes (e.g. circle, ellipse, square, etc.; size: ~ 5 degrees). Before we started the discrimination experiment, we first selected the optimal (within our stimulus set) circumference shape using a fixation task in which only 100% signal strength stimuli (see below) were presented. The preferred circumference shape, as determined in one of the two regions (varied daily), was subsequently used during the discrimination task. Stimuli were centered foveally on a grey background. The depth structure was defined solely by horizontal disparity as a two-dimensional radial basis Gaussian surface which could be either convex or concave (maximal disparity amplitude: 0.15 degrees). Stimuli were presented at 3 positions in depth, i.e. before, behind or at the fixation plane (±0.23 degrees depth variation). Task difficulty was manipulated by varying the percentage of dots defining the surface, i.e. the signal strength (or stereo-coherence). Dots that were not designated as defining the surface were assigned a disparity that was randomly drawn from a uniform distribution (support = [-0.50 degrees, 0.50 degrees]). During recording we used 3 different signal strengths (0%, 20% and 100% for monkey B1; 0%, 10% and 100% for monkey B2). For a particular circumference-shape all stimuli contained the same number of dots, regardless of the signal strength, the position in depth or the 3D-shape. For each experiment we used 20 different random dot patterns per signal strength. During some recording sessions we also presented a black or white square stimulus (with zero disparity; 5 degrees on a side) interleaved with the stereograms. The white square
stimulus contained a black aperture (size = 1.3 deg) in the centre in order to keep the fixation dot visible. All stimuli were presented on a grey background, rendering the black square a visible stimulus. Stimuli were presented dichoptically by means of a double pair of ferroelectric liquid crystal shutters (2 superimposed shutters in front of each eye; Displaytech, Longmont, CO). All 4 shutters operated at 60 Hz, synchronized with the vertical retrace of the display monitor (vertical refresh rate = 120Hz) equipped with a fast-decay P46 phosphor (VRG, Durham, NH, USA).

**Task**

Monkeys were required to maintain fixation (fixation window < 1.5 degrees on a side) on a small fixation point (size: 0.09 deg) for a fixed duration (425ms or 525ms in separate experiments; see below). Once fixation was achieved, a stimulus was presented for 800ms centered on the fixation dot. If the monkey maintained its gaze within the fixation window throughout the whole stimulus presentation, two response targets appeared on the left and right side of the fixation dot at 6 degrees eccentricity. The subject was required to make a saccade to one of these targets depending on whether he perceived a convex (to the right or left for monkey B2 and B1 respectively) or concave (to the left or right for monkey B2 and B1 respectively) shape (Fig. 1a). Correct responses were followed by a liquid reward. The 0% signal strength trials were randomly rewarded with a probability of 0.5. For the black and white square stimulus, the correct response was always indicated by a single response target that appeared immediately following the stimulus presentation (to the left and right side of the fixation dot for the white and the
black square respectively). All stimulus-response contingencies remained identical throughout the recording sessions.

**Recording of neural and eye signals**

For the simultaneous recordings in IT and AIP, two “Micro Matrix” microdrives (Thomas Recording Ltd, Marburg, Germany) with integrated single-channel preamplifier were mounted on a holder that was positioned on top of the recording chamber. For each microdrive, a quartz-platinum/tungsten microelectrode (~0.7 MOhm at 1kHz; 80 micron diameter) was lowered through a guide tube positioned in a grid (Thomas Recording Ltd, Marburg, Germany). Each electrode was referenced to its own guide tube that was situated >7 mm above the region in which the recordings were performed. Neural signals were amplified and filtered between 0.5 kHz and 5 kHz for spikes using an aperiodic Bessel Butterworth filter with a roll-off of 12dB/octave, and between 1 Hz and 141 Hz for local field potentials (LFPs) using an aperiodic Bessel Butterworth filter with a roll-off of 30dB/octave and 12dB/octave for low –and high pass filtering respectively. Stimulus onset was registered by a photodiode attached to the screen detecting the onset of a bright square (occluded and not visible to the monkey) appearing at the bottom of the display simultaneously with the stimulus. The horizontal positions of each eye and the vertical position of the right eye were monitored using an infrared-based camera system (EyeLink II, SR Research, Main, Canada). Eye position signals were sampled at 1kHz while spiking activity and photodiode pulses were sampled at 20 kHz on a DSP (C6000 series, Texas Instruments). The LFP signals were sampled at 1 kHz. Spikes were
discriminated online by the DSP using a dual time-window discriminator and displayed using LabView and custom-built software. Multi-unit activity (MUA) was obtained by setting the threshold for spike discrimination approximately 2 standard deviations below the mean extra-cellular spike signal of the fixation period.

**Data Analysis**

All analyses were performed using scripts written in Matlab (R2008a, MathWorks). LFPs were preprocessed by removing the power related to 50 Hz oscillations (i.e. power line artifact) and 60 Hz oscillations (i.e. stereo shutter artifact) using a 4th order Butterworth notch filter. Notch filtering produced a “dip” of limited bandwidth (~2Hz) in the LFP power spectrum around the respective center frequencies. The spectral smoothing inherent to the multitaper and wavelet analysis renders the influence of the narrow band spectral dips negligible. Hence, unless coherence was confined to these band limited “dips”, our results were not distorted by the filtering process. Note also that we obtained qualitatively identical results in 40 pairs of recording sites in which no shutter artifacts were present and therefore no 60Hz notch filtering was required. For each condition (i.e. a particular disparity signal strength, black or white square) and recording site, the mean of the LFP across trials (i.e. the visually evoked potential) was subtracted from the LFP traces of their respective trials. We used coherence (here defined as $|\text{coherency}|^2$) as a measure of functional connectivity between two regions (Bullmore and Sporns 2009). The coherence measures the degree of amplitude and phase correlation between two signals at a certain frequency (Priestley 1981). The LFP-LFP-coherence was calculated
using the continuous wavelet transform (complex Morlet wavelet; width = 7; \( \sim \)6Hz spectral resolution and \( \sim \)111ms temporal resolution at 20 Hz). The wavelet transform method (Lachaux et al. 2002; Tallon-Baudry et al. 1997) was employed because its time-frequency uncertainty is well adapted to the width and the dynamics of the different LFP frequency bands. However, we obtained very similar results using the multitaper method. We used a fixation period of 425ms in 40 sessions for monkey B1 and of 525ms in 7 sessions for monkey B1 and in all sessions for monkey B2. The LFP-data of the sessions with the 425ms fixation period were reflected about the first LFP-value of each trial which allowed the wavelet-convolution to start at 425ms before stimulus onset. In this way, we could show (Fig. 3 and 4) the dynamics of the LFP-power –and coherence during the entire 425ms fixation period without confining ourselves to the datasets with the 525ms fixation period. However, the average fixation period coherence-dynamics were highly similar when restricting our analyses to the datasets with a 525ms fixation period. That is, similar to the results for the complete dataset (see Results) we noticed a significant increase of the beta coherence during the fixation period.

We used multitaper analysis to estimate the spike-field and spike-spike coherence (5 discrete prolate spheroidal sequences (dpss) tapers; \( \pm \) 8.6Hz spectral resolution; 350ms sliding window). The multitaper method has been widely used for estimating the spike-field and spike-spike coherence (Gregoriou et al. 2009; Pesaran et al. 2002; Pesaran et al. 2008; Womelsdorf et al. 2006) and is especially suited when dealing with point processes such as MUA (Zeitler et al. 2006). Time-frequency representations of the spike-field and spike-spike coherence were obtained by using a sliding window analysis with a width of 350 ms that was progressed in time in steps of 10ms (time was designated to the center of
the window). The use of multiple tapers results in less variable coherence estimates but decreases the spectral resolution. We therefore verified whether multitapering affected the estimated peak coherence frequency. For this reason we used a 400ms sliding time window with only one dpss taper (spectral resolution of ±2.5 Hz). This analysis revealed very similar results with peak frequencies between 17.5Hz and 20Hz. Hence, multitapering had little influence on the estimated peak coherence frequency.

We employed spectral Granger causality analysis based on multivariate autoregressive (MVAR) modeling to measure directed connectivity between AIP and IT. One stochastic process \(X_1\) is said to “Granger cause” a second stochastic process \(X_2\) if the autoregressive predictability of \(X_2\) is improved by the inclusion of past values of \(X_1\) (Granger 1969). We used Geweke’s Granger causality (Geweke 1982), which has been used in various other studies (e.g. Brovelli et al. 2004; Gregoriou et al. 2009), as a measure of directional influences between two regions. The MVAR model assumes that the data are drawn from a second-order stationary process. This is generally not the case for neural processes such as LFPs. We therefore adopted a time-varying MVAR model approach based on a sliding window analysis (window length = 350ms; step duration = 10ms; time was designated to the center of the window; (Ding et al. 2000). This approach is based on the reasonable assumption of second-order stationarity of the LFP within a short time window. Note also that the ensemble mean of the LFP of each site was subtracted from the single LFP traces, rendering the data first-order stationary. For each time window and for each pair of LFP-traces the coefficient matrices of the MVAR model were estimated using the Vieira-Morf algorithm with unbiased covariance estimates. This algorithm is currently one of the most accurate estimation algorithms
The MVAR model of order 30 recovered many details of the coherence spectrum as estimated by the non-parametric wavelet method (See Fig. S3). Model stability was assessed by the roots $\lambda_i$ of the characteristic polynomial of the model, where the roots must satisfy the condition $|\lambda|<1$ (Ding et al. 2000). Only stable models were used in the analyses, resulting in the elimination of only $\sim0.01\%$ of all estimated models. For each trial and each temporal window the MVAR-model was fitted to the LFP-segment contained in that temporal window. Subsequently, for a particular location of the temporal window, the coefficient matrices and noise-covariance matrices were averaged across trials. These parameter estimates were used to calculate the spectral matrix which was used to calculate Geweke’s Granger causality. Geweke’s Granger causality from $X_2$ to $X_1$ quantifies the contribution of power (at frequency $f'$) of $X_2$ to the total power of $X_1$ (at frequency $f$). Another measure of directionality, i.e. the directed transfer function, produced qualitatively identical results (data not shown). All coherence or Granger causality estimates for the different conditions of a particular recording session were based on an equal number of trials to avoid differences due to finite sample bias. Unless stated otherwise, all statistical tests (t-tests and ANOVAs) are permutation tests. The beta band was defined as the frequencies between 17Hz and 25Hz.

Coherence and Granger causalities were computed for pairs of sites for which both regions displayed responsive MUA as tested by a 2-way split-plot ANOVA with “baseline vs. stimulus period” as repeated measure and “signal strength” (together with black and white squares if available) as between-condition factor. The baseline period was defined as the 400 ms immediately preceding stimulus onset. The stimulus period was identified as the 400ms period starting 50ms after stimulus onset (to account for
response latencies). The MUA of these periods was averaged over time per trial and square-root transformed before performing the ANOVA. Responsiveness was defined as a significant main effect of baseline vs. stimulus period ($\alpha = 0.05$). We calculated the response latency of each responsive MUA-site as the first of 2 consecutive 10ms-bins for which we observed a significant difference in spike rate with respect to the baseline period (paired permutation t-test; $\alpha = 0.05$; n = 15000 permutations).

**Results**

Two monkeys were trained to discriminate between concave and convex 3D shapes using as operant a saccade to one of two response targets that appeared immediately after stimulus presentation (Fig. 1a). On each trial, a static random-dot stereogram portraying either a concave or a convex surface was presented at one of three positions in depth, i.e. in front of, behind or at the fixation plane (Fig. 1b). This procedure enforces the use of perceptual strategies that are based on disparity variations within the stimulus (i.e. disparity gradients or curvature) rather than strategies relying on position-in-depth information (i.e. near or far decisions). Task difficulty was manipulated by varying the signal strength of the stimulus, i.e. the percentage of dots defining the 3D surface (see Materials and Methods). Average performance for the 100% signal strength stimuli ranged from 97% to 99% correct and decreased as a function of the signal strength of the stimulus (see Verhoef et al. 2010 for additional information).
Functional connectivity between AIP and IT

We simultaneously recorded multi-unit activity (MUA) and local-field potentials (LFPs) in area AIP and IT while the monkeys performed the 3D-shape discrimination task (Fig. 1c; N = 75 pairs of sites). Seventy-one pairs of sites displayed stimulus-driven MUA in both regions and were used for further analyses (monkey B1: N = 47; monkey B2: N = 24; see Materials and Methods). In line with (Srivastava et al. 2009), the response latency of the MUA in AIP was significantly shorter than in IT (Fig. 2; median response latency for monkey B1: AIP = 80ms, IT = 90ms; monkey B2: AIP = 90ms, IT = 110ms; p < 0.05, test for medians).

Figure 3 shows the LFP-spectrograms of each area for the different signal strengths. The average beta power in each area was markedly elevated prior to stimulus onset, but decreased significantly around 90 ms after stimulus onset ([−400ms, 90ms] vs. [90ms, 800ms], p < 0.001, paired t-test for each monkey). The beta power of both areas decreased monotonically with signal strength during the late stimulus period ([350ms, 800ms]; p<0.001; permutation ANOVA for each monkey). These beta power effects were present in each monkey but differed in magnitude between the two animals. In both the stimulus and prestimulus period, the average beta LFP power was significantly larger in monkey B2 than in monkey B1 (p<0.05 in IT and AIP) and the modulation by signal strength during the late stimulus period was stronger in monkey B2 (AIP: p<0.001; IT: p=0.051; interaction between monkey identity and signal strength, ANOVA). During the stimulus period, we additionally noticed a significant modulation of the high gamma power ([100ms, 800ms]; 60-100Hz; not for 30-60Hz) which was rather weak in AIP (p =
(p<0.001). Contrary to the beta-power modulation, the gamma power increased monotonically with signal strength. In the Supplemental Information we show that the beta-LFP-power was not influenced by the average MUA of a site.

We assessed possible synchronization between AIP and IT activity as a function of peristimulus time and frequency by computing LFP-LFP-coherograms for each stimulus strength (Fig. 4). Since results were very similar in each monkey (Fig. S1, S2), we pooled the data of the two animals. We observed strong synchronization of activity in AIP and IT that was mainly confined to the beta-band (17-25 Hz). No such synchronization was present in the low or high gamma band (i.e. 30Hz-60Hz and 60Hz-100Hz; see Fig. S4). The average beta-LFP-coherence was markedly elevated prior to stimulus onset, but decreased significantly around 90 ms after stimulus onset ([−400ms, 90ms] vs. [90ms, 800ms], p < 0.001, paired t-test for each monkey). The average beta coherence increased steadily throughout the fixation period, reaching its maximum around stimulus onset ([−400ms, −200ms] vs. [−200ms, 0ms], p<0.001, paired t-test for each monkey). The sharp drop in the average beta-LFP-coherence shortly after stimulus onset was followed by a more moderate increase in the average beta-LFP-coherence around 350ms after stimulus onset. Interestingly, the onset of this late increase in beta-LFP-coherence marked the instant at which the beta-LFP-coherence became significantly modulated by the signal strength of the stimulus (median number of trials per site per signal strength = 137). In the late stimulus period, the increase in LFP-coherence was significantly stronger for the lower signal strength stimuli compared to the 100% signal strength stimuli (p < 0.001, 1-way repeated measure ANOVA on the average coherence in [350ms, 800ms] for each monkey). The effect of signal strength on the coherence in
the late stimulus period did not differ between the two animals (ANOVA with monkey identity and signal strength as factors; \(p>0.05\) for the main effect of monkey identity and the interaction with signal strength). We did not observe any difference in the average coherence between convex and concave trials or between trials with stimuli at different positions in depth. In the Supplemental Information we show that the beta-coherence modulations were not caused by similar modulations in the beta-LFP-power.

Directed connectivity between AIP and IT

Interareal communication necessarily relies on action potentials while local field potentials represent mainly synaptic input to a region or local processing (Logothetis et al. 2001). Thus, if spiking activity of region A is synchronized to the LFP of region B but less so vice versa, this may indicate that A affects the neuronal activity in B and that the activity in B has little effect on the activity in A. These directed influences might also change during the course of the trial. Thus to investigate such potential directed functional connectivity and their time courses, we computed a coherogram on the LFPs in AIP and the spiking activity in IT and vice versa. The coherence between the spikes (MUA) of AIP and the LFP of IT showed a time course that appeared highly similar to the LFP-LFP coherence (Fig. 5a). The average beta-spike-field-coherence was clearly elevated prior to stimulus onset but declined soon after stimulus onset (baseline vs. stimulus period, \(p < 0.001\), paired t-test for each monkey). Also, the average beta-spike-field-coherence displayed significant modulation by the signal strength of the stimulus in the late stimulus period (i.e. [350ms, 800ms], \(p < 0.001\), 1-way repeated measure
ANOVA for each monkey). Monkey B2 displayed somewhat more beta spike-field coherence in the late stimulus period (p=0.01; coherence difference=0.001; see Fig. S1, S2) but the modulation by signal strength was comparable between monkeys (p>0.05, for the interaction between monkey identity and signal strength, ANOVA). As for the LFP-LFP coherence, no significant spike-field coherence was observed in the gamma band (see Fig. S4). The average coherence between the IT-spikes and the AIP-LFPs, however, differed in several aspects from the results obtained with the AIP-spikes and the IT-LFPs (Fig. 5b). First, the overall degree of beta coherence was significantly weaker compared to the beta coherence between the AIP-spikes and the IT-LFPs (p < 0.001, baseline –and stimulus period, paired t-test; p<0.01 for each monkey). Second, we did not observe any effect of signal strength on the beta coherence between the IT-spikes and the AIP-LFPs during the late stimulus period (p > 0.05, 1-way repeated measure ANOVA for each monkey).

Figure 6 shows the average spike-field coherence for the frequencies below 50Hz within each area (see Fig. S5 for the coherences at higher frequencies). For both areas we observed a decrease in the average beta coherence shortly after stimulus onset (baseline vs. stimulus period, p < 0.001, paired t-test for each monkey). Despite this similarity, the spike-field coherence within AIP was significantly stronger than in IT (p < 0.001, baseline –and stimulus period, paired t-test for each monkey). These effects were present in each monkey but the average beta spike-field coherence in IT was stronger in monkey B1 (p<0.05, ANOVA; coherence difference for baseline period=0.02; coherence difference for the late stimulus period=0.009) while the average spike-field coherence in AIP was stronger in monkey B2 compared to monkey B1 (p<0.01, ANOVA; coherence
difference for baseline period=0.13; coherence difference for late stimulus period=0.03). Only in AIP did we observe a modulation of the beta coherence by the signal strength of the stimulus (p < 0.001, 1-way repeated measure ANOVA in [350ms, 800ms] for each monkey; no significant interaction between monkey identity and signal strength, p>0.05 ANOVA). These results are in agreement with the above findings in that they show that the beta-oscillations in the input (~LFP) of area AIP are conveyed to its output (MUA) and subsequently transmitted to the input of area IT. These results also reveal that the signal strength-dependent component of the beta-oscillations in the IT-LFP are not or only weakly reflected in the output from IT. Accordingly, we observed elevated beta spike(AIP)-spike(IT) coherence in the prestimulus period that decreased around stimulus onset (p<0.01 for each monkey) but was not significantly modulated by (stereo) signal strength in the late stimulus period (see Fig.S7; p>0.05 for each monkey).

Although we subtracted the average evoked potential from the individual LFP-traces (see Materials and Methods), we checked whether any of the coherence measured between the two areas resulted from stimulus-locked oscillations by shuffling the order of trials for one of the neural signals, i.e. MUA or LFP, within each condition (i.e. signal strength) for each pair of sites. Because the shuffling was performed for each signal strength separately, it preserved all power differences between the conditions. The trial shuffling completely eliminated the observed coherence effects (effect of signal strength: p > 0.05; baseline vs. stimulus: p > 0.05; for field-field, spike-field –and spike-spike coherence and for each monkey). Hence, the observed coherence was not caused by stimulus-locked oscillations. We also assessed whether the asymmetric spike-field-coherence resulted from any differences in the spike rates of the two areas by equating
the average spike-trains for each condition and each pair of sites. As shown in the Supplemental Information, equating firing rate across conditions did not alter our findings. Finally, in the Supplemental Information we show that the beta spike-field and field-field coherence was not influenced by the average LFP-power, spike contamination of the LFP, the average MUA or single-trial MUA fluctuations.

The stronger AIP-spiking IT-LFP coherence compared to the IT-spiking AIP-LFP coherence suggests that the functional AIP-IT connectivity is mainly directed from AIP to IT. To further investigate the direction of the connectivity, we used spectral Granger causality (GC) analysis to assess the relative strength of influence of the AIP-LFPs on the IT-LFPs and vice-versa (see Materials and Methods). The Granger causality from signal X1 to signal X2 measures how much linear information is present in the past values of X1 that predicts the current value of X2 and is not already present in the past values of X2. The average GC in the beta-band in the AIP-to-IT direction was significantly higher than that in the reverse direction during both the baseline and stimulus periods (Fig. 7; p < 0.001 for both periods and each monkey, paired t-test), which agrees with the suggestion that the beta activity of AIP has a stronger influence on IT than vice-versa. The GC in both directions was modulated by the signal strength of the stimulus during the late stimulus period (p < 0.001 in both directions; 1-way repeated measure ANOVA). However, the effect of signal strength was stronger in the AIP-to-IT direction (p < 0.05; paired t-test on the difference between the 0% and 100% signal strength values of both directions). Each monkey showed the GC effects but the average GC in the IT to AIP direction, but not in the AIP to IT direction, was slightly larger in monkey B1 compared to monkey B2 (p=0.03, main effect of monkey identity; GC
difference=0.004; no significant interaction between monkey identity and signal strength; ANOVA).

As a final assessment of the directionality of the synchronized beta activity, we examined the phase differences between the neural signals of each area (see Supplemental Information). We observed that the AIP-beta-spikes tended to lead the IT-beta-LFPs by about 13 to 19ms. This latency difference resembles the response latency differences that we observed between the MUA of both areas (see above).

In summary, three converging lines of evidence, i.e. the spike-field coherence, the Granger causality findings and the phase lags between the neural signals of both areas, suggest that the source of the functional interactions between AIP and IT lies primarily in AIP.

**Stimulus modulated coherence was not caused by task difficulty**

We examined whether the effect of signal strength on the beta coherence was caused by task difficulty rather than by the visibility or saliency of the stimulus. For this purpose, we added a salient “white square stimulus” and a much less salient “black square stimulus” to our stimulus set (Materials and Methods; N=17 sites: 10 sites for monkey B2, 7 sites for monkey B1). These stimuli were presented during the discrimination task on trials that were randomly interleaved with the stereo-trials. Importantly, for the black and white squares, the correct response was indicated by a single response target that appeared immediately following stimulus presentation (instead of two response targets for the stereo stimuli; Materials and Methods). Hence, for these
two square stimuli, the factor task difficulty was eliminated (percentage correct for each
monkeys on both stimulus types ~100%) while the difference in stimulus saliency was
preserved. In both areas we observed significant responses to each shape (Fig. 2; p<0.05,
paired permutation test). We observed a clear difference in mean beta-coherence during
the stimulus periods when comparing trials in which a black or a white square was
presented (Fig. 4, 5, 6 and 7 lower panels). Specifically, after the initial decline, the
average beta coherence returned to the level of the pre-stimulus period during the
presentation of the black square (baseline vs. late stimulus period: p > 0.05 for all
coherence measures; paired t-test for each monkey) but not for the white square (baseline
vs. late stimulus period: p < 0.02 for all coherence measures; paired t-test; p<0.05 for
each monkey). The average beta coherence during the late stimulus period was greater for
the black than for the white square presentations (p < 0.009 for all coherence measures;
paired t-test; p<0.05 for each monkey). Consistent with the results obtained with the 3D
surfaces, the coherence observed during the presentation of the black square seemed to
originate in AIP (Fig. 7 lower panels; GC(AIP → IT) greater than GC(IT → AIP): p <
0.001; paired t-test in [350ms,800ms]; p<0.05 for each monkey). These findings clearly
demonstrate that the effect of stimulus strength on the mean beta-coherence between the
neural signals of these two areas is unrelated to task difficulty and not specific for the
task-relevant disparity signal. The results also reveal that the signal strength or saliency
of a stimulus, as defined in a broad sense (i.e. stereo-coherence or luminance/contrast),
can influence the coherence between two distant brain areas.
Regional specificity of the beta coherence and its relation with 3D-shape selectivity

The 3D-shape selective IT neurons were located in the lower bank of the STS, (Fig. 1b) while neurons recorded in the upper bank of the STS were unresponsive to these stimuli. This regional specificity of 3D-shape responses within the temporal cortex allowed us to assess the regional specificity of the observed beta coherence by comparing the beta-LFP-coherence of the AIP-IT recordings with the coherence measured between AIP and the upper bank of the STS (N = 7 sites in monkey B1). We observed significantly less beta coherence between the AIP-LFPs and the LFPs of the upper bank of the STS during both the stimulus and the baseline period (p < 0.001 for both periods, permutation t-test on [100ms, 800ms] and [-400ms, 0ms] respectively), although both STS positions were separated by only ~3mm. We observed a similar result when the AIP-IT and AIP-upper-bank-STS recordings were performed on the same day, with identical AIP positions in both recordings (Fig. 8 A, B; N = 5 sites; p = 0.008, permutation t-test). Despite the low coherence, we did observe a small but significant decrease of the beta-LFP-coherence of the AIP-upper-bank-STS recordings after stimulus onset (p = 0.035, paired permutation t-test). However, there was no effect of signal strength on the beta-LFP-coherence of the AIP-upper-bank-STS recordings (p > 0.05, 1-way repeated measure permutation ANOVA in [350ms, 800ms]). Furthermore, the interaction between signal strength and IT-position (i.e. lower versus upper bank) was statistically significant (p<0.05; split-plot ANOVA). These results show that the coherence effects are regionally specific and not caused by global changes in the behavioral state of the monkeys (e.g. due to arousal). Furthermore, these findings also exclude the possibility of “volume
conduction” as a cause of the observed AIP-IT coherence, since the upper bank of the STS is situated more closely to AIP compared to IT.

We compared the responsive pairs of sites in which neither site displayed 3D-shape selectivity (N=17; monkey B1: N=10; monkey B2: N=7) with the pairs of sites in which both (N=19; monkey B1: N=12; monkey B2: N=7) or only one of both (N=35; monkey B1: N=25; monkey B2: N=10) sites displayed 3D-shape selectivity. For all data selections we observed an elevated beta-coherence (field-field and spike-field) before stimulus-onset, which decreased significantly after stimulus onset (p<0.001, baseline vs. stimulus period). The mean beta coherence before stimulus onset did not differ between the different data selections (p>0.05). However, the modulation by stimulus signal strength during the later part of the stimulus period was only present for those pairs of sites in which at least one 3D-shape selective site was included (Fig. 8 C, E; p<0.001 for both field-field and spike(AIP)-field(IT) coherence) and not for the responsive but unselective pairs of sites (p>0.05 for both field-field and spike-field coherence). This finding was not a trivial consequence of a lack of modulation by stereo-signal strength in the unselective pairs of sites, since the average MUA of both areas within this data selection displayed a significant modulation by stereo-signal strength (p<0.05, repeated measures ANOVA). Furthermore, the significant coherence modulation by stereo-signal strength in 3D-shape selective pairs of sites was present in separate analyses in which we used only trials with either the preferred or non-preferred 3D shape of either IT or AIP (p<0.05 for each of the four analyses; 2-way ANOVA: p<0.001 for the main effect of stereo-signal strength; p>0.05 for the interaction between stereo-signal strength and preferred or non-preferred shape of IT or AIP). In addition, we show in the Supplemental

24
Information that the dependence of the coherence on the MUA selectivity of a site was not caused by spike rate differences between conditions. Although we had only few pairs of sites in which the preferred 3D shape of IT and AIP matched (N=11; monkey B1: N=7; monkey B2: N=4) or differed (N=8; monkey B1: N=5; monkey B2: N=3), we did observe similar modulations of the beta coherence in these data selections. However, probably due to the small sample size, these modulations failed to reach significance. Interestingly, the amplified beta coherence related to the black square in comparison to the white square was present in 3D-shape selective and unselective pairs of sites (Fig. 8 D, F; p<0.05 for both field-field and spike-field coherence). Hence, the modulation of the beta-coherence by the stereo-signal strength was only present in pairs of sites with at least one 3D-shape selective site, while the modulation by the luminance/contrast-signal strength was present in all responsive pairs of sites. These findings further demonstrate the high spatial resolution at which the synchronization effects occurred.

**Relating synchronized beta activity and behavior**

We considered whether the beta activity was in some way related to the monkey’s decision. For this purpose, trials were sorted according to whether the monkey made a response that was congruent or incongruent to the preferred 3D shape (i.e. convex or concave; based on the 100% signal strength stimuli) of the MUA-site. For example, for a concave selective site, we contrasted the beta activity of all trials in which the monkey responded concave (congruent) to the trials in which the monkey responded convex...
(incongruent). Note that we sorted according to the selectivity of the MUA but could not do the same for the selectivity of the beta power of a site since the beta power was rarely 3D-shape selective. Also, as the MUA was usually higher for the congruent trials (i.e. with the preferred 3D shape of a site), we first equated the firing rate (over time and for each site; see Supplemental information) between congruent and incongruent trials. Finally all comparisons are based on the same amount of trials to avoid a spurious effect due to finite sampling bias. We first examined the 0%-signal strength trials because of the elevated beta activity during the stimulus period and the distributed behavioral responses for this condition. Interestingly, we observed significantly increased beta-spike-field coherence in AIP during the late stimulus period when the monkey was about to respond congruently with the 3D-shape selectivity of the MUA-site compared to trials with incongruent responses (Fig. 9; \( p = 0.03 \), paired permutation test on [300ms, 800ms]). We did not find a similar effect during the baseline period. We observed similar, but smaller and non-significant trends for the 20%- and 100% trials \( (p>0.05) \), possibly caused by the decreased statistical power in these conditions (i.e. the behavioral responses were less distributed, resulting in fewer trials for a particular choice, and more spikes had to be removed to equate the firing rates between the two conditions). Without spike-rate correction the effect was significant in each monkey \( (p<0.05) \). With spike-rate correction the effect was still significant in monkey B2 \( (p=0.013) \) but not in monkey B1 \( (p>0.05) \) although a trend was still apparent. However, we have previously reported strong AIP-choice probabilities in monkey B1 that arose during the late stimulus period (i.e. around 300ms; Verhoef et al., 2010). The AIP-choice probabilities in monkey B2 were much weaker and were only present around stimulus offset. Hence, when correcting for
differences in the spike-rate between congruent and incongruent trials (see above), more
AIP-spikes of monkey B1 had to be removed. This explains why the effect was smaller in
monkey B1. We neither observed the congruency-effect in the spike-field coherence of
IT, nor in the beta power of each area (p>0.05; for any period of the trial). In addition, no
such effect was observed in the spike-field, spike-spike or field-field coherence between
pairs of sites with identical 3D-shape preferences in AIP and IT (p>0.05). However, this
could be the consequence of the relatively low number of such pairs of sites (N=11) and
the lower coherence we observed between areas as compared to within areas (see above).
We repeated all analyses for the gamma activity but did not find an effect. We also
compared correct and incorrect trials but observed no significant differences.

Thus, beta-spike-field synchronization in AIP seems to reflect the upcoming
behavioral choice of the monkey. One could wonder whether this modulation is caused
by the direction of the upcoming saccade or if it truly associates the upcoming behavioral
response with the selectivity of the MUA. To exclude the former possibility we sorted
trials according to the upcoming left- or rightwards saccade and repeated the same
analyses. For this data selection we did not observe a significant modulation of the beta-
spike-field coherence in AIP (p>0.05). Since we recorded in different hemispheres in
each monkey, we examined whether the AIP-spike-field coherence was modulated by the
laterality of the upcoming saccade. Yet, we did not find significant differences in the
AIP-spike-field coherence for saccadic responses that were ipsi- or contralateral to the
recording site. Hence, although we could not replicate this finding for the coherence
between areas, these analyses show a correlation between synchronized beta activity and
the behavioral choice of the monkey in the late stimulus epoch during a 3D-shape
discrimination task.

Discussion

We investigated the functional connectivity between the end-stages of the dorsal
and the ventral visual stream. We observed strong beta-band synchronization between IT
and AIP preceding stimulus onset that decreased shortly after stimulus onset and became
modulated by stimulus signal strength during the later portion of the stimulus period. We
showed that this beta-coherence modulation is unrelated to task difficulty but rather
influenced by general signal strength, be it stereo-coherence or luminance/contrast. In
addition, the elevated beta-coherence was regionally specific. Furthermore, even within
areas, we showed that the modulation of the beta coherence by stimulus signal strength
depended on the MUA-stimulus selectivities of the pairs of sites under study. During the
late stimulus period the spike-field coherence in AIP depended on the correspondence
between the MUA selectivity of that site and the upcoming behavioral choice of the
monkey. Finally, several convergent lines of evidence suggest AIP as the primary source
of the AIP-IT synchronized activity.

The observed synchronization between neural activities in AIP and IT was mainly
confined to the beta-band (17-25 Hz). Beta oscillations have been implicated in long-
range communication between remote brain areas (Brovelli et al. 2004; Gross et al. 2004;
Gross et al. 2006; Sehatpour et al. 2008) because beta oscillations are well suited to
synchronize over long conduction delays (Kopell et al. 2000). The functional significance of beta synchronization is still poorly understood but has been related to attention, vigilance and anticipatory processes (Buschman and Miller 2007; Engel and Fries 2010; Gross et al. 2004; Gross et al. 2006). For example, anticipatory beta-band synchrony has been observed in cats expecting a predictable upcoming sensory event (Roelfsema et al. 1997). Likewise, we used a fixed fixation period in our experiments which allowed the monkeys to anticipate stimulus onset. This anticipation seemed to be reflected in the beta coherence which increased steadily throughout the fixation period, reaching its maximum around stimulus onset. Such preparatory neural signals have been shown to be coherent over considerable distances in the cortex (Engel et al. 2001; Roelfsema et al. 1997) and our findings suggest that they also occur between temporal and posterior parietal cortex. We observed a drop in the beta coherence shortly after stimulus onset. Similar suppression of low-frequency population activity has been observed in several brain areas and in a variety of tasks (Donner et al. 2009; Gregoriou et al. 2009; Ray et al. 2008; Siegel et al. 2007). Such decreases in beta-band activity appear to be correlated to changes in the perceptual, cognitive or motor state throughout the cerebral cortex, possibly because beta oscillations may be related to mechanisms that maintain the status quo of the neural system (Engel and Fries 2010). A possible network-related explanation for the observed desynchronization after stimulus onset was given by a recent computational study (Lubenov and Siapas 2008). This study showed desynchronization in functionally connected neural networks shortly after a burst in the population activity and synchronization during random spiking activity under the influence of conduction
delays and Hebbian spike-time dependent plasticity. Indeed, population bursts are typical of activity in both AIP and IT after stimulus onset.

Shortly after stimulus onset we observed a rebound of the beta coherence which was modulated by the signal strength of the stimulus. Such modulations by signal strength have been frequently observed in the gamma band in both humans and macaques (Hall et al. 2005; Henrie and Shapley 2005; Ray et al. 2008; Siegel et al. 2007). Similarly, we also observed a monotonic increasing relation between signal strength and the high gamma power. Contrary to the gamma power and in agreement with previous studies, the beta activity displayed a monotonic decreasing relation with signal strength (Ray et al. 2008; Siegel et al. 2007). Hence, our results show that both the gamma and beta activity in AIP and IT are modulated by signal strength (i.e. stereo-signal strength or luminance/contrast) in a similar way as in other visual areas. We additionally show that this modulation is not the consequence of variations in task difficulty.

Although the functional significance of beta modulations is still poorly understood, our findings present some clues in this regard. First, the beta-coherence modulation was not specific to stimuli defined by disparity since synchronized beta activity was strongly modulated by the luminance/contrast of a stimulus containing no disparity. This demonstrates that the AIP-IT beta-coherence is a more general phenomenon that occurs in a variety of perceptual conditions. Second, the modulation of the beta coherence by signal strength defined by disparity was restricted to pairs of sites displaying selectivity for 3D shapes defined by disparity. This shows that for different perceptual conditions, a network of anatomically highly specific areas is recruited and suggests a functional role for the beta-coherence modulation during 3D-shape
discrimination. Third, we have previously shown that the activity in area AIP does not
contribute to the formation of perceptual decisions about 3D shapes in the present task
(Verhoef et al. 2010). Moreover, in the same study we have shown that monkey B1 and
B2 already formed their decision about 3D shape before 270ms and 415ms after stimulus
onset, respectively. However, the stimulus related beta coherence arose around 350ms
after stimulus onset, thus most likely after the monkeys had already formed their
decision. Hence, the reoccurrence of the beta coherence after stimulus onset seems
unrelated to perceptual- and decisional processes. However, since the monkey had to
retain the decision until the end of the trial and the beta coherence occurred shortly after
the formation of the perceptual decision and disappeared around stimulus offset, it seems
likely that the beta coherence was related to the maintenance of the perceptual state.
Consistent with this hypothesis, we observed that the spike-field coherence in AIP
reflected the upcoming choice of the monkey during the late stimulus period (i.e. ~350-800ms), that is, at a moment when the monkey had already decided. Although we could
not replicate this finding for the coherence between areas (see Results), we did show that
the beta activity in AIP synchronized to that of IT during the same time period.
Moreover, several lines of evidence suggest AIP as the source of the beta activity in IT
which could imply a similar role for the synchronized beta activity between AIP and IT.
A comparable role of synchronized beta oscillations in perceptual or cognitive
maintenance is also suggested by previous studies in both monkeys and humans (Tallon-
observed a relation between the level of beta synchronization during a delay interval and
the performance during a visual working memory task. In addition, a recent study by
Siegel et al. (2009) provided evidence for a role of synchronized beta activity in visual object maintenance during a short-term memory task. This study also found preparatory beta activity before stimulus onset that decreased during stimulus presentation and increased again during a delay period in which no stimulus was present.

Engel and Fries (2010) have suggested that beta activity is related to the maintenance of the current cognitive state of the system. Moreover, since novel input abruptly changes the system’s cognitive state, it should be accompanied by decreases in the beta activity of the system (Engel and Fries 2010). Our findings are in agreement with this proposal since beta coherence was stronger during stimulus presentations of low signal strength. That is, for the low signal strength stimuli, little or no (i.e. 0% signal strength) 3D-shape information was delivered by the stimulus and the current perceptual state of the system was more or less preserved. Conversely, much novel 3D-shape information was conveyed by stimuli of high signal strength (i.e. 100% signal strength), thereby changing the system’s perceptual state. Since 3D-shape-unselective pairs of sites were insensitive to 3D-shape information their perceptual state did not change by the amount of 3D-shape information (i.e. stereo-signal strength), which might explain the lack of modulation of the beta coherence by stereo-signal strength for these pairs of sites. Finally, since all pairs of sites were sensitive to luminance/contrast, which is necessary to represent any visual information, stimulus onset and the luminance/contrast of the stimulus seemed to change the perceptual state of all pairs of sites, thus explaining the decrease in beta coherence associated with these conditions. Hence, two stimulus features seem to change the system’s perceptual state and thereby influence the amount of beta coherence after stimulus onset: one is the amount of luminance/contrast which affects the
beta coherence in all responsive pairs of sites, the other is the amount of 3D-shape information, which is specific to 3D-shape selective pairs of sites.

Our findings suggest a distinct role for the beta activity in the pre- and post-stimulus period. While the former activity seems to reflect anticipation of stimulus onset, the latter activity might be related to perceptual maintenance. A similar functional dissociation between the beta activity in the pre- and post-stimulus period has been suggested by Donner et al. (2007). These authors hypothesized that the pre-stimulus beta activity and its stimulus-induced decrease acts globally on a large group of task-unrelated neurons. In agreement with this proposal, we observed pre-stimulus beta activity throughout IT, even some small activity in the upper-bank of the STS. The stimulus-induced beta increase though, is suggested to result from small pools of neurons that engage in coherent beta band oscillations (Donner et al. 2007). Correspondingly, we observed beta modulations which were spatially localized and depended particularly on the MUA selectivity of the site.

Where does the synchronized beta activity arise? One possibility is that beta oscillations are generated in a third region and subsequently transmitted to AIP and IT. Possible candidate regions are the Frontal Eye Fields (FEF) or the Lateral Intraparietal Area (LIP) as these areas have been related to decisional processes (Ferrera et al. 2009; Hanks et al. 2006; Stanford et al. 2010) and are known to contribute to saccadic behavior (which is the operant in our task). Alternative candidates are areas involved in perceptual maintenance such as the lateral prefrontal cortex (Siegel et al. 2009). Such top-down information could be useful for AIP in contexts in which familiar objects need to be grasped or when grasping perceptually ambiguous objects that are disambiguated through
contextual information. Our findings (i.e. the spike-field coherence, Granger causality
and phase differences between neural signals), together with the known anatomical
connections between IT and AIP (Borra et al. 2008, 2010), suggest the possibility that the
beta activity is relayed through AIP to IT. Alternatively, the synchronized beta activity
between IT and AIP could be due to common input arriving earlier in AIP. Further
studies using causal techniques (e.g. reversible inactivation) are needed to distinguish
between these and other possibilities.

Recently, there has been a considerable interest in possible functional interactions
between the dorsal and the ventral visual stream (Chinellato and Del Pobil 2009; Orban et
al. 2006; Sakata et al. 1997). We show that synchronized beta activity exists between AIP
and IT during 3D-shape discrimination. The synchronized beta activity appears directed
mainly from AIP to IT and seems to occur during perceptual anticipation and when the
system has stabilized to a particular perceptual state but not during active visual
processing. As a result, our findings provide evidence for a functional connectivity
between the two end-stages of the dorsal and the ventral stream during perceptual
discrimination.
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Figure legends

Figure 1. Task, stimuli and recording positions. (a) Trial sequence: trials started with 425ms fixation, followed by 800ms stimulus presentation. The monkeys were required to make a saccade to one of two response targets (i.e. left or right) that appeared immediately after stimulus presentation depending on whether they perceived a convex or a concave 3D shape. (b) Example of a convex random-dot stereogram positioned at the fixation plane at 100% signal strength. (c) Estimated recording positions in AIP (left) and IT (area TEs; right) indicated by a red arrow on a structural MRI.

Figure 2. Spike density plots of the MUA for all pairs of responsive sites. Black vertical lines indicate stimulus onset and offset. The position of the black arrow on the time axis indicates the response latency. IT: Left column. AIP: right column. Different signal strengths are indicated by color (stereo-signal strength) or line type (black or white square). The average spike trains of each site were first convolved with a Gaussian kernel (sd. 10ms) before being averaged across sites.

Figure 3. Wavelet LFP-spectrograms for AIP and IT. Time and frequency are represented on the horizontal and vertical axis respectively. Color indicates the percentage power change with respect to the baseline period (-400ms to 0ms). Black vertical lines indicate stimulus onset and offset. Rows from top to bottom: 100%, 10%-20%, 0% signal strength, black square, white square (see pictograms on the left). Note the
different color scales for AIP (a) and IT (b). As for the coherence analyses, the VEP of each site was subtracted from each LFP trace before computing the spectrograms.

**Figure 4.** Functional connectivity. Coherograms between the LPFs of both areas (Wavelet method; see Materials and Methods). Time and frequency are represented on the horizontal and vertical axis respectively. Average coherence is indicated by the color (see color bar at the bottom). Black vertical lines indicate stimulus onset and offset. Rows from top to bottom: 100%, 10%-20%, 0% signal strength, black square, white square (see pictograms on the left). The pairs of sites in which black and white squares were presented, represent a subset of the total dataset (see main text). This explains small differences in the average baseline coherence between these conditions and the stereo conditions.

**Figure 5.** Directed connectivity based on spike-field coherograms (multitaper method; see Materials and Methods). (a). Average coherence between the MUA from AIP and the LFP from IT. (b) Average coherence between the MUA from IT and the LFP from AIP. Time and frequency are represented on the horizontal and vertical axis respectively. Average coherence is indicated by the color (see color bars at the bottom). Black vertical lines indicate stimulus onset and offset. Rows from top to bottom: 100%, 10%-20%, 0% signal strength, black square, white square (see pictograms on the left). The pairs of sites in which black and white squares were presented represent a subset of the total dataset (see main text). This explains small differences in the average baseline coherence between these conditions and the stereo conditions.
Figure 6. Average spike-field coherence within IT (a) and AIP (b). Same conventions as in Figure 5. Note the different values on the colorbars of each column.

Figure 7. Directed connectivity. Spectral Granger causality between the LFPs from IT and AIP. Black vertical lines indicate stimulus onset and offset. Left column: Average Granger causality from AIP to IT. Right column: Average Granger causality from IT to AIP. Top row: red, green and blue lines plot the average Granger causality for the 0%, 10-20% and 100% signal strength trials, respectively (see legend). Bottom row: black and gray lines plot the average Granger causality for the black- and the white-square trials respectively. SEM (±) at each time point is indicated by shading over the lines.

Figure 8. Regional specificity of the beta coherence. Average field-field coherence as a function of time and frequency (averaged over different signal strengths). (a) Between the LFP from AIP and the LFP from IT (lower bank STS; TEs). (b) Between the LFP from AIP and the LFP from the upper bank of the STS. These plots are derived from the data from recording sessions with identical AIP positions. Same conventions as in Figure 4. (c) Average field-field coherence as a function of signal strength for the responsive pairs of sites in which both (green), only one (black) or neither site (red) displayed 3D-shape selectivity. (d) Same as in (c) but for the black and white square. (e,f) Same as in (c,d) but for the spike-field coherence between the AIP-MUA and the IT-LFP. No such effects were observed for the spike-field coherence between the IT-MUA and the AIP-LFP.
Figure 9. Average spike-field coherence in IT and AIP for trials in which the monkey made a response that was either congruent or incongruent with the preferred 3D shape of a MUA-site. Only data from the 0% signal strength condition are shown (see Results). Same conventions as in Figure 5.


