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Review article

Visual motion serves but is not under the purview of the dorsal pathway

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ABSTRACT

Visual motion processing is often attributed to the dorsal visual pathway despite visual motion's involvement in almost all visual functions. Furthermore, some visual motion tasks critically depend on the structural integrity of regions outside the dorsal pathway. Here, based on numerous studies, I propose that visual motion signals are swiftly transmitted via multiple non-hierarchical routes to primary motion-dedicated processing regions (MT/V5 and MST) that are not part of the dorsal pathway, and then propagated to a multiplicity of brain areas according to task demands, reaching these regions earlier than the dorsal/ventral hierarchical flow. This not only places MT/V5 at the same or even earlier visual processing stage as that of V1, but can also elucidate many findings with implications to visual awareness. While the integrity of the non-hierarchical motion pathway is necessary for all visual motion perception, it is insufficient on its own, and the transfer of visual motion signals to additional brain areas is crucial to allow the different motion perception tasks (e.g. optic flow, visuo-vestibular balance, movement observation, dynamic form detection and perception, and even reading). I argue that this lateral visual motion pathway can be distinguished from the dorsal pathway not only based on faster response latencies and distinct anatomical connections, but also based on its full field representation. I also distinguish between this primary lateral visual motion pathway sensitive to all motion in the visual field, and a much less investigated optic flow sensitive medial processing pathway (from V1 to V6 and V6A) that appears to be part of the dorsal pathway. Multiple additional predictions are provided that allow testing this proposal and distinguishing between the visual pathways.

Contents

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1. Visual motion is involved in almost all visual functions

Our visual system copes with ongoing visual motion, either induced by our own movements or by the movements of objects or events external to us. While the visual system relies on stabilization mechanisms such as the corollary discharge /efferent copy (Crapse and Sommer, 2008a,b) to counteract the significant visual motion changes induced by our movements (eye, head, or body), visual motion is inherently present even upon fixation (microsaccades, drift, and tremor (Yarbus, 1967; Martinez-Conde et al., 2004, 2013)). Over and above the optic flow changes we encounter when we move in the world, movements around us introduce additional visual motion (including the movements of our extremities). Put simply, the persistent visual motion encountered by our visual system dictates that visual motion will be inherent to all our visual experiences. These include the involvement of visual motion in visuo-vestibular and body balancing mechanisms (Paulus and Zihl, 1989; Shallo-Hoffmann and Bronstein 2003), in observation of stationary scenes as we scan them, in shape perception (for animated, non-animated, moving or stationary shapes), in smooth pursuit, saccades, hand-eye interaction and coordination, understanding facial expressions or body gestures, and even when we scan, skim and read across texts.

2. Visual motion processing is not under the purview of the dorsal pathway

A seminal theoretical account proposes that the visual system is segregated into two main processing pathways: the dorsal "where"/"how"/"action"/"spatial" pathway associated with aspects related to attention, spatial navigation, and preparation for action, and the ventral "what"/"perception"/"object" pathway associated with the computation of form and shape perception representations, such as edges, textures, surfaces, and colors (Ungerleider and Mishkin, 1982; Vaina, 1990; Goodale and Milner, 1992). However, there is evidence that speaks against the strict two-pathway hypothesis (Franz et al., 2000; McIntosh and Schenk, 2009; Hesse et al., 2012; Himmelbach et al., 2012). Numerous studies indicate involvement of ventral regions in dorsal-associated functions (e.g. depth or motion (Britten et al., 1992; Van Oostende et al., 1997; Grill-Spector et al., 1998; Janssen et al., 1999, 2000a,b; Kourtzi and Kanwisher, 2001; Gilaie-Dotan et al., 2002; Zhuo et al., 2003, 2013b; Li et al., 2013)), or the involvement of dorsal regions in ventral-associated functions (e.g. shape or face (Hasson et al., 2003; Janssen et al., 2008; Konen and Kastner, 2008; Srivastava et al., 2009; Romero et al., 2012, 2014; Freud et al., 2015; Theys et al., 2015)). Furthermore, other studies provide support for distributed processing in the visual cortex (e.g. (Schiller, 1993; DeYoe et al., 1994; Lennie 1998; Haxby et al., 2001)). Therefore the prevailing view is of a more complex and distributed visual cortex rather than the strict two-pathway segregation (Milner and Goodale, 2008; McIntosh and Schenk 2009).

Although visual motion is inherent in almost all visual functions, the received view is that visual motion processing and perception are under the purview of the dorsal pathway (e.g. (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992; Gross et al., 1993; Nassi and Callaway, 2009; Kravitz et al., 2011; Markov et al., 2013b, 2014)). The best example for this view is region MT/V5 (see below) which is (i) sensitive to visual motion across the visual field (Allman and Kaas, 1971; Dubner and Zeki, 1971; Desimone and Ungerleider, 1986; Fiorani et al., 1989; Weiner and Grill-Spector, 2011), (ii) its integrity is critical to visual motion perception as evident from primate (Newsome et al., 1985; Newsome and Pare, 1988; Salzman et al., 1990, 1992; Schiller, 1993; Pasternak and Merigan, 1994; Nichols and Newsome, 2002) and human studies [(Zihl et al., 1983; Marcar et al., 1997; Zihl and Heywood, 2015) and patients 9, 10, 26 in Schenk and Zihl (1997)], and (iii) it has been continually associated with and considered part of the dorsal pathway (e.g. (Shipp and Zeki, 1985; Livingstone and Hubel, 1987; DeYoe and Van Essen, 1988; Livingstone and Hubel, 1988; Regan et al., 1992; Kravitz et al., 2011; Pitzalis et al., 2012a; Markov et al., 2013a,b, 2014)).

But a more scrutinized observation paints a different and more complicated picture. For a start, some types of visual motion perception critically depend on regions *outside* the dorsal pathway. For example, basic motion perception skills, such as detecting visual motion or discriminating the direction of coherent motion when it is embedded in noise, critically depend on the integrity of the right ventral visual cortex (Gilaie-Dotan et al., 2013b). Recent studies also show that biological motion perception, which is the ability to visually perceive human movements, depends on the integrity of regions outside of the dorsal visual pathway, such as the posterior superior temporal sulcus (pSTS) and the ventral premotor cortex (vPMC) (Vaina and Gross, 2004; Saygin 2007; van Kemenade et al., 2012). In addition, the vermis, which is part of the cerebellum, is also critical to visual motion discrimination, irrespective of movement or motor influences (Nawrot and Rizzo, 1995, 1998; Thier et al., 1999; Jokisch et al., 2005; Cattaneo et al., 2014).

Second, visual motion perception loss can adversely affect functions that are associated with regions outside the dorsal pathway. LM, the motion blind patient (Zihl et al., 1983, 1991; Zihl and Heywood, 2015), who has suffered bilateral MT/V5 damage (Zihl et al., 1983; Shipp et al., 1994b), and lost the ability to perceive visual motion, complained that she perceived the visual world in discrete updates (as opposed to the continuous normal perception, see review Zihl and Heywood (2015)). This led to perceptual and functional deficits that went beyond dorsal pathway function. One such example is that she found it hard to maintain her visuo-vestibular body balance – which is not a function associated with dorsal pathway, and upon testing, she was found to be significantly impaired in this domain (Paulus and Zihl, 1989; Zihl and Heywood, 2015). To cope with this deficit, she walked slowly and fixated on fixed locations in the distance to allow her to slowly navigate through the environment. Another non-dorsal visual skill that was adversely affected following her lesion was her reading ability, as her reading was slow and she was unable to read faster (Zihl and Heywood, 2015). This is also consistent with a recent study reporting that transient lesions to MT/V5 induced by transcranial magnetic stimulation (TMS) can impair word recognition, a reading-related skill, in healthy individuals (Laycock et al., 2009).

In addition, some classical dorsal pathway functions can be preserved while visual motion perception is critically impaired. Although this argument, in and of itself, does not rule out the possibility that motion is still processed in parallel to other visual cues within the dorsal pathway, I find it important to highlight these findings. In LM, some dorsal visual functions were preserved

despite her severe visual motion deficits (Zihl and Heywood, 2015) including visual spatial functions such as localization, distance estimation and depth perception, stereopsis, calculations, temporal order, separation of visual stimuli, and eye movements when inspecting a scene (Zihl and Heywood, 2015). Additional studies support the dissociation between visual motion and stereopsis, which is a dorsal skill providing a clear advantage for prehension and eye-hand coordination through binocular vision (Servos et al., 1992; Fielder and Moseley, 1996; Melmoth et al., 2009). For example stereopsis is preserved in macaques with visual motion perception impairments following MT/V5 lesions (Schiller, 1993), leading the authors of that paper to conclude that there must be more than just two visual cortical pathways in the primate visual system. On the other hand, temporary disruption of the indirect pathway to MT through V2/V3 (not through the visual motion pathway, see below) adversely affects disparity-related behavior while hardly affecting the direction selectivity in MT (Ponce et al., 2008). Together these studies seem to indicate that motion-related processing and stereopsis-related processing, as investigated in these studies, are probably achieved in parallel and critically rely on different regions. Specifically, they show that stereopsis relies on dorsal V2/V3 (Ponce et al., 2008) but less so on motion MT/V5 or V4 (Schiller, 1993), and motion sensitivity relies on motion pathway MT/V5 (Schiller, 1993) but less so on dorsal V2/V3 (Ponce et al., 2008).

3. Limiting factors in studying visual motion perception

Visual motion perception is often considered a rather uniform perceptual entity (general or global motion perception). However, different types of visual motion perception have been shown to dissociate both behaviorally and neuropsychologically, indicating that visual motion is not a uniform perceptual category and that these different visual motion types rely on different neural and perceptual mechanisms. Some dissociations include first and second order motion perception in healthy individuals and in patients following selective/focal brain damage ((Lu and Sperling, 1995; Vaina and Cowey, 1996; Vaina et al., 1998, 1999; Vaina and Dumoulin 2011) but see (Hock and Gilroy, 2005), form-from-motion and motion detection in patients or developmental cases (Cowey and Vaina, 2000; Gilaie-Dotan et al., 2011), biological motion and motion coherence or other non-biological motion in healthy participants (Gilaie-Dotan et al., 2013a; Miller and Saygin, 2013), in patients (Vaina et al., 1990; Huberle et al., 2012; Gilaie-Dotan et al., 2013b, 2015) and in developmental cases (Gilaie-Dotan et al., 2011), and others (Regan et al., 1992; Vaina et al., 2014).

Most visual motion investigations are done with humans or non-human primates in fixed laboratory settings. Such investigations are not only detached from real world experiences, but normally investigate only apparent visual motion (as appears on screens (Ramachandran and Anstis, 1986)) rather than the real visual motion we experience in the real world when real things move around us or when we ourselves move. Furthermore, while investigations of non-human primates allow studying causal effects of focal predetermined lesions on behavior, these non-human primates are limited in their ability to report their perceptual experiences. Even when multiple measures are collected (e.g. eye movements and manual responses), language cannot serve as a reporting tool, and extensive training is often required to obtain good performance in a very specific task, when compared to humans.

The above limiting factors are some of the reasons why neuropsychological investigations of patients following brain damage are so critical for understanding visual motion processing and perception. Lesion studies have their limitations, as for example lesions are typically not confined to particular functional or anatomical regions, and damage to white matter cannot always be ruled out. However, such patients provide access to their motion perception deficits as experienced in real world situations (i.e. not lab controlled (Riddoch, 1917; Zihl et al., 1983; Vaina et al., 1990; Milner et al., 1991; Fine et al., 2003)) and thus provide a much broader perspective of visual motion perceptual experiences, the visual motion perception types that exist, associations and dissociations between processes (Vaina et al., 1990; Vaina and Cowey, 1996, 1998, 2000; Saygin, 2007; Gilaie-Dotan et al., 2011, 2013b, 2015), and can provide information about the criticality of different brain regions to specific visual motion perception subtypes by lesion-behavior correspondence (Vaina and Cowey, 1996; Vaina et al., 2000; Vaina and Gross, 2004; Saygin, 2007; Gilaie-Dotan et al., 2013b, 2015).

4. The visual motion pathway

Here, I provide a coherent framework for motion processing and perception to account for all these experimental findings. This framework incorporates evidence from human neuropsychological (including lesion-behavioral), perceptual and neuroimaging studies in healthy and in patients, as well as primate electrophysiological, cytoarchitectural, and connectivity studies; it applies to human and non-human primates despite inter-species differences (Orban et al., 2003; Sereno and Tootell, 2005; Peeters et al., 2009). I propose that visual motion is initially processed in a core lateral visual motion pathway that is distinct from the dorsal pathway (and the ventral pathway), not only anatomically, but also functionally, as it processes information much faster than the dorsal (or ventral) pathway, and covers the whole visual field in contrast to lower (upper) hemifield coverage in the dorsal (ventral) pathway. This core motion pathway swiftly propagates visual motion signals in a non-hierarchical fashion to multiplicity of regions across the brain – perhaps even before they reach awareness (Lamme and Roelfsema, 2000; Silvanto et al., 2005a,b; Moutoussis and Zeki, 2006). One explanation for this could be that reacting instantly to visual information that signifies how the environment changes relative to us (e.g. something moving towards us, someone reacting to us, how the structures around us are arranged and rearranged) is critical. While the idea of a visual motion pathway or motion analysis pathway has been used earlier to describe the flow of visual motion information (Boussaoud et al., 1990; Regan et al., 1992; Blake et al., 2003), a clear line between this lateral motion pathway (that includes MT/V5) and the dorsal pathway has never been drawn, and in fact in most cases these terms (dorsal and motion pathway) are used interchangeably. A few reasons/causes might have led to this apparent association including the dominance of magnocellular inputs feeding into MT/V5 and the dorsal pathway (Maunsell et al., 1990), the involvement of visual motion in some dorsal pathway functions (e.g. action perception of reaching, grasping), and perhaps even the observed sensitivity to disparity, which is a dorsal-related function, in the majority of MT/V5 neurons (e.g. (Maunsell and Van Essen, 1983b; DeAngelis et al., 1998; DeAngelis and Newsome, 1999)). Here I make a clear distinction between the motion and the dorsal pathways. I first describe the motion pathway's neuroanatomy and physiology, then describe secondary visual motion routes of the dorsal pathway that are not part of the motion pathway, and then explain the advantages associated with the visual motion pathway.

5. Neuroanatomy and physiology of the visual motion pathway

Visual motion information flows directly into middle-temporal motion-sensitive MT/V5 from separate subcortical and cortical parallel routes (Rodman et al., 1989, 1990; Girard et al., 1992;

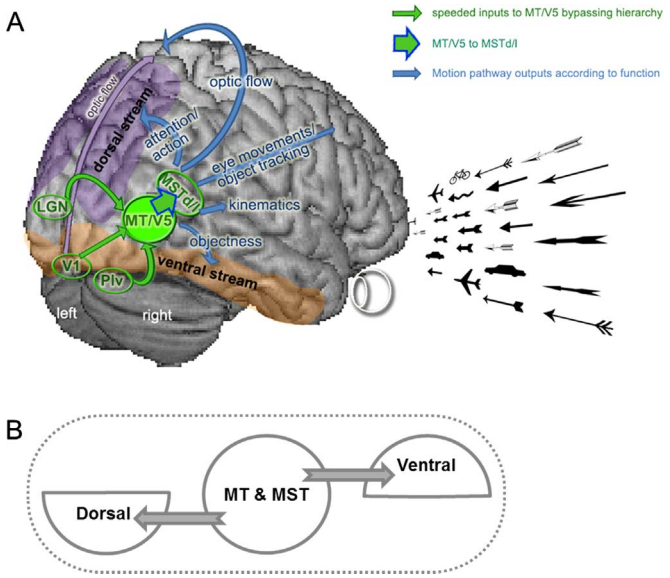

Fig. 1. Schematic visualization of the visual motion pathway. (A) Visual motion inputs swiftly propagate in parallel from subcortical regions and V1 directly into MT/V5 (thus bypassing the hierarchical information flow), and continue to MST subregions (MSTd, MSTl). From the MT/V5 and MST complex the information is transferred according to function to multiplicity of brain regions, reaching these regions significantly earlier than the hierarchical information flow. So for example information related to person or group kinematics is transferred to pSTS and vPMC, information related to eye movements to FEF, optic flow to V6 and V6A, information related to objectness to ventral pathway, information associated with action preparation to dorsal pathway, and so on. Note that wide field optic flow signals also propagate from V1 to V6 in a dorsal medial route that is not part of the motion pathway (depicted in purple, see "Secondary visual motion routes of the dorsal pathway, not part of the motion pathway"). Also note that this figure only illustrates the initial fast forward visual motion cortical sweep but does not capture the full processing complexity that follows. (B) Visual motion pathway's full field coverage facilitates transfer of visual motion information to all brain regions efficiently. In this example visual motion signals from upper [or lower] hemifield reach ventral [or dorsal] retinotopic areas. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Bridge et al., 2010; Ajina et al., 2015; Zeki, 2015), and from MT/V5 directly to middle superior temporal dorsal (MSTd) and lateral-ventral (MSTl or MSTp) regions (see Fig. 1A (Komatsu and Wurtz, 1988; Boussaoud et al., 1990)). Specifically, ***the first stage*** of this pathway includes the following inputs feeding in parallel directly into MT/V5 (Born and Bradley, 2005): (a) primary visual (V1) cortical direction-selective neurons along the retino-geniculate-cortical pathway are the major input to MT/V5 [e.g. (Maunsell and Van Essen, 1983a; Ungerleider and Desimone, 1986; Movshon and Newsome, 1996; Nassi and Callaway, 2006)], (b) pulvinar (thalamic) neurons that receive inputs from the superior colliculus (SC, retino-collicular pathway) project to MT/V5 [(Standage and Benevento, 1983; Shipp 2001; Berman and Wurtz 2010)], and (c) LGN neurons, that are mostly koniocellular, and amount to ~10% of the V1 inputs to MT/V5 (Sincich et al., 2004; Bridge et al., 2008; Nassi and Callaway, 2009; Gaglianese et al., 2012; Warner et al., 2012; Ajina et al., 2015). Because visual motion is so powerful, direction-selective neurons in V1 (*first stage)* are optimally activated not just by a contrast edge appearing in their visual field in the preferred direction, but also when that edge is in motion (Hubel and Wiesel, 1968; Movshon and Newsome 1996). The receptive field (RF) sizes of these cells are small, covering ~1–2° of the visual field (e.g. (Hubel and Wiesel, 1974)). Information transfer from the first stage to the second stage (MT/V5, see below) is extremely fast. For example the mean latencies of cortical MT responses relative to subcortical SC and pulvinar are < 5 ms (Berman and Wurtz, 2010). Even more conspicuous are the exceptionally short latencies of MT/V5 relative to their distant V1 inputs responses (< 2 ms) (Movshon and Newsome, 1996)[1] which are achieved by fast-conducting (Movshon and Newsome, 1996) and heavily myelinated axons between V1 and MT/V5 (Desimone and Ungerleider, 1986) that are 2–3 times thicker (2–3 μm in diameter) than other axons projecting from V1 (1 μm in diameter (Rockland, 1989, 1997)) to overcome the large V1 to MT/V5 distance.

The second stage, MT/V5, is the first region in this pathway that specializes in and is dedicated to visual motion processing, and therefore can be conceptualized as providing the "basic building blocks" for all visual motion processes (Zeki, 1974, 1978; Zeki et al., 1991; Watson et al., 1993; Huk et al., 2002; Born and Bradley, 2005; Amano et al., 2009). Furthermore, MT/V5 stands out as being developmentally unique compared to all other extrastriate visual areas (Rosa, 2002; Rosa and Tweedale 2005). For example, MT/V5 is the only extrastriate region that is already myelinated at birth, it functionally matures faster than other extrastriate areas, has a nearly constant proportion of size across all primates (Rosa, 2002; Rosa and Tweedale 2005), has been conceptualized as an additional primary visual area along with V1 based on its developmental trajectory (concurrent only with V1, A1, and S1) (Rosa and Tweedale, 2005; Bourne and Rosa, 2006), and it seems to be the only extrastriate region with a first order transformation of the visual field (Rosa, 2002). The RFs of MT/V5 cells are on average ~5.5–15° and < 20° of the visual field, 10-fold bigger than those of V1 (e.g. (Born and Bradley, 2005; Kolster et al., 2010)). MT/V5 cells are almost all sensitive to visual motion (direction and speed (Dubner and Zeki, 1971; Maunsell and Van Essen, 1983a; Albright, 1984; Desimone and Ungerleider, 1986; Zeki, 2015)) at almost any contrast, and are organized in a retinotopic fashion covering the upper and lower visual fields (Allman and Kaas, 1971; Dubner and Zeki, 1971; Desimone and Ungerleider, 1986; Fiorani et al., 1989; Weiner and Grill-Spector, 2011). MT/V5 is heavily myelinated (Van Essen et al., 1981; Orban, 1997; Zeki 2015) which could serve to speed up intrinsic local processing or inter-areal timing. MT/V5 projects directly to a manifold of brain regions including cortical V1, V2, V3, V3a, V6/DM/PO, V6A, V4, V4t, MST, VIP, LIP, FST, FEF, area 46, 46d, F2, and 9 (Maunsell and Van Essen, 1983a; Felleman and Van Essen, 1991; Galletti et al., 1996; Shipp et al., 1998; Markov et al., 2013a,b), and subcortical claustrum, putamen, caudate nucleus, inferior and lateral pulvinar, ventral LGN, reticular nucleus of thalamus, superior colliculus and pontine nuclei in the pons (Maunsell and Van Essen, 1983a; Ungerleider et al., 1984; Berman and Wurtz, 2010; Warner et al., 2012).

In *the* ***third stage*** of the visual motion pathway are the motion-sensitive regions MSTd and MSTl (Van Essen et al., 1981; Desimone and Ungerleider, 1986; Komatsu and Wurtz, 1988; Amano et al., 2009; Weiner and Grill-Spector, 2011; Ferri et al., 2012) that are adjacent to MT/V5 and receive robust and ascending projections from MT/V5 (Maunsell and Van Essen, 1983a; Ungerleider and Desimone, 1986). MST has larger RFs than those of MT/V5 (most MST cells: 15°–33+° (Van Essen et al., 1981; Desimone and Ungerleider, 1986; Komatsu and Wurtz, 1988; Celebrini and Newsome, 1995; Huk et al., 2002; Amano et al., 2009; Kolster et al., 2010; Mendoza-Halliday et al., 2014)), a proportion of which even contains the ipsilateral visual field (e.g. (Celebrini and Newsome, 1995; Huk et al., 2002; Amano et al., 2009)) and still retains crude retinotopy (Desimone and Ungerleider, 1986) with more sophisticated/function-specific motion-sensitivity (Tanaka and Saito, 1989; Andersen et al., 1990; Duffy and Wurtz, 1991a,b; Eifuku and Wurtz, 1998, 1999). MSTd appears to be more functionally specialized for non-object big-pattern "optic flow like" motion (Duffy

[1] The tuning properties of the subcortical inputs feeding directly into MT/V5 are less clear (Bridge et al., 2008; Gaglianese et al., 2012; Warner et al., 2012; Ajina et al., 2015).

and Wurtz, 1991a, 1997a,b,c), and MSTl appears to be more specialized for localized object-like motion-related functions (Komatsu and Wurtz, 1988; Eifuku and Wurtz, 1998, 1999). This is evident by (i) functionally-appropriate receptive field sizes (bigger RFs in MSTd and much smaller in MSTl (Eifuku and Wurtz, 1999; Huk et al., 2002; Kolster et al., 2010)), (ii) center-surround disparity sensitivity in MSTl but not in MSTd (Eifuku and Wurtz, 1998, 1999), (iii) causal involvement of MSTl (but not MSTd) in smooth pursuit (Komatsu and Wurtz, 1988, 1989), and more (see Komatsu and Wurtz (1988) and Wurtz et al. (1990)). In light of these characteristics, it is reasonable to assume that MSTd is more functionally-related to the analysis and integration of visual motion across the visual field resembling optic flow, while the functionality of MSTl is more associated with processing visual motion of moving elements in the visual field resembling object motion (see Eifuku and Wurtz (1999) and Huk et al. (2002)). Together, they can critically contribute to processes such as smooth pursuit and figure-ground segmentation in the dynamic environment. MST, as MT/V5, also projects to many brain regions including cortical regions as V2, posterior parietal V3A, V6/PO/DM, DP, parietal IPG, LIP, VIP, posterior temporal PP, MT/V5, FST, superior temporal STP (TPO, PGa, IPa), anterior temporal TEO, TF, frontal FEF (Boussaoud et al., 1990), as well as to subcortical regions as pulvinar, claustrum, striatum, reticular nucleus (thalamus), pontine nuclei and the nucleus of the optic tract (Boussaoud et al., 1992). Neuroimaging research substantiates the existence of the human homologues of macaque's MT/V5 and MST (Huk et al., 2002; Amano et al., 2009).

The propagation of visual motion information along the visual motion pathway is primarily hierarchical (see Fig. 2 (Andersen et al., 1990)), as is in the dorsal and ventral pathways, but faster (see also "Section 6" below). The hierarchical characteristics are evident by the direct connectivity between the different stages (Maunsell and Van Essen, 1983a; Ungerleider and Desimone, 1986; Rockland, 1989; Felleman and Van Essen, 1991; Movshon and Newsome, 1996; Sincich et al., 2004; Born and Bradley, 2005; Berman and Wurtz, 2010; Warner et al., 2012), the growing receptive field (RF) sizes and the increasing functional specialization that allow for a gradual build-up of visual motion integration across the visual field [V1 neurons tuned to very local "component" motion, a proportion of MT/V5 neurons show sensitivity to "global pattern" motion ((Movshon and Newsome, 1996) but see (Hedges et al., 2011)), and MST neurons show more specialized motion-sensitivity (see above)], and the growing response latencies along the hierarchical stages (Schmolesky et al., 1998; Lamme and Roelfsema, 2000).[2]

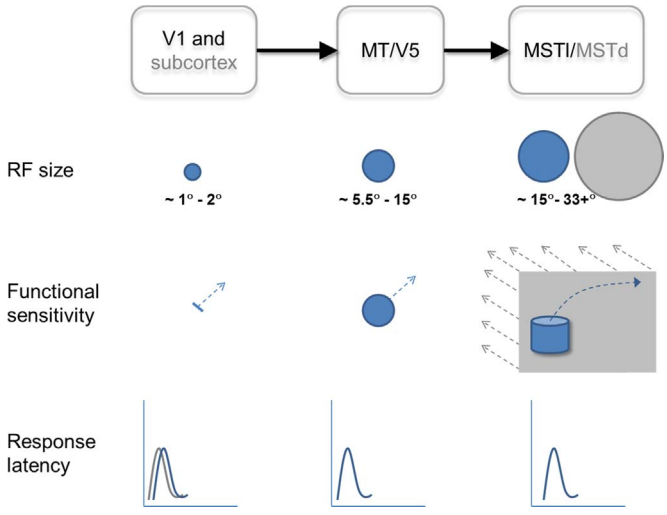

Fig. 2. Schematic illustration of the hierarchical characteristics within the visual motion pathway. Visual motion inputs propagate from subcortical and V1 contributions into MT/V5 and from there to MST subregions (MSTd, MSTl). Growing receptive fields, motion complexity (and response latencies to some extent) along the hierarchy.

6. Secondary visual motion routes of the dorsal pathway, not part of the motion pathway

The motion pathway described above is sensitive to any visual motion across the visual field (i.e. any retinal motion), including random non-coherent motion. In contrast to this "all-motion" primary visual pathway, two additional motion-sensitive cortical routes within the dorsal pathway, which I hypothesize are not part of the primary motion pathway, are described in this section. The first is a medial route which is driven by wide optic flow fields and is considered part of a direct visuo-somatosensory-motor medial pathway important for skeletomotor activity to control ones movements and actions in the environment. Thus, it is reasonable to consider this route as part of the dorsal pathway. It projects from V1 directly to visual V6 (also termed DM or PO (Galletti et al., 1996, 2001; Rosa, 2002)) on the medial wall near the parieto-occipital sulcus (POS) (Galletti et al., 1999), that then projects to the adjacent and not purely visual V6A (Galletti et al., 1996; Shipp et al., 1998). V6, which is sensitive and selective to wide-field optic flow (Galletti et al., 1999; Pitzalis et al., 2006, 2013b), has a full field retinotopic representation with a discontinuity in the upper visual field (Galletti et al., 1999; Rosa, 2002). Its cortical magnification factor is reduced, allowing an enhanced peripheral representation (Pitzalis et al., 2012a). For wide field optic flow, V6's response latencies are comparable to those of MT/V5 (Pitzalis et al., 2013a), although MT/V5 typically responds faster to other types of visual motion stimulation (Pitzalis et al., 2012b). Both V6 and V6A are connected to MT/V5, and according to V6 and MT/V5's intermediate connectivity patterns they are considered at the same hierarchical level, while V6A is considered one tier up the hierarchy (Galletti et al., 1996; Shipp et al., 1998). Another motion sensitive region, V3A, located at the posterior occipito-parietal cortex, also has a full-field retinotopic representation (Zeki, 1980; Galletti et al., 1990; Tootell et al., 1997; Fischer et al., 2012). However, studies show that at least half of V3A's motion sensitive cells are predominantly driven by real external motion (relative to head coordinates) rather than by retinal motion (Galletti et al., 1990; Fischer et al., 2012), and direct inputs from V1 to V3A mainly originate from peripheral V1 (Zeki, 1980), suggesting a peripheral bias in V3A, similar to that of V6's.

As both V3A and V6 are (i) not sensitive to all visual motion types, (ii) more sensitive to head-centered motion than to retinal motion, (iii) have a preferential bias for the periphery, and (iv) developmentally mature at a later stage than that of MT/V5 (see above), I do not consider V3A and V6 as part of the primary visual motion pathway described here, but rather as functionally-dedicated routes that parallel the motion pathway. Furthermore, as V3A and V6 are located within the dorsal cortex, and both show oculomotor modulated activity that might be involved in action planning (Galletti et al., 1990; Shipp et al., 1998, Galletti et al., 2001; Fischer et al., 2012; Pitzalis et al., 2012a), it is only reasonable to consider them as part of the dorsal pathway.

[2] Some studies reported a significant response latencies difference between V1 (first stage) and MT (second stage) only (Schmolesky et al., 1998), while others reported a significant response latencies difference only between MT (second stage) and MST (third stage (Lamme and Roelfsema, 2000)).

7. Benefits associated with a visual motion pathway

Here, I propose that since responding quickly to visual motion is critical for so many aspects of our survival (see above), the visual motion pathway's main role is to swiftly propagate visual motion information across the cortex, bypassing the visual hierarchical flow. In addition, the full visual field coverage of the visual motion pathway (cf. visual hemifield in dorsal or ventral retinotopic areas) allows efficient propagation of all visual motion signals across the brain (see Fig. 1B). I further hypothesize that the visual motion pathway also *critically supports our fluent and continuous visual perception by the spatio-temporal binding nature of visual motion*. Additionally, it is a core visual motion system necessary for *all visual motion perception types*.

7.1. Speeded transfer of visual motion information places MT/V5 at the 1st tier of the visual hierarchy

Visual motion sensitive region MT/V5 has been placed at the fourth (or even higher) tier of the visual hierarchy along with V4 and V4t based on anatomical connectivity and perhaps even on its anatomical locus ((Felleman and Van Essen, 1991; Markov et al., 2013b, 2014) and see also (Lamme and Roelfsema, 2000)). However, timing and temporal order of events are also critical factors for determining hierarchical relations. Therefore here I propose – based on the *timing* of activity – that **MT/V5 is actually at the first tier of the visual hierarchy**, along with V1 and *before* V2 or V3 (see Fig. 3). As already mentioned above, MT/V5's activity in response to visual motion starts at around the same time as that of V1 [MT/V5 at 30–39 ms (Maunsell, 1987; Raiguel et al., 1989, 1999; Lamme and Roelfsema, 2000; Zeki, 2015)[3] and fastest V1 at 25–45 ms (Maunsell, 1987; Raiguel et al., 1989; Nowak and Bullier, 1997; Lamme and Roelfsema, 2000); a few studies even report that MT/V5 *precedes V1* by 10 ms (Raiguel et al., 1989; ffytche et al., 1995; Buchner et al., 1997; Schoenfeld et al., 2002; Di Russo et al., 2012; Pitzalis et al., 2012b)], less than 40 ms following visual stimulation (Lamme and Roelfsema, 2000; Zeki 2015). This allows activity to reach MST (45 ms) and even FEF (43 ms) *before* it reaches V2 and V3 (Nowak and Bullier, 1997; Lamme and Roelfsema, 2000). It is true that it is difficult to properly distinguish the quicker magnocellular V2 or V3 latencies from the slower parvocellular latencies as these quicker dorsal (magno) and slower ventral (parvo) components of V2 (or V3) are not typically separated in reported analyses (but see Schmolesky et al. (1998)). Still, the earliest V2 (or V3) reported responses (V2: 37–82 ms (Raiguel et al., 1989; Nowak et al., 1995; Nowak and Bullier, 1997; Lamme and Roelfsema, 2000), V3: 50–70 ms (Schmolesky et al., 1998; Lamme and Roelfsema, 2000)) are lagging behind those of MT/V5 (35–39 ms) (Lamme and Roelfsema, 2000), indicating that MT/V5 should clearly be placed before V2 or V3 in the visual hierarchy. Even though the variance of the latencies in each region is not negligible (Raiguel et al., 1989; Nowak et al., 1995; Nowak and

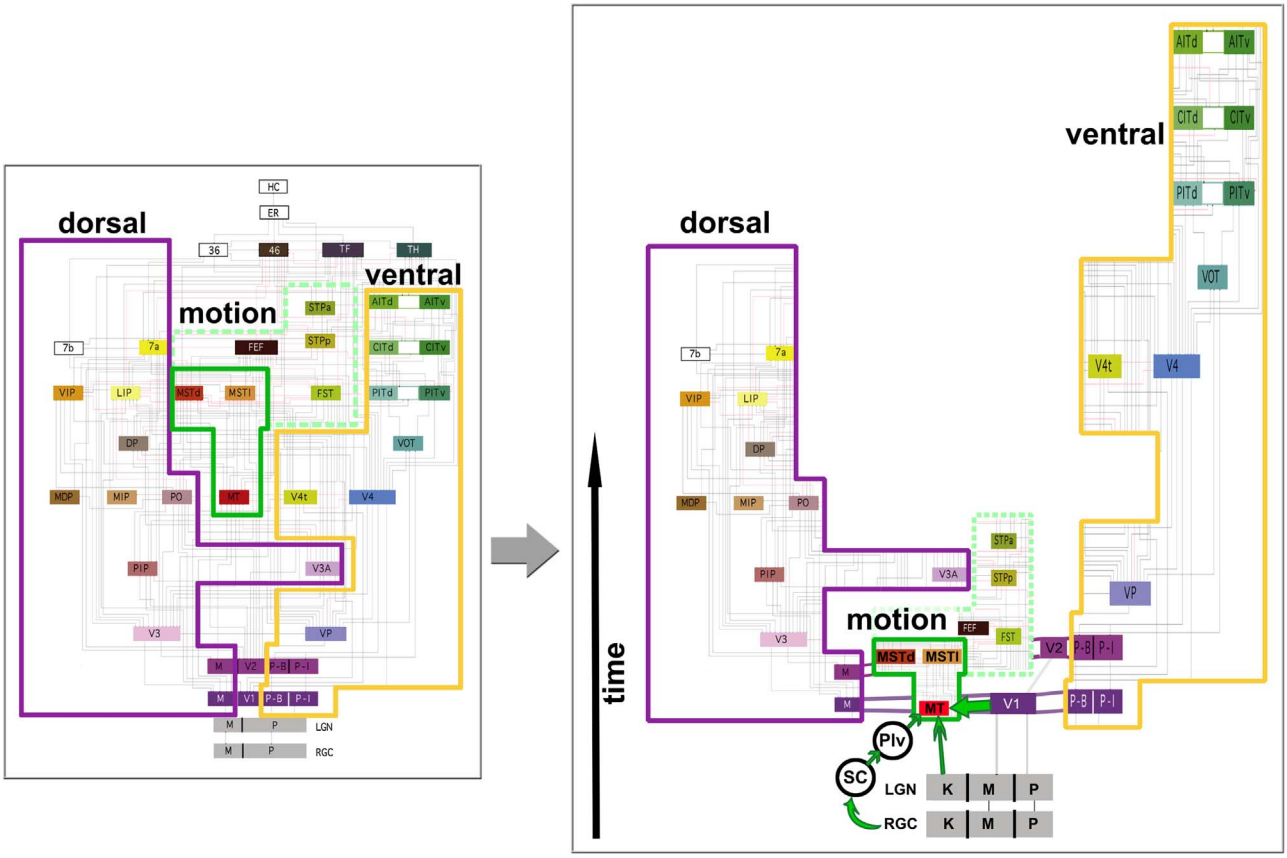

Fig. 3. The revised visual hierarchy according to timing (response latencies). Left – the original visual hierarchy proposed by Felleman and Van Essen (1991) based on ***anatomy*** (the anatomical inter-region connections are deemphasized here for presentation purposes), which is also consistent with recent anatomical studies (Markov et al., 2014). Approximate dorsal pathway is outlined in purple, ventral pathway in yellow, and motion pathway in green. Right – a revised ***temporal*** visual hierarchy proposal based on the temporal order of events, taking into account the speeded processing of the motion pathway, and the slowed processing of the ventral pathway. While originally according to its anatomical location, MT/V5 was placed at the 4th tier of the hierarchy, I now argue that MT/V5 is actually at the 1st tier along with V1 based on MT/V5's response latencies that precede those of V2 and V3 and are comparable to V1's. MT/V5 receives inputs from V1, koniocellular LGN layers, and pulvinar nuclei (Plv) through the superior colliculus (SC). MSTd/l and additional motion related regions (see dashed light green) are also moved to much earlier stages of the hierarchy. The motion pathway inputs are indicated by green arrows (as in Fig. 1). Parieto-occipital (PO) region is also known as V6/DM. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Bullier, 1997; Raiguel et al., 1999; Bullier, 2001), the above observations are not limited to the earliest responses in each region but are also true when the mean regional responses are taken into account (mean regional response latencies: V1 at 72 ms, MT/V5 at 76 ms, MST at 74 ms, V3 at 77 ms, and V2 at 84 ms (Lamme and Roelfsema, 2000)). Recently it has been proposed that visual motion signals are processed within the dorsal pathway in parallel, one route through MT/V5 and another through V6, in order to support different functions as space perception, action understanding and online action control (Kravitz et al., 2011; Pitzalis et al., 2012a, 2013a). I second that motion for optic flow and ego-motion stimulation. However, for most types of visual motion (apart from optic flow), activity in MT/V5 would probably start much earlier than that of V6's. Thus, the first main distinction between these propositions and the visual motion pathway proposal is based on timing and temporal order. According to the visual motion pathway proposed here, and according to electrophysiological studies (see above), visual motion signals reach MT/V5 earlier than other extrastriate regions (at 30–40 ms after stimulus onset (Raiguel et al., 1989; ffytche et al., 1995; Buchner et al., 1997; Lamme and Roelfsema, 2000; Schoenfeld et al., 2002; Zeki, 2015), probably apart from optic flow (Pitzalis et al., 2013a)). The second main distinction between these propositions and the visual motion pathway proposal is, I argue, that MT/V5 is not part of the dorsal pathway but part of an independent all-motion processing route that enables motion perception; importantly, it critically supports all processes involving visual motion cues.

7.2. Visual motion supports fluent and continuous visual perception through spatio-temporal binding

It is very hard to imagine what it would be like to perceive the visual world in a non-continuous fashion. Although we sample the world in a discrete fashion, our visual experience is smooth and continuous. Here I propose that this is due to the spatio-temporal binding nature of visual motion that allows us not only to link our vision at one point in time with what we viewed just an instant ago, but also to predict/anticipate where things will shortly be (e.g. time to collision (Hayward, 1972; Hoffmann and Mortimer, 1994; Vogel, 2003)). In other words, I suggest that visual motion signals are critical for our continuous visual perception across time and space. Rare reports exist of people who, following brain damage or neurological episodes, lost their continuous perception of the world. These critically occurred together with and as a function of the inability to perceive visual movements. For example, LM, the motion-blind patient, reported on her inability to see the world in a continuous fashion. For example, she would see liquid being poured as frozen, cars driving by as being still, and lips of people talking as jumping from one state to another (Zihl et al., 1983; Zihl and Heywood, 2015). These reports are not unique to LM, and similar reports have already been reported in the beginning of the 20th century. For example Pötzl and Redlich report of a lady not being able to follow a light moving in a room but rather seeing it as several lights (Pötzl and Redlich, 1911; Wertheimer, 1912). Another study reports on the inability to follow movement of objects or arm movements and seeing only successive still positions of moving items/arms (Goldstein and Gelb, 1918). An additional study describes a man that had a neurological episode where he was unable to perceive visual movements and saw the water pathway in the shower as separate droplets that hung up in midair (Ovsiew, 2014). This case is described in the context of the *Zeitraffer* phenomenon which relates to slowing down or speeding down of our perception. But importantly, in this context additional reports exist, such as having "cinematographic vision" (Sacks, 1992), where vision mimics rapidly flickering frames without the continuous sensation we typically have. Other reported cases of patients perceiving the world in freeze frames, slow motion, or "jumps", also occur along with visual motion perceptual deficits ((Cooper et al., 2012) and see review in Barton (2011)).

But losing visual movement perception is not the only evidence linking visual motion to our continuous and smooth perception of the visual world. Another line of evidence comes from the contribution of visual motion to our ability to segment the visual image into different entities, as in foreground and background. Imagine for example standing behind a dense fence and trying to see what is behind it. This can be a rather difficult task. However, walking along the fence makes this task much easier providing visibility behind the fence bars. Evidence for such spatio-temporal binding based on visual motion comes from abnormal development. For example, people born with bilateral congenital cataract that have gained their vision only at adolescence or later following surgical removal of their cataract (e.g. Project Prakash http://web.mit.edu/bcs/sinha/prakash.html), are not able to segment images into different components as neurotypically developed people would. Pawan Sinha and colleagues found that visual motion can significantly assist in allowing these patients to correctly segment the scene into different objects and sections (Ostrovsky et al., 2009). Another example is of an adult (MM) who recovered his vision at the age of 43 after 40 years of blindness. MM was very quickly successful in many visual motion tasks and these were helpful in assisting him in other tasks (such as scene segmentation (Fine et al., 2003)), maybe relying on the visual abilities developed until the age of 3 when he lost his vision.

7.3. Neural correlates of different visual motion perception tasks

Numerous studies, including electrophysiology and neuroimaging studies, have shown that MT/V5 and MST are responsive to almost any type of visually moving stimuli (e.g. (Zeki, 1974; Newsome et al., 1985, 1988; Wurtz et al., 1990; Duffy and Wurtz, 1991a,b; Kourtzi and Kanwisher, 2000; Rees et al., 2000; Vanduffel et al., 2002; Priebe et al., 2003; Majaj et al., 2007; Gilaie-Dotan et al., 2009; Tailby et al., 2010; Schwarzkopf et al., 2011; Urner et al., 2013; Vangeneugden et al., 2014)) and are involved in many visual functions such as segmentation of the visual scene, computation of structure, reducing noise, and more (see Born and Bradley (2005)). While these studies are of great importance, they do not provide evidence for MT/V5's or MST's causal and critical involvement in visual motion perception. In humans, early cases of neurological patients losing the ability to perceive visual motion (Pötzl and Redlich, 1911; Wertheimer, 1912; Goldstein and Gelb, 1918) were accompanied by additional symptoms (and thus not "pure enough" cases (Marotta and Behrmann, 2004)), and their anatomical descriptions were lacking as they were not followed by postmortem examinations (see Zeki (1991)).

Patient LM, with bilateral sustained brain damage in her parieto-occipital cortex matching the location of MT/V5 (Zihl et al., 1983, 1991), was the first relatively "clean case" of full visual field cerebral akinetopsia (also known as "motion blindness" (Zeki, 1991)) and thus the first most convincing evidence for the *critical* involvement of MT/V5 of the visual motion pathway in a multitude of motion perception tasks (Zihl and Heywood, 2015). LM's case, which was extensively investigated (Zihl et al., 1983; Hess et al., 1989; Paulus and Zihl, 1989; Baker Jr. et al., 1991; Zihl et al., 1991; Shipp et al., 1994a; Rizzo et al., 1995; McLeod et al., 1996; Campbell et al., 1997; Marcar et al., 1997; Zihl and Heywood, 2015), provides objective and subjective information about the multifaceted motion perception deficits accompanying MT/V5 lesion. For example,

[3] Schmolesky et al. (1998) is an exception reporting MT/V5 earliest latency at 72 ms after stimulus onset.

she had difficulty crossing the road since she could not anticipate when the cars would be approaching (they appeared to her in static snapshots and not continuously moving). She also found it difficult to be in crowded places where people kept appearing in unexpected locations (she was not able to follow their movements), or to engage in conversations since looking at a person's mouth (which she did not see as moving but rather as updated sporadically), which was not synchronized with their voice, was overwhelming (Campbell et al., 1997). In line with her subjective reports about losing visual movement perception, upon testing, although some residual motion perception for slow motion was preserved (for speeds < 10 deg/sec (Zihl et al., 1983)), many of her motion perception skills were confirmed to be significantly impaired. This included speed estimation, speed discrimination, detection of motion in noise (coherence thresholds), motion in depth, biological motion, reaching for objects, visuo-vestibular functions and apparent motion (Zihl et al., 1983; Paulus and Zihl, 1989; McLeod et al., 1996; Schenk et al., 2000; Zihl and Heywood, 2015). Although it is evident that LM's visual perception was impaired across the board following her bilateral MT/V5 lesion, her residual perception of slow motion might have been supported by spared alternative processing routes as the V6 complex (Galletti et al., 1996), V3A (Galletti et al., 1990; McKeefry et al., 2010), or perhaps even the ventral cortex (Britten et al., 1992; Zhuo et al., 2003; Gilaie-Dotan et al., 2013b).

Patient DF might also shed some light on the neural correlates of visual motion perception, even though the visual motion investigations she underwent are limited, and her lesion, following hypoxia due to carbon monoxide poising, is typically very difficult to detect and thus "borders" between affected and intact brain tissue remain equivocal. DF was diagnosed with acquired visual form agnosia following bilateral lateral occipital cortex damage but shows apparently normal action- (dorsal-) related skills. This led Goodale and Milner to propose the dorsal vision-for-action vs. ventral vision-for-perception pathways hypothesis ((Goodale et al., 1991; Goodale and Milner, 1992; Milner and Goodale 1993), but see (Schenk, 2012)). While DF demonstrates apparently normal dorsal related skills, she has severe visual motion perception difficulties as in estimating speed of bypassing vehicles (making it impossible for her to cross the road), identifying apparent motion, estimating motion direction when it was embedded is noise (coherence), and perceiving biological motion from point light displays (Johansson, 1973; Milner et al., 1991). These might not be surprising given that her lesion seems to invade her right MT/V5 (compare (James et al., 2003) with (Kolster et al., 2010) and with (Dumoulin et al., 2000)), in line with a recent neuroimaging study investigating her functional and structural visual cortex integrity (Bridge et al., 2013). Bridge et al. found that in contrast to neurotypical controls, DF's activations to visual motion were lacking in MT/V5, her V1's responses were abnormal, and the anatomical connectivity between LOC and MT was significantly reduced or absent. These findings support the necessity of MT/V5 for visual motion perception, and possibly also confirm the necessity of the right ventral cortex, which is damaged in DF, to various motion perception tasks (e.g. motion coherence (Gilaie-Dotan et al., 2013b)). They might also indicate that the spared routes conveying motion signals in DF's visual system allow for her dorsal related skills, emphasizing the differences in computational resources required for vision-for-perception vs. vision-for-action (Goodale, 2014).

It was also reported that lesions to human MST adversely affect the patient's ability to navigate in their surrounding (Vaina, 1998). Studies investigating visual motion detection and discrimination in cohorts of patients with unilateral brain lesions also suggest that visual motion impairments in the contralateral visual field are associated with damage to MT/V5 and MST (Plant et al., 1993; Barton et al., 1996; Greenlee and Smith, 1997; Vaina et al., 2001). Epileptic activity in MT/V5 has also been shown to elicit motion perception auras. One study describes a patient (Case 1) with ictal activity leading to a percept of colorless fog moving from peripheral vision and stopping abruptly in the midline (Plant et al., 1993), and another study describes seizures causing cars or real or illusory objects to move across the visual field from the left to the right (Laff et al., 2003).

Additional support for the causal involvement of MT/V5 in visual motion perception comes from stimulation studies in humans. Transcranial magnetic stimulation (TMS) in human MT/V5 elicits moving phosphenes when the eyes are closed (Pascual-Leone and Walsh, 2001; Antal et al., 2004; Silvanto et al., 2005b; Silvanto and Muggleton, 2008) as opposed to early visual cortex (V1/V2) stimulation eliciting stationary phosphenes (Silvanto et al., 2005b). Temporary disruption of MT/V5 function with TMS adversely affects motion direction perception (Beckers and Hömberg, 1992; Hotson et al., 1994; Schwarzkopf et al., 2011). MT/V5 is also linked to additional motion-related perceptual effects as the motion aftereffect (Theoret et al., 2002). Another study found significant motion perception impairments in the contra-lateral visual field after subdural electrical stimulation of MT/V5 (Blanke et al., 2002).

Studies in non-human primates also show that MT/V5 and MST are critical to motion perception tasks (Newsome and Pare, 1988; Salzman et al., 1990; Wurtz et al., 1990; Salzman et al., 1992; Schiller, 1993; Celebrini and Newsome, 1995; Britten and van Wezel, 1998; Liu and Newsome, 2005; Gu et al., 2012). For example lesions to primate MT/V5 significantly impair visual motion perception (Newsome and Pare, 1988; Wurtz et al., 1990; Schiller, 1993; Pasternak and Merigan, 1994) and these perceptual deficits closely resemble those of the motion blind patient LM following MT/V5 damage (Marcar et al., 1997). In addition, microstimulation of MT (Salzman et al., 1990, 1992) or MST (Celebrini and Newsome, 1995) neurons strongly influences perceptual performance on motion perception tasks.

While all the above provide clear-cut evidence for the visual motion pathway's necessary role in a variety of motion perception tasks, they do not argue for its sufficiency for perceiving visual motion or for being aware of visual motion. Indeed, different specialized regions outside the visual motion pathway critically contribute to specialized/specific motion perception types. This can explain why patients with lesions to MT/V5 (e.g. LM) suffer deficits in an extensive range of visual motion perception types while patients with lesions sparing MT/V5 have more specific motion perception impairments (Vaina and Cowey, 1996; Vaina et al., 2000; Vaina and Gross, 2004; Saygin, 2007; Gilaie-Dotan et al., 2011; van Kemenade et al., 2012, 2013b). For example, lesions to or abnormal function of the right ventral visual cortex that processes shape information and leads to shape perception, impair motion coherence, motion detection, and structure from motion perception, all tasks related to shape or surface definition (motion coherence displays are in essence detecting a moving surface in a cluttered display (Gilaie-Dotan et al., 2011, 2013b)) but do not impair biological motion perception (Gilaie-Dotan et al., 2011, 2015). Lesions to the pSTS and vPMC on the other hand, that process kinematics (Grossman et al., 2000; Saygin, 2007), are critical to biological motion perception (Vaina and Gross, 2004; Saygin, 2007; van Kemenade et al., 2012), but not to motion coherence thresholds (Saygin, 2007) or to motion tasks involving non-biological form (Vaina and Gross, 2004; van Kemenade et al., 2012). Lesions to intermediate visual regions cause selective visual motion perceptual deficits (Vaina et al., 2000; Cowey et al., 2006), highlighting their possible integratory role in these tasks (Vaina et al., 2005). And transient or temporary lesions to parts of the cerebellum (e.g. vermis and midline structures) can selectively

impair motion discrimination (e.g. (Nawrot and Rizzo, 1995, 1998; Jokisch et al., 2005; Cattaneo et al., 2014)).

To sum up, I assume that visual motion first quickly passes through the motion pathway to reach the specialized regions, each of which exploits the appropriate motion-related information (e.g. dorsal pathway uses hand and arm action information, ventral cortex uses surface and object information, regions along the STS and additional regions involved in kinematics are critical for the perception of single person, group, or social-related kinematics, FEF uses information related to eye movements and object tracking, visuo-vestibular regions use optic flow information). Even when visual motion cues are additionally propagated in parallel through alternative routes (e.g. optic flow from V1 directly to V6), the information streaming through the motion pathway seems to reach these target areas at the same time as or earlier than through the parallel routes (Pitzalis et al., 2013a). The quick flow of downstream information in the motion pathway might precede visual awareness, which seems to correspond to later stages of the processing that involve feedback information transfer (Lamme and Roelfsema, 2000; Hochstein and Ahissar, 2002; Silvanto et al., 2005a,b; Moutoussis and Zeki, 2006). In fact some types of visual motion perception, for example second-order motion, might depend on feedback from MT/V5 onto intermediate visual areas, and support for this comes from longer cortical latencies and reaction times for second-order motion relative to those of first-order motion (Ellemberg et al., 2003; Allard and Faubert, 2008; Ledgeway and Hutchinson, 2008). Furthermore, it is still unclear whether activation of MT/V5, relying only on subcortical inputs (Girard et al., 1992; Bridge et al., 2010; Ajina et al., 2015; Hervais-Adelman et al., 2015), might suffice for eliciting visual motion awareness (Moutoussis and Zeki, 2006). The Riddoch syndrome (Riddoch, 1917; Zeki and Ffytche, 1998) might actually suggest so, as patients with damaged V1 have awareness of visual movement in their blind field despite not being aware of *what* has moved. On the other hand blindsight (Weiskrantz, 1993; Azzopardi and Cowey, 1997; Stoerig and Cowey, 1997; Silvanto, 2015), which is probably a different neurological phenomenon than the Riddoch syndrome (Kentridge and Heywood, 1999; Zihl and Heywood, 2015), might suggest otherwise, as some blindsight patients show MT/V5 activity in response to visual motion in their blind field without being aware of it (Barbur et al., 1993; Goebel et al., 2001; Gaglianese et al., 2012; Ajina et al., 2015; Hervais-Adelman et al., 2015). In summary, the multiplicity of regions and networks contributing to various aspects of motion perception emphasizes the significant importance of visual motion to visual function.

8. Predictions to distinguish the motion visual pathway from the other visual pathways

Together with the conceptual proposal of a visual motion pathway that is functionally and anatomically distinct from the dorsal pathway, I provide a set of testable predictions for distinguishing between the motion, dorsal, and ventral pathways. These predictions, presented in Table 1 and in Fig. 4, and detailed more specifically below, are along spatial and temporal coding principles and sensitivities: retinal and retinotopic spatial sensitivities, spatial proximity of the visual stimuli to the observer (e.g. peripersonal vs. extra-personal space), and temporal sensitivities (e.g. high vs. low temporal frequencies). In general, I expect the ventral pathway to be highly sensitive to spatial information (even more so in the upper part of the visual field and in extra-personal space) and much less to temporal information. The dorsal pathway on the other hand would be highly sensitive to temporal information, and only sensitive to coarse spatial information, with higher sensitivity to spatial information in the lower visual field and in peri-personal space. Importantly I anticipate that the motion pathway would show high sensitivity to visual motion across the visual field, whether near or far from the observer, and would also be highly sensitive to the temporal aspects of the stimuli. This is in line with visual motion's spatio-temporal nature and the need to react to any visual motion in any part of the visual field. I further predict

Table 1
Proposed sensitivities to distinguish between the three pathways.

		Sensitivity			
		Spatial	**Temporal**	**Visual field**	**Proximity**
Pathway	**Ventral**	High	Low	Upper	Extrapersonal space
	Dorsal	Low	High	Lower	Peripersonal space
	Motion	Medium	High	Full	All

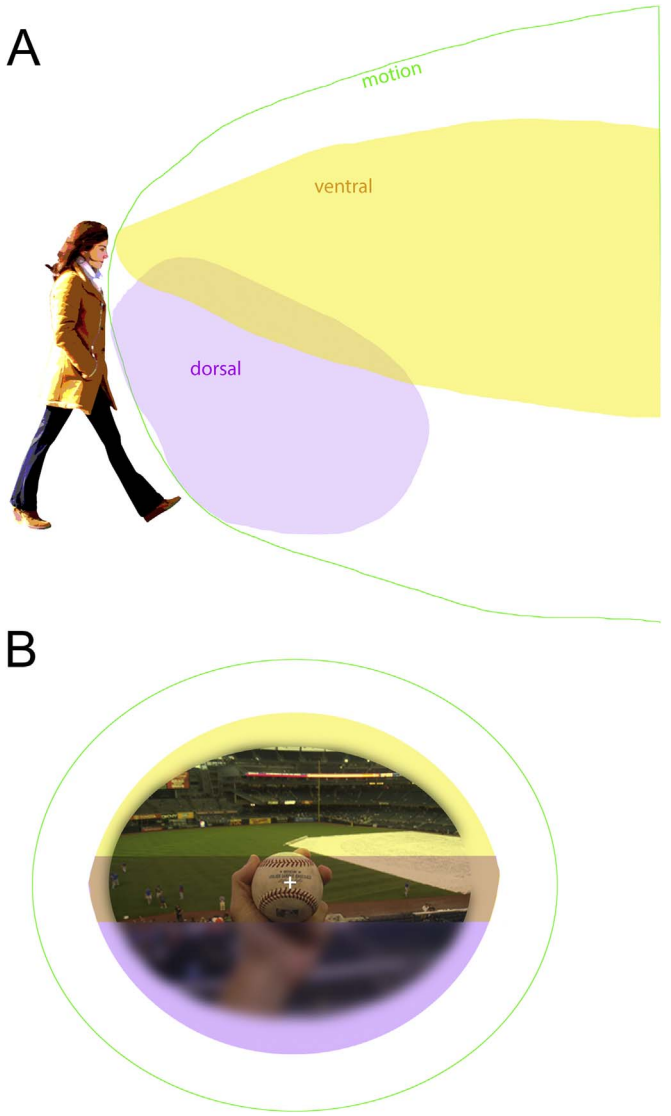

Fig. 4. Model predictions for spatial biases of the motion, dorsal and ventral visual pathways. (A) While ventral pathway shows sensitivity to the upper visual field and extra personal space, dorsal pathway shows sensitivity to lower visual field and peripersonal space, and motion pathway would be sensitive to visual motion across the visual field. (B) The pathways' spatial biases illustrated from the observer's point of view. The observer is fixating at the point indicated by the white cross on the baseball that they are holding. Note that dorsal pathway shows coarse spatial sensitivity in lower visual field, and that both ventral and dorsal pathways' biases cover the horizontal meridian. See also Table 1.

that deviations from these predictions should correspond to the statistical properties of the visual experience that humans encounter throughout their lifetime.

8.1. Spatial resolution sensitivities

The **ventral pathway** is highly sensitive to spatial information according to a center-periphery organizational principle (Levy et al., 2001, 2004; Grill-Spector and Weiner, 2014; Weiner et al., 2014). **Dorsal pathway** on the other hand, I hypothesize, does not require high spatial information and can achieve most of its functions based on low spatial resolution (e.g. grip, reach, grasp etc. see Fig. 4B) consistent with rather large receptive fields found in posterior parietal neurons (e.g. (Robinson et al., 1978)). For dorsal functions that require high spatial information (e.g. threading a needle or cutting nails) – these I hypothesize are performed in a slower manner than grasping or reaching and rely on dorsal-ventral interactions that support the high spatial information required to achieve them successfully. **The visual motion pathway** – I hypothesize – is sensitive to medium-to-high spatial information as it is critical that any motion of any size at any location in the visual field would be swiftly detected.

8.2. Retinal and retinotopically spatial sensitivities

A key principle guiding the organization of the visual cortex, and especially early visual cortex, is retinotopy. Retinotopic regions – starting from primary visual cortex (V1) and into V2, V3/VP and further, are organized such that the upper part of the visual field is represented in the ventral retinotopic regions (upper quadrants of the visual field), and the lower part of the visual field is represented in the dorsal retinotopic regions (dorsal quadrants). Although the ventral and dorsal portions of V1-V3 are assumed to be "neutral" with respect to ventral/dorsal pathway attribution to allow dorsal and ventral higher-order regions to use information from across the visual field (the majority of electrophysiological studies in early visual cortex do not even make this ventral-dorsal portion distinction; see also Nassi and Callaway (2009)), I suggest that this early retinotopic organization is of functional relevance to the higher more specialized visual regions along these pathways. Therefore I hypothesize that the **dorsal pathway** would be more sensitive to the lower half of the visual field (Previc, 1990; Rossit et al., 2013), relating to the dorsal involvement in preparation for actions (see Fig. 4B). This would be consistent with the conspicuous presence of one's hands in the lower visual field (Graziano et al., 2004), and with the lower visual field representing closer space than that appearing in the upper visual field, and thus requiring more attention when we move and act in the environment (see more below about peripersonal and extra-personal space), and even perhaps with better figure-ground segmentation in the lower visual field (Rubin et al., 1996) that might contribute to action preparation. This is supported by recent findings showing a lower VF bias in LO1/2 (Kolster et al., 2010) residing dorsally to MT/MST (Kolster et al., 2010; Weiner and Grill-Spector, 2011), a lower VF bias in V3d (Larsson and Heeger, 2006), and a lower VF bias in posterior parietal neurons (Robinson et al., 1978). Along the same line of reasoning, I propose that the **ventral pathway** that is involved in allowing us to perceive shapes, entities and places is more sensitive to the upper (vs. lower) part of the visual field (Previc, 1990; Boussaoud et al., 1991) as I hypothesize that we encounter these entities more frequently in the upper visual field as they are typically further away from us (see Fig. 4B). Upper visual field bias in ventral pathway is supported by recent findings of an upper VF bias in TEO and additional ventral regions (Boussaoud et al., 1991), in hV4 (Larsson and Heeger, 2006; Kolster et al., 2010) and in V3v (Larsson and Heeger, 2006), and by a case of acquired visual agnosia patient co-occurring with severely defective upper visual fields (Riddoch and Humphreys, 1987). Further support also comes from an upper visual field advantage for word discrimination (Goldstein and Babkoff, 2001), which are also associated with ventral pathway. A recent study reports that smaller upper visual field receptive fields are already present at the level of the primate superior colliculus supporting the idea that upper visual field is associated with "ventral-related" high resolution coding for form and structure (Hafed and Chen, 2016). I hypothesize that the human **motion pathway**, on the other hand, does not show an upper/lower visual field preference and is uniformly sensitive to any motion across the visual field. Furthermore, if there is any visual field preference in the human motion pathway then it should follow the visual motion distribution across the visual field that people experience across their lifetime (e.g. (Maunsell and Van Essen, 1987)). This full field coverage of the visual motion pathway regions is supported by human neuroimaging studies (Huk et al., 2002; Kolster et al., 2010; Weiner and Grill-Spector, 2011), and is consistent with MT's and MST's motion sensitivity across the whole visual field (MT and MST have full half field representation in each hemifield, MST with even ipsilateral representation (Huk et al., 2002; Weiner and Grill-Spector, 2011), whereas dorsal and ventral regions only represent quadrants of the visual field). This full field coverage in MT/V5 and MST (see Fig. 4A and B), along with their anatomical location between the two pathways (see Fig. 1A and B), further support the efficient transfer/propagation of visual motion information between the motion pathway and ventral and dorsal pathways (e.g. (Cerkevich et al., 2014)).

8.3. Sensitivity to spatial proximity of the visual stimuli

This actually relates to the ideas presented above about visual field sensitivities, and is illustrated to some extent in Fig. 4A. I expect the ***dorsal pathway*** to be more sensitive to peripersonal space (that can be associated with the lower visual field) than to extrapersonal space (that can be associated with the upper visual field) which is in line with the arguments that dorsal-associated stereopsis is most useful for interacting with the environment at an arm's length (Cutting et al., 1996; Arsenault and Ware, 2004). I also anticipate that ***ventral pathway*** would show the opposite effect with higher sensitivity to extrapersonal rather than peripersonal space. The *visual* ***motion pathway***, I anticipate, would not show any such sensitivities and would be equally sensitive to all visual motion across the visual field whether close or far from the observer.

8.4. Temporal sensitivities

The following predictions relate to the temporal information present in natural environmental stimuli (as compared with lab based artificially created flicker based temporal information). For such stimuli, I hypothesize that *the* ***ventral pathway*** would show low sensitivity to temporal information and would be sensitive mainly to the prominent changes in the spatial visual inputs that take place along the temporal axis, those which are informative about shape or form or surroundings that changed. If there are natural temporal frequencies occurring in natural scenes, then ventral pathway might be more tuned to them. *The* ***dorsal pathway*** should show high sensitivity to temporal information, especially for functions that are associated with action preparation, as these functions require high temporal precision. *The* ***motion pathway*** should show high sensitivity to all temporal information.

9. Conclusions

I propose here that visual motion is processed along a visual motion pathway that is distinct from the dorsal pathway. This pathway's foremost importance is to propagate visual motion quickly and efficiently throughout the brain. While this pathway is necessary for all types of visual motion perception, specific types of motion perception additionally depend on regions outside this pathway. Timing analyses place MT/V5 at the first level of the visual hierarchy along with V1. Predictions I provide might help to test these ideas in future research.

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