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Neuropsychologia 41 (2003) 1757–1768

NEUROPSYCHOLOGIA

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Similarities and differences in motion processing between the human and macaque brain: evidence from fMRI

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Received 8 May 2003; accepted 20 June 2003

Abstract

The present report reviews a series of functional magnetic resonance imaging (fMRI) activation studies conducted in parallel in awake monkeys and humans using the same motion stimuli in both species. These studies reveal that motion stimuli engage largely similar cortical regions in the two species. These common regions include MT/V5 and its satellites, of which FST contributes more to the human motion complex than is generally assumed in human imaging. These results also establish a direct link between selectivity of MT/V5 neurons for speed gradients and functional activation of human MT/V5 by three-dimensional (3D) structure from motion stimuli. On the other hand, striking functional differences also emerged: in humans V3A and several regions in the intraparietal sulcus (IPS) are much more motion sensitive than their simian counterparts.

Keywords: fMRI; Cortical regions; Intraparietal sulcus; Primates

1. Introduction

Motion has attracted a lot of interest in psychology and also neuroscience, as witnessed by the present special issue. One reason is that motion processing has many behavioral functions (Nakayama, 1985). Motion processing gives rise to perception of object motion and of self-motion. It is also used to control eye movements, pursuit and optokinetic nystagmus, as well as to guide movements of body parts and locomotion. Finally, it gives rise to the perception of two-dimensional (2D) shape (kinetic boundaries) and allows the extraction of three-dimensional (3D) structure (the kinetic depth effect and motion parallax). A second important reason for the continuing interest in motion processes is that direction selective cells have been identified as potential neural substrates of motion processing in striate cortex (Hubel & Wiesel, 1962) and extrastriate cortex (Allman & Kaas, 1971; Dubner & Zeki, 1971).

When attempting to relate human perception to single neurons recorded in the wake macaque one faces two important issues. The first concerns the part of the monkey brain where single neurons should be recorded from. For motion processing the standard answer has been MT/V5 (Britten, Shadlen, Newsome, & Movshon, 1992), because almost all MT/V5 neurons are direction selective (Albright, 1984; Dubner & Zeki, 1971; Lagae, Maes, Raiguel, Xiao, & Orban, 1994). Other regions also contain sizeable proportions of direction selective neurons and have received less attention (see Celebrini & Newsome, 1994). The second question relates to the homology between cortical areas explored with single-cell recording in the monkey and cortical regions in the human brain. Functional imaging, positron emission tomography (PET) and more recently, functional magnetic resonance imaging (fMRI) may help solve these two issues. Indeed, functional imaging reveals the overall pattern of regions involved in behavioral functions. In fact, fMRI and single-cell studies complement each other by operating at different levels of integration (Churchland & Sejnowski, 1988). The microelectrode provides a detailed account of the properties of single neurons, whereas the fMRI signals presumably reflect the pooled activity of large populations of neurons. Hence, most recent imaging studies in humans try to relate their findings to single-cell properties. For example, when we reported that several regions in the human brain in addition to hMT/V5+ were sensitive to motion (Dupont, Orban, De Bruyn, Verbruggen, & Mortelmans,

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doi:10.1016/S0028-3932(03)00177-5

1994), we related this finding to the many monkey cortical areas which contain sizable proportions of direction selective neurons. This assumes, however, that there is a one-to-one relationship between the different monkey cortical areas, e.g. the 30 or so extrastriate areas, and their human counterparts.

We know that a complete homology between cortical areas of humans and monkeys is highly unlikely, given the anatomical and behavioral differences between the two species, and the 30 million years that separate the emergence of the two species during evolution. Until recently, we had no technique to identify those cortical areas where the homology holds up and those where it does not. fMRI in the awake monkey holds the potential to resolve this issue and provides the missing link between human functional imaging and monkey single-cell recording. Although several groups have reported imaging in awake monkeys (Dubowitz et al., 1998; Logothetis, Guggenberger, Peled, & Pauls, 1999; Stefanacci et al., 1998), systematic studies have appeared only recently (Leite et al., 2002; Nakahara, Hayashi, Konishi, & Miyashita, 2002; Vanduffel et al., 2001, 2002). The more recent ones (Nakahara et al., 2002; Vanduffel et al., 2002) have also explicitly compared functional maps in human and non-human primates. This interspecies comparison for cortical regions involved in motion processing is the topic of the present report. It includes two sets of studies: those using simple random dot translation and those related to the extraction of 3D structure from motion. The latter draws on the material reported in Vanduffel et al. (2002), and to a lesser degree on the preceding human study (Orban, Sunaert, Todd, van Hecke, & Marchal, 1999). The translation part combines the two reports that dealt with human and monkey fMRI separately: Sunaert, van Hecke, Marchal, & Orban (1999) and Vanduffel et al. (2001), respectively. Initially, Vanduffel et al. (2001) emphasized the similarity between the activation pattern in the two species, with the exception of V3A. Yet, further experiments and the insight from the 3D structure from motion study have made it clear that the cortical networks processing translation stimuli include regions that are similar in the two species and others that are dissimilar. The part of the visual system that differs between humans and monkeys for both types of stimuli includes not only V3A, but also, and perhaps even more prominently, the intraparietal sulcus (IPS).

2. Methods

The detailed description of the methods is given in the original publications (Sunaert et al., 1999; Vanduffel et al., 2001, 2002). Only a brief summary is given here.

2.1. Subjects

Thirty human subjects of both sexes ranging in age from 20 to 33 years participated in the studies. They had normal or corrected vision, were right handed and had no history of neurological or psychiatric disease. Three male monkey subjects (3–5 kg) with normal vision also participated in the studies. The subjects' head was immobilized by using a bite bar in humans and a headpost cemented to the skull in monkeys. The subjects were told or trained to fixate a target on the display. Eye position was monitored in both species. In most conditions the subjects remained passive while viewing the stimuli, though in some experiments they were required to perform a demanding orientation monitoring task (attention − conditions) or a one-back task (attention + conditions). Although humans were trained much less on the orientation monitoring tasks than monkeys, performance level was similar for the two species. Subjects viewed the display binocularly in the translation studies and both monocularly and binocularly in the structure from motion experiments. Preliminary surgical procedures in monkeys were performed under anesthesia and all guidelines for use of laboratory animals were strictly adhered to. Human subjects gave their informed consent. All studies were approved by the ethical committee of the K.U. Leuven, Medical School.

2.2. Stimuli

Stimuli were projected onto a translucent screen positioned in the bore of the magnet by means of a video projector (Barco 6300 LCD projector). While the humans viewed the screen trough a mirror angled 45° with the line of sight, the monkey faced the screen directly. Distance between the eyes and the screen was always 28 cm in humans and it varied in monkeys from 18 to 54 cm.

For the translation studies a random textures pattern (referred to as random dots) was used (50% white dots of 4.5 arc min side) of 7° diameter in humans and 14° in monkeys. This pattern could be stationary or it could move 4–6°/sec in eight random directions.

For the 3D structure from motion studies the stimuli consisted of nine connected random lines undergoing translation in the image plane or rotation in depth. The translation displays appeared perceptually as a flat pattern, whereas the ones rotating in depth created a vivid 3D impression. These stimuli, used in humans and monkeys, are depicted in the lower left panel (labeled random) in Fig. 5 of Orban et al. (1999). In addition to these main 2D and 3D motion conditions, many other dynamic stimuli were tested in order to control for physical differences between the 3D and 2D displays. These controls are described in detail in Orban et al. (1999) and Vanduffel et al. (2002).

2.3. Scanning

A block design was used in all studies. A functional imaging time series typically consisted of 120 gradient-echo echoplanar imaging whole brain scans (Siemens Vision, upgraded to Sonata, 1.5T) with similar parameters in both species (TR ranging 3.6–2.4 s, TE 32–40 ms, 64 × 64

matrix). The two main differences were (1) a lower resolution in humans (typically 3 mm × 3 mm × 4.5 mm) compared to monkeys (2 mm × 2 mm × 2 mm) to offset the difference in brain size, and (2) the use of a contrast agent (Mion) in monkeys (4–12 mg/kg i.v.), while in humans fMRI relied on the BOLD effect. Mion depends only on blood volume, while the traditional BOLD measurements used in humans depend on blood volume, blood flow and oxygen extraction. Mion increases the contrast to noise ratio by a factor of 5 in a 1.5 T magnet and improves the localization of activation to the cortical rim (less effect from draining veins). The impulse function for Mion is similar to that of Bold, although the decay is somewhat slower (Leite et al., 2002; Vanduffel et al., 2001). The sign of the MR signal is opposite in Mion and BOLD measurements.

Within a times series the different conditions lasted typically 30 s and alternated in random order. For each subject anatomical images were obtained with a 3D MPRAGE sequence. In monkeys several of these MPRAGE sequences were acquired under anesthesia and averaged.

2.4. Analysis

The data were analyzed with SPM 99 and Freesurfer (for flattening). Analysis was similar in the two species, except that in monkeys the eye movement recordings were included as covariates of no interest in the general linear model. In humans random and fixed effects analysis was performed on the group data. In monkeys, single-subject analysis was performed. Thus, data were less smoothed in monkeys than in humans. The threshold for significant changes was set at $P < 0.05$ corrected for multiple comparisons in all studies.

3. Results

3.1. Motion sensitivity in human cortex: translating random dots

Only six subjects participated in the initial study of Sunaert et al. (1999). Since then, we have systematically tested the motion sensitivity in many human subjects, collecting two time series with stationary and moving RDs. Here, we present the results of the random effects analysis of 30 subjects (Fig. 1, Table 1), which confirms fully the original study. Motion sensitivity was observed in four occipital regions including the human MT/V5 complex in the ascending limb of the ITS (Dupont, Orban, De Bruyn, Verbruggen, & Mortelmans, 1994; McCarthy et al., 1995; Tootell et al., 1995a; Watson et al., 1993; Zeki et al., 1991). The next most significant activation is that of human V3A (Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998; Tootell et al., 1997). When using low contrast stimuli and a surface coil motion activation is largely restricted

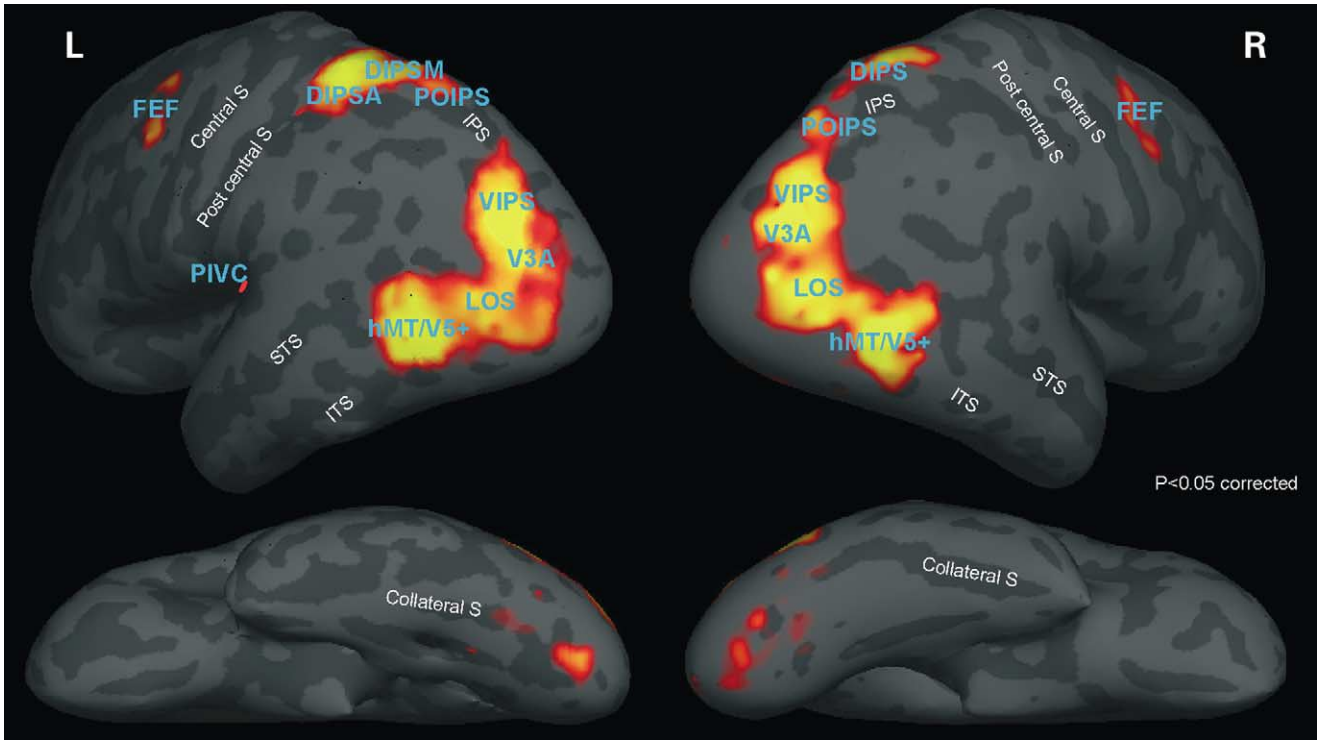

Fig. 1. Statistical parametric map (SPM) showing voxels that were significantly ($P < 0.05$, corrected random effects) more active when human subjects ($n = 30$) viewed moving RD than when viewing stationary RDs. The SPM is projected on inflated average left (L) and right (R) hemispheres of eight subjects. Top: postero-lateral view, bottom: ventral view. The different activation sites (see Table 1) are indicated in blue. STS: superior temporal sulcus, ITS: inferior temporal sulcus.

Table 1
Motion sensitive regions in human cerebral cortex

Region	Left hemisphere				Right hemisphere			
	x	*y*	*z*	*Z* score	*x*	*y*	*z*	*Z* score
hMT/V5+	−51	−72	0	6.87	51	−69	3	7.30
hV3A	−27	−90	12	7.27	33	−87	9	6.36
LOS/KO	−42	−81	6	5.96	42	−81	6	6.16
Ling	−27	−90	−9	5.52	15	−93	−9	6.47
VIPS	−27	−72	30	5.38	30	−78	27	6.04
POIPS	−18	−72	54	5.19	24	−75	45	5.94
DIPSM	−15	−63	60	5.67	18	−60	63	5.97
DIPSA	−36	−48	60	6.57	39	−36	54	4.23
FEF1	−33	0	63	5.34	39	0	60	5.34
FEF2	−42	0	51	5.24	48	3	48	5.13
PIC	−42	−33	21	5.08				
STS	−54	−51	12	4.34				
Fus					30	−66	−12	5.61
cing	−15	−21	39	4.78				

Fus: fusiform cortex; cing: cingulate cortex.

to these two regions (Tootell et al., 1997). In the present experiments, we used, however, high contrast stimuli and whole brain imaging. The other two occipital motion sensitive regions observed in our experiments are located in lingual gyrus and around the lateral occipital sulcus (LOS). Retinotopic mapping has shown that the lingual region corresponds to ventral V3, including in some instances ventral V2 or ventral V4 (Sunaert, van Hecke, Marchal, & Orban, 2000; Vanduffel et al., 2002). The LOS region is close to the kinetic occipital (KO) region which is also sensitive to simple translation (Rees, Friston, & Koch, 2000; van Oostende, Sunaert, van Hecke, Marchal, & Orban, 1997), hence the descriptive label LOS/KO used in the human reports.

There is a prominent motion activation in a string of regions along the IPS. Proceeding from occipital cortex to the post central sulcus, one encounters: (1) VIPS, in the occipital part of the IPS (Orban et al., 1999; Sunaert et al., 1999), (2) POIPS, at the junction of IPS and parieto-occipital sulcus (POS), (3) DIPSM, at the posterior end of the dorsal lips of IPS, and (4) DIPSA, at the anterior end of these dorsal edges, close to the junction with postcentral sulcus. The anatomical localization of these sites is illustrated in Figs. 3–5 (Sunaert et al., 1999). All these activation sites were observed in the two hemispheres, as was the activation of the frontal eye field (FEF, Table 1).

Finally, some motion sensitive sites reached significance only in one hemisphere, probably reflecting a weaker sensitivity. These include posterior insular cortical (PIC) region, close to vestibular cortex, superior temporal sulcus (STS) region supposedly involved in processing biological motion (Bonda, Petrides, Ostry, & Evans, 1996; Grossman & Blake, 2001; Puce, Allison, Bentin, Gore, & McCarthy, 1998), fusiform cortex and cingulate sulcus. Hence, most regions described by Sunaert et al. (1999) were obtained in this more extended analysis and their mean location is in good agreement in both studies (compare Table 1 with Table 2 of Sunaert et al., 1999).

3.2. Motion sensitivity in monkey cortex: translating random dots

Fig. 2 provides an overview of the motion sensitive regions in the macaque. These regions include V2 and V3, located in the lunate and inferior occipital sulci, MT/V5, FST, and MSTv, located in the superior temporal sulcus, VIP located in the intraparietal sulcus and FEF, located in the arcuate sulcus (Vanduffel et al., 2001). In one monkey, activation of a retroinsular region was observed.

Comparison with the human activation pattern reveals two important findings. First three of the four areas of the MT/V5 complex are activated by random dot motion and likely correspond to the hMT/V5+ activation observed in humans. These three areas include MT/V5 itself and FST and MSTv (Fig. 3). In particular, the FST activation matches that of MT/V5 itself in strength. Hence, assumptions based on single-cell recordings that the main components of the human MT/V5 complex are the homologues of MT/V5 and MSTd (Dukelow et al., 2000; Huk, Dougherty, & Heeger, 2002; Morrone et al., 2000) are not confirmed by our results.

Second, the number of motion sensitive regions is reduced in the monkey compared to humans. In addition to the almost classical absence of motion sensitivity in V3A (Tootell et al., 1997; Vanduffel et al., 2001), motion sensitivity tested with random dots is reduced in V4 compared to LOS/KO (but see Tolias, Smirnakis, Augath, Trinath, & Logothetis, 2001). Furthermore, the involvement of parietal cortex in motion processing is more restricted. VIP was motion sensitive in all monkeys, but its sensitivity is weak (Fig. 4).

3.3. 3D structure from motion sensitivity in humans and monkeys

In human occipital cortex, 3D SFM sensitivity was observed in hMT/V5+, LOS and hV3A (described in Orban et al., 1999 as TRIPS), as well as V2 and V3. In these two areas, activation was stronger in the ventral than dorsal cortex and corresponds to the lingual activation reported in the original study (Orban et al., 1999). In addition the four motion sensitive regions along the IPS were sensitive to 3D SFM: VIPS, POIPS, DIPSM and DIPSA. Finally, there might be some involvement of fusiform cortex (Fig. 5A). It is worth pointing out the excellent agreement between the human data in Vanduffel et al. (2002) and those reported in our original study (Orban et al., 1999). The only minor difference was a reduced inter-hemispheric bias in favor of the right hemisphere. This might reflect the small difference in stimuli between the studies (see Fig. 5 in Orban et al., 1999), or interindividual differences.

In monkeys (Fig. 5B) the sites engaged by 3D SFM included V2, V3, V4, MT/V5, FST, matching the activation

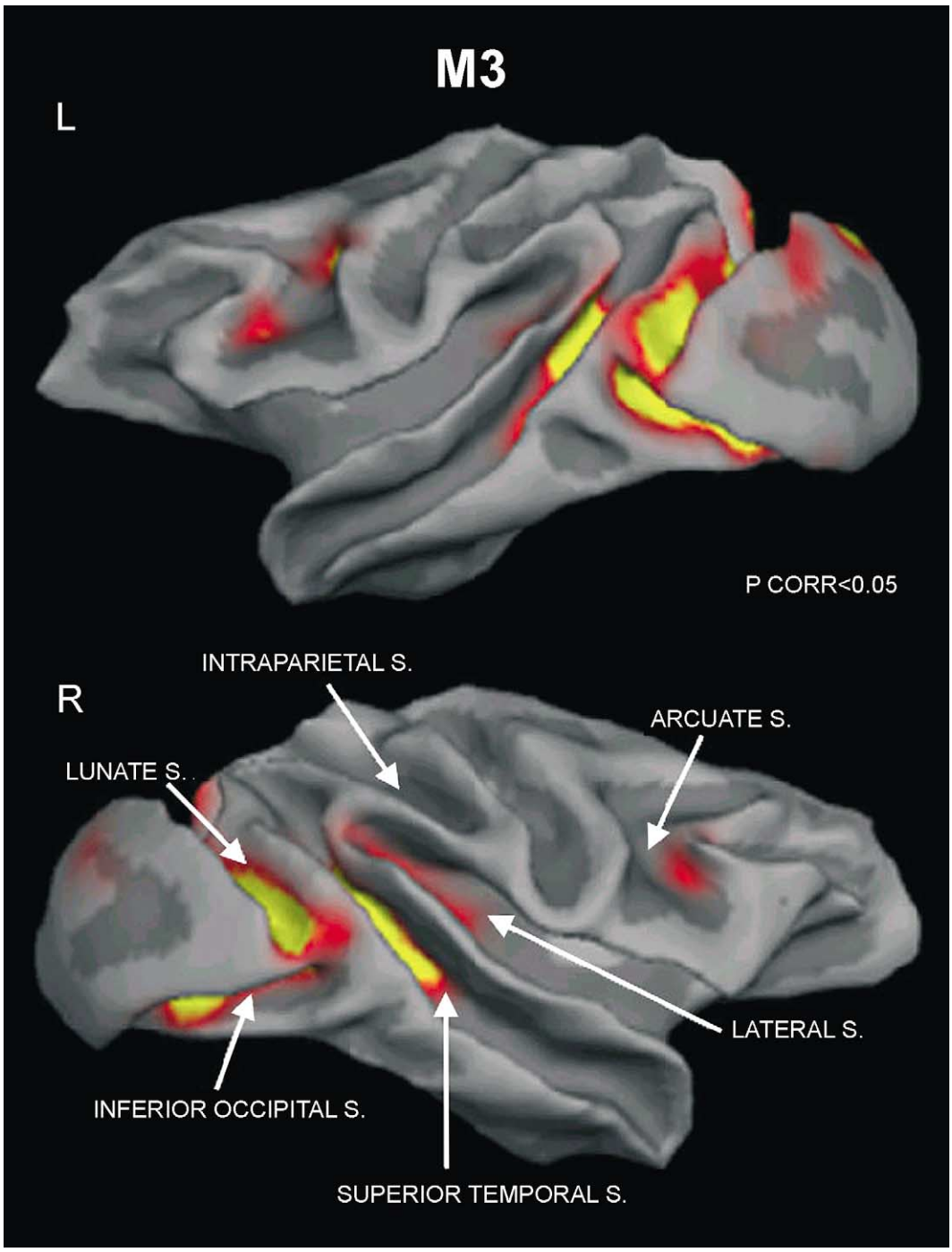

Fig. 2. Statistical parametric map showing voxels that were significantly ($P < 0.05$, corrected) more active when monkey subject M3 viewed moving RD than when viewing stationary RDs. The SPM is projected on the partially unfolded left (L) and right (R) hemispheres.

of early retinotopic regions, LOS and hMT/V5+ in humans. Notably, V3A and IPS regions were not activated at the standard significance level ($P < 0.05$ corrected). The activation of VIP (Fig. 6) reached only uncorrected level ($P < 0.001$). At that level activation was also observed in TE and anterior STS (Fig. 6). To ensure the generality of this result, we tested 3D SFM sensitivity in a range of conditions including the attention controls mentioned in the introduction and monocular and binocular viewing (for details of these tests, see Fig. 8). The grand average of all these tests for monkey VIP is compared to that of the four human IPS regions in Fig. 7. It is clear that the 3D SFM sensitivity is much stronger in human IPS compared to monkey IPS.

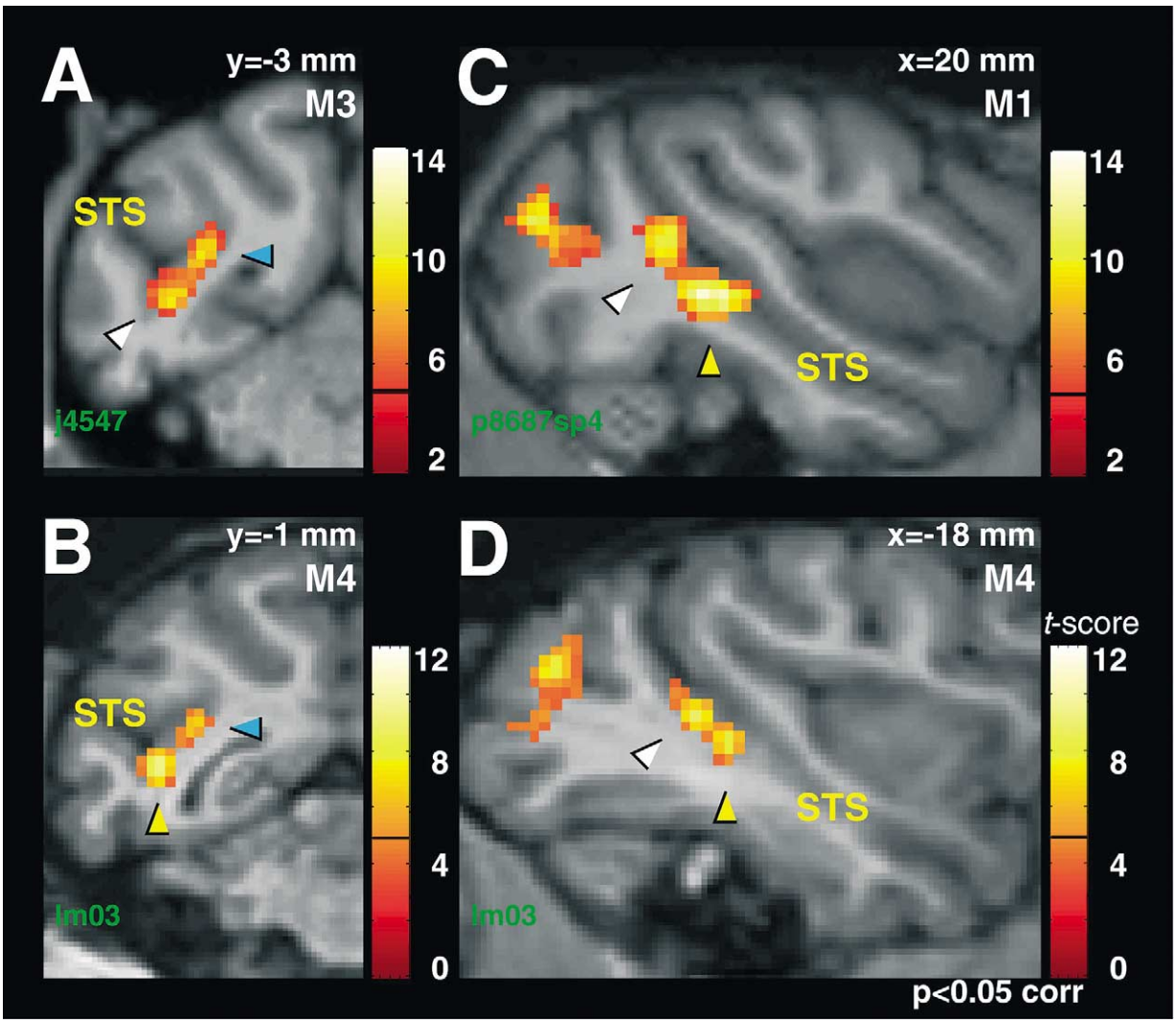

Fig. 3. SPMs for the motion-stationary subtraction thresholded at $P < 0.05$, corrected on coronal sections of monkey M3 (A) and M4 (B) 's brain and on sagittal sections of monkey M1 (C) and M4 (D) 's brain showing three functional regions in the superior temporal sulcus (STS): MT/V5 (white arrows), MSTv (blue arrows) and FST (yellow arrows). Color scales indicate *t* scores. Voxels in the lunate sulcus represent activation in V2 and V3.

In addition to attention controls, we also ran extensive controls to exclude effects of any of the physical differences between the 3D and 2D displays, other than those giving rise to the difference 3D structure. In humans most higher-order regions (hMT/V5+, LOS and the IPS regions) were significantly more active in the 3D rotation condition than in any of the 2D control conditions (Fig. 4 in Vanduffel et al., 2002 and Table 2 in Orban et al., 1999). In monkey, MT/V5+ and V4 behaved similarly (Fig. 4 in Vanduffel et al., 2002). The less significant activation sites in TE and VIP showed a similar tendency of functional specialization.

One of the regions that has enhanced activation for 3D SFM in both species is MT/V5. In the two species it was also the most significant and most consistent activation. Fig. 8 shows in detail all the experiments performed in humans and in monkeys, including 3D stimuli defined by moving random dots, portraying 3D planar surfaces. For all monkey subjects and all small subgroups of human subjects, MT/V5 or its human homologue was significantly active in both hemispheres.

4. Discussion

Motion sensitivity has been tested in humans with a variety of moving stimuli: translating gratings (e.g. Dupont et al., 1994 and Tootell et al., 1995a), translating random dots (Sunaert et al., 1999; Watson et al., 1993; Zeki et al., 1991), expanding and contracting circular gratings (Tootell et al., 1995b), expanding and contracting random dot patterns (Huk et al., 2002), and these stimuli have been presented in a wide variety of sizes. Little is know about how these variations in stimulus structure might influence MR motion sensitivity, although a few studies have tested

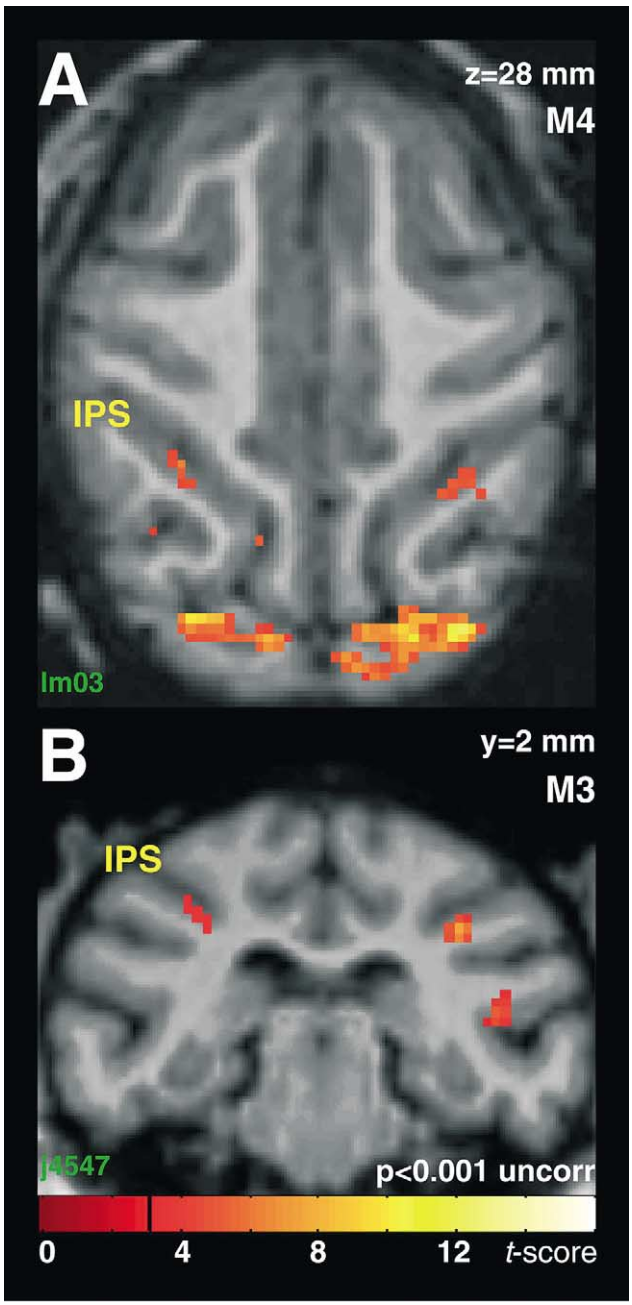

Fig. 4. SPMs for the motion-stationary subtraction on a horizontal (A) and a coronal section (B) of monkey M4 (A) and monkey M3 (B) 's brain. Same convention as in Fig. 3, except that threshold was lowered to $P < 0.001$, uncorrected. The few voxels in the intraparietal sulcus (IPS) correspond to VIP. Voxels in the lunate sulcus correspond to V2. Voxel size was 2 mm × 2 mm × 2 mm (compared to 3 mm × 3 mm × 3 mm in most of the initial study, Vanduffel et al., 2001).

the effects of contrast: (e.g. Tootell et al., 1995a) size (e.g. Sunaert et al., 1999) and speed (e.g. Chawla et al., 1999). To control for these factors in the present studies, it was important to use exactly the same stimuli in the two species. This was the case for the 3D structure from motion study (Vanduffel et al., 2002) and with exception of a minor difference in stimulus size, it was also true for the experiments investigating translatory motions. Sunaert et al. (1999) have reported that in humans the activation pattern obtained with translating RDs differs little between 7 and 14° diameter, and we have made similar observations in the monkey (Nelissen et al., unpublished). It is unlikely that the other small differences in experimental procedures explain the functional differences we observed (Leite et al., 2002; Vanduffel et al., 2001, 2002). Therefore, we conclude from our results that functionally V3A and intraparietal sulcus differ between humans and macaques. One should note that these differences concern regions processing motion information in the central visual field. Human imaging (Previc, Liotti, Blakemore, Beer, & Fox, 2000) and monkey imaging (Nelissen, unpublished) indicate that more peripheral stimuli yield a different activation pattern (see Galletti et al., this volume).

Despite these parietal differences, it is worth stressing that many regions are functionally similar in humans and monkeys, at least for the stimuli tested so far: notably the early retinotopic regions (Sereno et al., 1995), the MT/V5 complex and FEF. Although V4 seemed less sensitive to translating dots than its putative human counterpart, the 3D SFM sensitivity was similar, as is its sensitivity for kinetic patterns (Nelissen et al., 2000). Other experiments (Fize et al., 2002) also point to the conclusion that overall V4 is relatively similar in humans and monkeys. Therefore, we propose that human LOS/KO, that is located dorsally from human ventral V4, contains at least the homologue of monkey V4d. The homology between monkey MT/V5 and its human counterpart allows us to establish a direct link between the functional 3D SFM sensitivity measured with the fMRI and the selectivity for speed gradients reported for MT/V5 neurons reported by Xiao et al. (1997). To establish that link we tested 3D SFM sensitivity also with random dot stimuli portraying planar surfaces tilted in depth (Fig. 8), since the single-cell studies also used random dots and the speed gradients portrayed single-planar surfaces in depth. For the first time, we can make an explicit link between a single-cell property and a functional sensitivity measured in human fMRI. All three types of measurement point to the same functional specialization of MT/V5: extraction of depth from motion (Fig. 9).

Taken together the studies reviewed here clearly suggest that motion processing is much more prominent in human IPS than monkey IPS. This not completely surprising: in monkeys IPS separates a somatosensory area (area 5) from a visual one (area 7a). In humans, IPS is located in between two visual territories (SPL and IPL) and recently it has been suggested that IPL has no homologue in monkey (Karnath, 2001). An extensive study of IPS activation in a range of cognitive tasks has suggested that human IPS contains new regions not present in monkey (Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). This suggestion was based on the comparison of the human imaging results with monkey single-cell studies. With the technique reviewed here it is

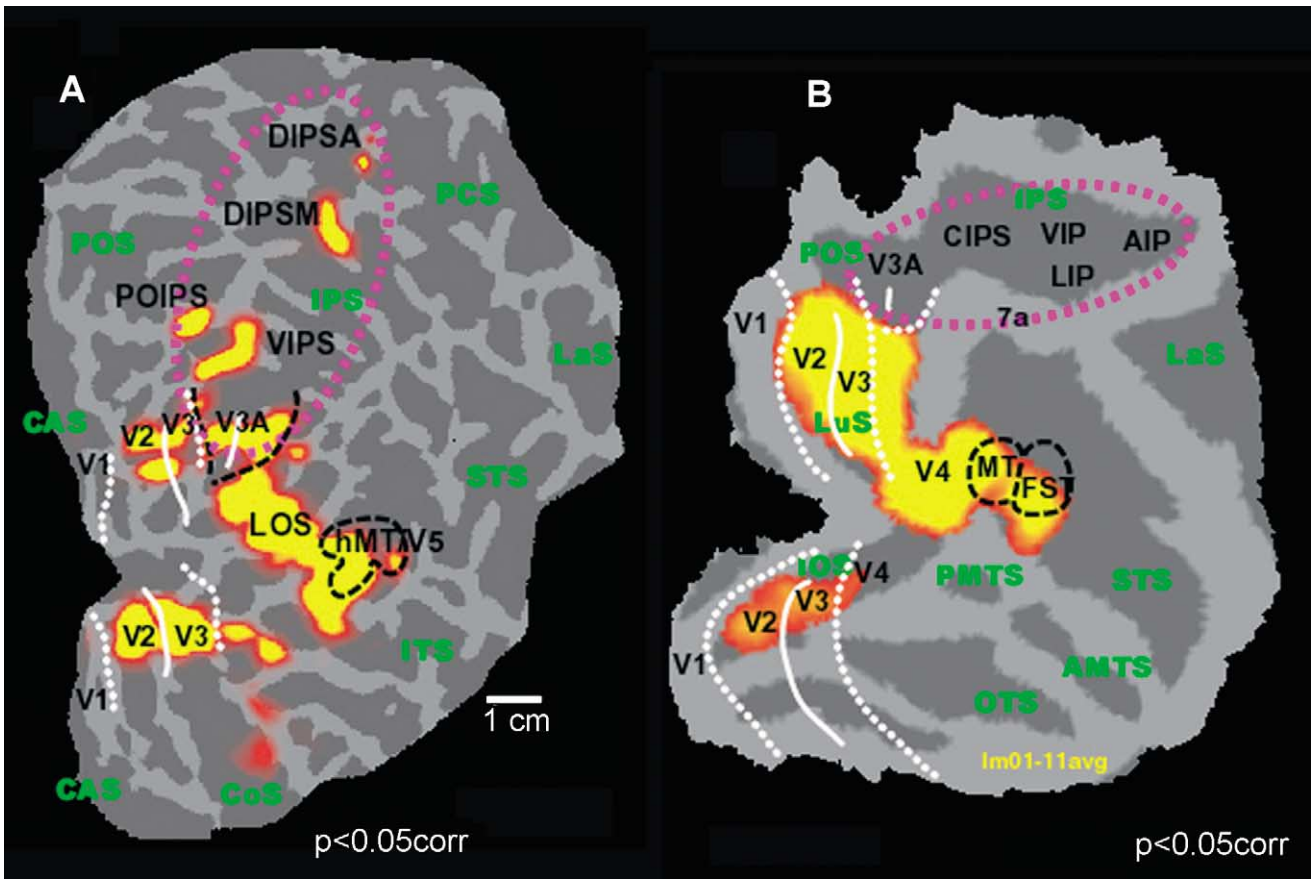

Fig. 5. SPM for the subtraction viewing of 3D rotating lines minus viewing of 2D translating lines ($P < 0.05$, corrected) of a single human (A) and monkey (M4: B) subject projected on the posterior part of the flattened right hemisphere. White stippled and full lines: vertical and horizontal meridian projections (from separate retinotopic mapping experiments); black stippled lines: motion responsive regions from separate motion localizing tests (as in Figs. 2–4); purple stippled lines region of interspecies difference encompassing V3 and intraparietal sulcus. PCS: post central sulcus, IPS: intraparietal sulcus, LaS: lateral sulcus, POS: parieto-occipital sulcus, CAS: calcarine sulcus, STS: superior temporal sulcus, ITS: inferior temporal sulcus, CoS: collateral sulcus, IOS: inferior occipital sulcus, OTS: occipito-temporal sulcus, PMTS: posterior middle temporal sulcus, AMTS: anterior middle temporal sulcus (modified from Vanduffel et al., 2002).

now possible to test this proposal experimentally. Our results are indeed consistent with the view that some of human IPS regions have no monkey counterpart. Another possible explanation, however, is that the species difference may be due to a simple difference in functional sensitivity of homologue areas, just as has been suggested for V3A (Tootell et al., 1997). It is important to recognize that these two interpretations are not mutually exclusive, as they may apply to different IPS regions. At present, as far as we are aware, no lesion data are available to support or challenge the motion processing differences in IPS of humans and monkeys. While the interpretation of the functional differences in parietal cortex is unclear, their source might be more tractable. It is well established that V3A in monkey projects to the posterior IPS regions (Nakamura et al., 2001) and that this posterior IPS region projects in cascade to more anterior parts. If the same connection pattern exists in humans, the motion sensitivity of the hV3A would then suffice to explain how additional motion information is injected into human IPS regions. In monkeys, motion information (concerning the central visual field) reaches IPS primarily through the MT/V5 and MSTd projections to VIP (Boussaoud, Ungerleider, & Desimone, 1990). In humans the motion information may well reach IPS in part through that route but more prominently through the projection from V3A.

There are many cues other than motion to extract 3D structure, e.g. stereo, texture and shading. Here, we have considered only 3D SFM. Single-cell evidence suggests that 3D orientation and 3D shape extracted from other cues is processed in posterior (Taira, Tsutsui, Jiang, Yara, & Sakata, 2000) and anterior IPS (Sakata, Taira, Murata, & Mine, 1995). We have recently begun to test some of these other cues in single-cell studies (Janssen, Vogels, & Orban, 1999, 2000) and in imaging (Janssen et al., 2002; Peuskens et al., 2002). It will be interesting to extend these imaging studies to the monkey (see also Sereno, Trinath, Augath, & Logothetis, 2002). It may well be that other 3D cues are equally well or perhaps more extensively processed in

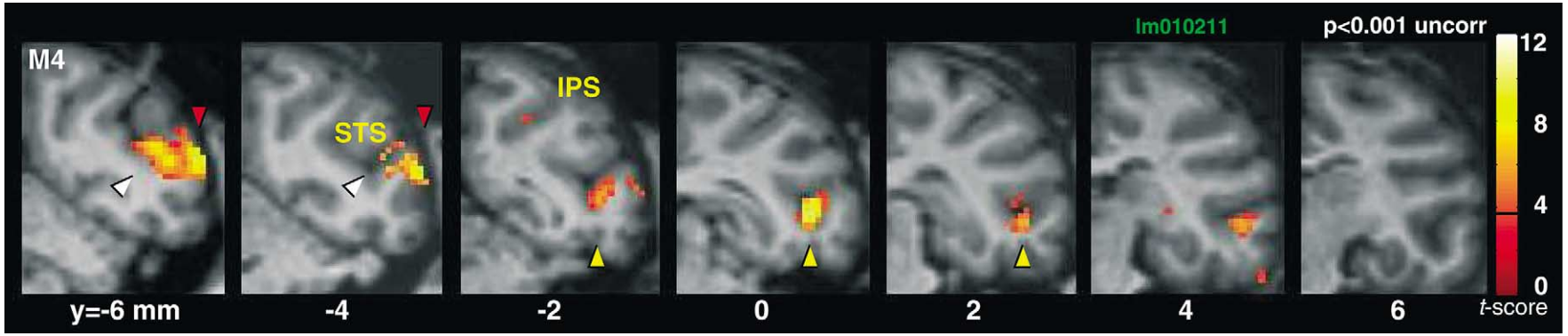

Fig. 6. SPMs for the subtraction 3D–2D on coronal sections of right hemisphere of monkey M4, thresholded at $P < 0.001$ uncorrected. Same conventions as Fig. 3. White arrow: MT/V5, yellow arrow: FST, brown arrow: V4. Notice weak activation in the intraparietal sulcus (IPS, level −2), the dorsal bank of superior temporal sulcus (STS, level 2) and the convexity of TE (level +4).

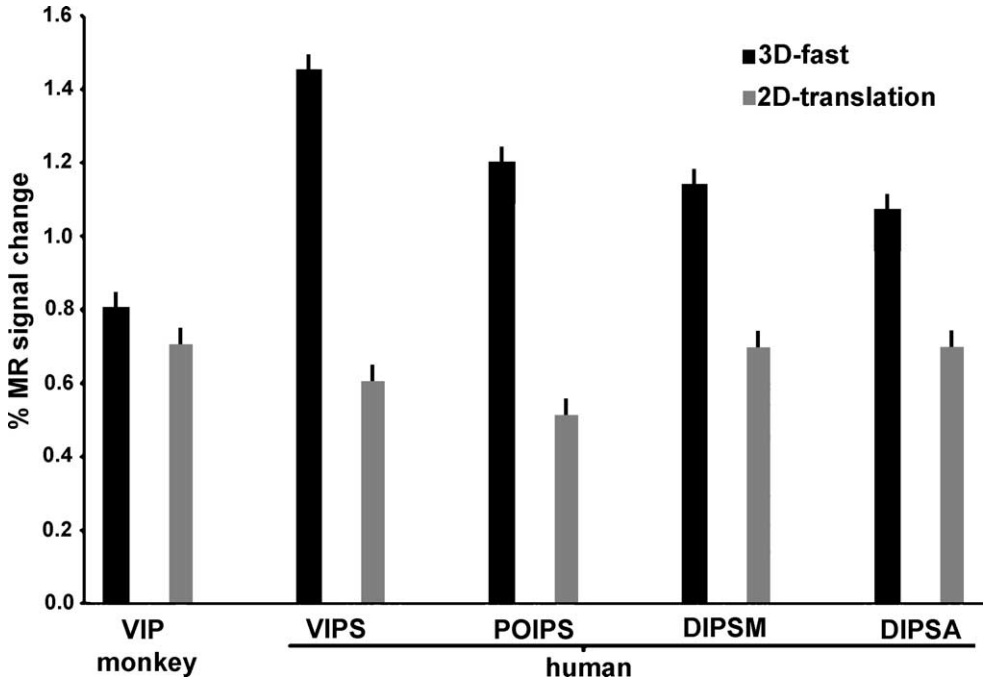

Fig. 7. Average percent MR signal change relative to stationary random lines when viewing 3D rotating lines (gray) and translating 2D lines (black) for monkey VIP and the four human IPS regions. The average is taken over all experiments in which random lines (and MION for monkeys) were used (the range of experiment is shown in next figure). Vertical bars indicate S.E.M.s (modified from the SOM of Vanduffel et al., 2002).

monkey IPS compared to human IPS. Thus, at this point we can only speculate about the behavioral significance of our fMRI findings. It is worth noting however, that in many instances the use of tools requires the control of motion (e.g. primitive ways of making fire). To a large degree this is also true for hunting with primitive weapons. In the same vein, primitive humans were omnivores who moved over large open territories to find food, while monkeys are herbivores living predominantly in trees. Thus, it may well be that motion processing became behaviorally much more important when humans emerged from the primate family millions of years ago, as also suggested by recent anatomical observations (Preuss & Coleman, 2002).

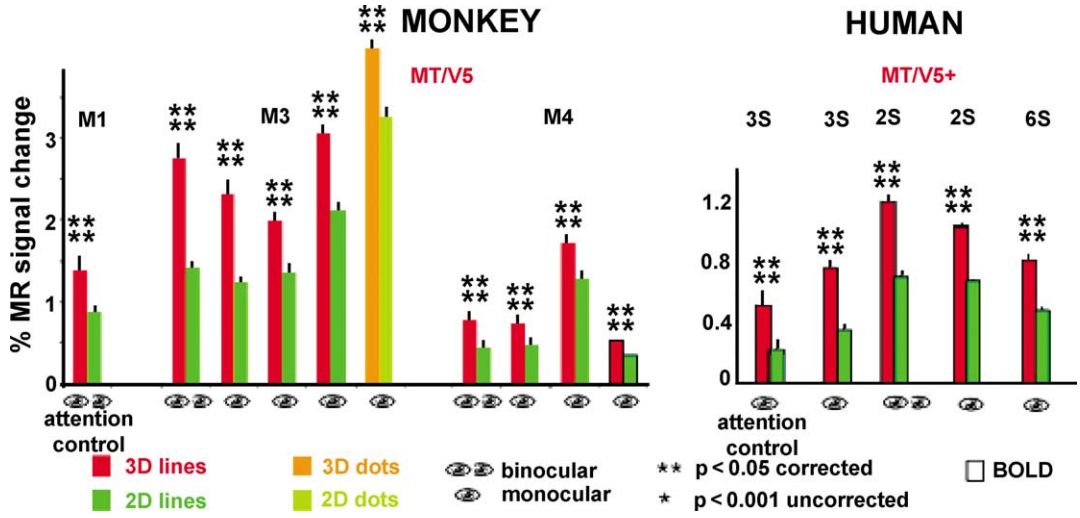

Fig. 8. Average percent MR change relative to stationary random dots in 3D conditions (red/orange) and 2D conditions (green/yellow) of MT/V5 and hMT/V5+ in different experiments involving three monkey subjects and different groups of human subjects (2–6 subjects): different attention states, monocular (one eye icon) or binocular (two eyes icon) presentation, random dots or random lines, BOLD and Mion. Vertical bars indicate S.E.M.s.

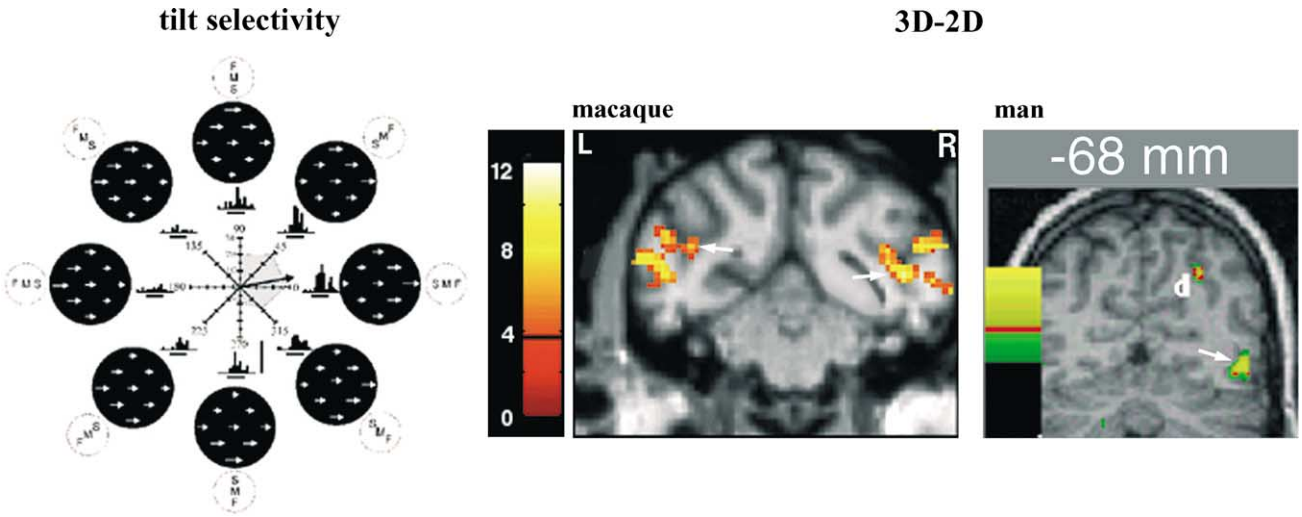

Fig. 9. Bridging the gap between monkey single cells and human fMRI: left panel tuning curve of a MT/V5 neuron selective for direction of speed gradient (from Xiao et al., 1997), middle and right panels: SPMs for 3D–2D on coronal section of monkey M3's (middle) and single human subject's (right, from Orban et al., 1999) brain. The white arrow points to MT/V5 in middle panel and to hMT/V5+ in right panel. Both SPMs thresholded at $P < 0.05$, corrected level.

Acknowledgements

The technical help of Y. Celis, A. Coeman, M. De Paep, W. Depuydt, C. Fransen, P. Kayenbergh, G. Meulemans and G. Vanparrijs is kindly acknowledged. This work was supported by the Queen Elisabeth medical foundation (GSKE), FWO G 0112.00, GOA 2000/11, IUAP P5/04 and EU project MAPAWAMO. W.V. is a research fellow of the FWO.

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