Local Motion Pooling Is Continuous, Global Motion Perception Is Discrete

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Perceiving the motion of an object is thought to involve two stages: Local motion energy is measured at each point in space, and these signals are then pooled across space to build coherent global motion. There are several theories of how local-to-global pooling occurs, but they all predict that global motion perception is a continuous process, such that increasing the strength of motion energy should gradually increase the precision of perceived motion directions. We test this prediction against the alternative that global motion perception is discrete: Motion is either perceived with high precision or fails to be perceived altogether. Data from human observers provides clear evidence that, whereas pooling local motion energy is continuous, the segmentation of local signals into coherent global motion patterns is a discrete process. This result adds motion perception to the growing list of processes that exhibit evidence of all-or-none visual awareness.

Public Significance Statement
Visual perception requires that objects are isolated from other objects, a process that is accomplished in part by analyzing motion energy across space. For example, although individual parts of a running dog may be moving in many directions at any moment, all of them share motion energy in the direction he's running, which helps the visual system to build the perception of a coherently moving object. This global motion process develops early in life, and deficits in it have been identified in disorders including autism, dyslexia, and schizophrenia. Whereas current theories of global motion perception predict that motion perception is analog, taking on any value from weak to strong, here we show that it is discrete: coherent motion is either perceived nearly perfectly, or not at all. This finding suggests that current models of global motion perception, and theories of why deficits in this process occur, may require substantial revision.

A fundamental goal in the study of perception is to understand how physical stimuli map on to conscious awareness. Early researchers including Leibniz (see Boring, 1950) and Fechner (1860) proposed a perceptual threshold that causes perception to be discrete: a weak stimulus is either experienced completely or not at all (see Rouder & Morey, 2009). This discrete theory was later formalized into mathematical models (Blackwell, 1953; Stevens, 1972), which have been crucial for theory development across many domains. However, the idea of a perceptual threshold was largely discarded in favor of continuous models with the advent of signal detection theory (Green & Swets, 1966), which

assumes that all stimulation leads to some perceptual strength that increases with increasing signal. Many contemporary models of perception follow this continuous framework (Knill & Richards, 1996; Ma, 2010). However, the question of whether mental processes are continuous or discrete has become the focus of recent work, which includes evidence for discrete perception (Swagman et al., 2015), discrete working memory (Rouder et al., 2008; Zhang & Luck, 2008), and discrete long-term memory (Province & Rouder, 2012). Determining whether conscious experiences are continuous or discrete is a critical step toward understanding the processes that underlie perceptual and cognitive functions.

Theories of visual processing have been especially rooted in the assumption that perception is continuous. For example, a crucial step in vision involves determining how objects are moving through space. Most theories of how motion perception is achieved assume that motion energy is first measured at each point within the visual field, and that this *local motion* information is represented in early cortical visual areas (Hubel & Wiesel, 1968). However, this noisy local motion energy must then be used to somehow identify the overall motion directions of coherently moving objects. Such *global motion* directions are thought to be computed in midlevel cortical visual areas (Britten et al., 1992) by

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pooling local motion signals across space within an object (Heeger, 1987; van Santen & Sperling, 1984). There have been several proposals regarding how this pooling occurs, (see Webb et al., 2007), but critically, all such pooling models predict that motion perception is continuous: the accuracy with which local signals can be pooled to generate a global signal should gradually increase with increasing global motion energy. Here we test this prediction against the alternative possibility that global motion perception is a discrete, all-or-none process whereby you either see global motion precisely or fail to see global motion altogether.

In typical studies of global motion perception, participants view a field of moving dots in which most dots move in random directions, while some move in a single coherent direction (see Figure 1A). The number of coherently moving dots determines the strength of the global motion signal, and the global direction can be identified above chance even when only 5% of the dots are moving coherently (Scase et al., 1996). Increasing coherence leads to better motion identification performance, which is typically measured as accuracy in a discrimination task (e.g., leftward vs. rightward motion). Here we measure performance by instead asking participants to report their perceived global motion direction, which allows us to compare theories of how performance varies with global motion coherence. If global motion perception is continuous as predicted by local-pooling theories, then increasing coherence should produce gradual increases in the precision of motion responses, as pooling more signal dots produces more precise representations (see Figure 2B). Alternatively, if

global motion perception is discrete, then responses will arise from a mixture of pure guesses when motion perception fails and highly accurate responses when it is successful (see Figure 2A). Moreover, increasing coherence should only affect the probability of successful motion perception, whereas the precision of responses on successful trials should remain constant (see Figure 2C). These predictions of continuous verses discrete motion perception were tested by constructing formal models of motion identification responses and comparing their ability to account for various stimulus conditions across five experiments. The results reveal a striking dissociation: motion perception is discrete when it is accomplished by segmenting local motion energy into signal and noise but is continuous when local motion directions are pooled to derive an average direction.

## Experiments 1a and 1b

Method

Participants

Thirty-one adults participated Experiment 1a (22 women, *Mdn* age = 19), and thirty participated in Experiment 1b (17 women, *Mdn* age = 19), in exchange for course credit. Simulation studies suggest that this sample size provides for highly reliable model recovery (see Table S1 in the online supplemental material). One participant in Experiment 1a did not finish the experiment, and for

Figure 1

Stimuli and Design for Experiments 1 Through 3
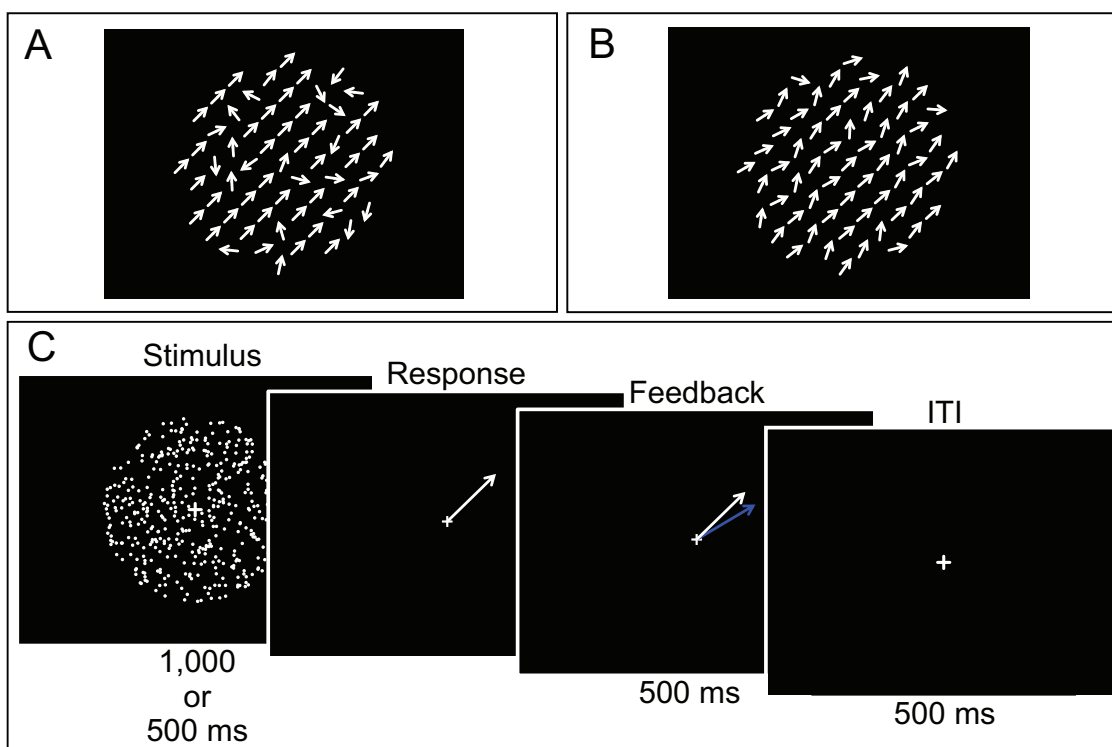
Note. Transparent motion stimuli (A) are composed of noise dots with random directions and some proportion of signal dots that all move in the same direction (termed coherence). Gaussian motion stimuli (B) are composed of dots with motion directions sampled from a circular Gaussian distribution, and coherence is defined by the standard deviation of that distribution. The trial structure (C) was similar for all experiments. See the online article for the color version of this figure.

Figure 2
Model Predictions
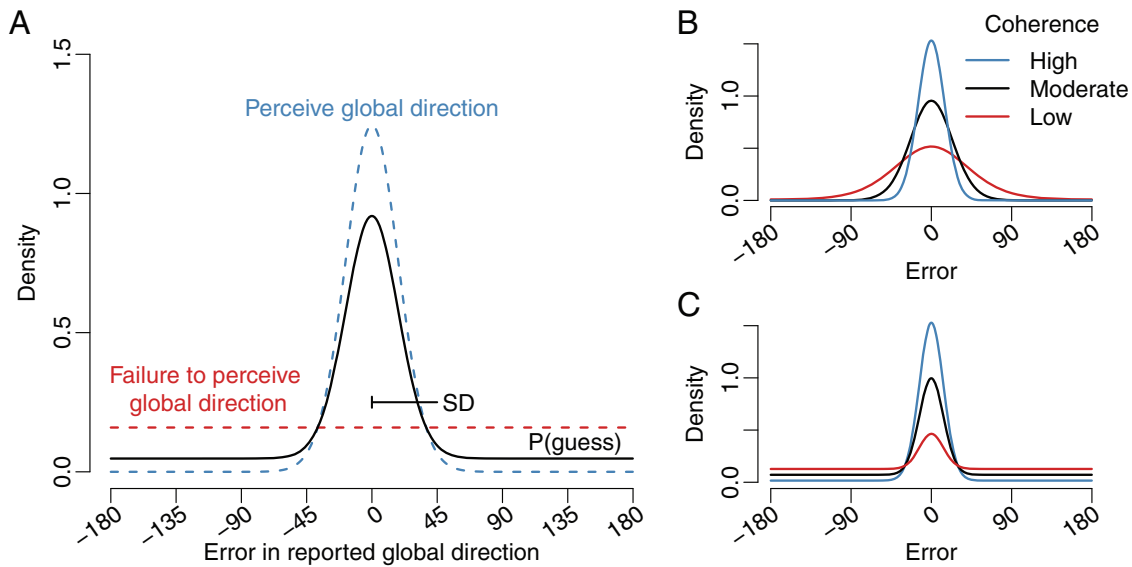
Note. According to the mixture model (A), when the global motion direction is perceived response errors follow a von Mises distribution centered at zero, with standard deviation (*SD*) that measures the precision of these reports. When participants fail to perceive the global motion direction entirely, response errors follow a uniform distribution. When averaged over trials, response errors follow a mixture of these two distributions (solid line). The continuous model predicts that only *SD* should vary with manipulations of motion coherence (B), whereas the discrete model predicts that only the probability of being in the guessing state should vary with coherence level (C). See the online article for the color version of this figure.

four participants in Experiment 1a and four in Experiment 1b, a pure-guessing model (uniform distribution) fit response errors better (ΔBIC > 3) than a model that also allowed for target responses, suggesting that they did not follow task instructions. Analyses were conducted on the remaining 26 participants in Experiment 1a and 26 in Experiment 1b, respectively. All studies were approved by the Mississippi State University Institutional Review Board.

Stimuli

The Psychophysical Toolbox (Kleiner et al., 2007) for Octave (Eaton et al., 2020) running on the Linux operating system was used to display stimuli on 24-in. LCD monitors (BenQ, Model Number XL2420-B). Motion stimuli comprised small round white dots spanning approximately .1° visual angle (created using antialiasing). Dots were presented on a black background within a circular aperture spanning 1° to 9° visual angle. Dots had an average density of 3 dots/degree² and moved at a rate of 5°/s. Dots had a limited lifetime, each presented for 200 ms (with random initial lifetime) before being repositioned to a new random location. Dots that reached the aperture boundary were repositioned to the opposite side of the aperture. Each dot followed a linear trajectory, with motion direction that could be one of two types: signal dots all moved in the same global motion direction, whereas noise dots moved in random, uniformly distributed directions (see Figure 1A). This type of motion stimulus has been referred to as "transparent" motion (Schütz et al., 2010), because the signal dots appear to form their own moving surface. Global motion coherence is defined as

the percentage of dots assigned as signal, such that higher coherence yields a higher global motion signal to noise ratio.

Procedure

The structure of a trial is shown in Figure 1C. A white cross (.4°) was presented at the center of the screen throughout the experiment, and participants were asked to maintain fixation throughout the experiment. Motion stimuli were displayed for 1,000 ms (Experiment 1a) or 500 ms (Experiment 1b). Following the stimulus, an arrow (3.5°) appeared, emanating from fixation with a random orientation. Participants used a computer mouse to orient the arrow in the global motion direction of the stimulus and clicked the mouse button to confirm their response. The response period (median response time = 1.80 s) effectively imposes a brief interval during which participants must retain the motion direction in working memory. However, any effect of this memory requirement is likely to be small, as single feature values can be retained in memory for extended periods of time with little loss of precision (Magnussen et al., 1991). Moreover, if there is any loss of precision due to the memory interval, the effect should be similar across coherence conditions, such that any effect of coherence on performance does not reflect the memory requirement. Following confirmation of their response, a blue arrow pointing in the true global direction was presented for 500 ms to provide performance feedback. The next trial began after a 500-ms intertrial interval, and a break was provided every 80 trials.

Participants completed 20 practice trials, followed by 800 experimental trials. On each trial the global motion direction was randomly sampled from a uniform distribution (0° to 360°).

Coherence levels (10%, 15%, 22%, 33%, and 50%) were sampled with even frequency and randomly ordered across trials, providing 160 trials for each coherence condition. Pilot studies were conducted to identify coherence levels that resulted in highly accurate motion identification performance, and those that resulted in very poor performance, while avoiding ceiling and floor effects. These values served as coherence for the easiest and most difficult experimental conditions, respectively, and intermediate levels were evenly spaced on a logarithmic scale between them.

Mixture Model Analysis

Motion identification errors were characterized using the Zhang and Luck (2008) two-component mixture model. This model was initially developed for characterizing working memory performance, but has since been applied in many domains including motion perception (Bae & Luck, 2019), although not to identify signatures of continuous verses discrete motion perception. According to this mixture model the error in identifying motion direction on each trial arises from one of two processes (see Figure 2A). If the global motion direction is perceived successfully, the report error arises from a von Mises distribution (similar to the circular normal) centered at zero with a standard deviation that reflects the precision of responses. Alternatively, if the motion direction fails to be perceived altogether, response errors are guesses that necessarily follow a uniform distribution due to the circular nature of the motion direction space. Fitting this model to response errors provides an estimate of the rate of guessing (g) and the amount of noise in responses on nonguess trials (SD). Whereas continuous models predict that manipulations of motion coherence should primarily affect standard deviation (see Figure 2B), discrete models predict that only the rate of guessing should vary with motion coherence (see Figure 2C).

The mixture model was first fit separately to each participant and each coherence level condition using standard maximum likelihood estimation procedures (see model fitting in the online supplemental material). This approach provides estimates of guess rate (g) and response variability (SD) for each coherence condition, and the critical question is whether these parameters change across coherence levels. Although it seems reasonable to address this question by performing significance testing on the parameter estimates resulting from this full model, simulation studies suggest that this approach is seriously flawed (see model recovery in the online supplemental material). To more rigorously assess whether guessing and standard deviation vary with motion coherence, restricted models that force one or both parameters to be fixed across conditions were also fit to each participant's data. The Bayesian information criterion (BIC; Schwarz, 1978) was used to compare these restricted models with each other, and to the full model in which both g and SD are free to vary. For example, comparing the full model with one where the guess rate is restricted across conditions provides for an omnibus test of whether guess rates vary across two or more conditions. With five coherence levels the full model has 10 free parameters, both the fixed SD and fixed guess rate models have six free parameters, and the null model that forces both SD and g to be fixed across coherence levels has two parameters. BIC penalizes model complexity based on the number of parameters in a manner motivated by Bayesian inference and provides for reliable model recovery (see Table S1 in the online

supplemental material). However, the results are similar if models are compared using Akaike's information criterion (AIC; Akaike, 1973; see Table S2 in the online supplemental material), with any exceptions noted in the following text.

Results

Figure 3A shows error distributions for each of the five coherence conditions in Experiment 1a. When coherence was high (50%, right), most response errors were tightly centered around zero, indicating that participants were often highly accurate in identifying the true motion direction. However, there are also trials on which the errors were extremely large and uniformly distributed, indicated by the long flat tails in the error distribution. Moreover, as coherence is lowered the central part of the distribution does not appear to widen, but rather, there are more and more extremely large errors. In line with this pattern, fitting the full mixture model separately to each condition suggests that the rate of pure guessing increases substantially as coherence is lowered (see Figure 3B), but the standard deviation of responses that are not guesses is nearly constant across coherence levels (see Figure 3C).

To investigate whether guess rate and standard deviation vary across conditions, a common approach is to test whether parameter estimates from the full model differ significantly across conditions. For example, a repeated measures analysis of variance (ANOVA) confirms that the rate of pure guessing increases as coherence is lowered, $F(4, 100) = 282.60$, $p < .001$, $\eta_P^2 = .92$. However, whereas mean estimates of SD appear to be nearly identical across coherence levels, an ANOVA suggests a small but significant effect, $F(4, 100) = 2.85$, $p = .03$, $\eta_P^2 = .10$. This ANOVA approach, however, is inappropriate for several reasons. First, whereas null-hypothesis significant testing can only reveal evidence against the null hypothesis, and may be biased toward doing so (Berger & Sellke, 1987), our goal is to identify invariances in parameters across conditions, so we must be able to accurately quantify evidence for the null as well as against it. One way to do so is with a Bayesian approach to ANOVA, and a Bayes factor (BF) ANOVA with default priors (Rouder et al., 2012) confirms that guess rates vary across coherence levels ($BF_{10} > 100$), but suggests that there is only weak evidence (Raftery, 1995) that SD varies with coherence ($BF_{10} = 1.55$). This result is similar to that provided by the standard ANOVA, however, the Bayes factor ANOVA shares several other potential problems with applying an ANOVA to parameter estimates from the full model. First, significance tests on parameter estimates ignore the shape of the likelihood function, and so might mischaracterize biases in parameter estimates as true effects. In particular, SD estimates from the mixture model are biased high when guess rates are greater than 60% (Sutterer & Awh, 2016), such as in the most difficult conditions here. Consequently, whereas the ANOVA approach characterizes the small increase in SD at the lowest coherence condition in Figure 3C as a true effect, it is possible that this small increase reflects a bias in parameter estimation. To make matters worse, several assumptions of the ANOVA are violated, as variance in the parameter estimates changes with overall performance, and the bounded parameter estimates are not normally distributed.

Not surprisingly, simulation studies revealed that the ANOVA approach yields inflated Type I error rates, suggesting significant effects in SD when in fact there are none (see model recovery in the

Figure 3
Experiment 1a Results
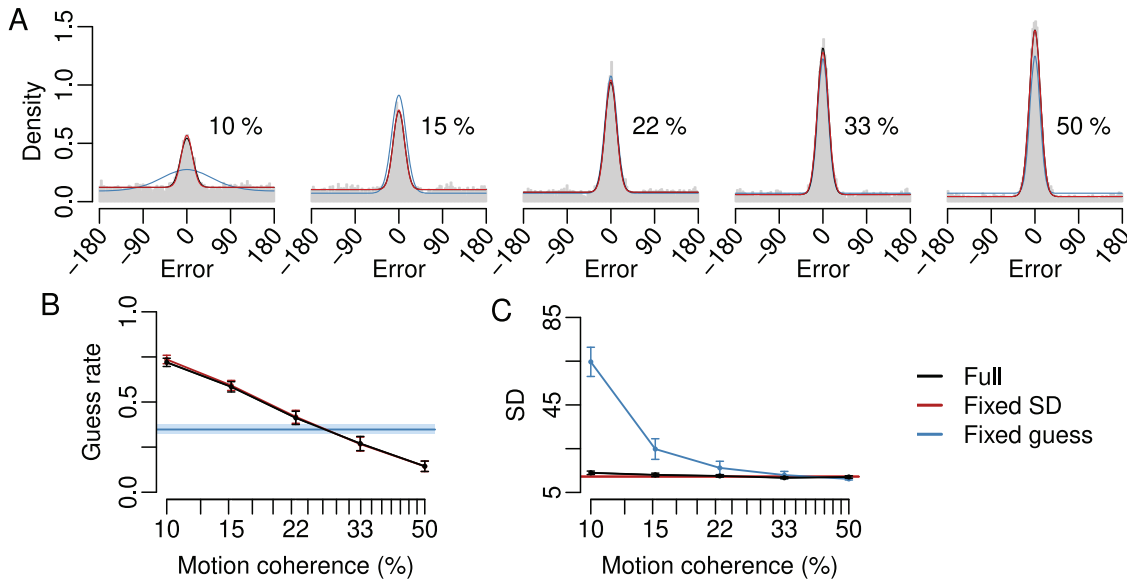
Note. Error distributions were aggregated across participants (A), and models were fit to these averaged distributions (lines) for display purposes. Fitting the full model to individuals suggests that whereas guess rates decrease substantially as coherence is increased (B), the standard deviation of nonguessing responses is nearly invariant across conditions (C). Error bars in all figures denote standard errors of parameter estimates across participants. See the online article for the color version of this figure.

online supplemental material). Fortunately, however, the simulations reveal that formal model comparison using the BIC statistic provides for a reliable way to assess whether parameters do or do not change across conditions. For example, in the fixed guess model the guess rate is forced to be constant across coherence levels. This model clearly provides a poor fit to the data (see Figure 3A), and BIC favors the full model over this fixed guess model (average ΔBIC = 71), suggesting that guess rates indeed vary across conditions. Alternatively, the fixed *SD* model, in which guess rate varies across coherence levels but *SD* is constant, provides an almost identical fit to the data as the full model (see Figure 3A), and BIC favors the fixed *SD* model over the full model (ΔBIC = 22). Table 1 shows average BIC values and the number of participants fit best by each model (in parentheses), and clearly suggests that in Experiment 1a guess rate varies with motion coherence, whereas *SD* is constant.

The amount of time that a motion stimulus is displayed may have a substantial influence on global motion processing (Watamaniuk, 1993). In particular, it is possible that our failure to observe changes in response precision (*SD*) with coherence in Experiment 1a was due to the long 1,000-ms stimulus period, which may have caused precision on nonguess trials to be at ceiling. To test whether *SD* varies with coherence when less time is available to process the motion stimulus, in Experiment 1b the stimulus duration was shortened to 500 ms. The same full and restricted models were fit to these data, and the results again suggest that the fixed *SD* model provides a better fit to the data than either the full model or the fixed guess model (see Table 1 and Figure S2 in the online supplemental material), replicating the result from Experiment 1a that motion coherence affects only guess rates. Comparing the fixed *SD* model parameters across experiments (see Figure S3 in the online supplemental material) suggests that stimulus duration did not affect *SD*, $t(50) = .79$, $p = .43$, $d = .22$. A BF *t* test (Rouder et al., 2009) applied to these parameter estimates also suggests that precision is invariant with stimulus duration ($BF_{01} = 2.80$). Alternatively, comparing guess rates across conditions (analyzed with a mixed-effects ANOVA) suggests that

Table 1
Model Comparison Using Bayesian Inference Criterion (BIC) for Experiments 1 Through 3

Model	Experiment 1a (N = 26)	Experiment 1b (N = 26)	Experiment 2a (N = 29)	Experiment 2b (N = 29)
Full model	22 (0)	20 (0)	8 (3)	10 (5)
Fixed *SD* model	**0 (26)**	**0 (24)**	31 (4)	39 (2)
Fixed guess rate model	93 (0)	46 (1)	**0 (22)**	**0 (22)**
Null model	112 (0)	63 (1)	142 (0)	183 (0)

Note. BIC values were averaged over participants. Items in bold represent the preferred model. Values in parentheses indicate number of participants for which respective model was preferred.

shortening the stimulus duration increased the rate of guessing, $F(1, 50) = 5.25$, $p = .03$, $\eta_P^2 = .09$, $BF_{10} = 1.67$, and a significant interaction suggests that this effect was slightly larger when coherence was high ($F(4, 200) = 3.41$, $p = .01$, $\eta_P^2 = .06$, $BF_{10} = 3.14$).

Discussion

Most theories of global motion perception follow a standard encoding-decoding framework, in which local motion directions are first encoded by a population of motion-sensitive units, and a global estimate is derived by pooling across units (see Webb et al., 2007). The models are highly similar to working memory models that utilize an encoding-decoding framework (e.g., Bays, 2014), and differ from one another primarily in the algorithm that dictates how local signals are pooled. To assess whether these models can account for the results of Experiment 1, responses were simulated from the models assuming the design and stimulus properties of Experiment 1, and the mixture-model analysis was applied to the resulting synthetic data. Critically, the estimated variability in response errors (SD) increased with coherence for all such models, regardless of the particular pooling algorithm used (see Table S3 in the online supplemental material). This result is not surprising, as decreasing coherence necessarily leads to more noise in the local motion signals, such that any global direction estimate that pools over all local signals will become gradually less precise. However, the empirical results of Experiment 1 suggest that the precision of responses is constant across a range of coherence levels, whereas coherence has large effects on the rate at which global motion perception fails entirely. These results suggests that, for the transparent motion stimuli in Experiment 1, global motion perception is a discrete process that either occurs with highly accurate direction perception or fails completely.

Whereas these results cast doubt on the idea that all local motion signals within the stimulus region are pooled, they are in line with the proposal that signal dots are first segmented from noise dots, and then the direction of this subset is identified (Braddick, 1993). There is some evidence for segmentation, such as the finding that the perceived speed of signal dots does not vary with coherence (Schütz et al., 2010), suggesting that properties of the signal dots can be perceived without any influence from noise dots. Our results follow if the segmentation process is discrete: successfully segmenting the signal dots on some trials leads to very high precision regardless of coherence because the motion direction of the subset is obvious. However, rather than segmentation occurring only partially on other trials, segmentation fails altogether, and global motion is not perceived at all. Such a discrete segmentation stage seems reasonable in natural viewing conditions, where some minimal amount of local motion energy in precisely the same direction should be required for the visual system to combine disparate parts of space together into a coherent moving object. The transparent motion stimulus used in Experiment 1, in which all signal dots move in the same direction, mimics such natural situations and has therefore been used extensively to study motion perception (e.g., Scase et al., 1996). However, there are many ways to build global motion stimuli, and some of them may be less likely to evoke the segmentation process (Dakin et al., 2005; Schütz et al., 2010). In Experiment 2, such a motion stimulus was tested for signatures of continuous and discrete processing.

If our observation of all-or-none direction identification in Experiment 1 reflects discrete segmentation, then we should not observe discrete processing in Experiment 2 when signals are not segmented from noise.

Experiments 2a and 2b

Method

Participants

Thirty adults participated in Experiment 2a (22 women, Mdn age = 19) and thirty in Experiment 2b (24 women, Mdn age = 19). One participant was excluded from Experiment 2a and one from Experiment 2b as the pure-guessing model fit their data better than a model that additionally allowed for target responses.

Stimuli and Procedure

Experiment 2 was identical to Experiment 1 with the following exceptions. Whereas in Experiment 1 the motion direction of each dot was designated as either signal or noise, in Experiment 2 motion directions for each dot were sampled from a wrapped Gaussian distribution (see Figure 1B and Watamaniuk et al., 1989). The mean of this distribution determined the global motion direction on each trial, and the concentration around this mean determined motion coherence. Coherence is defined as the mean resultant length of the distribution (R), which is a function of the variance of the underlying Gaussian distribution (σ^2, $R = e^{-\sigma^2/2}$). Coherence was manipulated across five levels ($R = 19^{\circ}, 26^{\circ}, 35^{\circ}, 43^{\circ}, 51^{\circ}$) that were chosen to provide similar overall performance as the five coherence conditions in Experiment 1. Stimuli were presented for 1,000 ms in Experiment 2a and 500 ms in Experiment 2b.

Results

The overall accuracy of responses in Experiment 2a (see Figure 4A) was qualitatively similar to that in Experiment 1a (see Figure 3A). However, whereas in Experiment 1 the effect of coherence was in guess rate but not SD, the opposite pattern held for the Gaussian motion stimuli in Experiment 2. The full model was now preferred over the fixed SD model (ΔBIC = 23), suggesting that the variability in motion direction estimates (SD) increased with decreasing coherence. This pattern was supported by a significant effect of coherence on SD parameters as estimated in the full model (see Figure 4C), $F(4, 112) = 51.00$, $p < .001$, $\eta_P^2 = .65$, $BF_{10} > 100$. Moreover, the fixed guess model was preferred over the full model (ΔBIC = 8), suggesting that only response precision varied with motion coherence, whereas guess rate was invariant (see Table 1). However, the fixed guess model and full model provided similar performance when assessed using AIC (see Table S3 in the online supplemental material), and estimates of guess rates from the full model (see Figure 4B) do appear to vary somewhat across coherence conditions ($F(4, 112) = 50.06$, $p < .001$, $\eta_P^2 = .64$, $BF_{10} > 100$). Critically, although it is not entirely clear whether guess rates varied with coherence in Experiment 2a, precision clearly did vary with coherence as is predicted by local pooling models.

The results of Experiment 2b, in which stimulus duration was reduced from 1,000 ms to 500 ms, largely replicate Experiment 2a:

Figure 4
Experiment 2a Results
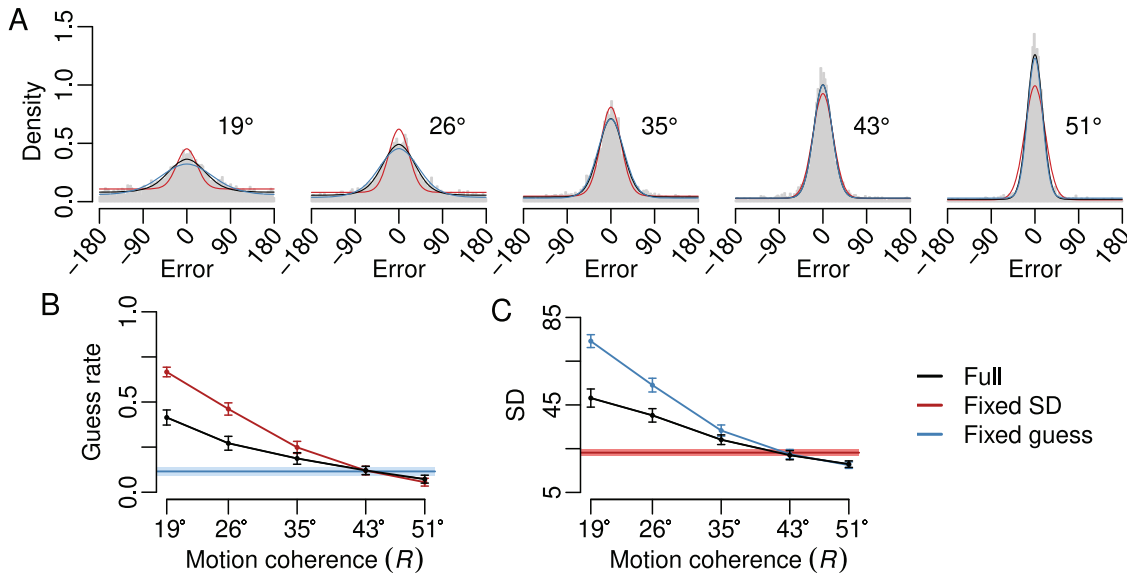
Note. Error distributions were aggregated across participants (A), and models were fit to these averaged distributions (lines) for display purposes. Fitting the models to individuals suggests that guess rates may decrease somewhat as coherence is increased (B), but unlike Experiment 1 the standard deviation (*SD*) of nonguessing responses now varies substantially with motion coherence (C). See the online article for the color version of this figure.

There was clear evidence that *SD* varied with motion coherence, and mixed evidence that guess rates varied as well (see Table 1 and Figure S4 in the online supplemental material). Comparing parameters from the fixed guess model across Experiments 2a and 2b (the preferred model by BIC in both experiments) suggests that stimulus duration had no effect on guess rate, $t(56) = .03$, $p = .97$, $d = .00$, $BF_{01} = 3.84$, or *SD*, $F(1, 56) = 1.00$, $p = .32$, $\eta_P^2 = .02$, $BF_{01} = 4.54$; see Figure S5 in the online supplemental material. But taken together, Experiments 2a and 2b clearly show that the precision of responses varies with coherence for a Gaussian motion stimulus, and that this pattern holds for a range of stimulus durations.

Discussion

The all-or-none direction identification of transparent motion in Experiment 1 may have reflected a discrete segmentation of signal and noise dots. If so, then identifying the global direction of Gaussian motion in Experiment 2 should not be discrete, as it is unlikely to be segmented into signal and noise. In line with this prediction, varying the coherence of Gaussian motion clearly affected the precision of identification reports. This pattern implies a continuous process in which the direction of all dots in the stimulus are pooled to derive an average heading direction, in line with standard models of global motion perception.

The dissociation between transparent and Gaussian motion is remarkable given that they are so similar, which raises a question: are the differences observed across Experiments 1 and 2 driven by the blocked nature of the stimulus types? For example, perhaps the repeated exposure to transparent or Gaussian

motion within each experiment caused participants to adopt a particular strategy that differed across experiments. Alternatively, the motion-identification process might be determined by statistical properties of particular stimuli: Segmentation occurs when a small subset of dots share nearly identical directions, and pooling occurs when local directions are similar but not identical. To test these possibilities, in Experiment 3 transparent and Gaussian motion trials were mixed within the same experiment. If segmentation and pooling are dynamic processes that depend on the stimulus, then the dissociation observed across Experiments 1 and 2 should replicate in this mixed design, such that identification is discrete for transparent motion and continuous for Gaussian motion.

Experiment 3

Method

Participants

Forty-nine adults (22 women, *Mdn* age = 19) participated in Experiment 3 in exchange for course credit. Fifteen were excluded from analysis because a pure-guessing model fit their data better than the full model in one or both stimulus conditions. One additional participant was excluded because their performance was exceptionally poor in the more difficult conditions, leading to unreliable parameter estimates. Although this exclusion rate is higher in Experiment 3 than in the previous four experiments, the results largely replicate those from Experiments 1 and 2. It is therefore unlikely that participant exclusion criteria are affecting the results.

Stimuli and Procedure

Experiment 3 was similar to Experiments 1 and 2, with the following exceptions. Each trial consisted of either a transparent motion stimulus or a Gaussian motion stimulus with a 500-ms duration. Motion coherence was either low or high for transparent motion (15% or 33% signal dots) and Gaussian motion (26° or 43° mean resultant length). These coherence levels match the second-to-lowest and second-to-highest conditions from Experiments 1 and 2, with the goal of observing robust effects of coherence that maximally differentiate between the fixed guess and fixed-precision models. In this 2 × 2 factorial design, stimulus type and coherence level were counterbalanced and presented in random order, providing 200 trials for each condition (800 total).

Results and Discussion

Figure 5 shows the resulting response error distributions, and visual inspection suggests that the differential effects of coherence across stimulus types was replicated: For transparent motion (top), coherence primarily affected the rate of guessing, seen as a rise in the long flat tails, whereas for Gaussian motion (bottom) coherence affected SD, seen as a widening of the central part of the distribution. A full model, in which guess rate and SD parameters were free to vary across both stimulus and coherence conditions, was compared with a restricted model in which model parameters were differentially fixed depending on the stimulus type: For transparent motion only guess rate varied across coherence, and for Gaussian motion only SD varied across coherence. Both models fit well (see Figure 5), and BIC suggests that the restricted model provided a better account than the full model (ΔBIC = 6.4, N = 28/33). However, AIC results were less clear, and the full model provided a better fit (ΔAIC = 3, N = 21/33), possibly because guess rate varied slightly across coherence levels for Gaussian motion as in Experiment 2. To test this possibility, the restricted model was amended to allow guess rate to vary for both transparent and Gaussian motion, whereas SD was again fixed across coherence conditions for transparent motion. This model was preferred over the full model according to both BIC (ΔBIC = 4.7, N = 32/33) and AIC (ΔAIC = .07, N = 21/33), although AIC was more ambiguous. Overall, these results replicate the patterns observed across Experiments 1 and 2, implying that motion segmentation and pooling processes can be deployed

Figure 5
Experiment 3 Results
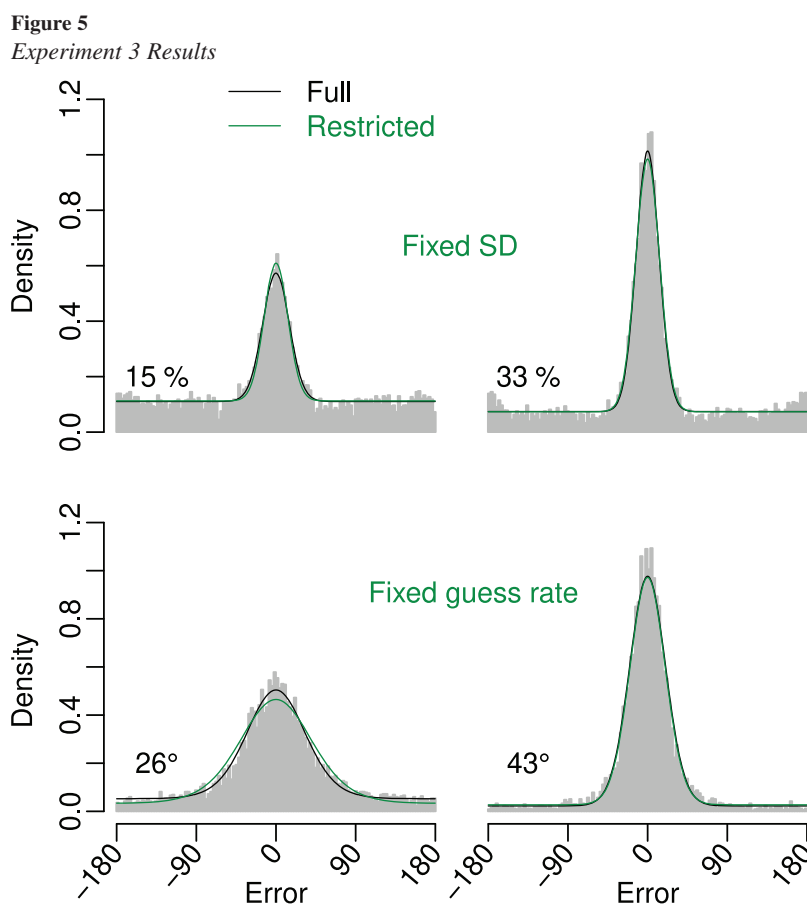
Note. Response errors are aggregated over participants for transparent motion (top) and Gaussian motion trials (bottom). When transparent and Gaussian motion trials were mixed within the same experiment, fitting the model to individuals suggests that guess rate varies with coherence for transparent motion, but the SD of nonguess responses varies with coherence for Gaussian motion. See the online article for the color version of this figure.

differentially on a trial-by-trial basis, driven by statistical properties of the motion stimulus.

General Discussion

Most theories of global motion perception assume that global directions are derived by pooling local motion signals over space. We tested a straightforward prediction of such models: identifying global motion directions should become gradually less precise as motion coherence decreases. However, in Experiment 1a lowering the coherence of a transparent motion stimulus led to more pure guessing responses, whereas the precision of successful identification was identical across a large range of coherence levels. This result was replicated with a shorter stimulus duration (Experiment 1b), and when another type of motion stimulus was present (Experiment 3). This finding of all-or-none global motion identification is among several perceptual processes that have been shown to be discrete, including word identification (Swagman et al., 2015), sensory memory (Pratte, 2018), and the attentional blink (Asplund et al., 2014). Although such claims go against decades of work rooted in signal detection theory, going forward we believe it will be essential to consider that many cognitive and perceptual mechanisms might involve discrete processing stages.

We hypothesized that the all-or-none nature of motion identification in Experiment 1 reflected a discrete segmentation process, such that the subset of signal dots is either successfully isolated from noise dots, or global motion fails to be perceived altogether. The results of Experiment 2 support this proposal: for Gaussian motion, in which local motion is not easily segmented into signal and noise components, direction identification was no longer discrete but exhibited signatures of local pooling. This dissociation in how motion is processed for different stimulus types was replicated in Experiment 3 when both motion types were presented intermixed, suggesting that the particular properties of these stimuli drive discrete segmentation or continuous pooling processes in real time. Local pooling is at the heart of many models of global motion perception, and it is interesting that the visual system can utilize such a process for Gaussian motion. However, doing so is akin to finding the average heading direction of a flock of birds, which hardly seems like the primary purpose of the visual motion system. Instead, we suggest that true global motion perception should be characterized by the all-or-none segmentation of visual space into discrete, coherently moving subsets. For example, knowing that a single bird is just that: a coherent object with an overall global motion direction, even though its wings, head, and tail have motion energy in many directions simultaneously.

Segmenting the visual world into coherently moving objects, and pooling motion energy within those objects to determine their heading, are both important processes when viewing natural scenes comprised of many moving things. Indeed, some models seek to accomplish both segmentation and pooling from local motion energy (e.g., Grossberg et al., 2001; Tlapale et al., 2010). Moreover, area MT includes some neurons that represent pooled motion directions, whereas others represent segmented directions (McDonald et al., 2014; Xiao & Huang, 2015). The results of Experiments 1 through 3 suggest that segmentation and pooling can be measured in isolation by using different types of motion stimuli. Although this result may seem surprising given how similar transparent and Gaussian motion are at face value, previous

studies have also shown that subtle stimulus differences can have substantial impacts on how motion is perceived. For example, one approach for testing local pooling algorithms utilizes motion stimuli comprising asymmetrical or bimodal distributions of local motion directions, as particular pooling algorithms make unique predictions for how such stimuli should be perceived (Zohary et al., 1996; see also Webb et al., 2010). Critically, the results suggest that the way local motion signals are combined depends on statistical properties of the motion stimulus: when one direction has substantially more energy than the others, this maximum is the perceived direction ("winner take all"). Alternatively, when multiple directions have similar energy, their average is the perceived direction ("vector averaging"). Similarly, when two coherent motion signals overlap, they are perceived independently as if segmented from one another, if their motion directions are sufficiently different. But if the directions are similar their average direction is perceived (Nichols & Newsome, 2002; Treue et al., 2000). Taken together, these results suggest that the visual system can pool motion directions in cases where such pooling seems reasonable, such as with Gaussian motion, and can explicitly segment visual signals from one another and from the background when a subset of local elements have highly similar directions, as is the case with transparent motion.

Winner-take-all decision algorithms, in which the strongest of multiple local motion signals is taken as the perceived direction, are sometimes equated with the process of segmenting signal from noise (e.g., Medathati et al., 2017; Salzman & Newsome, 1994; Zohary et al., 1996). However, it is important to distinguish between merely taking the maximum local motion response as the global motion direction, and true segmentation in which coherently moving local elements are grouped together and isolated from other stimuli (e.g., Schütz et al., 2010). For example, we show in simulation studies that a winner-take-all decision algorithm predicts that precision should decrease as coherence is decreased, even for transparent motion stimuli (see the online supplemental material). This isn't surprising: as coherence is lowered, the maximum neural response to local motion signals becomes more likely to be further from the true coherent direction, as the maximum response must be taken across both signal and noise dots. However, the results of Experiments 1a, 1b, and 3 suggest that, for transparent motion, response precision is constant and remarkably high across a range of coherence levels. This result implies that the subset of coherent signal dots can be explicitly segmented from the noisy background, even at very low coherence levels, such that accurately identifying the direction of this subset is trivial. We initially suspected that the motion system might revert to pooling across both signal and noise dots when the segmentation process fails for transparent motion, particularly in Experiment 3 where both transparent and Gaussian motion stimuli were intermixed. But even in this case response precision was the same for low- and high-coherence transparent motion stimuli, suggesting that when segmentation fails, global motion simply fails to be perceived altogether. However, more work is needed to identify the conditions that trigger segmentation, and whether there might be cases in which segmentation and pooling can operate simultaneously.

Many previous results in motion perception stemmed from exploring a variety of stimulus parameters and stimulus types (e.g., Webb et al., 2007), and this approach provides a promising avenue for further testing the notions of continuous pooling and discrete

segmentation. For example, we observed discrete segmentation with typical transparent motion stimuli in which all signal dots move in precisely the same direction and suspect that it is the presence of highly similar motion across local elements that evokes the segmentation process. However, the motion directions of signal dots could instead be drawn from a Gaussian distribution to examine whether, for example, local motions are only segmented if the similarity of their directions is above some threshold. Likewise, stimulus characteristics such as dot speed (Braddick, 1993) and dot lifetime (Pilly & Seitz, 2009) might affect whether signal dots are segmented from noise. For example, although Bae and Luck (2019) did not conduct formal model comparisons, their results suggest that manipulating the coherence of a transparent motion stimulus might affect both guess rate and precision when the lifetime of dots is extremely short ($\approx$16 ms). One consequence of such brief dot durations is a marked decrease in signal strength for each dot's local motion direction, which might undermine the segmentation process in a similar manner as adding noise to the local signal directions. Exploring how the signatures of discrete and continuous processing vary across this large stimulus space provides a promising avenue for further testing and refining the mechanisms that underlie continuous pooling and discrete segmentation.

Here we have compared predictions of discrete and continuous processing by modeling errors in an identification task, but several other approaches have been used to accomplish the same goal. The most common approach is to draw receiver operating characteristic (ROC) curves in a detection task: these curves should be straight lines if they arise from a discrete process, and curved lines if from a continuous process. ROC curve analysis has revealed evidence for continuous processing in some cases (e.g., Green & Swets, 1966) and discrete processing in others (e.g., Rouder et al., 2008). However, using ROC curves to distinguish between continuous and discrete processing has serious limitations, whether they are constructed by manipulating response bias or by using confidence ratings (e.g., Bröder & Schütz, 2009; Rouder et al., 2021). More recently, formal modeling of confidence rating distributions (Province & Rouder, 2012) and reaction time (RT) distributions (Zhou et al., 2021) has been used to compare discrete and continuous theories. There is not a consensus on which of these approaches is the most appropriate for comparing discrete and continuous processing, and in most applications an entire cognitive process (e.g., working memory, recognition memory, perception) is determined to be mediated by either continuous or discrete processing, making it difficult to directly compare purportedly continuous and discrete cases. Here, however, using the Zhang and Luck (2008) mixture-model approach we observe a remarkably clear dissociation between two highly similar stimuli in the same task: Discrete processing of transparent motion and continuous processing of Gaussian motion. Going forward, these motion stimuli may therefore provide a powerful platform for comparing the various approaches to discerning continuous and discrete processing.

Although the Zhang and Luck (2008) mixture model has been ubiquitous in working memory research, several alternatives have been proposed that make substantially different assumptions, such as eschewing the existence of guessing altogether (Bays, 2014; Schurgin et al., 2020; Van Den Berg et al., 2012). These models can produce error distributions with long tails that look similar to the uniform tails that arise from guessing, without the explicit assumption of pure guessing. However, we suspect that all such

single-process models predict that when data are fit with the two-process mixture model, both *SD* and guess rates should vary at least somewhat with any manipulation of stimulus strength, such as coherence. Therefore, our finding that precision is completely invariant across a range of coherence conditions for transparent motion, whereas guess rates vary substantially, provides strong evidence for a pure guessing process. Our results also have important implications for studies that examine deficits in motion perception, such as deficits found in autism (Manning et al., 2015) and schizophrenia (Chen et al., 2003), as they might occur in the discrete segmentation or continuous local-pooling processes. More generally, examining the continuous and discrete nature of motion processing across a variety of conditions will provide critical evidence for understanding how the visual system carves the world into coherent, moving objects.

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