

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

ScienceDirect

Journal homepage: [www.elsevier.com/locate/cortex](http://www.elsevier.com/locate/cortex)

Special issue: Review

# Functional interactions between the macaque dorsal and ventral visual pathways during three-dimensional object vision

Peter Janssen <sup>a,\*</sup>, Bram-Ernst Verhoef <sup>a,b</sup> and Elsie Premereur <sup>a</sup><sup>a</sup> Laboratorium voor Neuro- en Psychofysiologie, KU Leuven, Leuven, Belgium<sup>b</sup> Department of Neurobiology, University of Chicago, Chicago, IL 60637, USA

## ARTICLE INFO

## Article history:

Received 11 October 2016

Reviewed 9 December 2016

Revised 23 January 2017

Accepted 25 January 2017

Published online xxx

## Keywords:

Disparity

fMRI

Microstimulation

Reversible inactivation

Coherence

## ABSTRACT

The division of labor between the dorsal and the ventral visual stream in the primate brain has inspired numerous studies on the visual system in humans and in nonhuman primates. However, how and under which circumstances the two visual streams interact is still poorly understood. Here we review evidence from anatomy, modelling, electrophysiology, electrical microstimulation (EM), reversible inactivation and functional imaging in the macaque monkey aimed at clarifying at which levels in the hierarchy of visual areas the two streams interact, and what type of information might be exchanged between the two streams during three-dimensional (3D) object viewing. Neurons in both streams encode 3D structure from binocular disparity, synchronized activity between parietal and inferotemporal areas is present during 3D structure categorization, and clusters of 3D structure-selective neurons in parietal cortex are anatomically connected to ventral stream areas. In addition, caudal intraparietal cortex exerts a causal influence on 3D-structure related activations in more anterior parietal cortex and in inferotemporal cortex. Thus, both anatomical and functional evidence indicates that the dorsal and the ventral visual stream interact during 3D object viewing.

© 2017 Elsevier Ltd. All rights reserved.

## 1. Introduction

The concept of the dorsal and ventral visual pathway, as originally proposed by Ungerleider and Mishkin almost four

decades ago (Ungerleider & Mishkin, 1982), emerged from the differential behavioral effects of lesions of the temporal and parietal cortex in macaque monkeys. Since then, numerous studies in monkeys have consistently corroborated this

*Abbreviations:* 3D, three dimensional; AIP, anterior intraparietal area; aAIP, anterior AIP; AIT, anterior inferotemporal area; CIP, caudal intraparietal area; EM, electrical microstimulation; F5, premotor area F5; FEF, Frontal Eye Fields; fMRI, functional magnetic resonance imaging; FST, fundus of the superior temporal sulcus; FWE, family wise error; ITC, inferior temporal cortex; IPS, intraparietal sulcus; LFP, local field potential; LIP, lateral intraparietal area; MIP, medial intraparietal area; MT, middle temporal area; pAIP, posterior AIP; PIP, posterior intraparietal area; PIT, posterior inferotemporal area; PRR, Parietal Reach Region; TE, anterior inferotemporal area; TEO, posterior inferotemporal area.

\* Corresponding author. Herestraat 49-O&N2-bus 1021, 3000 Leuven, Belgium.

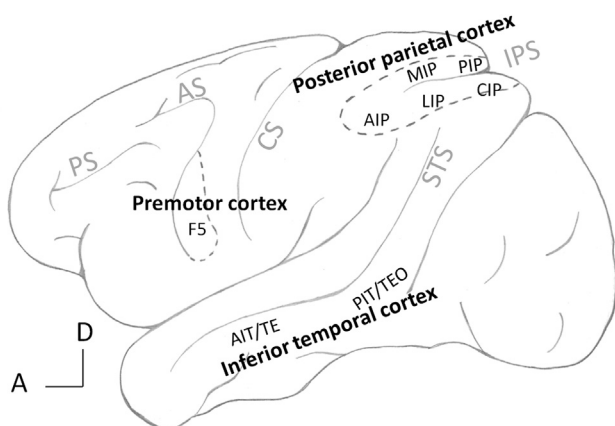
E-mail address: [Peter.Janssen@kuleuven.be](mailto:Peter.Janssen@kuleuven.be) (P. Janssen).

<http://dx.doi.org/10.1016/j.cortex.2017.01.021>

0010-9452/© 2017 Elsevier Ltd. All rights reserved.

dichotomy by highlighting the specialized properties of individual neurons in both visual pathways for object recognition versus spatial vision (as proposed by Ungerleider and Mishkin (1982)), or for perception versus action (Goodale & Milner, 1992). As a result of these studies, the structure and organization of the macaque extrastriate cortex is currently much better understood. Posterior parietal cortex, for example, consists of a large number of distinct cortical areas (Lewis & Van Essen, 2000). Several areas in the intraparietal sulcus (IPS) seem to be organized according to the effector (Fig. 1): the lateral intraparietal area (LIP) more posteriorly in the lateral bank is primarily active during saccadic eye movements (Pesaran, Pezaris, Sahani, Mitra, & Andersen, 2002; Premereur, Janssen, & Vanduffel, 2015; Premereur, Vanduffel, & Janssen, 2011; Snyder, Batista, & Andersen, 1997; Wardak, Olivier, & Duhamel, 2002); the medial intraparietal area (MIP) on the medial bank (also referred to as the Parietal Reach Region, PRR) is active during reaching movements (Bhattacharyya, Musallam, & Andersen, 2009; Premereur, Janssen, et al., 2015; Snyder et al., 1997); and the anterior intraparietal area (AIP) anteriorly in the lateral bank is crucial for object grasping (Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Nelissen & Vanduffel, 2011; Romero, Pani, & Janssen, 2014).

These visuomotor areas in the IPS project to specific cortical areas in the frontal lobe that are part of the motor system. For example AIP projects to ventral premotor cortex or area F5 (Borra et al., 2008; Premereur, Van Dromme, Romero, Vanduffel, & Janssen, 2015), area LIP to the Frontal Eye Fields (FEF) (Schall, Morel, King, & Bullier, 1995; Stanton, Bruce, & Goldberg, 1995) and area MIP to dorsal premotor cortex (Johnson, Ferraina, & Caminiti, 1993; Johnson, Ferraina, Bianchi, & Caminiti, 1996; Tanne, Boussaoud, Boyer-Zeller, & Rouiller, 1995). More caudal IPS areas, such as the caudal intraparietal area CIP, are primarily visual and seem to be



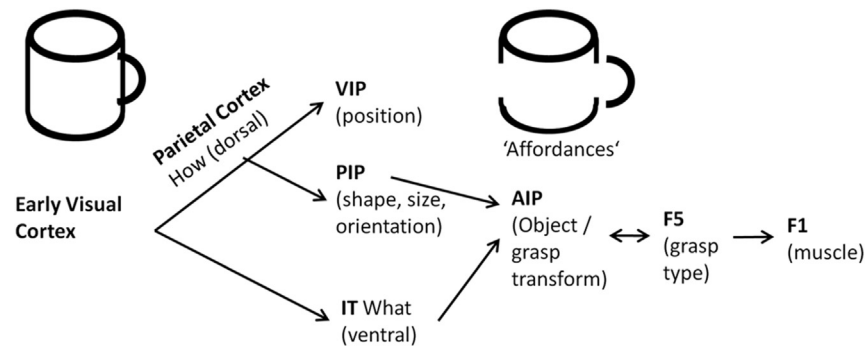
**Fig. 1 – Overview of anatomical regions.** IPS: intraparietal sulcus; STS: superior temporal sulcus; CS: central sulcus; PS: principal sulcus; AS: arcuate sulcus; AIT: anterior inferotemporal cortex; PIT: posterior inferotemporal cortex; AIP: anterior intraparietal area; MIP: medial intraparietal area; LIP: lateral intraparietal area; CIP: caudal intraparietal area; PIP: posterior intraparietal area; F5: premotor area F5; AIT: anterior inferotemporal area; PIT: posterior inferotemporal area; A: anterior; D: dorsal.

involved in three-dimensional (3D) vision (Katsuyama et al., 2010; Rosenberg, Cowan, & Angelaki, 2013; Tsutsui, Sakata, Naganuma, & Taira, 2002). In contrast, the inferior temporal cortex (ITC), one of the end stages of the ventral pathway, appears to be organized according to specific object classes or object features. The ITC consists of area TEO (or PIT) posteriorly and area TE (or AIT) anteriorly, and even within area TE multiple subareas have been identified that are specialized for processing specific object classes or object features: faces (Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003), bodies (Popivanov, Jastorff, Vanduffel, & Vogels, 2012), color (Conway & Tsao, 2006), 3D shape (Janssen, Vogels, & Orban, 1999; Vaziri, Carlson, Wang, & Connor, 2014), glossiness (Nishio, Goda, & Komatsu, 2012) and disparity (Verhoef, Vogels, & Janssen, 2012). Most if not all of these parietal and inferotemporal macaque areas have putative homologues in humans (Culham & Kanwisher, 2001; Downing, Jiang, Shuman, & Kanwisher, 2001; Grefkes & Fink, 2005; Shikata et al., 2008; Tsao, Moeller, & Freiwald, 2008). While many studies have focused on the response properties of neurons in either parietal or inferotemporal cortex (Freud, Plaut, & Behrmann, 2016), much less is known about whether and how areas in both pathways interact with each other. Here, we will focus on recent scientific progress in our understanding of dorsal–ventral stream interactions in the macaque monkey, based on a series of anatomical, electrophysiological and functional imaging studies.

## 2. Theoretical and anatomical studies

When we grasp an object, prior knowledge about the object's estimated weight, size, surface properties, temperature, usability, etc. can guide the grasping action. Almost two decades ago Fagg and Arbib (1998), proposed a model of visually-guided grasping that explicitly hypothesized the existence of a pathway between the ITC and posterior parietal cortex that transmits object information to the dorsal visual pathway (Fig. 2).

The FARS (Fagg–Arbib–Rizzolatti–Sakata) model was inspired by studies in patients with either occipitotemporal lesions (Goodale, Milner, Jakobson, & Carey, 1991) or parietal lesions (Jeannerod, 1986; Jeannerod, Decety, & Michel, 1994). Whereas patient DF is strongly impaired in recognizing objects but has no problem in grasping objects, a patient with a parietal lesion showed a deficit in preshaping of the hand during grasping (without a deficit in object recognition). Importantly, such a preshaping deficit was not observed when grasping familiar objects. In the latter case, stored information about the object's size and geometry was presumably available in the intact ventral visual stream, and subsequently transmitted to the dorsal visual stream and finally to motor cortex to guide the grasping action. A typical everyday example where dorsal–ventral stream interactions are likely to play a role is grasping a mug: once we have recognized the object as a mug we can grasp it by the handle (for drinking), or if we want to move the mug we may grasp it by the body or the upper edge. The FARS model hypothesized that visual object information relevant for grasping (termed ‘affordances’) is represented in area AIP based on inputs from more caudal



**Fig. 2 – FARS model.** According to the FARS model, AIP uses visual input to extract affordances, which are object features that are relevant for grasping. F5 then applies various constraints to select a grasp for execution and to inform AIP of the status of its execution, thus updating AIP's active memory. Area F5 projects to F1 to execute the grasping movement. The areas shown are VIP (ventral intraparietal area); PIP (posterior intraparietal area); IT (inferotemporal cortex); AIP (anterior intraparietal cortex); area F5 (of the ventral premotor cortex) and area F1 (primary motor area).

parietal regions and the ITC, and then transmitted to ventral premotor cortex (area F5) where object information is transformed into motor commands that ultimately drive primary motor cortex and the spinal cord. It is noteworthy that even to date, very little experimental evidence has confirmed the inputs from the end stage of the ventral stream (ITC) to the dorsal stream (AIP) at the functional level.

At the anatomical level, however, more evidence for a connection between the ITC and posterior parietal cortex is available. Several anatomical tracer studies in monkeys showed that the ITC and the areas in the lateral bank of the intraparietal sulcus are interconnected. One of the earliest studies (Webster, Bachevalier, & Ungerleider, 1994) injected retrograde and anterograde tracers in the ITC (both in TEO and in TE) and observed labeling in posterior parietal cortex: TEO is connected to both the ventral and dorsal subdivision of area LIP, and to the more caudal area V3A, whereas TE is primarily connected to a more anteriorly located part of dorsal LIP, which most likely corresponds to the posterior subsector of area AIP (see section on causal studies). Importantly, all connections between the ITC and parietal cortex were bidirectional, but the type of connectivity (feedforward or feedback) differed depending on the direction: projections from parietal cortex to area TE were more feedforward-like (originating in layer III) whereas the projections from TE to parietal cortex were more feedback-like (terminating in all layers). This observation is highly relevant for the interpretation of the recent microstimulation and inactivation studies (see below). In a more recent anatomical tracer study (Borra et al., 2008), the authors injected in two locations in area AIP, which was identified based on anatomical landmarks (one more anterior and one more posterior site), and observed strong labeling in areas TEO and TE in the ITC. The labelling in area TE was located on the temporal convexity in the more posterior part of TE, and more anteriorly primarily in the ventral bank of the anterior part of the Superior Temporal Sulcus (STS). Again, the projection from AIP to the ventral bank of the anterior STS was of the feedforward type, although some projections to other parts of the ITC were also of the feedback type. Overall,

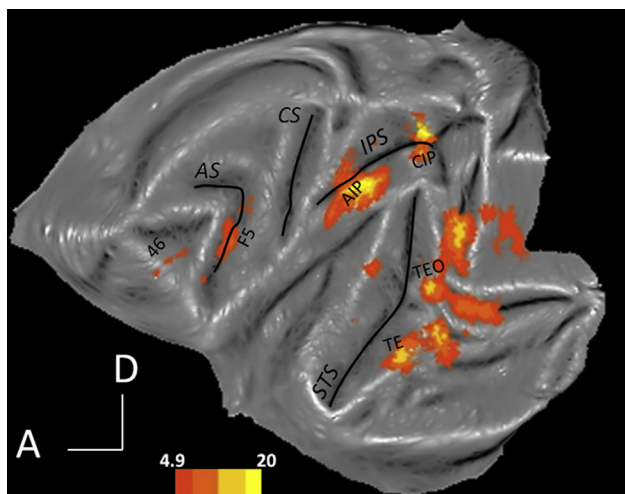
consistent anatomical evidence indicates that the end-stage areas of the dorsal (area AIP) and the ventral (area TE) stream are interconnected, and that the feedforward projections primarily run from parietal cortex to area TE.

### 3. Neural selectivity for disparity-defined 3D object structure in dorsal and ventral visual stream

Many stimulus features and stimulus categories are processed in either the ventral or the dorsal visual stream. For example, the ventral stream contains several patches that are sensitive to color (Conway & Tsao, 2006), glossiness (Nishio et al., 2012), complex shapes such as faces (Tsao, Freiwald, et al., 2003) and bodies (Popivanov et al., 2012), whereas many dorsal stream areas are sensitive to stimulus motion (Britten, Shadlen, Newsome, & Movshon, 1993; Colby, Duhamel, & Goldberg, 1993; Cook & Maunsell, 2002; Maunsell & Newsome, 1987; Maunsell & Van Essen, 1983; Saito et al., 1986; Tanaka & Saito, 1989). In contrast, binocular disparity, one of the strongest visual cues for depth perception, is processed in both the dorsal and the ventral visual stream. A large number of fMRI studies in monkeys (Durand et al., 2007; Joly, Vanduffel, & Orban, 2009; Tsao, Vanduffel, et al., 2003; Van Dromme, Premereur, Verhoef, Vanduffel, & Janssen, 2016; Van Dromme, Vanduffel, & Janssen, 2015; Verhoef, Bohon, & Conway, 2015) and in humans (Bridge & Parker, 2007; Chandrasekaran, Canon, Dahmen, Kourtzi, & Welchman, 2007; Georgieva, Todd, Peeters, & Orban, 2008) have observed widespread activations related to disparity in occipital, parietal and temporal visual cortex (Fig. 3).

At the single cell level, neurons selective to binocular disparity have been described in almost every visual area (for reviews see (Parker, 2007; Verhoef, Vogels, & Janssen, 2016)), and even in the motor system (Ferraina, Pare, & Wurtz, 2000; Theys, Pani, van Loon, Goffin, & Janssen, 2012).

Binocular disparity is not only a powerful cue to estimate the distance of stimuli with respect to the fixation plane (near



**Fig. 3 – The cortical network of areas sensitive to 3D structure in the macaque measured with fMRI ( $p < .05$ , Family-wise error (FWE) corrected). Abbreviations as in Fig. 1. Data from (Van Dromme et al., 2016).**

or far), but can also provide accurate information about the 3D structure of objects, since the visual system is very sensitive to the variation of disparity along a curved surface (e.g., concave or convex). The ventral bank of the anterior STS – part of area TE – contains a population of neurons that is exquisitely sensitive to 3D structure defined by binocular disparity (Janssen, Vogels, & Orban, 2000; Janssen et al., 1999; Yamane, Carlson, Bowman, Wang, & Connor, 2008). These neurons signal the 3D structure of surfaces independent of the mean disparity (i.e., position in depth), position and size of the stimulus, and can detect very small differences in 3D structure (Janssen et al., 2000), similar to the perceptual performance of human observers when judging disparity gradients (Rogers & Cagenello, 1989). Contrary to many neurons in primary visual cortex and dorsal stream area MT/V5 (Cumming & Parker, 2000; Krug, 2004), TE neurons do not respond to disparity in anticorrelated random dot stereograms, in which no depth is perceived (Janssen, Vogels, Liu, & Orban, 2003). Hence the properties of 3D structure-selective TE neurons and their position in the hierarchy of visual areas (at the end of the ventral visual stream) make them ideally suited to support 3D object perception.

Following these single-cell investigations in the ventral stream and guided by monkey fMRI data (Durand et al., 2007; Joly et al., 2009), a series of studies investigated the coding of 3D structure from disparity in the dorsal visual stream, more specifically in AIP and its target area in the premotor cortex area F5a (Srivastava, Orban, De Maziere, & Janssen, 2009; Theys, Pani, et al., 2012; Theys, Pani, van Loon, Goffin, & Janssen, 2013; Theys, Srivastava, van Loon, Goffin, & Janssen, 2012). Here too, a large fraction of the neurons signal differences in 3D structure, as predicted by the fMRI data, but the properties of the neurons differ from those in the ITC: AIP neurons signal 3D structure considerably faster (50–70 msec compared to 80–90 msec in TE) but are less sensitive to small differences in disparity. Moreover, neurons

selective for 3D structure are almost invariably strongly active when monkeys grasp real-world objects, and are co-localized with neurons that are active during grasping in the dark (Theys et al., 2013). Thus, the fast and coarse neural coding of 3D structure from disparity in the dorsal stream seems suitable to provide visual object information that can guide the preshaping of the hand during grasping, whereas the highly detailed – but slower – representation in TE is ideal for object recognition, consistent with the dorsal–ventral division of labor.

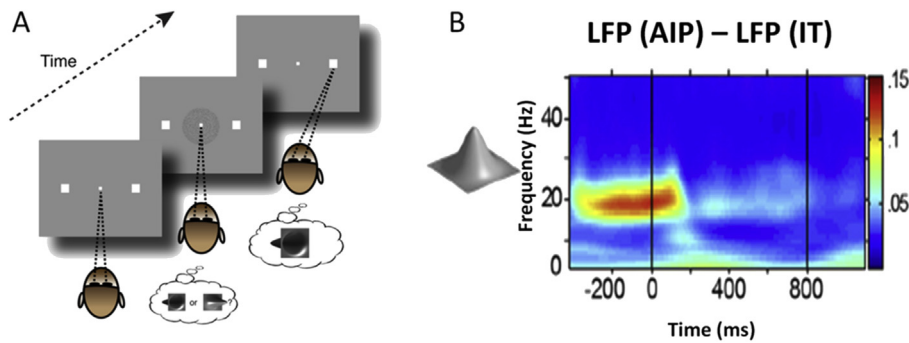
Hence the end-stage areas of the dorsal and ventral visual streams each contain a neural representation of 3D object structure. The question naturally arises then whether these two neural representations functionally interact. Why would the visual system spend considerable resources to compute the same object feature twice in two remote areas that are anatomically connected? The answer to these questions was sought in studies investigating the correlation between neural activity in AIP and TE, and in studies that employed causal manipulations of neural activity.

#### 4. Choice-related activity and synchronization between dorsal and ventral stream areas during 3D structure categorization

Several studies have employed random-dot stimuli to probe depth perception in monkeys. These stimuli have the advantage that no other cue besides disparity is available to solve the task. One can train monkeys to indicate their perceptual report by means of a motor response (an eye movement or a hand movement), while one can parametrically manipulate the amount of information in the stimulus by changing the disparity coherence, i.e., the percentage of dots that define the surface (the other dots take on random disparities).

Verhoef, Vogels, and Janssen (2010) trained monkeys to indicate whether they perceived a surface – presented at, in front of, or behind the fixation point for a fixed duration – as either concave or convex by means of an eye movement, while simultaneously recording neuronal activity in 3D-structure selective sites in AIP and TE. The trial-by-trial correlation between neural activity and the perceptual choice of the monkeys (the choice probability) arose early after stimulus onset in TE, but much later in area AIP. Based on an analysis of the eye deviations during stimulus presentation, the estimated period in which the perceptual decision was made (decision time, approximately 100–250 msec after stimulus onset) occurred during the period of high choice probability in TE but before the choice probability in AIP. Hence the activity in TE but not that in AIP correlated with the perceptual decision in the epoch when monkeys were accumulating perceptual evidence. This finding supports the view that visual information in the ventral, but less so in the dorsal, pathway is used for visual recognition purposes.

One way to probe whether areas in the ventral and the dorsal pathway functionally interact with each other is by simultaneously recording in AIP and TE during 3D structure categorization. Verhoef, Vogels, and Janssen (2011) analyzed the coherence (a measure of correlation) between the neural



**Fig. 4 – Simultaneous inferotemporal-parietal recording during 3D structure categorization.** A. After a brief period of fixation, a 3D stimulus was presented foveally. The animal indicated whether he perceived a concave or convex stimulus by making a saccade to, respectively, right or left. B. Beta coherence between the LFP signals in AIP and IT. Time and frequency are represented on the horizontal and vertical axis, respectively. 0 indicates stimulus onset; black lines indicate stimulus onset and offset. Color bar indicates average coherence. Data from (Verhoef et al., 2011).

activity (spikes and local field potentials (LFP)) simultaneously recorded in AIP and TE while the monkeys were categorizing 3D surfaces with a fixed stimulus duration (Fig. 4A). They observed strong coherence between AIP and TE in the beta band (17–25 Hz) prior to stimulus onset, which fell shortly after stimulus onset and reappeared approximately 350 msec after stimulus onset (Fig. 4B).

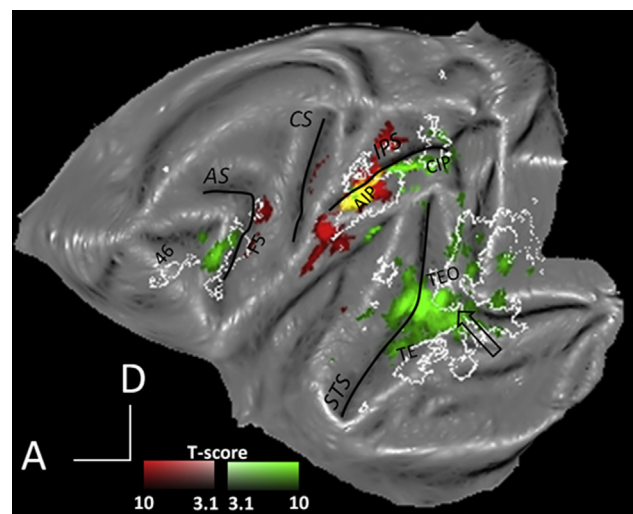
This synchronized LFP activity was regionally-specific since significantly less beta band coherence was measured between the LFPs of AIP and those recorded in the (unresponsive) upper bank of the STS. The elevated beta band coherence between AIP and TE could be interpreted as indicating information exchange between the two areas, but appeared to be unrelated to the 3D-shape discrimination task: the coherence was low in the epoch when the animals were deciding on the 3D structure of the stimulus, and was highest when the animals were viewing a task-irrelevant black square. Several additional analyses (including spike-field coherence and Granger causality analysis) strongly suggested that the functional AIP–TE connectivity was mainly directed from AIP to TE, consistent with the laminar pattern of an anatomical connectivity between the two areas (Borra et al., 2008; Webster et al., 1994).

The synchronized activity between AIP and TE suggests some form of connectivity between both areas, in agreement with the known anatomical connections between both areas. However, the interpretation of the synchronized activity is complicated by the correlational nature of the findings. Hence, a thorough understanding of these dorsal–ventral stream interactions requires causal perturbation techniques.

## 5. Causal evidence for functional interactions between dorsal and ventral visual stream during 3D object processing

A large part of the anterior IPS is activated more strongly by curved surfaces than by flat surfaces at different disparities (Durand et al., 2007) (Fig. 3). However, at the single-cell level this large fMRI activation consists of at least two patches of neurons selective for disparity-defined 3D structure (Van

Dromme et al., 2015): one in anterior AIP and one in posterior AIP, immediately adjacent to area LIP, surrounded by regions lacking such selectivity. Both subsectors of AIP also contain many neurons that are strongly active during object grasping (Romero et al., 2014). To chart the effective connectivity of these two functionally-defined patches of neurons in AIP, we applied electrical microstimulation during fMRI (EM-fMRI) in both AIP subsectors (Premereur, Van Dromme, et al., 2015). The anterior subsector of AIP (aAIP) was connected to a set of cortical areas that is known to be involved in somatomotor processing (Fig. 5; red activations): ventral premotor cortex (F5a, in the posterior bank of the lower ramus of the arcuate sulcus, Figs. 1 and 5), area MIP, area PFG on the



**Fig. 5 – AIP-microstimulation.** Areas significantly activated during microstimulation of posterior AIP compared to no microstimulation are shown in green; areas active by microstimulation of anterior AIP microstimulation are shown in red.  $p < .001$ , uncorrected. Yellow indicates overlap. White outlines indicate the stereo network as in Fig. 3. Arrow indicates area TEO activated by both stereo-stimuli and pAIP-microstimulation. Abbreviations as in Fig. 1. Data from Premereur et al., 2015.

parietal convexity, and the secondary somatosensory area S2 (in which neurons are active when monkeys actively explore objects with their hands (Ishida, Fornia, Grandi, Umiltà, & Gallese, 2013)). However, the posterior subsector of AIP (pAIP), with neuronal properties virtually identical to those in anterior AIP, showed a very different pattern of connectivity (Fig. 5; green activations): EM in pAIP activated area 45B in the anterior bank of the lower ramus of the arcuate sulcus, areas PIP and CIP in the caudal IPS and, surprisingly, also areas TEO and TE in the ventral visual stream. Note that EM-fMRI in area LIP also evoked a distinct pattern of activations (mainly in area FST). Thus, EM-fMRI in functionally-defined clusters of neurons in the IPS can chart distinct patterns of effective connectivity of small subsectors of areas, often localized only a few millimeters apart.

The sum of all functional activations measured during EM-fMRI in aAIP and pAIP provides a remarkably consistent replication of the anatomical tracer results described in Borra et al. (2008). However, Premereur, Van Dromme, et al. (2015) mapped the effective connectivity of patches of neurons that were identified and studied by means of extensive single-cell recordings, so that we can draw conclusions about specific neuronal populations rather than an entire area.

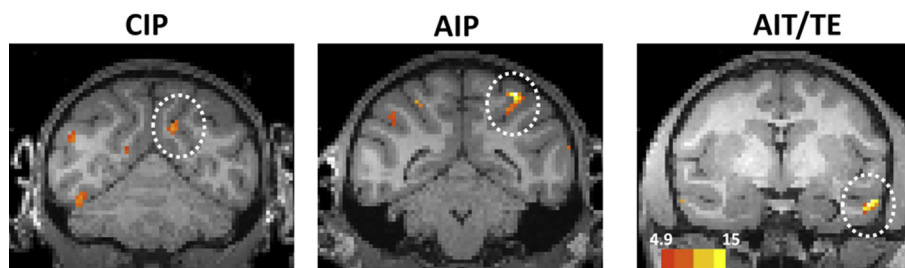
The overlap in the 3D structure network (Fig. 5; white outlines) and the fMRI activations observed during pAIP-EM (Fig. 5; green activation patterns) in area TEO (marked with an arrow in Fig. 5) clearly demonstrates that pAIP is connected to 3D-structure sensitive regions in the ventral visual stream, although also other ITC regions were activated by pAIP-EM.

Previous electrophysiological recordings had demonstrated that 3D structure selectivity is clustered in area TE, i.e., patches of neurons that prefer convex surfaces are separated from patches with neurons preferring concave surfaces (Verhoef et al., 2012). When neuronal properties are clustered in the cortex, it becomes possible to investigate the effect of artificially enhancing the activity in one of these clusters on perceptual reports (DeAngelis, Cumming, & Newsome, 1998; Salzman, Murasugi, Britten, & Newsome, 1992). Electrical microstimulation (EM) during 3D structure categorization causes very different effects in the dorsal compared to the ventral visual stream. In a reaction-time version of the 3D structure categorization task (i.e., the monkey could make his eye movement response as soon as he reached a decision), the injection of small electrical currents in clusters of neurons in area TE caused robust and highly consistent effects on the

perceptual report (Verhoef et al., 2012): EM in clusters of neurons preferring convex shapes caused the animals to choose convex much more frequently, whereas EM in clusters of neurons preferring concave shapes led to much more concave choices. Moreover, EM caused significantly shorter reaction times when the animals opted for the choice target associated with the preference of the stimulation site, and increased reaction times when the animals chose the other target. These observations are consistent with the idea that the monkeys' choices arise from a competition between two populations of neurons (one for convex and the other for concave), which is biased by adding EM, similar to previous studies (DeAngelis et al., 1998; Ditterich, Mazurek, & Shadlen, 2003). However, when the same animals received EM in clusters of neurons in parietal area AIP (with similar selectivity and clustering as in TE) the effects on behavior were very different (Verhoef, Vogels, & Janssen, 2015): EM caused either small or inconsistent effects on perceptual categorization, and almost invariably caused an increase in the reaction times of the animals. Combining these behavioral results with the EM-fMRI study described earlier (Premereur, Van Dromme, et al., 2015), we can hypothesize that AIP-EM may have caused variable activation of TE clusters (in some animals or in some sessions more than in others depending on the location in AIP), and therefore also variable and inconsistent effects on perception.

The most straightforward test of a possible dorsal stream contribution to ventral stream areas during 3D object vision consists of reversible inactivation of a dorsal stream area while measuring its effect on the ventral stream. Van Dromme et al. (2016) injected muscimol, a GABA-A agonist, into an area in the most posterior part of the IPS, area CIP, while monkeys were viewing curved and flat surfaces during fMRI. As expected, reversible inactivation of area CIP caused a significant reduction in fMRI activations related to 3D structure processing in area AIP (Fig. 6).

More surprisingly, however, CIP inactivation also caused a significant reduction in fMRI activations in area TE, but not in area TEO. Furthermore, CIP inactivation during 3D structure categorization caused a small but significant reduction in performance in both monkeys. EM-fMRI of CIP did not activate area AIP nor TE, suggesting that the observed inactivation effects arose by means of an indirect effect (most likely through dorsal LIP). It is likely that CIP inactivation caused a reduction in activity in area AIP, which in turn caused a reduction in 3D structure-related activations in area TE and



**Fig. 6 – Reversible CIP-inactivation.** T-score maps show areas with significantly decreased stereo-activations during CIP-inactivation compared to no-inactivation. Dashed circles mark the labeled areas (CIP, AIP and AIT/TE).  $P < .05$ , FWE corrected. Data from (Van Dromme et al., 2016).

thereby also a perceptual deficit. These observations constitute the first evidence for a causal contribution of the dorsal stream to 3D structure-related activations in the ventral visual stream. However, the exact role of these dorsal-pathway areas on the ITC requires further research.

## 6. Conclusions

This review has focused on dorsal–ventral stream interactions during 3D structure processing in the macaque monkey. However, similar interactions may also exist for the computation of 2D shape contours. Neurons in pAIP respond very selectively to small shape features (Romero & Janssen, 2016; Romero et al., 2014), and pAIP is effectively connected to ventral stream areas TEO and TE (Premereur, Van Dromme, et al., 2015).

Highly specific causal perturbation methods in combination with psychophysics, electrophysiology and functional imaging represent powerful tools to unravel how cortical networks operate. A recent study (Klein et al., 2016) showed that EM primarily evokes orthodromic activations of feedforward connections, similar to cell-type specific optogenetics. The EM-fMRI data described above are consistent with this idea, as well as with the known pattern of anatomical connectivity between IPS areas and ventral stream areas (Borra et al., 2008). Although feedback connections are abundant in the primate brain, EM-fMRI may predominantly show the much more powerful feedforward (“driving”) connections.

At first glance, one might reason that object shape is analyzed in the ventral visual stream and then transmitted to the dorsal stream IPS areas to provide visual object information for grasping. Several lines of evidence argue against this idea. First of all, the response latencies are invariably shorter in AIP than in TE, on average by 10–30 msec. Secondly, the properties of AIP neurons differ markedly from those of neurons in TE or TEO. Besides the differences related to the representation of 3D structure described above, the most intriguing difference is that pAIP neurons do not signal shape independent of position, i.e., they lack position tolerance: the preference for small shape features can be very different when tested at another position within the receptive field of the neuron (Romero et al., 2014). Ventral stream areas TEO and TE, in contrast, achieve high selectivity and position tolerance (DiCarlo, Zoccolan, & Rust, 2012). Finally, all experimental evidence to date (anatomical connectivity, synchronization, microstimulation and reversible inactivation during fMRI) indicates an influence of the IPS areas in the dorsal stream upon the ventral stream, but much less in the opposite direction. (It should be noted that no EM-fMRI or inactivation-fMRI study has targeted areas TE or TEO.) Thus, theoretical arguments (e.g., the FARS model) suggest that ventral stream object information should be transmitted to the dorsal stream (e.g., when grasping a coffee mug), but experimental evidence so far suggests an influence of the dorsal stream IPS areas on the ventral stream. Several possibilities might explain this apparent conflict. First of all, the tasks that have been used so far may not have been optimal to reveal a ventral stream contribution to the dorsal stream. A task in which the grasp type would depend on some typical object feature processed

exclusively in the ventral stream (e.g., texture) might be more suitable to demonstrate a ventral pathway contribution to the dorsal stream. Moreover, introducing a delay might be important since the ventral pathway of humans may be more recruited when grasping objects after a delay but not during immediate grasping (Cohen, Cross, Tunik, Grafton, & Culham, 2009; Singhal, Monaco, Kaufman, & Culham, 2013). Furthermore, the presence of monocular depth cues during prehension may also increase the functional coupling between parietal and temporal areas (Verhagen, Dijkerman, Grol, & Toni, 2008). Alternatively, a species difference could also play a role: humans grasp objects in different ways depending on what the goal of the action is (e.g., drinking or placing), but monkeys may not have this capacity in their behavioral repertoire – at least not to the same degree as humans. Finally, although the dorsal and the ventral streams clearly – and possibly at multiple levels – interact, visual object information may not simply be transferred from one visual stream to the other. After all, patient studies have demonstrated that both pathways can function independently, since reaching and grasping can be relatively preserved after ventral stream lesions and object recognition can be intact after dorsal stream lesions (Goodale et al., 1991).

## Conflict of interest

The authors declare no conflict of interest.

## Funding sources

Bram-Ernst Verhoef is a postdoctoral fellow of the Flemish fund for scientific research (FWO). The authors received funding from PFV/10/008 and FWO grants G071309 and G0A2213. The funding sources had no role in study design; data collection, analysis or interpretation; writing of the report or the decision to submit the article for publication.

## Acknowledgements

We thank Anne Coeman, Marc De Paep, Sara De Pril, Wouter Depuydt, Chantal Franssen, Astrid Hermans, Piet Kayenbergh, Gerrit Meulemans, and Stijn Verstraeten for technical and administrative assistance. Special thanks to Christophe Ulens and Inez Puttemans for assistance during the experiments.

## REFERENCES

- Bhattacharyya, R., Musallam, S., & Andersen, R. A. (2009). Parietal reach region encodes reach depth using retinal disparity and vergence angle signals. *Journal of Neurophysiology*, 102(2), 805–816. <http://dx.doi.org/10.1152/jn.90359.2008>.
- Borra, E., Belmalih, A., Calzavara, R., Gerbella, M., Murata, A., Rozzi, S., et al. (2008). Cortical connections of the macaque anterior intraparietal (AIP) area. *Cerebral Cortex*, 18(5), 1094–1111. <http://dx.doi.org/10.1093/cercor/bhm146>.

- Bridge, H., & Parker, A. J. (2007). Topographical representation of binocular depth in the human visual cortex using fMRI. *Journal of Vision*, 7(14). <http://dx.doi.org/10.1167/7.14.15>, 15–11–14.
- Britten, K. H., Shadlen, M. N., Newsome, W. T., & Movshon, J. A. (1993). Responses of neurons in macaque MT to stochastic motion signals. *Visual Neuroscience*, 10(6), 1157–1169.
- Chandrasekaran, C., Canon, V., Dahmen, J. C., Kourtzi, Z., & Welchman, A. E. (2007). Neural correlates of disparity-defined shape discrimination in the human brain. *Journal of Neurophysiology*, 97(2), 1553–1565. <http://dx.doi.org/10.1152/jn.01074.2006>.
- Cohen, N. R., Cross, E. S., Tunik, E., Grafton, S. T., & Culham, J. C. (2009). Ventral and dorsal stream contributions to the online control of immediate and delayed grasping: A TMS approach. *Neuropsychologia*, 47(6), 1553–1562. <http://dx.doi.org/10.1016/j.neuropsychologia.2008.12.034>.
- Colby, C. L., Duhamel, J. R., & Goldberg, M. E. (1993). Ventral intraparietal area of the macaque: Anatomic location and visual response properties. *Journal of Neurophysiology*, 69(3), 902–914.
- Conway, B. R., & Tsao, D. Y. (2006). Color architecture in alert macaque cortex revealed by fMRI. *Cerebral Cortex*, 16(11), 1604–1613. <http://dx.doi.org/10.1093/cercor/bhj099>.
- Cook, E. P., & Maunsell, J. H. (2002). Dynamics of neuronal responses in macaque MT and VIP during motion detection. *Nature Neuroscience*, 5(10), 985–994. <http://dx.doi.org/10.1038/nn924>.
- Culham, J. C., & Kanwisher, N. G. (2001). Neuroimaging of cognitive functions in human parietal cortex. *Current Opinion in Neurobiology*, 11(2), 157–163.
- Cumming, B. G., & Parker, A. J. (2000). Local disparity not perceived depth is signaled by binocular neurons in cortical area V1 of the Macaque. *The Journal of Neuroscience*, 20(12), 4758–4767.
- DeAngelis, G. C., Cumming, B. G., & Newsome, W. T. (1998). Cortical area MT and the perception of stereoscopic depth. *Nature*, 394(6694), 677–680. <http://dx.doi.org/10.1038/29299>.
- DiCarlo, J. J., Zoccolan, D., & Rust, N. C. (2012). How does the brain solve visual object recognition? *Neuron*, 73(3), 415–434. <http://dx.doi.org/10.1016/j.neuron.2012.01.010>.
- Ditterich, J., Mazurek, M. E., & Shadlen, M. N. (2003). Microstimulation of visual cortex affects the speed of perceptual decisions. *Nature Neuroscience*, 6(8), 891–898. <http://dx.doi.org/10.1038/nn1094>.
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, 293(5539), 2470–2473. <http://dx.doi.org/10.1126/science.1063414>.
- Durand, J. B., Nelissen, K., Joly, O., Wardak, C., Todd, J. T., Norman, J. F., et al. (2007). Anterior regions of monkey parietal cortex process visual 3D shape. *Neuron*, 55(3), 493–505. <http://dx.doi.org/10.1016/j.neuron.2007.06.040>.
- Fagg, A. H., & Arbib, M. A. (1998). Modeling parietal-premotor interactions in primate control of grasping. *Neural Networks*, 11(7–8), 1277–1303.
- Ferraina, S., Pare, M., & Wurtz, R. H. (2000). Disparity sensitivity of frontal eye field neurons. *Journal of Neurophysiology*, 83(1), 625–629.
- Freud, E., Plaut, D. C., & Behrmann, M. (2016). ‘What’ is happening in the dorsal visual pathway. *Trends in Cognitive Sciences*, 20(10), 773–784. <http://dx.doi.org/10.1016/j.tics.2016.08.003>.
- Georgieva, S. S., Todd, J. T., Peeters, R., & Orban, G. A. (2008). The extraction of 3D shape from texture and shading in the human brain. *Cerebral Cortex*, 18(10), 2416–2438. <http://dx.doi.org/10.1093/cercor/bhn002>.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20–25.
- Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, 349(6305), 154–156. <http://dx.doi.org/10.1038/349154a0>.
- Grefkes, C., & Fink, G. R. (2005). The functional organization of the intraparietal sulcus in humans and monkeys. *The Journal of Anatomy*, 207(1), 3–17. <http://dx.doi.org/10.1111/j.1469-7580.2005.00426.x>.
- Ishida, H., Fornia, L., Grandi, L. C., Umilta, M. A., & Gallese, V. (2013). Somato-motor haptic processing in posterior inner perisylvian region (SII/piC) of the macaque monkey. *PLoS One*, 8(7), e69931. <http://dx.doi.org/10.1371/journal.pone.0069931>.
- Janssen, P., Vogels, R., Liu, Y., & Orban, G. A. (2003). At least at the level of inferior temporal cortex, the stereo correspondence problem is solved. *Neuron*, 37(4), 693–701.
- Janssen, P., Vogels, R., & Orban, G. A. (1999). Macaque inferior temporal neurons are selective for disparity-defined three-dimensional shapes. *Proceedings of the National Academy of Sciences of the United States of America*, 96(14), 8217–8222.
- Janssen, P., Vogels, R., & Orban, G. A. (2000). Three-dimensional shape coding in inferior temporal cortex. *Neuron*, 27(2), 385–397.
- Jeannerod, M. (1986). Mechanisms of visuomotor coordination: A study in normal and brain-damaged subjects. *Neuropsychologia*, 24(1), 41–78.
- Jeannerod, M., Decety, J., & Michel, F. (1994). Impairment of grasping movements following a bilateral posterior parietal lesion. *Neuropsychologia*, 32(4), 369–380.
- Johnson, P. B., Ferraina, S., Bianchi, L., & Caminiti, R. (1996). Cortical networks for visual reaching: Physiological and anatomical organization of frontal and parietal lobe arm regions. *Cerebral Cortex*, 6(2), 102–119.
- Johnson, P. B., Ferraina, S., & Caminiti, R. (1993). Cortical networks for visual reaching. *Experimental Brain Research*, 97(2), 361–365.
- Joly, O., Vanduffel, W., & Orban, G. A. (2009). The monkey ventral premotor cortex processes 3D shape from disparity. *NeuroImage*, 47(1), 262–272. <http://dx.doi.org/10.1016/j.neuroimage.2009.04.043>.
- Katsuyama, N., Yamashita, A., Sawada, K., Naganuma, T., Sakata, H., & Taira, M. (2010). Functional and histological properties of caudal intraparietal area of macaque monkey. *Neuroscience*, 167(1), 1–10. <http://dx.doi.org/10.1016/j.neuroscience.2010.01.028>.
- Klein, C., Evrard, H. C., Shapcott, K. A., Haverkamp, S., Logothetis, N. K., & Schmid, M. C. (2016). Cell-targeted optogenetics and electrical microstimulation reveal the primate koniocellular projection to supra-granular visual cortex. *Neuron*, 90(1), 143–151. <http://dx.doi.org/10.1016/j.neuron.2016.02.036>.
- Krug, K. (2004). A common neuronal code for perceptual processes in visual cortex? Comparing choice and attentional correlates in V5/MT. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359(1446), 929–941. <http://dx.doi.org/10.1098/rstb.2003.1415>.
- Lewis, J. W., & Van Essen, D. C. (2000). Mapping of architectonic subdivisions in the macaque monkey, with emphasis on parieto-occipital cortex. *The Journal of Comparative Neurology*, 428(1), 79–111.
- Maunsell, J. H., & Newsome, W. T. (1987). Visual processing in monkey extrastriate cortex. *Annual Review of Neuroscience*, 10, 363–401. <http://dx.doi.org/10.1146/annurev.ne.10.030187.002051>.
- Maunsell, J. H., & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology*, 49(5), 1127–1147.
- Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the shape, size, and orientation of



- objects for grasping in neurons of monkey parietal area AIP. *Journal of Neurophysiology*, 83(5), 2580–2601.
- Nelissen, K., & Vanduffel, W. (2011). Grasping-related functional magnetic resonance imaging brain responses in the macaque monkey. *The Journal of Neuroscience*, 31(22), 8220–8229. <http://dx.doi.org/10.1523/JNEUROSCI.0623-11.2011>.
- Nishio, A., Goda, N., & Komatsu, H. (2012). Neural selectivity and representation of gloss in the monkey inferior temporal cortex. *The Journal of Neuroscience*, 32(31), 10780–10793. <http://dx.doi.org/10.1523/JNEUROSCI.1095-12.2012>.
- Parker, A. J. (2007). Binocular depth perception and the cerebral cortex. *Nature Reviews Neuroscience*, 8(5), 379–391. <http://dx.doi.org/10.1038/nrn2131>.
- Pesaran, B., Pezaris, J. S., Sahani, M., Mitra, P. P., & Andersen, R. A. (2002). Temporal structure in neuronal activity during working memory in macaque parietal cortex. *Nature Neuroscience*, 5(8), 805–811. <http://dx.doi.org/10.1038/nn890>.
- Popivanov, I. D., Jastorff, J., Vanduffel, W., & Vogels, R. (2012). Stimulus representations in body-selective regions of the macaque cortex assessed with event-related fMRI. *NeuroImage*, 63(2), 723–741. <http://dx.doi.org/10.1016/j.neuroimage.2012.07.013>.
- Premereur, E., Janssen, P., & Vanduffel, W. (2015). Effector specificity in macaque frontal and parietal cortex. *The Journal of Neuroscience*, 35(8), 3446–3459. <http://dx.doi.org/10.1523/JNEUROSCI.3710-14.2015>.
- Premereur, E., Van Dromme, I. C., Romero, M. C., Vanduffel, W., & Janssen, P. (2015). Effective connectivity of depth-structure-selective patches in the lateral bank of the macaque intraparietal sulcus. *PLoS Biology*, 13(2), e1002072. <http://dx.doi.org/10.1371/journal.pbio.1002072>.
- Premereur, E., Vanduffel, W., & Janssen, P. (2011). Functional heterogeneity of macaque lateral intraparietal neurons. *The Journal of Neuroscience*, 31(34), 12307–12317. <http://dx.doi.org/10.1523/JNEUROSCI.2241-11.2011>.
- Rogers, B., & Cagenello, R. (1989). Disparity curvature and the perception of three-dimensional surfaces. *Nature*, 339(6220), 135–137. <http://dx.doi.org/10.1038/339135a0>.
- Romero, M. C., & Janssen, P. (2016). Receptive field properties of neurons in the macaque anterior intraparietal area. *Journal of Neurophysiology*, 115(3), 1542–1555. <http://dx.doi.org/10.1152/jn.01037.2014>.
- Romero, M. C., Pani, P., & Janssen, P. (2014). Coding of shape features in the macaque anterior intraparietal area. *The Journal of Neuroscience*, 34(11), 4006–4021. <http://dx.doi.org/10.1523/JNEUROSCI.4095-13.2014>.
- Rosenberg, A., Cowan, N. J., & Angelaki, D. E. (2013). The visual representation of 3D object orientation in parietal cortex. *The Journal of Neuroscience*, 33(49), 19352–19361. <http://dx.doi.org/10.1523/JNEUROSCI.3174-13.2013>.
- Saito, H., Yukie, M., Tanaka, K., Hikosaka, K., Fukada, Y., & Iwai, E. (1986). Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *The Journal of Neuroscience*, 6(1), 145–157.
- Salzman, C. D., Murasugi, C. M., Britten, K. H., & Newsome, W. T. (1992). Microstimulation in visual area MT: Effects on direction discrimination performance. *The Journal of Neuroscience*, 12(6), 2331–2355.
- Schall, J. D., Morel, A., King, D. J., & Bullier, J. (1995). Topography of visual cortex connections with frontal eye field in macaque: Convergence and segregation of processing streams. *The Journal of Neuroscience*, 15(6), 4464–4487.
- Shikata, E., McNamara, A., Sprenger, A., Hamzei, F., Glauche, V., Buchel, C., et al. (2008). Localization of human intraparietal areas AIP, CIP, and LIP using surface orientation and saccadic eye movement tasks. *Human Brain Mapping*, 29(4), 411–421. <http://dx.doi.org/10.1002/hbm.20396>.
- Singhal, A., Monaco, S., Kaufman, L. D., & Culham, J. C. (2013). Human fMRI reveals that delayed action re-recruits visual perception. *PLoS One*, 8(9), e73629. <http://dx.doi.org/10.1371/journal.pone.0073629>.
- Snyder, L. H., Batista, A. P., & Andersen, R. A. (1997). Coding of intention in the posterior parietal cortex. *Nature*, 386(6621), 167–170. <http://dx.doi.org/10.1038/386167a0>.
- Srivastava, S., Orban, G. A., De Maziere, P. A., & Janssen, P. (2009). A distinct representation of three-dimensional shape in macaque anterior intraparietal area: Fast, metric, and coarse. *The Journal of Neuroscience*, 29(34), 10613–10626. <http://dx.doi.org/10.1523/JNEUROSCI.6016-08.2009>.
- Stanton, G. B., Bruce, C. J., & Goldberg, M. E. (1995). Topography of projections to posterior cortical areas from the macaque frontal eye fields. *The Journal of Comparative Neurology*, 353(2), 291–305. <http://dx.doi.org/10.1002/cne.903530210>.
- Tanaka, K., & Saito, H. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology*, 62(3), 626–641.
- Tanne, J., Boussaoud, D., Boyer-Zeller, N., & Rouiller, E. M. (1995). Direct visual pathways for reaching movements in the macaque monkey. *NeuroReport*, 7(1), 267–272.
- Theys, T., Pani, P., van Loon, J., Goffin, J., & Janssen, P. (2012). Selectivity for three-dimensional shape and grasping-related activity in the macaque ventral premotor cortex. *The Journal of Neuroscience*, 32(35), 12038–12050. <http://dx.doi.org/10.1523/JNEUROSCI.1790-12.2012>.
- Theys, T., Pani, P., van Loon, J., Goffin, J., & Janssen, P. (2013). Three-dimensional shape coding in grasping circuits: A comparison between the anterior intraparietal area and ventral premotor area F5a. *The Journal of Cognitive Neuroscience*, 25(3), 352–364. [http://dx.doi.org/10.1162/jocn\\_a\\_00332](http://dx.doi.org/10.1162/jocn_a_00332).
- Theys, T., Srivastava, S., van Loon, J., Goffin, J., & Janssen, P. (2012). Selectivity for three-dimensional contours and surfaces in the anterior intraparietal area. *Journal of Neurophysiology*, 107(3), 995–1008. <http://dx.doi.org/10.1152/jn.00248.2011>.
- Tsao, D. Y., Freiwald, W. A., Knutsen, T. A., Mandeville, J. B., & Tootell, R. B. (2003). Faces and objects in macaque cerebral cortex. *Nature Neuroscience*, 6(9), 989–995. <http://dx.doi.org/10.1038/nn1111>.
- Tsao, D. Y., Moeller, S., & Freiwald, W. A. (2008). Comparing face patch systems in macaques and humans. *Proceedings of the National Academy of Sciences of the United States of America*, 105(49), 19514–19519. <http://dx.doi.org/10.1073/pnas.0809662105>.
- Tsao, D. Y., Vanduffel, W., Sasaki, Y., Fize, D., Knutsen, T. A., Mandeville, J. B., et al. (2003). Stereopsis activates V3A and caudal intraparietal areas in macaques and humans. *Neuron*, 39(3), 555–568.
- Tsutsui, K., Sakata, H., Naganuma, T., & Taira, M. (2002). Neural correlates for perception of 3D surface orientation from texture gradient. *Science*, 298(5592), 409–412. <http://dx.doi.org/10.1126/science.1074128>.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.
- Van Dromme, I. C., Premereur, E., Verhoef, B. E., Vanduffel, W., & Janssen, P. (2016). Posterior parietal cortex drives inferotemporal activations during three-dimensional object vision. *PLoS Biology*, 14(4), e1002445. <http://dx.doi.org/10.1371/journal.pbio.1002445>.
- Van Dromme, I. C., Vanduffel, W., & Janssen, P. (2015). The relation between functional magnetic resonance imaging activations and single-cell selectivity in the macaque

- intraparietal sulcus. *NeuroImage*, 113, 86–100. <http://dx.doi.org/10.1016/j.neuroimage.2015.03.023>.
- Vaziri, S., Carlson, E. T., Wang, Z., & Connor, C. E. (2014). A channel for 3D environmental shape in anterior inferotemporal cortex. *Neuron*, 84(1), 55–62. <http://dx.doi.org/10.1016/j.neuron.2014.08.043>.
- Verhagen, L., Dijkerman, H. C., Grol, M. J., & Toni, I. (2008). Perceptuo-motor interactions during prehension movements. *The Journal of Neuroscience*, 28(18), 4726–4735. <http://dx.doi.org/10.1523/JNEUROSCI.0057-08.2008>.
- Verhoef, B. E., Bohon, K. S., & Conway, B. R. (2015). Functional architecture for disparity in macaque inferior temporal cortex and its relationship to the architecture for faces, color, scenes, and visual field. *The Journal of Neuroscience*, 35(17), 6952–6968. <http://dx.doi.org/10.1523/JNEUROSCI.5079-14.2015>.
- Verhoef, B. E., Vogels, R., & Janssen, P. (2010). Contribution of inferior temporal and posterior parietal activity to three-dimensional shape perception. *Current Biology: CB*, 20(10), 909–913. <http://dx.doi.org/10.1016/j.cub.2010.03.058>.
- Verhoef, B. E., Vogels, R., & Janssen, P. (2011). Synchronization between the end stages of the dorsal and the ventral visual stream. *Journal of Neurophysiology*, 105(5), 2030–2042. <http://dx.doi.org/10.1152/jn.00924.2010>.
- Verhoef, B. E., Vogels, R., & Janssen, P. (2012). Inferotemporal cortex subserves three-dimensional structure categorization. *Neuron*, 73(1), 171–182. <http://dx.doi.org/10.1016/j.neuron.2011.10.031>.
- Verhoef, B. E., Vogels, R., & Janssen, P. (2015). Effects of microstimulation in the anterior intraparietal area during three-dimensional shape categorization. *PLoS One*, 10(8), e0136543. <http://dx.doi.org/10.1371/journal.pone.0136543>.
- Verhoef, B. E., Vogels, R., & Janssen, P. (2016). Binocular depth processing in the ventral visual pathway. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1697). <http://dx.doi.org/10.1098/rstb.2015.0259>.
- Wardak, C., Olivier, E., & Duhamel, J. R. (2002). Saccadic target selection deficits after lateral intraparietal area inactivation in monkeys. *The Journal of Neuroscience*, 22(22), 9877–9884.
- Webster, M. J., Bachevalier, J., & Ungerleider, L. G. (1994). Connections of inferior temporal areas TEO and TE with parietal and frontal cortex in macaque monkeys. *Cerebral Cortex*, 4(5), 470–483.
- Yamane, Y., Carlson, E. T., Bowman, K. C., Wang, Z., & Connor, C. E. (2008). A neural code for three-dimensional object shape in macaque inferotemporal cortex. *Nature Neuroscience*, 11(11), 1352–1360. <http://dx.doi.org/10.1038/nn.2202>.