

# Temporal Frequency Modulates Reaction Time Responses to First-Order and Second-Order Motion

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This study investigated the effect of temporal frequency and modulation depth on reaction times for discriminating the direction of first-order (luminance-defined) and second-order (contrast-defined) motion, equated for visibility using equal multiples of direction-discrimination threshold. Results showed that reaction times were heavily influenced by temporal frequency, especially in the case of second-order motion. At 1 Hz, reaction times were faster for first-order compared with second-order motion. As temporal frequency increased, reaction times for first-order motion decreased slightly, but those for second-order motion decreased more rapidly. At 8 Hz, reaction times for second-order motion were, in many cases, faster than those for first-order motion. Reaction times decreased as stimulus modulation depth increased at approximately the same rate for both motion types. The findings demonstrate that behavioral response latencies to first-order and second-order motion are dependent on specific stimulus parameters and may, in some cases, be shorter in response to second-order compared with first-order motion.

*Keywords:* reaction time, first-order motion, second-order motion, temporal frequency, modulation depth

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Whenever objects move, the patterns of light converging on the retina convey information that can be subdivided into two categories: first-order (variations in luminance) and second-order motion (variations in textural properties such as contrast; Cavanagh & Mather, 1989; Chubb & Sperling, 1988). Examples are shown in Figure 1 and are explained fully in the Method section. Psychophysical and neurophysiological evidence suggests that first-order and second-order motion are encoded separately in the mammalian vision, at least initially (e.g., Baker, 1999; Cavanagh & Mather, 1989; Ledgeway & Hess, 2002; Ledgeway & Hutchinson, 2005; Nishida, Ledgeway & Edwards, 1997; Smith, 1994a; Smith & Ledgeway, 1997, 1998; Sperling & Lu, 1998; Vaina, Cowey, & Kennedy, 1999; Zhou & Baker, 1993).

There are a number of conditions under which the mechanisms responsible for encoding second-order motion exhibit inferior temporal resolution compared with those that encode first-order motion. (a) Temporal sensitivity and acuity for discriminating the direction of second-order motion is poorer (e.g., Hutchinson & Ledgeway, 2006; Schofield, Ledgeway & Hutchinson, 2007; Smith & Ledgeway, 1998). (b) Observers can discriminate first-order motion direction at brief stimulus exposure durations (~26 ms), but cannot discriminate second-order motion direction (contrast modulations of noise and spatial beats) at exposure

durations of  $\leq \sim 200$  ms (Derrington, Badcock, & Henning, 1993; Ledgeway & Hess, 2002). (c) Even when matched for visibility, reaction times for detecting first-order motion onset are faster than those for detecting second-order motion across a range of drift rates (Ellemerberg et al., 2003). This is also true for tasks that require observers to judge the direction of the two classes of motion, at least at moderate temporal frequencies (1 Hz; Ledgeway & Hutchinson, 2008).

There is an assumption that visual response latencies are linked to the complexity of processing required to encode a stimulus. As such, the relative temporal sluggishness of the visual system to second-order motion is attributed to the proposed additional processing (e.g., filter–rectify–filter) that second-order information must undergo before motion energy is extracted (Wilson & Kim, 1994; Yo & Wilson, 1992). Models of motion (e.g., Baker, 1999; Chubb & Sperling, 1988; Wilson, Ferrera, & Yo, 1992) assume that after orientation-selective and spatial frequency-selective filtering, first-order and second-order motion are encoded by two separate streams. First-order local motion energy is extracted using simple Reichardt-like detection units, but for second-order motion, a nonlinear rectification stage follows initial filtering. The rectification stage demodulates the image and turns second-order information into first-order information. This is followed by a second stage of orientation-selective filtering at a different spatial scale before local motion energy is finally extracted. Local first-order and second-order motions are then pooled for spatiotemporal integration.

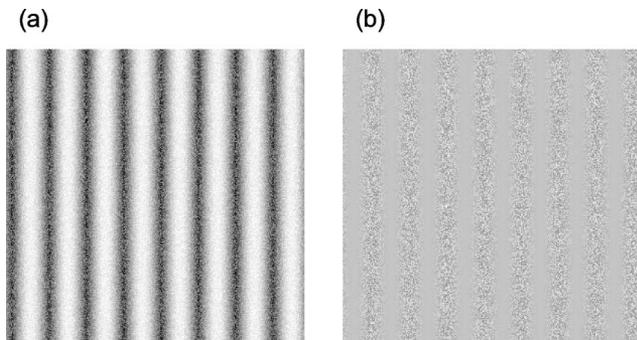
The time taken to encode a stimulus is dependant on specific stimulus parameters. Behavioral response latencies decrease as stimulus amplitude (Ejima & Ohtami, 1987; Ellemerberg et al., 2003; Harwerth & Levi, 1978; Ledgeway & Hutchinson, 2008; Murray & Plainis, 2003; Plainis & Murray, 2000) and drift rate (Burr, Fiorentini

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*Figure 1.* Stimulus examples: (a) first-order (luminance-modulated) and (b) second-order (contrast-modulated) dynamic noise patterns. Luminance-modulated dynamic noise was constructed by adding a drifting sinusoidal luminance grating to a field of spatially two-dimensional random visual noise. Contrast-modulated dynamic noise was constructed by multiplying a drifting sinusoidal luminance grating by the noise field.

& Morrone, 1998; Hohnsbein & Mateeff, 1992; Tynan & Sekuler, 1982) increase and increase as spatial frequency increases (Ludwig, Gilchrist, & McSorley, 2004; Manahilov, Calvert, & Simpson, 2003; Murray & Plainis, 2003). Electrophysiological evidence also shows that increases in stimulus amplitude and temporal frequency lead to decreased response latencies. These effects occur throughout the visual processing hierarchy, from the retina to visual cortex across a range of species including turtles, flies, cats, and monkeys (e.g., Baylor, Hodgkin, & Lamb, 1974; Bolz, Rosner, & Wassle, 1982; Carandini, Heeger, & Movshon, 1997; Maunsell et al., 1999; Maunsell & Gibson, 1992; Raiguel, Xiao, Marcar, & Orban, 1999; Warzecha & Egelhaaf, 2000).

A number of parameters have been shown to differentially affect response latencies to first-order and second-order patterns. Manahilov et al. (2003) measured reaction times at near-threshold contrast for detecting static stimuli. At 0.5 c/deg, reaction times were slower to second-order than to first-order stimuli, but at 7 c/deg, they were similar for the two patterns. Variable reaction time responses have also been noted for color. Burr et al. (1998) measured simple reaction times to the onset of moving luminance and chromatic gratings as a function of drift rate and contrast. Reaction times to luminance gratings were faster than to chromatic gratings, but the magnitude of the difference depended on contrast and speed. At low speeds ( $\leq \sim 1$  deg/s), reaction times were faster for luminance. As speed increased, the difference was less pronounced. Reaction times also decreased as contrast increased for low (0.25 deg/s) but not for high speeds (10 deg/s).

The effects of stimulus drift rate on behavioral response latencies for judging first-order and second-order motion direction are currently unknown. The present study investigated the effect of temporal frequency on reaction times for discriminating the direction of first-order (luminance-defined) and second-order (contrast-defined) motion.

## Method

### Participants

Four participants, CVH (an author), SH, AM, and DPM, acted as observers in the study. All had normal or corrected-to-normal visual acuity.

### Apparatus and Stimuli

Stimuli were presented using a Macintosh G4 and a Sony Trinitron monitor with software written in the C programming language. The number of luminance intensity levels available was increased from 8 to 14 bits using a Bits++ attenuator (Cambridge Research Systems, Kent, England). Mean display luminance was 58.4 cd/m<sup>2</sup>. Images were viewed binocularly and in darkness at a distance of 139 cm. One screen pixel subtended 0.94 arc min, resulting in a display subtending 8 degrees vertically and horizontally. To ensure that second-order stimuli did not contain luminance artifacts, the monitor was gamma corrected using a photometer, look-up-tables, and psychophysically (e.g., Gurnsey, Fleet, & Potechin, 1998; Ledgeway & Smith, 1994; Scott-Samuel & Georgeson, 1999). A control experiment confirmed that the second-order stimuli were not contaminated by such artifacts (see Supplemental Materials, Figure 4).

Stimuli (Figure 1) were 1 c/deg first-order (luminance-modulated dynamic noise) or second-order (contrast-modulated dynamic noise) motion, drifting at either 1, 2, 4, or 8 Hz. Luminance-modulated dynamic noise was constructed by adding a drifting sinusoidal luminance grating to a field of spatially two-dimensional random visual noise (Michelson contrast: 0.25). Contrast-modulated dynamic noise was constructed by multiplying a luminance grating by the noise field.

The strength or modulation depth of each stimulus was determined by the following general equation:

$$\text{Modulation depth} = (A_{\max} - A_{\min}) / (A_{\max} + A_{\min}), \quad (1)$$

where  $A_{\max}$  and  $A_{\min}$  represent the maximum and minimum values of each stimulus type, respectively. For luminance-modulated dynamic noise,  $A_{\max}$  and  $A_{\min}$  refer to the maximum and the minimum luminances, respectively, averaged over adjacent noise elements with opposite polarity in the image. For contrast-modulated dynamic noise,  $A_{\max}$  and  $A_{\min}$  refer to the maximum and minimum local Michelson contrasts in the image computed over adjacent noise elements with opposite polarity, respectively.

### Procedure

**Direction-discrimination thresholds.** Direction-discrimination thresholds were measured for each motion type at each temporal frequency. A single-interval forced-choice task was employed. Trials were self-paced and self-initiated. On each trial, observers were presented with a fixation cross, after which the motion stimulus was presented for 500 ms. The task was to judge motion direction (either leftward or rightward chosen with equal probability). Grating modulation depth varied from trial to trial according to an adaptive 1-up 3-down staircase designed to converge on the modulation depth corresponding to 79.4% correct performance. At the beginning of each run of trials, the modulation depth was set to a suprathreshold level (typically  $\sim 6$  dB above threshold). The initial staircase step size was chosen to be half this value. On subsequent reversals, the step size was halved, and testing terminated after 16 reversals. Threshold estimates were taken as the mean of the last four staircase reversals. Each observer completed a minimum of six runs of trials for each condition. The order of testing was randomized. The mean threshold and *SEM* were calculated for each condition.

Thresholds were used to equate each motion pattern in terms of visibility by presenting them at equal multiples of threshold, which has become conventional practice in the literature. Although this assumes that the two motion types will elicit the same effective amplitude of neural signal when at the same threshold multiple, there is good evidence that this is not unreasonable (e.g., see Culham et al., 1998; Smith, 1994b). For example, the perceived speeds of first-order and second-order motion are identical when their physical speeds are matched, but only when they are presented at the same multiple of direction-discrimination threshold (Ledgeway & Smith, 1995).

**Reaction times.** Choice reaction times for discriminating the direction of each pattern were measured as a function of stimulus modulation depth using a fixed set of modulation depth values (expressed as multiples of direction-discrimination threshold). Each modulation depth was presented 25 times in a random order within each run of trials. Each observer completed a minimum of eight runs per condition (200 trials per point), and order of testing was randomized. Mean reaction times (calculated conventionally from correct responses only) were computed *within* each run. These means were used to calculate the grand mean and SEM across runs. Similar to previous studies (e.g., Ledgeway & Hutchinson, 2008; Murray & Plainis, 2003; Plainis & Murray, 2000), only reaction times within a particular range were included in the analysis. Those that were less than 100 ms or greater than 2,000 ms were excluded and were subsequently retested by randomizing the order of trials within that run (see Ledgeway & Hutchinson, 2008, for details).

## Results

In agreement with previous studies (e.g., Hutchinson & Ledgeway, 2006; Schofield et al., 2007; Smith, Hess, & Baker, 1994), thresholds for luminance-defined motion were markedly lower than those for contrast-defined motion (see Figure 2a). The modulation depths of the motion patterns were set at twice the direction-discrimination threshold, and reaction times were measured for discriminating motion direction as a function of stimulus temporal frequency (see Figure 2b).<sup>1</sup> At 1 Hz, reaction times for judging first-order motion direction were faster than those for second-order motion. As temporal frequency increased beyond 2 Hz, reaction times to second-order motion decreased, whereas those for first-order motion remained reasonably flat, exhibiting only a slight improvement in performance as temporal frequency increased. At 8 Hz, reaction times were typically faster to second-order motion than to first-order motion.

To further quantify the effects of temporal frequency on response latencies, reaction times were measured as a function of stimulus modulation depth. Figure 3 shows reaction times plotted as a function of modulation depth (expressed as multiples of direction-discrimination threshold) at stimulus temporal frequencies of 1, 2, 4, and 8 Hz. Similar to previous studies (e.g., Ledgeway & Hutchinson, 2008; Murray & Plainis, 2003; Plainis & Murray, 2000), the data were fit with the following equation:

$$y = a + k/m, \quad (2)$$

where  $a$  is the asymptotic reaction time, and  $k$  is the parameter describing the rate of decrease in reaction times with increasing stimulus modulation depth ( $m$ ). A nonparametric (bias corrected

and accelerated) bootstrapping technique was used to estimate 68% confidence intervals for  $a$  and  $k$  (as approximations to the standard error around each parameter). 10,000 bootstrapped replications were made of each fitted function, and the resulting distributions were used to generate a confidence interval for each parameter, without assuming a Gaussian distribution for the raw data or the residuals (Efron & Tibshirani, 1993). The values of  $a$ ,  $k$ , and  $R^2$  are given in Table 1.

There was good agreement between observers in that as stimulus modulation depth increased, reaction times decreased. At 1 Hz, reaction times for judging first-order motion direction were typically faster than for second-order motion when presented at the same multiple of threshold (see Figure 3a). For a given threshold multiple, the relative differences in reaction times for the two types of motion were such that they resulted in almost parallel curve fits. At 2 Hz, the degree to which reaction times for judging first-order motion direction were superior to those for judging second-order motion direction was less pronounced (see Figure 3b), a trend marked by an overall decrease in reaction times for second-order motion. Again, curve fits exhibited comparable fall-offs. At 4 Hz, reaction times were similar and in some cases faster for second-order motion (see Figure 3c). At 8 Hz, reaction times were markedly faster for second-order motion than for first-order of motion, and slopes were shallower for both than at lower temporal frequencies (Figure 3d).

## Discussion

In agreement with previous studies (e.g., Baylor et al., 1974; Bolz et al., 1982; Burr et al., 1998; Carandini et al., 1997; Ejima & Ohtami, 1987; Ellemberg et al., 2003; Harwerth & Levi, 1978; Hohsbein & Mateeff, 1992; Ledgeway & Hutchinson, 2008; Maunsell et al., 1999; Maunsell & Gibson, 1992; Murray & Plainis, 2003; Plainis & Murray, 2000; Raiguel et al., 1999; Tynan & Sekuler, 1982; Warzecha & Egelhaaf, 2000), this study showed that reaction times for discriminating motion direction decrease as stimulus temporal frequency and modulation depth (amplitude) increase. At 1 Hz, reaction times were faster for first-order than for second-order motion. As temporal frequency increased, reaction times for first-order motion decreased slightly. In comparison, those for second-order motion decreased rapidly, and at 8 Hz were actually faster than for first-order motion. Reaction times decreased as a function of modulation depth and, irrespective of which motion type elicited faster responding, did so at approximately the same rate.

That reaction times for discriminating first-order (luminance-defined) and second-order (contrast-defined) motion direction varied with temporal frequency is in agreement with previous findings for luminance-defined and chromatically defined motion. Burr et al. (1998) found that at slow drift rates (0.25 Hz), reaction times to the onset of chromatically defined motion were slower than those to equivalent luminance-defined motion, but at higher drift rates (10 Hz), reaction times were similar. Also in agreement with Burr et al., we found that reaction time slopes (i.e., the rate at which

<sup>1</sup> The highest stimulus modulation depth possible was limited by absolute sensitivity to contrast-modulated dynamic noise at high temporal frequencies (i.e., thresholds were close to unity at 8 Hz; see Figure 2a).

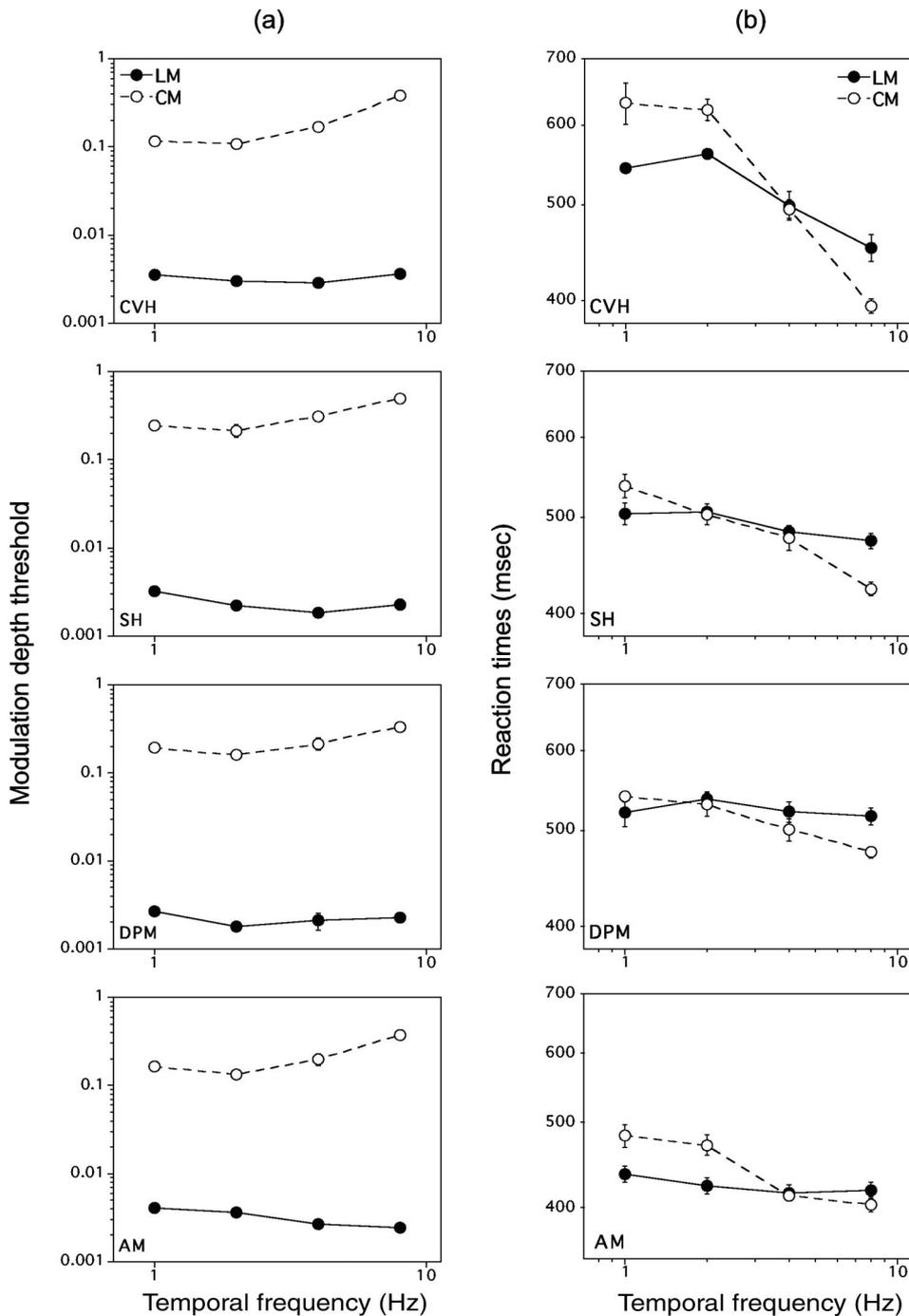


Figure 2. (a) Direction discrimination thresholds (corresponding to 79.5% correct) for first-order and second-order motion as a function of drift temporal frequency (Hz). (b) Reaction times for discriminating the drift direction of suprathreshold first-order and second-order motion as a function of temporal frequency. Motion patterns were presented at modulation depths that were twice the direction-discrimination threshold. Error bars represent  $\pm 1$  SEM.

reaction times decreased as contrast increased) became shallower at faster stimulus drift rates. The present results are not in agreement with those of Elleberg et al. (2003), however. In the present study, reaction times for first-order and second-order motion con-

verged at temporal frequencies  $\geq 4$  Hz. Using 1 c/deg patterns drifting at 6 Hz that had been equated for stimulus visibility, Elleberg et al. found that reaction times were slower for second-order than for first-order motion. Whereas the present study mea-

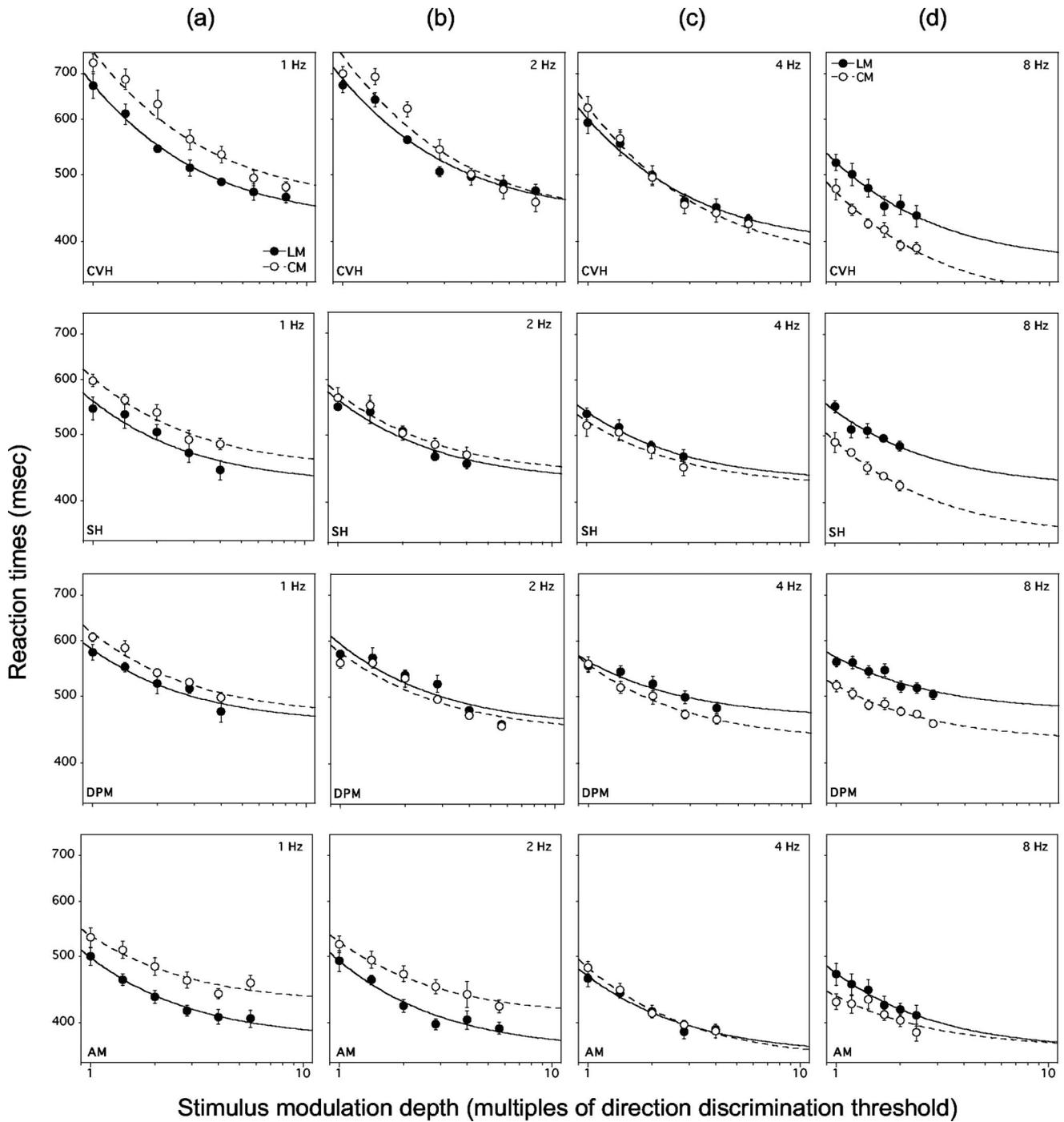


Figure 3. Reaction times for discriminating the drift direction of first-order and second-order motion as a function of stimulus modulation depth (expressed as multiples of the direction-discrimination threshold) at (a) 1, (b) 2, (c) 4, and (d) 8 Hz. Error bars represent  $\pm 1$  SEM.

sured reaction times for discriminating stimulus direction (choice reaction times), Ellemberg et al. measured reaction times to motion onset (simple reaction times). As such, our findings may be specific to direction-selective first-order and second-order motion mechanisms rather than mechanisms responsible for detecting a temporal change.

Despite being differentially affected by temporal frequency changes, at given temporal frequency, reaction times for both types of motion exhibited a comparable dependence on stimulus modulation depth (i.e., the shapes of the functions were similar for both types of motion). The overlap of the 68% confidence intervals of the  $k$ -parameter for the majority (10/16) of the curve fits, derived

Table 1  
Curve Fit Parameters and  $R^2$  Values for Each Observer for First-Order and Second-Order Motion

Observer	Temporal frequency (Hz)	First-order motion			Second-order motion		
		$a$ [68% CI]	$k$ [68% CI]	$R^2$	$a$ [68% CI]	$k$ [68% CI]	$R^2$
CVH	1	428.21 [425.1, 432.37]	245.65 [239.75, 253.4]	.99	456.51 [444.38, 470.67]	295.1 [267.71, 317.66]	.96
	2	437.17 [428.84, 448.79]	249.47 [230.5, 266.59]	.96	433.24 [416.65, 455.91]	307.67 [270.52, 342.49]	.92
	4	394.48 [389.2, 401.22]	206.89 [196.19, 216.84]	.99	373.93 [367.6, 379.98]	252.74 [242.04, 263.92]	.99
	8	372.64 [363.71, 378.11]	148.06 [137.58, 157.68]	.97	326.32 [320.07, 332.67]	145.41 [136.63, 155.08]	.98
SH	1	423.11 [409.6, 436.61]	135.76 [112.05, 156.76]	.9	445.8 [438.14, 455.09]	158.13 [144.04, 171.22]	.97
	2	427.18 [415.9, 441.87]	134.11 [111.49, 154.61]	.9	437.36 [432.04, 451.79]	136.18 [120.98, 149.93]	.94
	4	427.9 [425.4, 436.02]	112.57 [103.8, 119.52]	.98	421.23 [411.72, 434.14]	102.69 [84.1, 121.63]	.90
	8	420.57 [401.95, 428.3]	122.21 [106.6, 140.33]	.91	357.53 [354.28, 362.13]	132.95 [127.54, 137.76]	.99
DPM	1	455.9 [446.11, 464.11]	127 [112.91, 141.5]	.94	467.44 [460.24, 477.62]	148.64 [135.58, 162.81]	.96
	2	451.62 [436.96, 466.43]	142.9 [113.76, 166.14]	.85	443.96 [431.58, 458.4]	134.55 [109.59, 157.12]	.86
	4	465.32 [457.08, 473.9]	95.93 [80.4, 109.06]	.92	431.55 [427.78, 436.55]	123.74 [117.29, 131.17]	.98
	8	475.08 [467.41, 485.22]	93.33 [79.82, 106.04]	.88	430.49 [425.05, 434.7]	86.52 [79.39, 93.9]	.96
AM	1	379.27 [377.12, 382.4]	118.11 [113.9, 123.12]	.99	426.89 [420.34, 433.59]	108.42 [95.77, 119.35]	.94
	2	365.79 [359.21, 371.11]	126.1 [113.77, 135.16]	.96	409.15 [405.17, 412.28]	115 [107.55, 120.37]	.98
	4	360.12 [352.8, 365.6]	107.14 [95.35, 116.31]	.96	354.07 [351.11, 357.38]	126.84 [120.47, 131.11]	.99
	8	365.3 [361.8, 369.92]	106.52 [100.65, 111.91]	.98	367.67 [356.31, 380.08]	69.65 [53.45, 87.07]	.74

Note. The rate of change in reaction times as a function of stimulus modulation depth is well described by Equation 2. The 68% confidence intervals were estimated from 10,000 iterations of a nonparametric bootstrap procedure. See text for details.

from Equation 2 and shown in Table 1, for the two types of motion supports this conclusion.<sup>2</sup> If, as suggested by Murray and Plainis (2003), reaction times versus modulation depth functions represent contrast gain of mechanisms in the visual system, our findings suggest that the mechanisms that encode luminance-defined and contrast-defined motion operate using similar gain producing a similar change in response per unit change in contrast (threshold multiple). Although equating stimuli in terms of multiples of threshold introduces the possibility of multiplicative error, as accurate matching depends critically on accurate threshold measurement, we are confident this cannot account for the our results for a number of reasons: (a) Individual threshold measurements exhibited little variability across different runs of trials (indicated by the error bars in Figure 2a) and observers and are directly comparable to those reported previously (Hutchinson & Ledgeway, 2006; Ledgeway & Hutchinson, 2005, 2008; Schofield et al., 2007); (b) reaction times decreased at similar rates for both types of motion as stimulus modulation depth increased would not be expected if the stimuli were erroneously presented at different multiples of threshold; and (c) the differences in reaction times for first-order and second-order motion patterns (e.g., Figure 3d) were sufficiently large that they were unlikely to have resulted from a mismatch in stimulus visibility.

For luminance, there is consensus on the existence of two (or perhaps three) channels, broadly tuned for temporal frequency. It has been suggested that the visual system employs these channels separately for encoding slow and fast temporal frequencies or speeds (e.g., Anderson & Burr, 1985; Hammett & Smith, 1992; Hess & Snowden, 1992; Kulikowski & Tolhurst, 1973; Mandler & Makous, 1984). There is also evidence that second-order motion perception may be particularly affected by changes in temporal frequency. It has been posited that first-order and second-order motion are encoded by separate mechanisms at low temporal frequencies, but they are encoded by a common mechanism at higher temporal frequencies (e.g., Allard & Faubert, 2006; Burr et

al., 1998; Gegenfurtner & Hawken, 1996; Stoner & Albright, 1992). First-order and second-order gratings begin to form a coherently moving plaid at around 3 Hz (Stoner & Albright, 1992), and velocity gains are different for luminance, chromatic, and amplitude-modulated (second-order) stimuli at low temporal frequencies, but they are similar at  $\geq 4$  Hz (Gegenfurtner & Hawken, 1996). It has also been proposed that luminance-defined and chromatically defined motion are encoded separately at low temporal frequencies but are encoded by a single mechanism at high ( $\geq \sim 4$  Hz) temporal frequencies (Burr et al., 1998; Gegenfurtner & Hawken, 1996). The operation of a common mechanism at high temporal frequencies is conducive with reaction time results such as those of Burr et al. (1998), but this does not fully explain the current finding that reaction times were faster for second-order motion at higher temporal frequencies. Although the reaction time responses in the present study did show more contrast-dependence at low temporal frequencies, which may fit with the notion of separate motion-detecting mechanisms at low and high temporal frequencies, for a given temporal frequency the results for first-order and second-order motion were qualitatively similar. This does not support the notion that first-order and second-order motion are encoded separately at low temporal frequencies but are encoded by the same mechanisms at higher temporal frequencies. However, it is worth noting that the lowest temporal frequency employed in the present study was 1 Hz.

The findings of the current study suggest that two separable mechanisms may mediate first-order and second-order motion processing. Neuropsychological case studies also support this.

<sup>2</sup> If two standard error bars overlap (equivalent to overlap of the 68% confidence intervals) one can conclude that the difference is not statistically significant, but the converse is not true. That is, even if there is no overlap the difference may not be statistically significant (e.g. Schenker & Gentleman, 2001; Payton, Greenstone & Schenker, 2003).

Vaina and colleagues have presented evidence from a number of neuropsychological patients for a double dissociation between first-order and second-order motion processing. Patient RA (Vaina & Cowey, 1996; Vaina et al., 1999) suffered a unilateral lesion close to the medial surface of the occipital lobe, just above the calcarine fissure including parts of extrastriate cortex, particularly areas V2 and V3. RA's lesion also involved white matter and could therefore have disrupted connections between V1 and the dorsal set of visual areas. Patient JV (Vaina & Soloviev, 2004) suffered small unilateral infarcts centered on the ventral occipital region, in particular, in areas V2 and VP. Both patients demonstrated a selective impairment on tests of first-order motion but intact performance on tests of second-order motion. Patient FD (Vaina et al., 1999; Vaina, Makris, Kennedy, & Cowey, 1998) suffered a small, shallow cortical lesion in his left hemisphere, just dorsal to area MT. Patient TF (Vaina, Soloviev, Bienfang, & Cowey, 2000) suffered small unilateral infarcts centered in the dorsal regions on areas V2 and V3. FD demonstrated a selective deficit for second-order motion but showed normal performance on tests involving first-order motion. Patient TF performed at a very impaired level on second-order motion tasks but showed normal performance on first-order motion tasks.

Faster reaction times for second-order motion are at odds with the notion that second-order motion perception is necessarily delayed compared with first-order motion perception and may represent some important functional role. Second-order motion rarely occurs in isolation in the world but rather occurs in conjunction with first-order motion. Johnson and Baker (2004) have simulated the responses of spatial filters, which mimic neurons in the mammalian visual system, to natural images containing first-order and second-order information. They found evidence for a structured relationship between the first-order and second-order response statistics within natural scenes and proposed that second-order image statistics convey additional information that augments first-order information. It has also been suggested that second-order information is useful for disambiguating shadows; handling transparency; breaking camouflage; and detecting moving, texture-covered objects whose constituent texture motion is irrelevant, such as pouncing predators or fleeing prey (Baker, 1999; Daugman & Downing, 1995). Therefore, it makes sense that second-order motion information may be most important in situations where objects are moving quickly (e.g., a predator). In such instances, it would be advantageous for the visual system to respond rapidly to second-order motion. That second-order motion perception can be faster than first-order motion perception is certainly an intriguing and somewhat unexpected finding, one that warrants further study. By investigating other instances where second-order motion perception is as good as, or better than, first-order motion perception may help illuminate the functional importance of its role in visual processing.

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