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Motion Perception as a Partnership: Exogenous and Endogenous Contributions

Robert Sekuler

William James portrayed perception as a partnership: "Whilst part of what we perceive comes through our senses from the object before us, another part (and it may be the larger part) always comes . . . out of our own head."¹ On this view, visual experience is constructed not only from exogenous resources such as the raw material provided by the eye, but also from endogenous resources, including knowledge, memory, and expectation. This review shows that visual motion, like other forms of perception, emerges from a Jamesian partnership between endogenous and exogenous influences.

LIVING WITH UNCERTAINTY

For one study of motion detection, Karlene Ball and I devised conditions that would maximize or min-

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imize the validity of the observer's expectations, a key endogenous influence.² In the first of these conditions, the target's direction was constant over trials so that an observer could be certain about the motion that had to be detected; in the second condition, randomization kept the observer uncertain about what direction to expect. We reasoned that certainty might allow an observer to attend to the one appropriate direction. Our stimuli, spatially random dots moving in the same direction at a common, constant speed, covered the entire display of 8° diameter. As a result, there was no advantage in looking at or attending to any particular location. Instead, the observer could attend to the expected direction by monitoring signals within neurons that are tuned to the expected direction.³

Each trial comprised two 600-ms intervals. Selected at random, one interval contained low-contrast, spatially random, moving dots; the other interval contained only a uniform, veiling luminance. The experiment interleaved two types of blocks. In certainty blocks, dots always moved in the same, predictable direction, upward. In uncertainty blocks, the direction was unpredictable, alternating randomly between upward and rightward. The subject was not asked to judge di-

rection of motion, but merely to identify which interval contained the stimulus.

In the certainty condition, the 3 subjects averaged approximately 75% correct detection (Fig. 1). With uncertainty, detection of the upward-moving dots declined to only slightly above chance, 53%. So, without altering any property of the stimulus, but reducing the value of endogenous information, we rendered a moving stimulus virtually invisible.

Thus, expectation of a particular direction of motion modulates the detectability of a moving target. In another study, to learn how rapidly such expectations can be constructed or changed, on each trial, we gave the subject a hint about the motion that might be presented.⁴ The direction in which the dots moved varied randomly from trial to trial, over a range of 360°. On some trials, a cue to the upcoming direction was presented for 50 ms. This cue, which appeared at various times before or after the test interval, was a line radiating out from the center of the display, and its orientation corresponded to the dots' direction of motion. Results with the cue were compared with results from two control conditions without a cue. In one control condition, the direction of motion varied randomly from trial to trial; in the other control condition, the direction of motion was fixed (upward), allowing the subject to be certain about which direction would be presented. Figure 2 illustrates the sequence of events in the trials.

On half the trials, low-contrast,

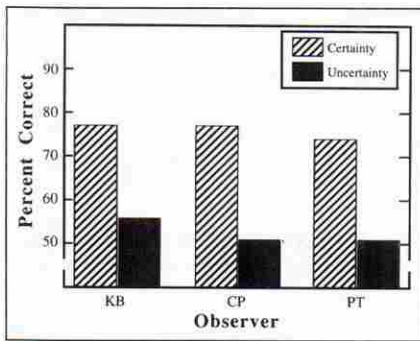


Fig. 1. Mean percentage correct for certainty and uncertainty conditions in the experiment on detection of a moving target.² Data are shown for 3 observers.

moving dots were presented in a 500-ms test interval; otherwise, the test interval was blank. Using a numerical rating scale, subjects judged whether dots had been presented and rated their confidence in that judgment (e.g., 1 = *certain that a stimulus was presented*; 4 = *not sure at all, but a stimulus might not have been presented*). Performance was indexed by a nonparametric measure of detectability, $zP(A)$. As shown in Figure 3, a cue before the test interval is very helpful: As the interval between cue and test motion increases, detectability improves dramatically. A cue after the test interval does no good, however. Performance in this condition is the same as with no cue and total uncertainty.

RESPONDING TO CHANGE

Expectation is not the only endogenous influence on motion perception. For example, Allison Sekuler, Erica Sekuler, and I showed that information extracted early in a target's trajectory can shape the processing of information later in the trajectory.⁵ In these experiments, a disc appeared at the display's center and moved along a straight path. After traveling for a short, random duration, the disc changed direction abruptly by 30° clockwise. The observer pressed a key to signal when the change was detected; response time (RT) was the dependent variable. The independent variables were duration and predictability of the motion prior to the change in direction. To vary predictability, the initial direction was either constant (in some blocks of trials) or a random choice, from a range of 360°. When the motion lasted just a short time before changing direction (e.g., 300 ms), unpredictable prechange motion produced much longer RTs than did predictable prechange motion. When the initial trajectory reached 500 to 700 ms, the initial direction's randomness ceased to matter: RTs for unpredictable prechange motion dropped to the same level as RTs for predictable motion. Because other

experiments showed that brief presentations produce highly variable judgments of direction, our hypothesis is that 500 to 700 ms are needed before the trajectory's representation reaches its maximal precision.

Allison Sekuler and I extended this initial work by identifying several factors that can retard the development of an accurate representation of direction, or even disrupt this process altogether.⁶ These disruptive factors include a momentary cessation of the motion or a brief disappearance of the target. From other related experiments, Ehtibar Dzhafarov, Jyri Allik, and I were able to develop a mathematical model of how the visual system detects a change in motion direction, speed, or both.⁷

"PLAYED UPON FROM TWO DIRECTIONS"

For a clue to how expectation or other endogenous influences might actually facilitate perception, we can go back to William James, who offered a metaphor that has proven to be prophetic:

The natural way of conceiving all this is under the symbolic form of a brain-cell played upon from two directions. Whilst the object excites it from without, other brain-cells, or perhaps spiritual forces, arouse it from within.⁸

James went beyond this metaphor, suggesting that local variations in cerebral blood flow could track shifting brain activity that was provoked by shifts in attention. After reviewing results from several crude but ingenious methods for measuring blood flow, James commented that fluctuations of the brain's blood flow

... followed the quickening of mental activity almost immediately. We must suppose a very delicate adjustment whereby the circulation follows the needs of the cerebral activity. Blood very

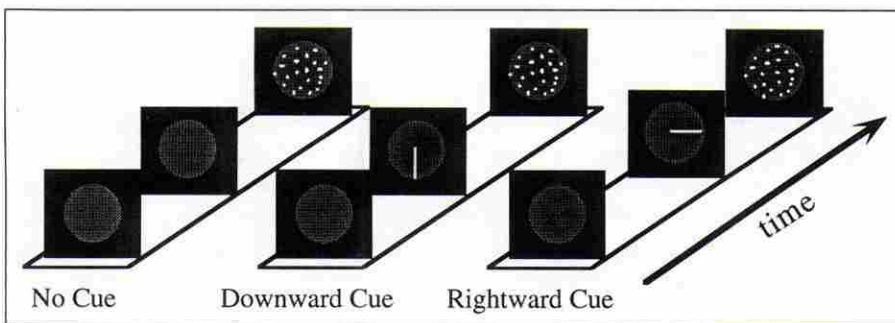


Fig. 2. Schematic representation of three types of trials in the experiment with motion cuing.⁴ From left to right, the sequences represent trials with no cue, with a cue for downward motion, and with a cue for rightward motion. In each sequence, a trial began with a blank screen, after which a cue line could be presented, followed by a 500-ms interval during which dim, moving dots could be presented. Not shown are trials on which the cue followed the motion and trials on which no moving dots appeared. Variation in the interval between cue and motion is suggested by the different temporal positions of the cues in the rightmost two sequences.

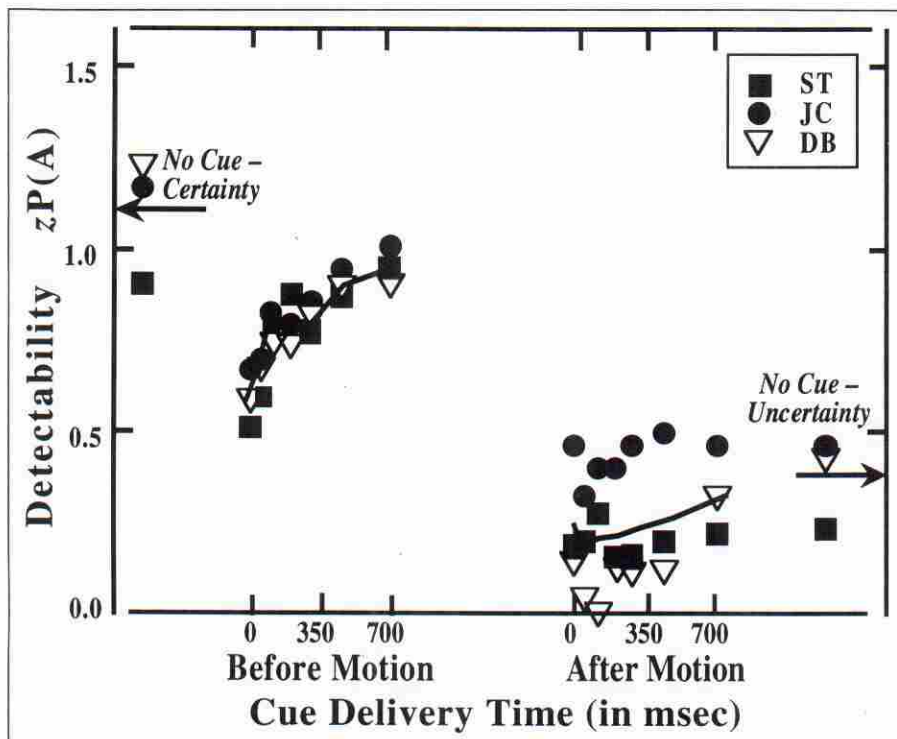


Fig. 3. Detectability of motion as a function of the interval between delivery of a cue and the onset of motion. The measure, $zP(A)$, plotted on the vertical axis is linearly related to the more familiar measure d' . The series of data points at the left shows performance when the cue preceded the motion; data points at the right show performance when the cue followed the motion. Also shown are data for two control conditions, in which cues were not used: blocks of trials on which the constancy of the dots' direction afforded the observer certainty (extreme left, "Certainty") and blocks of trials on which the dots' directions varied randomly (extreme right, "Uncertainty"). Data are shown for 3 observers. Arrows indicate interobserver means for the two control conditions.

likely may rush to each region of the cortex according as it is most active, but of this we know nothing.⁹

A century later, James's lament—"of this we know nothing"—has far less validity than it once did. Sophisticated brain-imaging techniques, including positron emission tomography, have localized functionally significant changes in cerebral blood flow, including changes that follow hard on a "quickening of mental activity." These techniques have identified the loci of various sensory and cognitive functions, including the loci of several circuits involved in attention.¹⁰ In the human cerebral cortex, an area known variously as the medial temporal area (MT) or area V5 is strongly and selectively activated when a subject looks at a moving target or at a stationary tar-

get that produces illusory motion.¹¹ This area is rich with directionally selective neurons, which respond vigorously to particular directions of motion and less vigorously, or not at all, to other directions. Activity in this area is enhanced when the structure of the psychophysical task focuses attention to a target's motion.¹² This finding does not prove that attention to motion is mediated by enhanced activity only in MT, but it does implicate MT as one target of attentional processes.

Area MT's preponderance of direction-selective neurons is consistent with the idea that any stimulus is recognized by the particular distribution of activity that it evokes across many different neural units. In such a scheme, called a coarse code, each encoding unit is broadly

tuned (i.e., responds to many different stimuli). For visual motion, this means that any neuron in an area such as MT responds to a broad range of directions. Further, in a coarse code, different neurons are sensitive to different sets of inputs, and each input stimulates many different neurons. Any moving stimulus activates many differently tuned directionally selective neurons. Perceived direction reflects the distribution of activity across neurons.

In both sensory and motor systems, similarly tuned neurons tend to share common neighborhoods. For instance, in area MT, neighboring neurons tend to "prefer" similar directions.¹³ The grouping of neurons according to direction preference makes it possible to transform Cartesian coordinates to more abstract coordinates: direction of motion. For example, minute current pulses applied locally to area MT of a monkey boost the activity of particular neurons, thereby altering the direction in which the monkey perceives a visual stimulus to be moving.¹³ Grouping of neurons by direction preference would allow influences originating in other brain structures to boost activity selectively within areas such as MT. Such localized influences on MT could be the basis for direction-selective effects of attention. There are several different means by which localized alterations of activity could boost the signal-to-noise ratio within a group of neurons and thereby improve detectability.¹⁴ For instance, narrowing the tuning of direction-selective neurons would improve signal-to-noise ratio; so too would selective gating, or monitoring, of particular direction-selective neurons. Changing expectations permit adjustments in which direction-selective mechanisms are monitored.

Alterations in signal-to-noise ratio affect the stimulus's coarse-coded representation and can have two different kinds of consequences, a change in detectability and a change

in perceived direction. If the observer expects—and then attends to—the direction-selective mechanism that is optimally tuned for the target's direction, detectability is enhanced, as Ball and I found. But if the observer expects a direction slightly different from the one actually presented, monitoring a suboptimal mechanism will decrease the signal level and increase the noise level, thereby diminishing the target's detectability. Additionally, monitoring the wrong mechanism will boost the potential response in that mechanism, altering the resulting coarse-coded representation, and thereby causing the direction of movement to be misperceived. Preliminary results by Allison Sekuler and me suggest that this second effect can be quite potent.

Each trial in our experiments began with a directional cue (a line radiating out from the center of the screen). The cue was followed by an interval during which very low-contrast moving dots could be presented or the display could remain blank. Ninety percent of the time, the cue was consistent with the direction in which the dots would move; on 10% of the trials, however, the cues differed from the dots' direction by varying amounts. After judging whether dots had been presented, subjects estimated the direction those dots had taken (using a protractor surrounding the display).

As before,² stimuli were more easily detected when they moved in a direction consistent with the preceding cues. More important, some erroneous cues altered perceived direction. Perceived directions were "pulled toward" the cues, and the strength of this attraction was directly related to the separation between the cued direction and the true direction of motion. For example, a discrepancy of 15° between cue and motion caused a perceptual shift of nearly 10°, but a discrepancy of 90° had no effect on perceived direction. A slightly wrong expecta-

tion, then, biases the perceived direction.

The idea that the visual system represents motion in a coarse code has been used in quantitative models of various psychophysical phenomena: the perceived unidirectional flow in a stimulus comprising many different, spatially intermingled direction vectors¹⁵ and the existence of motion metamers, stimuli that are perceptually indistinguishable from one another despite their considerable physical differences.¹⁶ Psychophysical studies suggest also that neurons tuned to similar directions can join in mutually facilitatory coalitions, whereas units tuned to very different directions tend to inhibit one another.¹⁷ These selective facilitatory and inhibitory interactions increase the effective signal-to-noise ratio.

USING WHAT WE HAVE LEARNED

Ball and I wondered whether motion cues could be harnessed in a human–electronic partnership to improve the safety of drivers and pilots.⁴ Suppose that a high-speed electronic-vision device, such as a highly miniaturized electronic chip with optical sensors, analyzed the optic array, detected important motion vectors, and fed that information to the driver in a timely fashion. The driver might be able to exploit this information to improve his or her own extraction of motion information. But the electronic partner in this hybrid electronic–human system would not be able to provide precise information quickly enough. Therefore, the system would be plausible only if the crude information the electronic partner could provide quickly would be effective.

To determine how useful a crude cue might be, we introduced varying degrees of unreliability into the cue

in the motion detection experiment described earlier.⁴ Previously, the oriented line had been a trustworthy guide to the direction that would be presented (at least on trials when motion actually was presented). Now, however, once the computer had randomly selected the direction of motion for a trial, it randomly selected the cue's orientation. The cue was chosen from a uniform distribution centered about whatever direction of motion would be presented. This distribution ranged from 0° (perfectly valid cue) to 360° (utterly invalid cue). Compared with no cue at all, a cue that was mismatched to the motion by as much as 30° still improved detectability significantly. Thus, even relatively crude cues improve detectability, probably because directionally selective mechanisms are broadly tuned.

A partnership between a human driver and an electronic helper was an intriguing idea several years ago when we first proposed it. Recently, the idea's feasibility was increased substantially by the development of a simple, robust algorithm that can speedily extract important aspects of optical flow.¹⁸ This algorithm is particularly well suited for implementation as a circuit on a miniaturized electronic chip. However intriguing the scheme may be, several questions must be answered before prototype hardware is considered more seriously. For one thing, some visual motion that is crucial in driving involves three-dimensional components. As a result, it will be important to confirm whether cues to three-dimensional components of motion can facilitate detection in the same way that cues to two-dimensional components do. Another concern is the quality of the information that the electronic partner would provide. A misleading cue impairs detection of motion. In the cue-reliability study just discussed, when the cue signaled a direction very different from the one that was actually presented, performance fell well be-

low the uncued level. Attention is a double-edged sword: It amplifies activity evoked by the attended stimulus but suppresses activity produced by a nonattended stimulus.¹⁰ This means that misleading information from the electronic partner, like mistaken advice from a human backseat driver, could be worse than no information at all. In any Jamesian partnership, after all, the perceptual outcome is only as good as each partner's contribution.

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Simultaneous Numerical and Temporal Processing in the Pigeon

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The question of whether animals are capable of counting is currently being hotly debated. Some researchers contend that animals routinely and automatically count sequences of events,¹ but others argue that animals have shown few of the properties of human counting systems.²

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Whatever the outcome of this debate eventually may be, it is clear that animals can make relative numerical judgments or numerical discriminations. For example, a rat can be trained to press one lever after it has heard two bursts of white noise and to press another lever after it has heard four bursts of white noise. Because the interburst interval is varied between trials, the discrimination is based on number of bursts and not on the time duration of the sequence.

Animals also show excellent ability to estimate time intervals.³ On fixed-interval schedules of reinforce-

ment, animals show time estimation by rate of responding. A rat or pigeon is presented initially with a light or sound signal and is then rewarded for the first response made after a fixed period of time from the signal's onset. On test trials in which the signal is continued without reward, animals show a *break-run-break* pattern of responding; that is, after a period of little or no responding, the animals respond at a high rate for a period of time and then return to a low level of response. The average time taken to reach the midpoint of the period of rapid responding closely estimates the time at which reward normally is delivered, indicating accurate time estimation.⁴ Animals also readily discriminate time intervals. In studies similar to number discrimination experiments, rats and pigeons learn to make different responses to signals of short and long durations.

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