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# Linking Neuronal Direction Selectivity to Perceptual Decisions About Visual Motion

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All rights reserved**Keywords**

motion perception, direction discrimination, speed discrimination, area MT, prefrontal cortex, strobe-reared cats, working memory

**Abstract**

Psychophysical and neurophysiological studies of responses to visual motion have converged on a consistent set of general principles that characterize visual processing of motion information. Both types of approaches have shown that the direction and speed of target motion are among the most important encoded stimulus properties, revealing many parallels between psychophysical and physiological responses to motion. Motivated by these parallels, this review focuses largely on more direct links between the key feature of the neuronal response to motion, direction selectivity, and its utilization in memory-guided perceptual decisions. These links were established during neuronal recordings in monkeys performing direction discriminations, but also by examining perceptual effects of widespread elimination of cortical direction selectivity produced by motion deprivation during development. Other approaches, such as microstimulation and lesions, have documented the importance of direction-selective activity in the areas that are active during memory-guided direction comparisons, area MT and the prefrontal cortex, revealing their likely interactions during behavioral tasks.

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## INTRODUCTION

Long before the neuronal mechanisms underlying motion perception could be examined directly, the opponent nature of perceptual phenomena associated with visual motion suggested that these mechanisms are selective for motion direction (Nakayama 1985). One of the best-known examples of such selectivity for motion direction is the waterfall illusion, also referred to as the motion aftereffect (MAE), in which, following prolonged viewing of objects moving in a single direction, stationary objects appear to move in the opposite direction. The MAE was explored in many psychophysical studies involving direction-specific adaptation, characterizing in some detail the underlying direction-specific channels (Levinson & Sekuler 1975a, Sekuler & Ganz 1963, Sekuler & Levinson 1977). These and many other psychophysical studies lead to the conclusion that image motion, like color and form, is a fundamental visual dimension with its own distinct neuronal mechanism (Nakayama 1985). With the advent of recordings from single cortical neurons and the discovery of neurons displaying selectivity for motion direction in the cortex of cats and monkeys (Hubel & Wiesel 1962, 1965, 1968), it became possible to compare the properties of directional motion channels revealed psychophysically to direction-selective (DS) activity of cortical neurons, providing more direct links between brain and behavior. In this review, we focus on such links. We first discuss parallels between the nature of the motion mechanisms revealed with behavioral and physiological approaches and the transition from the local directional signals in early cortical processing to motion signals that correlate with perception. We then provide an overview of the cortical regions carrying DS signals and document their utilization in perceptual decisions during simple motion discrimination tasks, as well as during more complex tasks requiring shifts of attention and memory storage. We then examine the contribution of direction selectivity to visual function by outlining the perceptual effects of a widespread elimination of cortical direction selectivity, followed by a discussion of the behavioral effects of localized lesions in regions carrying motion signals.

## PARALLELS IN MOTION MECHANISMS REVEALED BY PSYCHOPHYSICS AND PHYSIOLOGY

Psychophysical and physiological studies have provided a detailed account of the visual system's response to image motion. In many cases, these two distinct empirical strategies have converged on a consistent set of general principles that characterize visual processing of motion information. Both approaches have shown that the direction and speed of target motion are among the most important encoded stimulus properties, revealing many parallels between psychophysical and physiological responses to motion.

Early psychophysical studies demonstrated the existence of independent mechanisms sensitive to opposite directions of motion (Levinson & Sekuler 1975a, Sekuler & Ganz 1963, Sekuler & Levinson 1977), showing that these mechanisms are most sensitive at low spatial frequencies (Watson et al. 1980) and are narrowly tuned for speed (Tolhurst et al. 1973). Physiological recordings also revealed that many cortical neurons increase their firing rates in response to a particular direction of motion while reducing their activity in response to motion in the opposite direction. Such selectivity for motion direction, first encountered in the striate cortex, is even more common in such extrastriate cortical areas as V3 or MT in the monkey (Born & Bradley 2005, Gegenfurtner et al. 1997, Maunsell & Van Essen 1983, Wood et al. 1973) and the lateral suprasylvian area in cats and ferrets (Dunn-Weiss et al. 2019, Hubel & Wiesel 1969, Spear & Baumann 1975, Toyama et al. 1994). Consistent with the motion mechanisms that have been revealed psychophysically, neurons selective for direction generally prefer lower spatial frequencies moving at higher speeds (Gegenfurtner et al. 1997, Hawken et al. 1988, Morrone et al. 1986). Investigation

of the basic properties of motion processing remains an active research area, with recent work revealing that tuning preferences of MT neurons shift to higher spatial frequencies at high contrast (Pawar et al. 2019).

Both neural and psychophysical responses to motion change with stimulus properties, often in very similar ways. For example, early studies revealed that responses to motion of single neurons in MT and limits of motion perception exhibit very similar scaling with eccentricity (Baker & Braddick 1985, Mikami et al. 1986). Both neural responses to motion and motion perception saturate very quickly with increasing contrast, a property that differentiates motion from other visual modalities (Sclar et al. 1990). Neuronal DS responses exhibit rapid adaptation to motion (<100 ms), mirroring perceptual motion aftereffects that can occur on the same timescale (Glasser et al. 2011). Another example illustrating parallels between physiology and behavior comes from a series of classic psychophysical studies involving the use of moving patterns consisting of components that must be integrated to produce a coherent motion percept. This work opened the door to the study of higher-order processing of complex motion in extrastriate cortical neurons, revealing mechanisms for integrating local signals that are likely to underlie the perception of complex motion (Gegenfurtner et al. 1997, Huk & Heeger 2002, Khawaja et al. 2013, Li et al. 2001, Movshon et al. 1985, Ouellette et al. 2004, Pack et al. 2001, Rust et al. 2006, Wang & Movshon 2015).

These examples are just a sample among many parallels between motion perception and physiology (for a comprehensive review, see Park & Tadin 2018). While they are both numerous and informative, these links are still largely correlational, falling into the analogy class of linking propositions (Teller 1984). Below, we focus on links that directly implicate DS signals in perceptual decisions about visual motion.

## FROM LOCAL DIRECTION-SELECTIVE SIGNALS TO SIGNALS THAT LINK TO VISUAL BEHAVIOR

As mentioned above and detailed below, DS responses are found in several brain areas. In the relatively high-level brain areas, these signals typically correspond to perceived visual motion directions. However, that is not the case for early DS signals in the brain, where responses of DS neurons pick up local motion signals that are best characterized as building blocks for what eventually becomes perceived visual motion. In many cases, perceived motion direction differs rather dramatically from these local motion signals. A classic example involves a class of motion stimuli known as plaids (Adelson & Movshon 1982). In this case, two superimposed gratings moving in oblique directions are perceived as a vertically moving plaid—a global motion direction that differs from the component directions that make up the stimulus. Another example comes from the various types of random-dot stimuli, which are usually perceived as having a global motion direction but are composed of individual dots whose directions often differ greatly from the perceived direction (Britten et al. 1992, Pasternak et al. 1990, Williams & Sekuler 1984).

This transition from local to global motion signals starts with area V1. With their small receptive fields (RFs), DS V1 neurons are selective for local motion energy within small apertures. Such signals are often ambiguous with respect to both their direction and their speed, an ambiguity known as the aperture problem (Pack & Born 2001, Wallach 1935). For plaid stimuli, DS V1 neurons signal directions of components that make up the plaid, rather than the coherently moving plaid direction perceived by human observers (Movshon et al. 1985). For random-dot stimuli, V1 does not show monotonically increasing responses with increasing motion coherence, in contrast to both responses in MT and motion perception (Braddick et al. 2001; Britten et al. 1992, 1996; Celebrini & Newsome 1994; Newsome et al. 1989). While these properties of DS neurons in V1 represent a critical local stage in motion processing, the ambiguities that are present in these

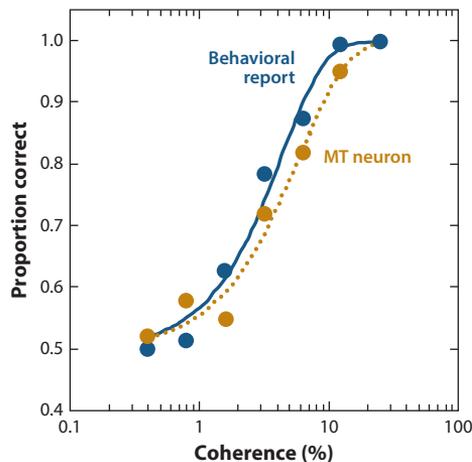
signals need to be resolved. Evidence indicates that this resolution is accomplished by integrating V1 responses at later stages of motion processing, a process that has been extensively studied in area MT (Born & Bradley 2005). MT, with its strong connections with V1, robust direction selectivity, and relatively large RFs, is particularly well suited for integration and interpretation of local motion signals. Indeed, for plaid stimuli, many MT neurons faithfully represent perceived pattern motion direction (Movshon et al. 1985, Pack et al. 2001, Rust et al. 2006). Similarly, temporal evolution of DS signals in MT reveals a solution to the aperture problem inherited from V1 (Pack & Born 2001). For random-dot stimuli, MT responses increase with increasing motion coherence (Bisley et al. 2004, Britten et al. 1996, Zaksas & Pasternak 2006) and reflect qualitative perceptual changes of dot motion (Qian et al. 1994, Zaksas & Pasternak 2006). Thus, with a few notable exceptions (e.g., Hedges et al. 2011), DS signals in MT are closely linked to the perception of global motion.

This evolution of DS mechanisms going from V1 to MT has been captured by a class of models that incorporate motion detection by linear spatiotemporal filters in V1 and spatial integration by MT neurons, paired with nonlinear mechanisms at each processing stage (Rust et al. 2006, Simoncelli & Heeger 1998). These models can explain not just MT responses to simple lab-based stimuli (Rust et al. 2006), but also MT responses to more naturalistic stimuli (Nishimoto & Gallant 2011) and even functional magnetic resonance imaging blood-oxygen-level-dependent signals in response to natural movies (Nishimoto et al. 2011).

While the studies discussed above highlight the importance of spatial integration, perceiving motion of objects in the real world also requires limiting spatial integration to signals belonging to a single object and not pooling signals from multiple moving objects or their background. The solution requires balancing competing demands between spatial integration and processes that highlight differences in local motion signals (Braddick 1993). However, despite remarkable efficiency of motion segregation revealed in behavioral tests (Nawrot et al. 1996, Tadin et al. 2019), this is a relatively unexplored issue. Spatial segregation can be accomplished using suppressive center-surround mechanisms (Allman et al. 1985, Rao & Ballard 1999). In MT, neurons with suppressive surrounds respond poorly to large uniform moving stimuli and respond strongly to small motions, and in some cases, their responses are further enhanced by surround motion in the antipreferred direction (Allman et al. 1985). Such neural mechanisms, also found in other motion-processing areas (Tadin 2015), are theoretically well suited to visually segment moving objects (Nakayama & Loomis 1974). A microsimulation study (Born et al. 2000) has linked center-surround MT neurons with the encoding of direction of moving objects, while neurons that prefer large moving stimuli have been linked with signaling background motion. Parallel work in humans has focused on spatial suppression (Tadin et al. 2003), a putative behavioral correlate of neural surround suppression. These behavioral results have been linked with human MT+ (Tadin et al. 2011) and physiological center-surround mechanisms in MT (Liu et al. 2016, Pack et al. 2005). Notably, recent work has linked spatial suppression with visual segmentation of moving objects (Tadin et al. 2019). In sum, converging evidence paints a picture of a flexible motion system that favors integration when noise or ambiguities are present and takes advantage of computational benefits afforded by suppressive mechanisms when motion signals are strong. The end results are DS signals that, in most cases, accurately represent motion directions of visual objects.

## **DIRECTION-SELECTIVE NEURONS REFLECT DEMANDS OF MOTION DISCRIMINATION TASKS**

Parallels in the psychophysical and physiological characterizations of motion mechanisms provide compelling evidence in support of the theory that DS neurons underlie motion perception. However, addressing whether and how signals by DS neurons are utilized in perceptual decisions



**Figure 1**

Physiological and psychophysical data obtained simultaneously from a rhesus monkey, relating neuronal and behavioral responses to different levels of dot coherence (% of dots moving in the same direction in the presence of random motion). Figure adapted with permission from Newsome et al. (1989).

requires recordings from these neurons taken while animals are performing motion discrimination tasks.

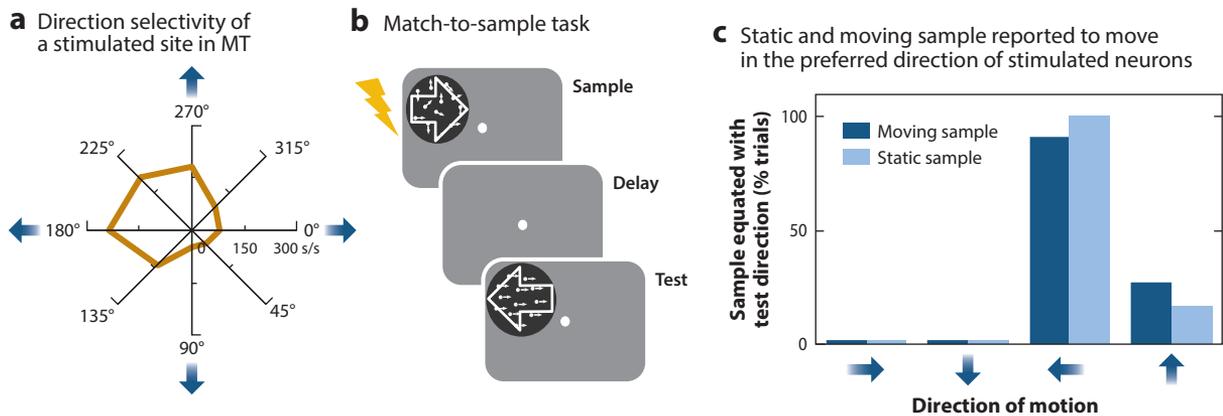
### Area MT

Most of the work linking direction selectivity to behavior have focused on the extrastriate area MT, since the majority of its neurons have been shown to be DS (Maunsell & Van Essen 1983) and play an important role in perceptual decisions about motion direction (Newsome & Pare 1988). In a series of influential experiments, Newsome and his colleagues introduced an approach that, for the first time, allowed direct comparison between psychophysical and physiological responses of neurons in areas MT and MST (Britten et al. 1992, 1996; Celebrini & Newsome 1994; Newsome et al. 1989). By varying the strength of the motion signal in a field of randomly moving dots and recording neuronal activity during the performance of a direction discrimination task, these authors generated neurometric and psychometric functions relating perceptual decisions and neuronal sensitivity to motion coherence (**Figure 1**). This work revealed a strong similarity between the shapes of the psychometric and neurometric functions of many MT neurons, with some neurons showing sensitivity that is nearly identical to that measured behaviorally (Britten et al. 1992). The comparison of neurometric functions recorded in area MT and the behaviorally measured psychometric functions was subsequently extended to motion speed, linking MT activity to speed judgements (Liu & Newsome 2005, 2006).

These and other studies that related neuronal activity to perceptual decisions on a trial-by-trial basis showed that the activity in MT was predictive of the choice made by the animals, leading to the widely accepted view that DS signals in MT are likely to be utilized in perceptual decisions about visual motion (Liu & Newsome 2005, 2006; Lui & Pasternak 2011; Price & Born 2010; Zaksas & Pasternak 2006; Zohary et al. 1994).

### Microstimulation Demonstrates that Area MT Signals Are Utilized in Perceptual Decisions

The observation of strong correlation between neuronal and behavioral sensitivities during motion discrimination provided a powerful link between neuronal direction selectivity and its role



**Figure 2**

Effect of microstimulation of a direction-selective (DS) site in MT. (a) Preference of the example site for leftward motion. (b) Behavioral task. The monkey was rewarded for reporting whether the sample moved in the same direction as or a different direction than the test. Stimulation was applied during the sample in 25% of trials. (c) In stimulation trials, the monkey always reported that the sample direction was the same as the test moving to the left, the preferred direction of the stimulated site, irrespective of the actual sample direction or the presence of motion during the sample. This result shows that signals introduced by microstimulation of MT are interpreted as visual motion. Figure adapted with permission from Bisley et al. (2001).

in direction judgements. A more direct confirmation that motion signals in MT and MST are utilized in perceptual decisions was provided by elegant microstimulation studies (Celebrini & Newsome 1995, Ditterich et al. 2003, Gu et al. 2012, Murasugi et al. 1993, Nichols & Newsome 2002, Salzman et al. 1992).

This work revealed that motion coherence thresholds for reporting a motion direction improved when microstimulation was applied to neuronal clusters preferring that direction. Low-coherence stimuli that could not be reliably identified became detectable when microstimulation was applied. These studies convincingly showed that signals originating in MT affected perception by biasing the decision in favor of the direction represented by stimulated neuronal clusters, most likely by strengthening signals elicited by visual stimulation. However, the simple direction identification task used in these studies did not provide insights into the visual experience produced by microstimulation of directional columns. These insights were provided by a study involving a more complex task in which monkeys compared directions of two sequentially presented random-dot moving stimuli, the sample and the test (Bisley & Pasternak 2000) (**Figure 2b**). Microstimulation was applied to clusters of MT neurons during the presentation of the sample in 25% of the trials (Bisley et al. 2001). Thus, the monkey compared the direction of the sample perceived during microstimulation to the direction of the nonstimulated test. Bisley et al. found that, on trials with the test moving in the direction preferred by the stimulated neurons (**Figure 2a**), the monkeys nearly always equated the direction of the sample with the direction of the test, irrespective of the actual direction presented during the sample (**Figure 2c**). The monkeys even reported the presence of motion in the stimulated direction when the sample contained static dots (**Figure 2c**). This conclusion was supported by the retinotopic specificity of the effect: Microstimulation was effective only when delivered to neurons with RFs in the same contralateral portion of the visual field as the stimuli being discriminated during the behavioral task. Thus, stimulation applied during the sample produced signals interpreted by the monkeys as directional motion, leading to the conclusion that the directional information used by the monkeys is likely to be provided by neurons in area MT.

## Posterior Parietal Cortex

Since DS neurons in MT project directly to several regions in the parietal cortex, including areas MST and LIP (Barbas 1988, Boussaoud et al. 1990, Ninomiya et al. 2012, Petrides & Pandya 2006, Schall et al. 1995), the presence of DS signals in these areas is not surprising. Area MST receives direct inputs from MT (Boussaoud et al. 1990, Desimone & Ungerleider 1986) and displays prominent selectivity for visual motion. Its neurons, with their large RFs, show robust selectivity for the directions of rotation, expansion, and other types of complex motion but also respond to simpler translational motions of smaller stimuli (Takahashi et al. 2007, Tanaka & Saito 1989). MST has been implicated in processing of the optic flow and in integrating vestibular and visual motion signals during navigation and self-motion (Boussaoud et al. 1990, Desimone & Ungerleider 1986, Duffy & Wurtz 1991, Egger & Britten 2013, Gu et al. 2012, Recanzone et al. 1997, Tanaka & Saito 1989, Tanaka et al. 1986, Thiele & Hoffmann 1996). MST signals have also been linked to perceptual decisions involving judgements of heading direction (Gu et al. 2007).

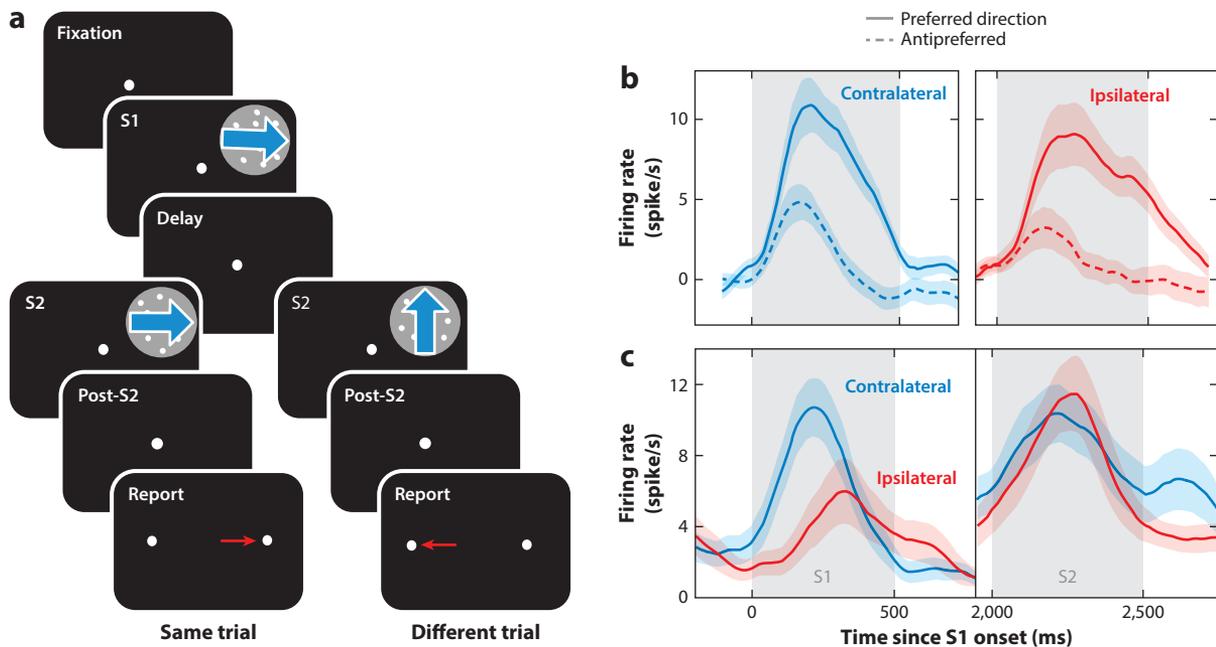
The parietal cortex receives direct inputs from both MT and MST, and the participation of its neurons in decisions about motion direction has been studied quite extensively (Freedman & Assad 2016, Huk et al. 2017). Much of this work has focused on principles of decision making, rather than on the way that these neurons utilize different aspects of visual motion in this process. Area LIP, located in the posterior parietal cortex (PPC), is perhaps the most-studied parietal region, and most of the work on this area has involved visual motion. Its neurons show DS responses during tasks requiring perceptual decisions but also during passive fixation (Andersen 1997, Eskandar & Assad 2002, Fanini & Assad 2009). Motion stimuli have also been used to examine decision-related aspects of LIP activity, including its predictive nature in response to bistable apparent motion (Williams et al. 2003), its ability to form flexible visual categories (Freedman & Assad 2006, Swaminathan & Freedman 2012), and the strong link between its activity and perceptual decisions (Huk & Shadlen 2005, Huk et al. 2017, Roitman & Shadlen 2002, Shadlen & Newsome 2001). This region is strongly interconnected with the dorsolateral prefrontal cortex (dlPFC), and both areas have been implicated in integrating bottom-up and top-down signals and in attentional control (Freedman & Ibos 2018).

## Lateral Prefrontal Cortex

The ventral prearcuate region of the prefrontal cortex (area 8Av) is of particular interest for this review because of its direct reciprocal connections with ipsilateral MT, which inform it about contralateral visual motion (Barbas 1988, Ninomiya et al. 2012, Petrides & Pandya 2006, Schall et al. 1995). This region also receives information about ipsilateral motion from the MT in the opposite hemisphere (Wimmer et al. 2016), most likely by way of callosal connections from the opposite lateral prefrontal cortex (LPFC) (Schwartz & Goldman-Rakic 1984).

Thus, while the bottom-up motion signals reach the LPFC from MTs from both hemispheres, direct top-down projections can only reach the LPFC from the MT within the same hemisphere (Barbas 1988, Ninomiya et al. 2012, Petrides & Pandya 2006). The presence of both direct and indirect inputs from MT is reflected in the LPFC's well-documented selectivity for behaviorally relevant motion direction and speed (Hussar & Pasternak 2009, 2012, 2013; Zaksas & Pasternak 2006) and in its relatively balanced representation of ipsilateral and contralateral motion (Wimmer et al. 2016) (**Figure 3b**).

It is important to note that, unlike neurons in area MT and area LIP, DS responses of the LPFC neurons show strong dependence on task demands and weaken dramatically during passive fixation, when animals are not required to attend to stimulus direction (**Figure 4**), and when



**Figure 3**

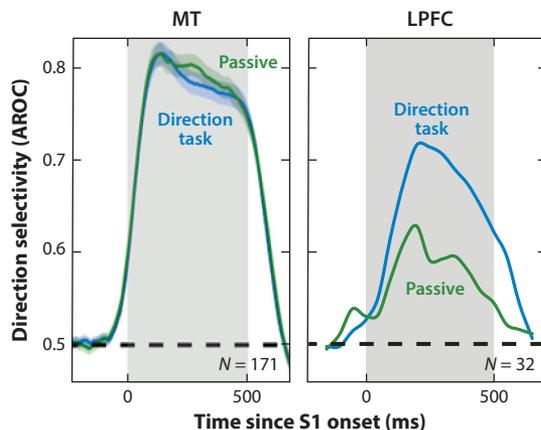
(a) Behavioral task used to study representation and memory for visual motion during neuronal recordings. Monkeys compared directions of two moving random-dot stimuli, S1 and S2, separated by a brief delay. (b) Similar average direction-selective (DS) activity recorded in the lateral prefrontal cortex (LPFC) in response to ipsilateral and contralateral motion ( $n = 42$ ). Responses to the preferred (solid) and antipreferred directions (dashed) were recorded during S1 during the direction comparison task shown in panel a. Baseline activity was subtracted for each neuron. (c) The LPFC response of an example neuron to ipsilateral motion was weaker during S1 but was enhanced during the comparison stage of the task. Note that, despite the difference in the response strength between S1 and S2, direction selectivity for ipsilateral and contralateral motion was comparable. Figure adapted with permission from Wimmer et al. (2016).

the animal's attention is directed to stimulus speed (Hussar & Pasternak 2009). Not only is direction selectivity in the LPFC strongly enhanced with attention, but there is also evidence that the LPFC's responses to motion can reflect even subtle differences in task demands. For example, during a memory-guided direction comparison task, in which monkeys compared the directions of two stimuli, S1 and S2, separated by a brief delay (see the task in **Figure 3a**), the response to the ipsilateral motion during S1 was often substantially weaker than the response to the contralateral motion (Wimmer et al. 2016) (**Figure 3c**). However, this response was dramatically enhanced when the same stimulus was presented during S2, when the task placed additional demands on the animal (Wimmer et al. 2016). The importance of task demands to the way that the LPFC represents motion information raises the questions of what the functional significance of these DS signals is and what their contributions to tasks requiring motion discrimination are. These questions are addressed below.

## COGNITIVE SIGNALS IN NEURONS REPRESENTING VISUAL MOTION

### Spatial and Feature-Based Attention for Motion

Extensive work has been devoted to the effects of attention on the representation of sensory information in the primate cortex. The seminal work of Moran & Desimone (1985) demonstrated changes in RF properties in areas V4 and IT in response to shifts in spatial attention. Subsequently,



**Figure 4**

Direction-selective responses in the LPFC, but not in MT, are affected by task demands. Direction selectivity in MT (*left*) and the LPFC (*right*) in a direction comparison task (see **Figure 2a**) and during a passive fixation task. Sensory conditions in the two tasks were identical, but during passive fixation, monkeys were rewarded without having to report direction differences. The LPFC plot was adapted with permission from Hussar & Pasternak (2009). Abbreviations: AROC, area under the receiver operating characteristic curve; LPFC, lateral prefrontal cortex.

the effects of attention have also been examined in areas MT and MST (Anton-Erxleben et al. 2009; Katzner et al. 2009; Martinez-Trujillo & Treue 2002; Maunsell & Treue 2006; Patzwahl & Treue 2009; Treue & Martinez Trujillo 1999; Treue & Maunsell 1996, 1999). This work has revealed that both spatial and feature-based attention exert modest modulatory influences on the activity of MT and MST neurons, largely via multiplicative gain, but do not fundamentally change the processing of motion information in these areas. Parallel beneficial effects of attention on motion thresholds have also been observed in human subjects (Ling et al. 2009). However, when monkeys are not required to attend to stimulus direction and are rewarded for simply maintaining fixation, the effects of this drastic change in task demands were not detectable in the spiking activity of DS neurons in MT (Zaksas & Pasternak 2006).

In contrast, robust selectivity of the LPFC neurons for behaviorally relevant motion direction or speed is dramatically reduced when animals are not required to make a perceptual report and are rewarded for passively fixating on the display (Hussar & Pasternak 2009, 2012, 2013) (**Figure 3**). These observations highlight the difference between the nature of motion representation in the two areas. In area MT, although responses to motion can be modulated by attention (e.g., Treue & Maunsell 1996), they continue to faithfully represent DS signals, even in the absence of explicit demands to attend to motion. In contrast, in the LPFC, selectivity for stimulus direction requires that the stimulus be behaviorally relevant. However, this sensitivity to task demands does not appear to be reflected in the LPFC's top-down influences on the spiking activity of MT neurons, suggesting that DS signals in the LPFC are unlikely to play a key role in processing of visual motion in MT. This possibility is supported by the intact motion coherence thresholds measured at very short delays during a direction discrimination task in monkeys with LPFC lesions (see **Figure 11a** below) (Pasternak et al. 2015).

### Working Memory for Visual Motion

Tasks involving comparisons of moving stimuli occurring at different times provide an opportunity to study processing of visual motion. Importantly, such tasks also allow the study of the

mechanisms underlying the retention of visual information and the process of comparison needed to form perceptual decisions. In other words, the use of such tasks extends motion processing work to more complex natural behavior. Several groups have been examining the neuronal mechanisms underlying temporary storage and memory-guided comparisons of motion stimuli, focusing not only on areas MT and MST but also on the posterior parietal area LIP and the prefrontal cortex. These studies used various versions of the match-to-sample (MTS) task, in which monkeys compared directions of two moving stimuli, sample (S1) and test (S2), separated by a brief memory delay.

In one version of the MTS task, animals were rewarded for signaling a match at the appearance of a test matching the sample by releasing a bar or button (Masse et al. 2017, Mendoza-Halliday et al. 2014). The data provided by such studies allow the analysis of activity during the memory delay. Using this approach, Mendoza-Halliday et al. (2014) recorded from MT while sample stimuli were presented in neurons' RFs, and subsequent comparison test stimuli (match or nonmatch) appeared in a different quadrant of the visual field. The analysis revealed virtually no DS signals in spiking activity during the delay, although DS signals were detectable in local field potentials. However, recordings from MST, which has RFs large enough to accommodate spatially separated sample and test stimuli, during the same task showed many neurons displaying robust DS signals, leading to highly accurate population encoding of remembered motion direction. Similar results were found in the LPFC, where delay activity was more sustained. These observations led to the conclusion that both MST and the LPFC, but not MT, participate in the retention of motion information. However, the difference in RFs between MT and MST complicates this interpretation of the difference between the two areas. Specifically, given spatial separation of the comparison test from the RF, the representation of the sample may have been transferred to the location of the upcoming test, avoiding detection by recordings that are limited to neurons with RFs that overlap only with the sample stimulus. Such shifts have been documented in tasks with samples and tests presented in separate hemifields (Pasternak & Zaksas 2003, Zaksas et al. 2001).

In another version of the MTS task, monkeys report after the offset of the comparison S2 whether the two comparison stimuli moved in the same or different directions (**Figure 3a**). This approach allows not only the analysis of memory-related delay activity but also the examination of whether responses during S2 are modulated by the remembered S1 direction (e.g., Zaksas & Pasternak 2006). Recordings from MT during this version of the task, with both sample and test appearing in the neuron's RF, revealed more delay activity than was observed in Mendoza-Halliday et al.'s (2014) study (Zaksas & Pasternak 2006). These signals, however, were largely transient, appearing at different times in different neurons, and were nearly absent at the end of the delay. The lack of memory-related signals late in the delay suggests that MT may be an unlikely site of memory storage using representations that rely on the spiking activity (Masse et al. 2019). However, lesion and microstimulation results, discussed below, strongly implicate MT in remembering motion direction during the delay period, suggesting a storage mechanism that does not rely on the spiking activity code. Even though there appeared to be no explicit DS signals at the end of the delay, MT responses to the comparison S2 were affected by the S1 direction (Lui & Pasternak 2011). Thus, responses during S2 reflect the comparison between the current and the remembered stimulus, indicating that, at the time of the comparison, MT neurons have access to storage of directional signals.

Recordings from the LPFC during the same task revealed DS delay activity reflecting the remembered S1. As in MT, these signals were largely transient and asynchronous among neurons, but unlike in MT, this activity persisted until the end of the delay (Hussar & Pasternak 2012, 2013). Weakening of this activity during the passive fixation task, when the monkeys were not required to attend to motion, suggests that this activity is behaviorally relevant. During the comparison S2,

like neurons in area MT, neurons in the LPFC also carried comparison signals between the current and remembered stimuli. These signals were similar to those found in MT, suggesting potential interactions between the two areas during the comparison process (Wimmer et al. 2016).

In summary, this work highlights active participation of neurons in areas MT and MST, as well as in the LPFC, in the processes of retention and comparison of visual motion information. The presence of memory-related signals in both sensory and prefrontal neurons strongly suggests that the ability to retain motion information requires active interactions among multiple regions during memory-guided comparisons of motion directions.

## **PSYCHOPHYSICAL CONSEQUENCES OF A WIDESPREAD LOSS OF CORTICAL DIRECTION SELECTIVITY**

In cats, as in primates, direction selectivity emerges in the striate cortex (Pasternak et al. 2003) and, as in primates (Ferrera et al. 1994, Tolias et al. 2005), is present in extrastriate areas 18 and 19 and in large numbers in PMLS, an area analogous to monkey MT (Bisti et al. 1985, Dreher et al. 1996, Toyama et al. 1994). Neuronal selectivity in the visual cortex, however, is not limited to direction and speed, and the same neurons are often also tuned for other stimulus features, such as orientation, disparity, or spatial frequency (for a review, see Pasternak et al. 2003). Selective elimination of direction selectivity across the visual cortex without affecting other RF properties and without tissue damage would offer a unique opportunity to examine specialized contributions of the DS mechanism to visual function.

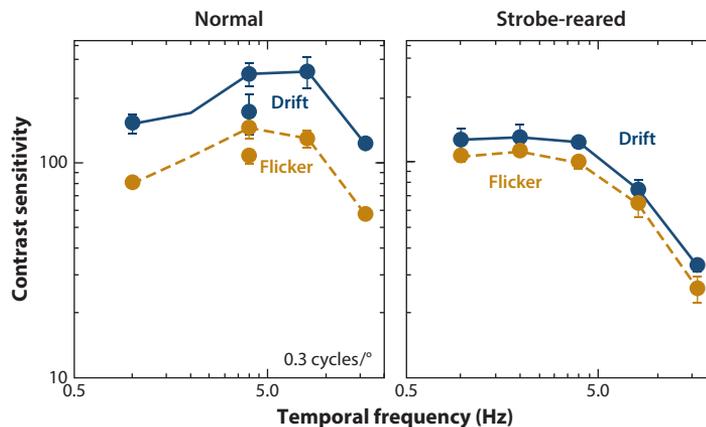
In one example, cats were reared in an environment illuminated by a short-duration (3  $\mu$ s) strobe light flashed at 8 Hz (Cynader & Chernenko 1976, Pasternak et al. 1985). Under these conditions, the animals were exposed to a series of still images and were thus deprived of exposure to continuous motion while still experiencing static spatial form. This type of rearing resulted in a massive and permanent reduction in the proportion of DS neurons in the striate cortex and in the extrastriate areas 18 and PMLS, leaving largely unaffected selectivity for other stimulus dimensions (Cynader & Chernenko 1976, Kennedy & Orban 1983, Pasternak et al. 1985, Spear et al. 1985) and consequently allowing detailed psychophysical characterization of the residual motion mechanisms in these animals.

### **Detecting of Drifting but Not of Counterphase Gratings Is Affected by the Reduced Direction Selectivity**

Sensitivity for moving gratings has been shown to be approximately a factor of two higher than that for counterphase (flickering) gratings generated by combining two gratings moving in opposite directions (Camisa et al. 1977, Levinson & Sekuler 1975a, Pasternak 1986, Watson et al. 1980) (**Figure 5**).

There have been several interpretations for this difference: One suggested that counterphase gratings are detected by independent DS mechanisms, each sensitive to only one half-contrast component (Levinson & Sekuler 1975b, Watson et al. 1980), while the other postulated the existence of a less sensitive nondirectional flicker mechanism (Wilson 1985). The first model predicted that the sensitivity for counterphase gratings would increase as a result of summation of contrasts of the two oppositely moving components. The second model (Wilson 1985), however, predicted that, in the absence of DS mechanisms, both moving and counterphase gratings would be detected by the same less sensitive flicker mechanism, lowering the sensitivity for moving gratings.

Empirical results in strobe-reared cats (Pasternak 1986) (**Figure 5**) provided strong evidence in support of the second model: While the sensitivity for counterphase gratings did not appear to



**Figure 5**

Widespread loss of cortical direction selectivity reduces sensitivity for detecting drifting, but not flickering, gratings. Contrast sensitivity for detecting counterphase and drifting gratings measured in normally reared and strobe-reared cats. The cats discriminated between a grating and a blank screen with the same mean luminance. Figure adapted with permission from Pasternak (1990).

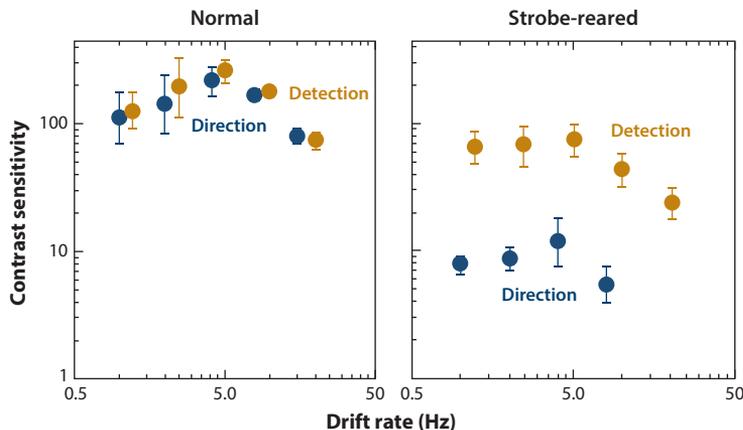
be affected by the loss of cortical direction selectivity, the sensitivity for detecting moving gratings was below the intact levels (approximately 0.3 log units). As a result, sensitivity for the two types of gratings was nearly identical. Evidently, the presence of DS mechanisms boosts sensitivity for detection of moving stimuli, but in their absence, the residual mechanisms still adequately signal the presence of moving stimuli even at very low contrasts.

### Discrimination of Motion Directions Requires High-Contrast Stimuli when Direction Selectivity Is Reduced

To learn whether the mechanisms supporting the detection of moving gratings also carry signals about their direction, Pasternak & Leinen (1986) and Pasternak et al. (1985) measured contrast thresholds during both detection and direction discrimination tasks. In the detection task, the animals viewed two displays of equal mean luminance and were rewarded for selecting the display containing the moving grating. During the discrimination task, the animals viewed two displays, each with identical gratings moving in opposite directions, and were rewarded for selecting the display containing the rightward-moving grating. The comparison of thresholds measured during the two tasks revealed a striking difference between normal and strobe-reared cats.

While the normal cats had nearly identical sensitivity for detecting and discriminating moving gratings, cats with severe loss of DS neurons required 10 times higher contrasts to discriminate direction than to detect it (Figure 6). In other words, strobe-reared cats were only able to identify the direction of moving gratings at high contrasts—a finding that parallels results found for humans with V1 lesions (Ajina et al. 2015). Measurements of spatial contrast sensitivity, thresholds for orientation, low-speed thresholds, and temporal resolution revealed no serious abnormalities, with the exception of slightly reduced contrast sensitivity for high spatial frequencies.

The selectivity of the behavioral deficits is consistent with few, if any, abnormalities in other RF properties, a conclusion confirmed by physiological recordings (Pasternak et al. 1985, Spear et al. 1985). Greatly reduced but still measurable sensitivity for direction is likely a reflection of the activity of the few remaining neurons with residual directional bias that survived deprived rearing and/or an alternate, less sensitive, mechanism that does not rely on canonical motion selectivity.



**Figure 6**

Cats with widespread loss of direction selectivity can detect low-contrast moving gratings but cannot discriminate their direction. Contrast sensitivity for detecting and discriminating directions of motion measured at low spatial frequency (0.3 c/d) in strobe-reared (*right*) and normally reared cats (*left*). Figure adapted with permission from Pasternak et al. (1985).

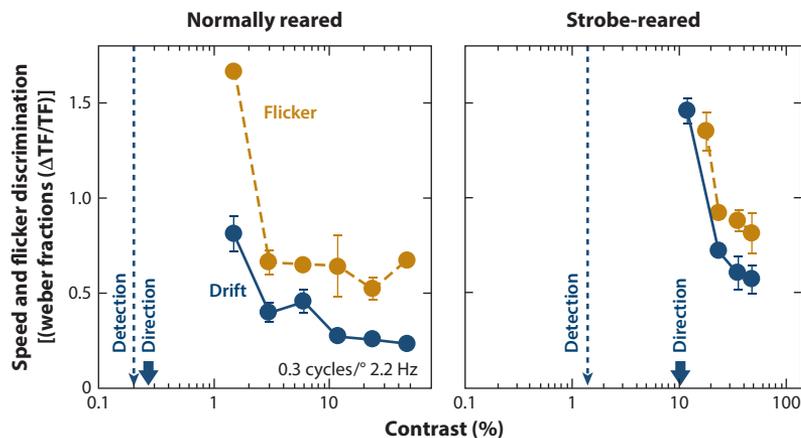
### Discrimination of Speeds and Flicker Depends on Intact Direction-Selective Mechanisms

The strong effects of strobe-rearing on direction sensitivity, described above, provided a unique opportunity to determine whether the ability to judge differences in speed and in flicker rates also depends on having intact DS mechanisms. Taking advantage of the discovery that the residual directional mechanisms in strobe-reared cats can only operate at high contrasts (Pasternak et al. 1985, Spear et al. 1985), subsequent work measured speed discrimination of moving gratings and temporal frequency discrimination for counterphase gratings over a range of contrasts (Pasternak 1987) (**Figure 7**). The results revealed that both speeds and flicker rates could only be discriminated at contrasts at which the cats could reliably discriminate stimulus direction. Both normal and strobe-reared cats were more accurate in discriminating speeds than temporal frequencies, a difference also observed in intact monkeys (Pasternak & Merigan 1994) and in human observers (McKee et al. 1986).

However, in strobe-reared cats, the contrast threshold for detection of gratings was much lower than thresholds for discriminating grating direction, and this difference revealed the importance of directional mechanisms for speed and flicker rate judgements. Thus, despite being able to detect the presence of both moving and flickering gratings at relatively low contrasts (see **Figures 5** and **7**), the animals could not discriminate their speed or flicker rate unless they could also discriminate their direction. These results suggest that discriminations of speeds and temporal frequencies are likely to depend on a common DS mechanism.

### Widespread Loss of Direction Selectivity Severely Weakens Motion Perception with Noisy Stimuli

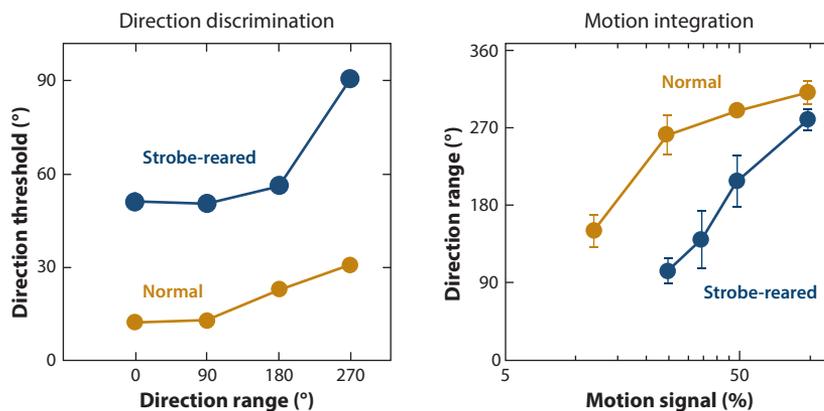
Pasternak et al. (1990) examined motion perception of animals with reduced direction selectivity with moving high-contrast random dots, revealing additional deficits in direction discrimination. Although strobe-reared cats were able to reliably discriminate opposite directions of motion, they showed more than a fourfold loss in the precision of their direction judgements (**Figure 8**). In



**Figure 7**

Precision of speed and flicker discrimination depends on the sensitivity for motion direction. Speed and flicker discrimination thresholds as a function of grating contrast measured in a normal and in a strobe-reared cat. The individual contrast threshold for detecting the grating is indicated by a vertical broken line, and the contrast threshold for direction discrimination is indicated by an arrow. Note that the two thresholds are similar in normal cats, but in strobe-reared cats, they differed by nearly a log unit. Figure adapted with permission from Pasternak (1990).

the same series of experiments, moving random-dot stimuli consisting of many localized vectors were used to assess pooling of local motion signals into a global motion percept (Pasternak et al. 1990). Strobe-reared cats performed nearly as well as the normal cats in discriminating opposite directions when all dots in the display were directionally biased, demonstrating that even a small number of DS neurons can perform spatial pooling of local directional signals. However, in the presence of directional noise, discrimination of opposite directions was severely compromised (**Figure 8**). Finally, strobe-reared cats showed a surprising superiority in discriminating directions of random dots at large spatial displacements ( $D_{max}$ ), suggesting that motion integration occurs



**Figure 8**

Cats with widespread loss of direction-selective neurons show severe deficits in the precision of direction judgements and in motion integration in the presence of noise. Figure adapted with permission from Pasternak et al. (1990).

at larger than normal spatial scales, indicative of a change in sampling strategy in a system with reduced direction selectivity (Rudolph et al. 1994).

### **Summary of the Perceptual Effects of Reduced Direction Selectivity**

Overall, several aspects of motion perception were seriously compromised by the widespread loss of cortical direction selectivity. These include the ability to discriminate directions at low contrasts or in the presence of motion noise, demonstrating the insensitivities of the residual directional mechanism. Work in this area also revealed nearly identical sensitivity for detecting moving and flickering gratings, suggesting the detection of both stimuli by nondirectional mechanisms. Despite the nearly intact contrast sensitivity for detecting such stimuli, the cats could only discriminate their speeds and temporal frequencies at contrasts at which they could also discriminate motion direction, linking speed and flicker discrimination to directional mechanisms. Finally, these animals also showed a dramatic deficit in discriminating small differences in direction, highlighting the importance of intact DS mechanisms for the precision of directional judgements.

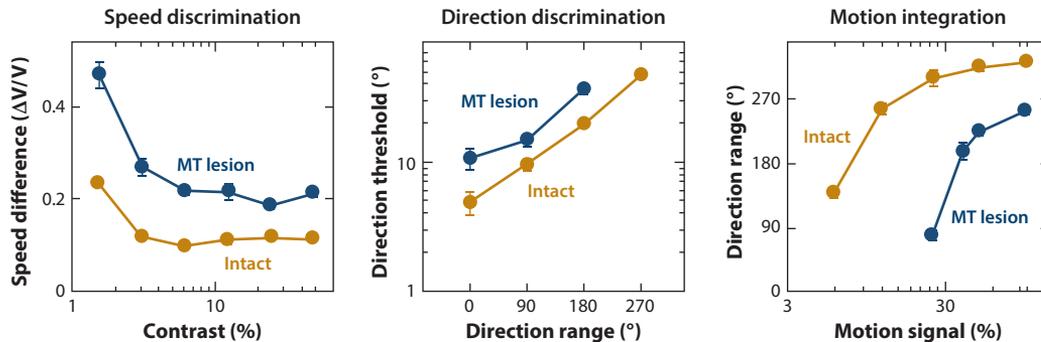
### **BEHAVIORAL EFFECTS OF LESIONS OF CORTICAL AREAS CARRYING MOTION SIGNALS**

#### **Deficits in Motion Perception Associated with Lesions of Early Visual Cortex**

Studies of cats with widespread loss of direction selectivity provided a strong functional link between DS mechanisms and many aspects of motion perception. However, they did not address the questions of whether and how the role of DS neurons in motion perception depends on the neurons' cortical location. These questions were addressed by studies that relied on the lesion approach, beginning with studies of the effects of localized lesions in the cat early visual cortex, areas 17 and 18. DS neurons are common in both areas (Cynader & Chernenko 1976, Orban et al. 1981, Pasternak et al. 1981), but they differ in their spatiotemporal sensitivity and in the size of their RFs. Neurons in area 17 have smaller RFs that prefer finer stimuli moving at lower speeds, while the RFs of area 18 prefer faster coarse stimuli and are larger (Orban et al. 1981). These spatiotemporal differences between the two areas were reflected in distinct behavioral effects of lesions to them. Area 17 lesions resulted in reduced sensitivity for the direction of slowly moving, higher-spatial-frequency gratings but left largely intact sensitivity for motion direction of coarse stimuli (Pasternak et al. 1995). In contrast, area 18 lesions abolished the ability to discriminate direction of these coarse stimuli, although the animals were still able to detect their presence (Pasternak & Maunsell 1992). This result demonstrates the contribution of directional signals carried by area 18 neurons to motion perception. It is noteworthy that the spatiotemporal properties of these neurons match the spatiotemporal characteristics of behaviorally measured motion mechanisms (Pasternak 1990, Watson et al. 1980).

#### **Lesions of Extrastriate Regions Rich in Direction Selectivity Result in Deficits in Motion Perception**

Extrastriate area PMLS is a region in the cat cortex with high incidence of DS neurons and other neuronal properties consistent with its role in motion perception (Spear 1991). Bilateral lesions of this area resulted in pronounced deficits in discriminating speeds of moving gratings, particularly pronounced at lower contrasts and higher speeds, but no detectable deficits in contrast sensitivity for discriminating opposite directions (Pasternak et al. 1989). PMLS also plays a role in the perception of more complex motion, as is evident from lesion-induced deficits in motion integration,



**Figure 9**

Bilateral MT/MST lesions result in severe deficits in motion perception. In the presence of MT/MST lesions, the monkeys displayed substantially lower precision in discriminating speeds of moving gratings (*left*) and in fine direction discrimination of random-dot stimuli (*middle*) and the inability to discriminate motion directions in the presence of motion noise (*right*). Figure adapted with permission from Pasternak & Merigan (1994).

particularly in the presence of noise and in the perception of structure from motion (Rudolph & Pasternak 1996). Notably, these selective deficits in motion perception in cats are analogous to those observed in monkeys with bilateral MT/MST lesions, as discussed below (Pasternak & Merigan 1994).

MT contribution to motion perception in nonhuman primates has been documented by several lesion studies, beginning with the work of Newsome & Pare (1988), who injected ibotenic acid, a neurotoxin that selectively eliminates neurons, into physiologically identified portions of MT. They showed that the MT lesion had a profound effect on motion coherence thresholds for stimuli presented in the lesioned hemifield but no effect on contrast thresholds for discriminating the orientation of stationary gratings presented at the same location. It is noteworthy that, with continued training, these thresholds recovered to nearly normal levels. Similar findings of initially severe deficits produced by ibotenic acid lesions in MT, followed by partial or even complete recovery, have been reported in later papers by Pasternak and colleagues (Bisley & Pasternak 2000, Pasternak & Merigan 1994, Rudolph & Pasternak 1999).

These studies examined in detail the effects of bilateral and, later, unilateral large ibotenic acid lesions involving MT and MST on a range of motion discrimination tasks, including contrast thresholds for detection and direction discrimination of moving gratings; thresholds for speed, direction difference, and motion integration; and coherence (Figure 9). In one study, bilateral MT/MST lesions in free-viewing monkeys lead to severe losses in the precision of judgements of differences in direction and speed, as well as a deficit in motion integration, particularly in the presence of motion noise (Pasternak & Merigan 1994) (Figure 9). The latter result is analogous to the deficit observed in cats with reduced direction selectivity (see Figure 8). This deficit in extracting the veridical directional signal out of a noisy background produced by the loss of MT and MST is likely to be of major functional significance, since moving objects of interest often contain irrelevant direction vectors. It is noteworthy that contrast sensitivity for detection and discrimination of opposite grating directions was largely unaffected by the MT/MST lesion (Pasternak & Merigan 1994, Rudolph & Pasternak 1999), consistent with work in humans that found no deficits in discriminating the direction of high-contrast gratings after transcranial magnetic stimulation (TMS) of MT (Tadin et al. 2011).

The effects of a unilateral MT/MST lesion were examined in animals with controlled fixation (Bisley & Pasternak 2000, Rudolph & Pasternak 1999). This allowed a direct comparison of

motion thresholds for stimuli in the intact and the lesioned hemifield in the same animal, often on the same day. Consistent with earlier findings, the results showed only a transient drop in contrast sensitivity for direction but persistent deficits in direction discrimination of moving gratings and random dots in the presence of noise (Rudolph & Pasternak 1999). Similar susceptibility to noise have been reported for motion-blind patients with extensive extrastriate lesions, whose performance deficits were most pronounced when noise was added to the stimulus (Baker et al. 1991, Rizzo et al. 1995). The relatively preserved sensitivity for direction with pronounced deficits in speed discrimination that has been observed with both bilateral and unilateral MT/MST lesions is consistent with largely unaffected sensitivity for direction but a severe deficit in discriminating speed differences in a human patient with unilateral extrastriate damage (Plant & Nakayama 1993).

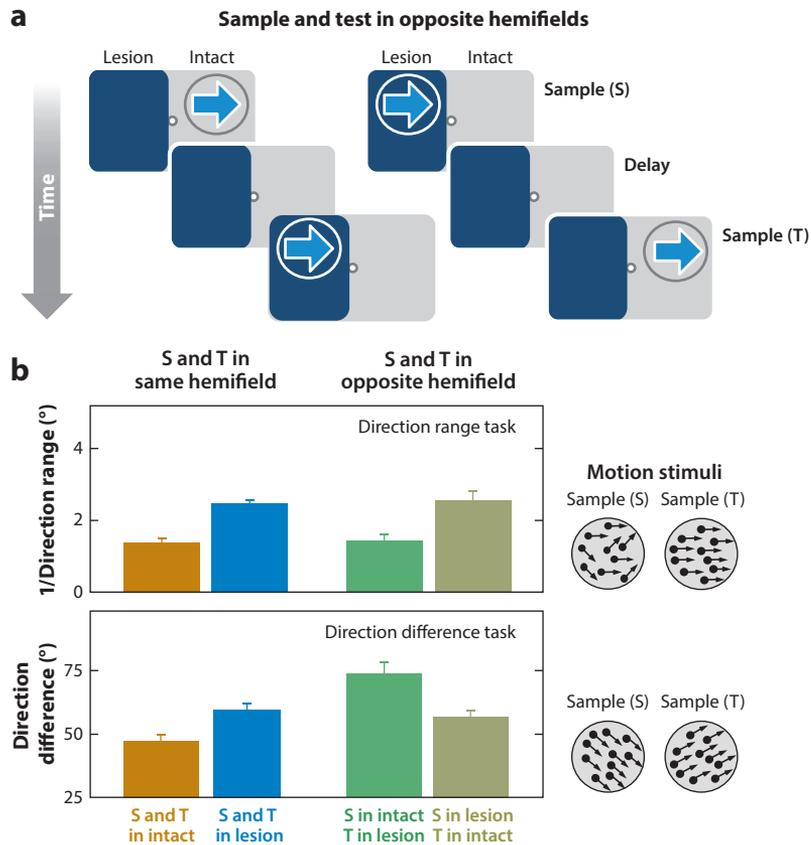
Monkeys with MT/MST lesions also showed a reduction in the precision of direction judgments, particularly at smaller spatial displacements of random dots, similar to that found in strobe-reared cats with greatly reduced direction selectivity (Pasternak & Merigan 1994, Rudolph et al. 1994). This effect suggests an increase in the spatial scale of the residual directional mechanisms, indicative of the change in the sampling strategy in the system with reduced DS mechanisms. The loss in the precision of direction discriminations suggests broader direction tuning functions or increased neuronal variability (Wilson & Gelb 1984).

One striking observation of the effects of MT lesions in monkeys and of PMLS lesions in cats is that selective deficits in motion thresholds often partially or even completely recover with additional training (Newsome et al. 1985, Pasternak & Merigan 1994, Rudolph & Pasternak 1999, Yamasaki & Wurtz 1991). While these studies strongly support functional specialization of areas MT/MST in the monkey and PMLS in the cat for signaling visual motion during behavioral tasks, they also demonstrate that, even in cases of nearly complete removal of these regions, with training, other cortical areas appear to be capable of partially assuming the disrupted functions. Indeed, in humans, there are at least 17 brain areas that are responsive to moving stimuli (Sunaert et al. 1999). Evidence for compensatory reorganization was also provided by a recent study that examined the effects of reversible inactivation of MT on motion discrimination and discovered that inactivation effects depend on training experience and the type of stimuli used during that training (Liu & Pack 2017). The authors of this work suggest that experience with specific motion stimuli can alter the readout during the task, shifting it to earlier or later stages of motion processing.

The idea that training with specific motion stimuli can shift the site of a readout from MT to the stage of processing that matches the task demands is consistent with an earlier finding that the contribution of MT to motion perception depends on the nature of the motion discrimination task (Bisley & Pasternak 2000). In this study, monkeys with unilateral MT/MST lesions compared two random-dot stimuli separated by a delay, sample and test, during two different motion tasks, a direction range task and a direction difference task, each making different demands on the subject.

During the direction range task (**Figure 10a,b**), task difficulty was manipulated by varying the range of local directions only during the sample, while the test moved coherently. In this case, the challenging stage was the sample, since the task required the extraction of the mean direction from a broad distribution of local directions.

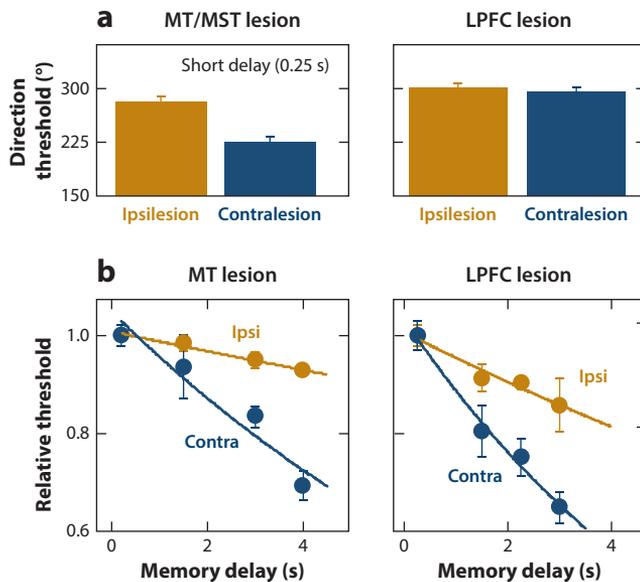
In the direction difference task (**Figure 10b**), the task difficulty was manipulated by changing the difference in direction between the coherently moving sample and test. In this task, the challenging stage was the comparison test, since during this period the monkeys had to compare its direction to the relatively similar direction of the sample (**Figure 10b**). To examine the effect of the MT/MST lesion on different components of each of these tasks, the sample and test were spatially separated; either the sample was placed in the lesioned (contralateral) hemifield and the test in the intact field or the other way around.



**Figure 10**

The effects of a unilateral MT/MST lesion depend on the nature of motion discrimination. (*a*) Behavioral task and the locations of sample and test in intact and lesioned hemifields. (*b*) Thresholds measured during the direction range task (*top*) and during the direction difference task (*bottom*). The left columns show the performance when both sample and test appeared in the lesioned or in the intact hemifields. The right columns show thresholds measured when the sample and test were placed in opposite hemifields. Figure adapted with permission from Bisley & Pasternak (2000).

During the direction range task, the deficit was observed when the sample was placed in the lesioned hemifield. In contrast, during the direction difference task, the deficit was present only when the test was placed in the lesioned hemifield (**Figure 10b**). These results suggest that the role of MT critically depends on the nature of discrimination required by the task. When the task demands integration of local signals, MT appears to play a key role in both processing and remembering such stimuli (**Figure 10**). However, when the motion is coherent, the key contribution of MT/MST to the comparison between the current and remembered motion becomes apparent. Subsequent neurophysiological recordings during the same task revealed that MT neurons integrate local directional vectors of such stimuli (Bisley et al. 2004, Zaksas & Pasternak 2006) and, during the test, carry signals reflecting comparisons between the current and the remembered stimulus (Lui & Pasternak 2011), highlighting the likely participation of these neurons in the memory processes. This role is also supported by the dramatic increase in deficits at longer memory delays produced by a unilateral MT/MST lesion (**Figure 11b**), leading to the hypothesis that



**Figure 11**

Effects of unilateral ibotenic acid lesions of MT/MST and the lateral prefrontal cortex (LPFC) on motion thresholds. (a) Direction range thresholds measured at a short memory delay with stimuli in contralesional and ipsilesional locations. Contralesional deficit was produced by MT/MST but not by LPFC lesions. (b) Effect of memory delay on direction range threshold. Performance across delays was normalized to thresholds measured at the shortest delay (0.25 s). Both MT/MST and LPFC lesions produced similar deterioration of performance with increasing memory delay. Figure adapted with permission from Bisley & Pasternak (2000) and Pasternak et al. (2015).

neurons participating in the processing of visual motion are also involved in its retention (Bisley & Pasternak 2000). The role of MT in retaining the motion stimuli that it processes was also supported by the observation that performance dropped to chance during the direction comparison task when microstimulation of MT was introduced in the middle of the memory delay (Bisley et al. 2001). The dramatic disruption of performance by microstimulation during the memory delay suggests that, during the delay, MT neurons either maintain an active connection with the circuitry involved in storage or are an integral component of that circuitry. Despite the apparent absence of DS activity in late delay, this finding, along with comparison signals during S2, which indicate that MT has access to the remembered direction, and the increased deficits in motion thresholds at longer delays, strongly implicates MT in the retention and retrieval aspects of memory-guided motion comparisons. This is consistent with the finding that applying TMS over human MT during the delay impairs working memory for motion (Zokaei et al. 2013).

### Lesions of the Lateral Prefrontal Cortex Lead to Deficits in Remembering Visual Motion

As in MT, LPFC neurons are active during all stages of the memory-guided direction comparison task (Hussar & Pasternak 2012, 2013; Zaksas & Pasternak 2006). When the task involves complex random-dot stimuli consisting of a broad range of directions, firing rates in the LPFC are affected by direction range, a response property that is likely inherited from MT (Zaksas & Pasternak 2006). Nevertheless, a unilateral LPFC lesion did not affect direction range thresholds at the

shortest memory delay (**Figure 11a**), suggesting that the signals in the LPFC responses to complex motion, unlike those recorded in MT, may not be essential for the process of motion integration (Pasternak et al. 2015).

However, the deficits in direction range thresholds emerged at longer memory delays (Pasternak et al. 2015) (**Figure 11b**). These delay-specific deficits were exclusively contralateral and similar to those produced by the MT/MST lesions (**Figure 11b**), suggesting that both areas contribute to the retention of direction and are likely to actively interact during the task. It is noteworthy that, although both contralateral and ipsilateral motion are represented in the LPFC (Wimmer et al. 2016), the delay-specific threshold deficits were exclusively contralateral. Furthermore, the deficits at longer delays became even more pronounced if the test (S2) appeared at an unpredictable location within the contralateral visual field, requiring rapid shifts of spatial attention.

The contralateral nature of these deficits highlights the importance of the communication between the LPFC and the motion processing neurons, which provide it with activity signaling contralateral motion and are the target of top-down influences arriving from the LPFC. During this interaction, the LPFC is likely to play an important role in accessing the remembered motion during the delay and facilitating its utilization in the comparison process. Studies of patients with lesions of the corresponding region of the prefrontal cortex, the dlPFC, also revealed deficits in working memory attention for contralateral stimuli (Barbey et al. 2013). This observation is consistent with the proposed role of the prefrontal cortex in directing attention to behaviorally relevant stimuli and in manipulating and assisting in selecting appropriate action (Curtis & D'Esposito 2003, Szczepanski & Knight 2014).

In summary, the observed effects of lesions of the areas active during memory-guided discriminations of motion, area MT and the LPFC, provided strong support for the contribution of these areas to perceptual decisions about visual motion. These reciprocally interconnected regions carry both sensory and memory-related signals, and the nature of the deficits that these lesions produce highlights the importance of active interactions between them during behavioral tasks.

## CONCLUDING COMMENTS AND FUTURE DIRECTIONS

In this review, we examine the evidence that links neuronal selectivity for motion direction to perceptual decisions. Parallels in the properties of DS mechanisms revealed by neurophysiological and psychophysical studies, together with strong correlations between neuronal activity and behavioral choices, convincingly show that DS signals are utilized in judgements about motion direction. The necessity of DS signals in perceiving direction, as well as other aspects of motion perception, was demonstrated by psychophysical studies of animals with developmentally induced widespread selective elimination of cortical direction selectivity. Subsequently, the effects of selective lesions of cortical regions with high incidence of DS neurons, notably areas MT and MST in monkeys and PMLS in cats, provided further confirmation of the role that these neurons play in perceptual decisions about visual motion.

While these findings are compelling in showing the behavioral relevance of direction selectivity and the contribution of area MT, they provide only partial understanding of the mechanisms that allow the animal to succeed in the task. One reason for this is that DS neurons are encountered not only in area MT, but also in several other cortical regions that are active during tasks involving visual motion. In addition, DS activity is also present in the PPC during both passive fixation and other, more complex naturalistic tasks such as memory-guided comparisons of directions. While this activity bears similarity to signals recorded in area MT, with which it is interconnected, the LPFC neurons also carry memory-related signals and contribute to further elaboration of

these signals, consistent with task demands. Neurons in the LPFC are also active during motion comparisons, showing motion-selective responses to behaviorally relevant motion, in addition to carrying memory-related signals. While these observations demonstrate the likely participation of these regions in sensory and cognitive aspects of motion comparisons, we know relatively little about how each contributes to performance in real time and the nature of their interactions on a trial by-trial basis. Future studies involving simultaneous multielectrode recordings from all three regions while monkeys perform motion discriminations will undoubtedly bring us closer to understanding the circuitry that underlies perceptual decisions.

As we consider other future directions, a theme emerges that builds on the work described above on memory comparisons. In contrast to our detailed knowledge of how DS signals are used for simple motion direction discriminations, we know a lot less about the roles that these signals play in more complex perceptual and cognitive judgements. While there is evidence that insights derived from simple motion tasks can predict behavioral responses to complex natural stimuli (Burge & Geisler 2015), there are still many unanswered questions about motion processing during natural behavior. For example, most motion research uses stimuli that have a fixed spatial location; we historically have favored spatially fixed stimuli to isolate motion from global changes in position. This is in contrast with the real world, where motion is almost always paired with such global changes in position. Indeed, recent work shows that human motion perception takes advantage of this inherent interdependency of motion and position signals (Kwon et al. 2015). However, as neural recordings are typically done with spatially fixed stimuli confined to single RFs, we know very little about how motion information is extracted from multiple spatially separate RFs. Such studies will be essential for gaining deeper understanding of the way that signals conveyed by the DS neurons during natural behaviors.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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## Errata

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