Attentional modulation of visual motion perception

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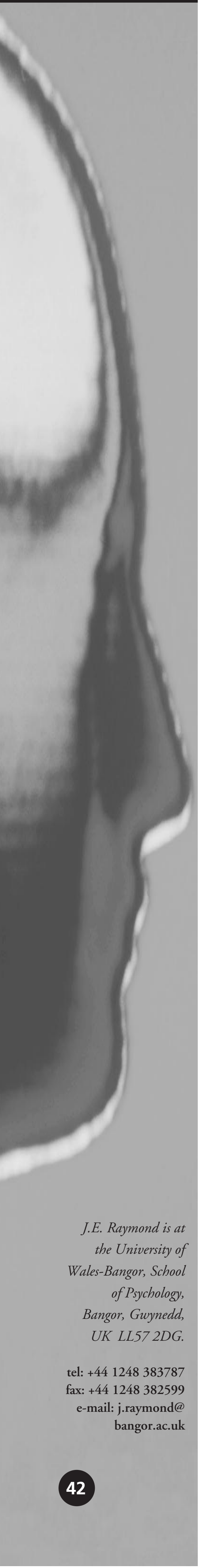

How is the perception and processing of visual motion affected by attention? This review examines recent research in cognition, perception and neurophysiology that explores how ongoing behavioural tasks (and the attentional states they impose) modulate the processing of visual motion. Although traditional views hold that motion is processed in an obligatory, 'pre-attentive' manner, evidence for processing in a task-independent manner is scant. Recent studies of human perception that have measured motion priming, motion aftereffects, uncertainty effects, and motion-interaction effects indicate instead that even simple aspects of motion processing may be substantially affected by whether motion information in a task is used or ignored by the perceiver. Single-unit studies in brain areas sensitive to visual motion in monkeys, and functional imaging studies on humans, also indicate that task and attentional state affect activity levels in brain regions thought to be important in motion perception. This review brings together these converging findings of attentional modulation of motion perception and considers them in light of object-oriented theories of attention.

Is motion information that is relevant to a visually guided task processed by the brain in the same way as task-irrelevant motion? Imagine two people viewing a rural scene with a tree swaying in the wind. One is attempting to judge the force of the wind and the other is planning to take a photograph of the landscape. The former will have attention focused on the swaying tree, with an active interest in its movement. The latter will adopt a more global perspective, ignoring the tree's irrelevant motion. Even though the visual image on the retinae of each individual might be the same, their awareness of the tree's motion is surely different. To yield different perceptual experiences, the neural processing of visual motion must also be different. Where in the visual pathways does processing become dependent on the visual task and in what way does task relevance alter visual motion information?

Broadly speaking there are two possible answers to the first question. One is that information about the task alters the initial (early) stages of sensory processing, either by modulating activity or via selection, so that different perceptual data are produced. The other is that visual motion is processed in an obligatory, or stimulus-driven, fashion yielding the same perceptual data regardless of task. High level, task-related brain activity then determines whether the motion information is made accessible to awareness. These extreme alternatives describe early and late notions of attentional control, respectively. By 'attention', I mean those neural processes (at any stage) that promote preferential processing of stimuli relevant to a particular task and inhibit processing of task-irrelevant stimuli. Although early versus late operation of attention has been a subject of much controversy in the last several decades, most models of visual motion processing assume a late site of attentional control, that is, after motion-specific processing[1–4].

Early in this decade, the prevailing view was that visual motion is processed by a separate motion 'module', or sub-system, in the brain and that this processing occurs without the benefit of feedback from other feature-specific visual sub-systems or from other brain areas activated by the task at hand. These ideas resulted from influential models, such as Marr's[1], that espouse a feed-forward view of visual processing. The discovery of multiple visual 'maps' in the brain[5], feature-specific deficits in neuropsychology patients (including 'motion blindness', or akineotopsia[6,7]), and psychophysical data indicating feature independence for perception of simple stimuli[8] promoted the idea of feature modularity in visual processing. At the same time, influential visual search studies (described below) were widely interpreted to indicate that motion[9] and other simple visual features were processed 'pre-attentively', acting as visual 'primitives' or perceptual building blocks[10]. Attention was seen by many as an 'add-on' mechanism to perception, rather than an integral part of visual processing.

Work in the last decade has cast doubt on this view. Physiological data show that motion and depth information interact within the so-called motion 'module', or sub-system[11],

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Box 1. Studying simple integrative motion perception

Studies of the object-relevant level of motion processing have been conducted using primarily ‘plaids’ and dynamic random-dot kinematograms (RDKs). Plaids consist of two grating patterns oriented differently and moving with different motion vectors. They can appear as two separate stripe patterns slipping across one another or as a single plaid surface moving in a unitary direction partway between the two component directions. What makes pairs of grating patterns slip versus cohere has been used to understand how information from the two motion vectors is combined (Ref. a). Recent work suggests that surface perception and segmentation play a critical role (Ref. b).

RDKs consist of a large number of moving dots randomly positioned within a restricted area. Each dot is assigned a particular motion vector (see Fig. I). With these stimuli, a variable percentage of dots can be moved in a single coherent (signal) direction whilst remaining dots are moved in random directions (noise). Even when the percentage of signal dots is quite low (e.g. 10%), observers perceptually group all the dots into a unified surface and report seeing a coherently moving texture with a global motion in the signal direction. Using such stimuli, sensitivity to global motion can be quantified by determining the minimum percentage of coherent dots needed for just accurate identification of the signal direction. This is known as the motion coherence threshold.

Such stimuli have also been used to study the global nature of motion processing in monkey brain. In an elegant set of experiments using RDK stimuli, Newsome and colleagues recorded from single units in macaque area MT while simultaneously measuring motion coherence thresholds behaviourally (Ref. c). They reported that neural firing rates varied with the percentage of signal dots and that behavioural coherence thresholds closely matched the minimum coherence needed to just elevate activity levels in single MT neurones above baseline.

Specialized RDKs have also been developed to research motion transparency (Ref. d) and the perception of shape derived from motion (Ref. e). These studies support the idea that the object-relevant level of processing is closely related to the mental invention of object and surface representations.

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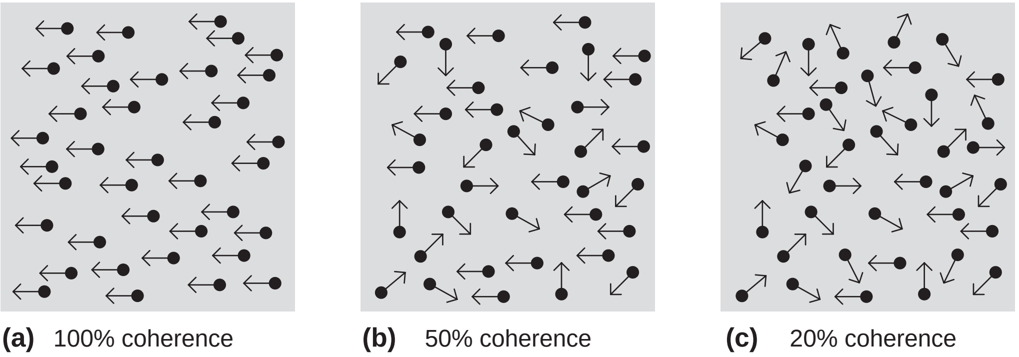

(a) 100% coherence **(b)** 50% coherence **(c)** 20% coherence

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Fig. I. Random-dot kinematograms (RDKs). A fully coherent RDK **(a)** and two partially coherent RDKs **(b and c)** are shown. The direction of each dot’s movement, indicated here by an arrow, is separately controlled so that the percentage of dots moving in the same direction (called % coherence) can be manipulated. Even with low % coherence, the RDK’s dotted surface is perceived as having a global movement direction matching that of the coherently moving dots.

as do information about colour and motion[12]. Evidence now exists to support the possibility of significant cortical reentrant pathways in motion-processing areas[13,14] and notions of pre-attentive versus attentive perceptual processing have changed[15,16]. Conventional modular, data-driven models of motion processing are now inadequate and the possibility of attentional modulation of motion processing is currently being re-evaluated.

Traditional ‘pre-attentive’ views of motion processing

Perhaps motion perception has been traditionally viewed as a purely data-driven process because motion appears to be so very easily detected, and indeed seems to ‘attract’ attention. These observations have been used to imply that motion processing is ‘pre-attentive’, that is, proceeds without the aid of attention.

The ease of detecting moving objects has been studied experimentally using visual search paradigms[9,17–19]. Observers are asked to press a key as quickly as possible to indicate the presence or absence of a target object that is defined by its motion in the presence of a number of distractor objects. When target motion is ‘short range’, that is, produced by apparent motion sequences involving small spatial displacements and short intervals, the speed of target detection is rapid and independent of the number of distracter items[17–19]. When target motion is ‘long range’, that is, created using large spatial displacements and long intervals, target detection is slow and increases as the number of distracters is increased. The presence of distracter set size effects in visual search studies has been interpreted to indicate that the to-be-detected feature requires focused attention[10]. The motion visual search experiments were thus interpreted to

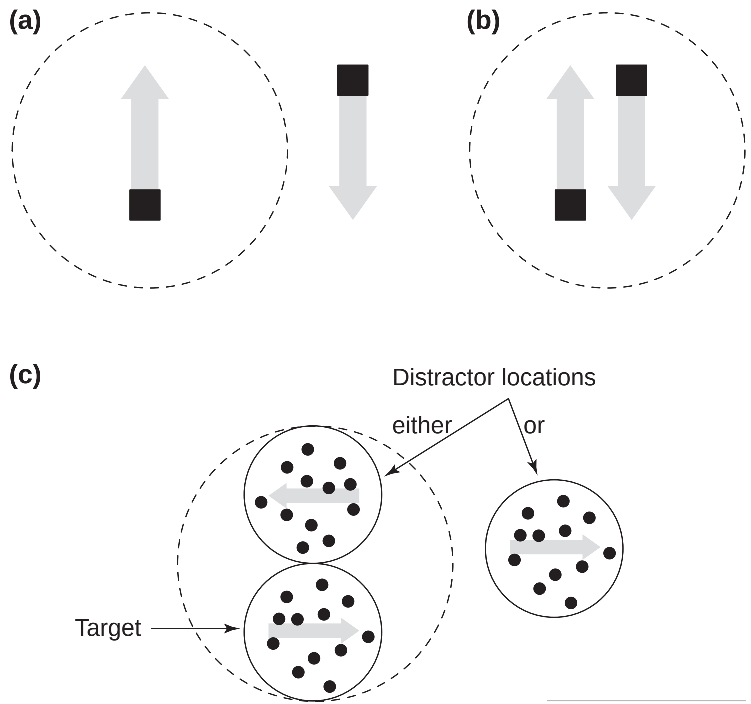

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Fig. 1. Stimuli used in single unit studies of attention in monkey MT/MST. Dotted circles represent the cell's receptive field. **(a,b)** The stimuli used by Treue and Maunsell[38]. One stationary square (target) was presented before the other and then both oscillated in counterphase. Monkeys maintained central fixation and were rewarded for a key press whenever the target, but not the distractor, changed speed. With the configuration shown in (a) firing rates were greater when the target, as opposed to the distractor, was within the cell's receptive field. For the configuration shown in (b) firing rates were maximal when the attended square moved in the cell's preferred direction and decreased substantially when the unattended square moved in the cell's preferred direction. **(c)** Seidemann and Newsome[40] used RDKs and required monkeys to make a global direction judgement on a spatially defined RDK. They found only modest attentional modulation (an order of magnitude smaller than that reported by Treue and Maunsell[38]), perhaps because targets were defined solely by a static spatial location.

mean that short-range motion (or luminance-defined, 'first-order' motion) is 'pre-attentive', that is, occurring as a result of parallel data-driven processing and operating without attention, and that long-range (feature-defined) motion requires the serial allocation of focussed attention. However, interpretation of the presence and absence of set size effects as reflecting serial attention versus parallel data-driven mechanisms, respectively, has been criticized[15,16] because both results can be accounted for by parallel processes operating with or without attention at different speeds. Moreover, subsequent studies have shown that short- and long-range distinctions were not particularly good at predicting the presence or absence of set size effects in visual search[20,21]. Rather, aspects of perceptual organization leading to target segmentation and distracter grouping (e.g. motion contrast) seem to determine set-size effects. In summary, these visual search studies have not clarified whether attention modulates motion processing and they do not unambiguously support a late-selection view of motion processing.

Another key observation leading to the belief that motion is 'pre-attentive' is that motion seems to attract attention. In an effort to assess this experimentally, Hillstrom and Yantis[22] used visual search displays in which a single object moved but its movement was unrelated to its status as target or distracter. They found that object motion had no effect on speed of detecting targets defined by other (non-motion) features, neither helping when it was the target that moved nor hindering detection when a distracter was moved. These results indicate that when motion is task-irrelevant, it does not afford object representations any particular advantage in competing for response selection, that is, in 'capturing' attention. It suggests that when motion *is* task relevant, motion may aid rapid detection of targets because motion-processing mechanisms receive attentional facilitation.

Neither the ease of detecting motion nor the idea that motion attracts attention supports the idea that motion processing is purely pre-attentive. Moreover, neither point speaks directly to the issue of whether attentional processes are able to modulate motion processing.

Two levels of visual motion processing

Broadly speaking, processing of visual motion undergoes two levels of processing, a motion data level and an object-relevant level. (These are not meant to correspond to discrete neural locations and each level is likely to comprise several computational stages.) The motion data level, primarily involving V1, uses image filtering mechanisms to extract motion signals generated by first-order (i.e. luminance-defined)[2,4] or second-order (e.g. texture-, stereo-, or motion-defined)[23] information present in the visual array. This level has been generally viewed as a purely stimulus-driven filtering process, uncomplicated by processes responsive to task relevance[2–4,18,23]. Psychophysical data indicating attentional modulation at this level of processing is lacking although recent neuro-physiological and neuro-imaging data support the possibility of attentional modulation at this level's assumed neural correlate (i.e. V1)[24–27].

The object-relevant level is needed to account for motion perception of complex stimuli containing multiple motion vectors, such as transparent motion stimuli, structure-from-motion displays, or partially coherent 'noisy' dynamic dot displays (see Box 1). This level probably integrates and segments motion information collected from the motion data level into discrete object representations[28–32]. Processing here may also generate motion signals based on changes in location of salient features or objects, accounting for motion perception without motion data, that is, when first- or second-order motion is weak (as in some types of 'long-range' motion), conflicting[33,34], or entirely absent[35]. The dorsal extrastriate cortex, especially the human analogue to monkey MT/MST complex (sometimes referred to as hMT+) is thought to be a critical cortical site for this type of integrative motion processing[7,13,27,36–40]. An emerging consensus is that object-based perceptual and attentional mechanisms may interact with integrative motion processing at this level.

Neurophysiological findings

Significant contributions to understanding how attention and motion processing brain mechanisms interact comes from single-unit studies in area MT/MST of the monkey brain[38–40], and from functional imaging[25,27,36,37,41] and event-related potential (ERP) studies[26] in humans. (The stimuli and approach used in some of these studies are shown in Figs 1 and 2, respectively.)

Findings from single-unit studies in MT/MST indicate that when motion stimuli are presented inside a cell's receptive field (see Fig. 1), its response rate will depend on whether the animal is required to use the information in a concurrent task. The magnitude of attentional modulation may depend on the type of motion judgement required, whether motion is a target-defining feature in the stimulus configuration, and whether the target stimulus is inside or outside the cell's receptive field. Although of obvious importance, single unit data are limited in what they can tell us about motion *perception*. Without adequate concurrent behavioural measures, these studies cannot reveal the *qualitative* effects of attentional modulation on either motion sensitivity (i.e. gains versus losses) or on perception (e.g. the presence or absence of direction distortions) because the effect of increments or decrements in neural activity of these units on other perceptually relevant units is not known. Because in all these studies, a subset of single units are reported as remaining unmodulated by attention, these, or non-attentional, motion-responsive units in other unstudied areas, could mediate behavioural thresholds, leaving open the question of how attention affects perception.

Attentional modulation of motion-generated neural activity in humans has recently been observed using ERPs[26] and fMRI[25,27,36,37,41]. Using two superimposed, 'transparent' random-dot kinematograms (RDKs), Valdes-Sosa *et al.*[26] reported that ERP responses (P1 and N1) were suppressed for the unattended versus attended RDK even though the two dot arrays occupied the same spatial location. These data support the idea that attentional modulation of very early levels of motion processing can be object-based. Recent functional imaging studies also provide evidence that task relevance affects activity levels of motion sensitive areas in the brain. Stimuli used in some of these studies are shown in Fig. 2. The general result is that several areas in the brain (including hMT+, areas at the V1/V2 border, and V3a) change activity levels depending on the attentional state of the observer. A critical problem for imaging studies is designing conditions that isolate changes to motion alone, as opposed to changes in other stimulus features (as in the O'Craven *et al.* experiment[35]), shifts in general arousal and decision criteria (as in the 'no-attention' condition of Büchel *et al.*[27]), or differences in task difficulty (as in the Beauchamp *et al.* study[37]). Moreover, attention or perception during imaging has either not been assessed or only grossly measured, making links between observed changes in brain activity and perceptual experience somewhat tentative. Behavioural studies that have used greater precision in assessing perception and controlling attention will now be considered.

Perception of moving stimuli

Surprisingly few studies have measured the effects of attention on the perception of visual motion. Most of these measured the effect of instruction sets on the *illusory* perception of motion of stationary or directionally ambiguous stimuli, with only a few measuring the effect of attention on the perception of actually moving stimuli.

In a recent study, my colleagues and I measured the effects of attention on global motion sensitivity by assessing the motion coherence threshold, using RDKs as stimuli[42] (see Box 1). We chose this approach because performance of the RDK task probably involves hMT+[7,13,34] and attention affects activity levels in this structure[36–40]. We combined a well-studied paradigm for measuring attention (the negative priming paradigm[43]) with an observation Isaak and I had made earlier[44]. We showed that brief (about 500 ms) exposure to a coherently moving RDK (prime) caused the motion coherence threshold of a subsequently presented, similar RDK (probe) to be significantly elevated (compared with a no-prime condition), if the global direction in both RDKs matched. If they were opposite, coherence thresholds were lowered.

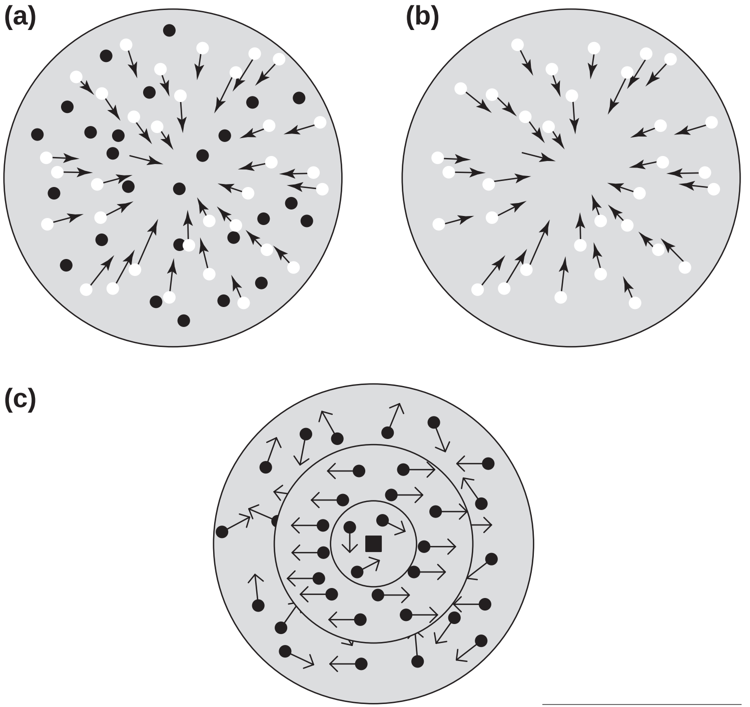

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Fig. 2. Stimuli used in fMRI studies of attention and motion in humans. (a) The dual random-dot flow field used by O'Craven *et al.*[36] In one experiment observers attended alternately (every 20 s) the moving white dots or the stationary black dots. Differences in activity levels in hMT+ for the two attention states were observed but could have been due to either colour or motion changes in the to-be-attended stimuli. In a second experiment, similar stimuli were used but the colour of the moving dots alternated every 20 s and observers were told to attend to the black dots only. Activity in hMT+ was reduced when moving dots were white and observers attended black dots compared with when moving dots were black and black dots were attended. Observers were not required to use the visual information in any way (attention was not actually measured) in either experiment. **(b)** Büchel *et al.*[27] used a single radial flow field display and compared activity levels when observers were asked to monitor subtle speed changes (performance was not measured) versus a 'no attention' condition. Differences in activity levels in hMT+ as well as V3a and the V1/V2 border were observed. **(c)** Beauchamp *et al.*[37] used an annular array of coherently moving dots (indicated by the solid lines) viewed against a zero coherence RDK and a central fixation square. Stimuli remained unchanged throughout the experiment and, in different episodes, observers made judgements about (1) the movement of dots in the annular ring, (2) the colour of the dots in the annulus, or (3) luminance changes of the fixation spot. Activity in hMT+ was greatest when attention was directed at the location of the motion stimulus and when the task was movement versus colour based.

To explore whether attention played a role in these priming effects, we elaborated the procedure by asking observers to use selective attention to make a judgement about the prime stimulus (see Fig. 3). On most trials the prime was composed of two transparent sheets of orthogonally moving dots (e.g. 50% of dots moved downwards and 50% moved leftwards). The probe had only one global direction (chosen randomly from four alternatives) and its coherence was varied so the coherence thresholds for the probe stimulus could be measured. On other trials, the prime had only one coherent direction (with 50% noise elements). On each trial,

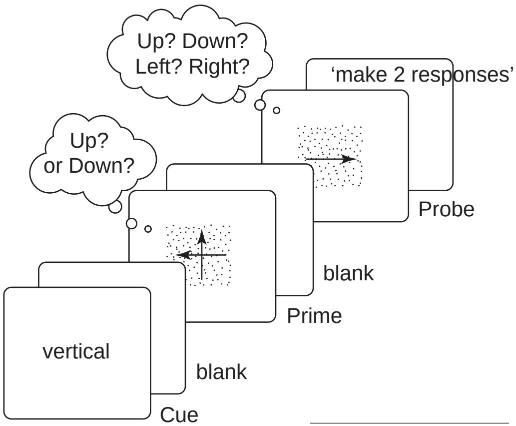

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Fig. 3. An example trial in the motion-priming experiment[42]. After pressing a button, the observer viewed a cue, a prime, and a probe, presented successively with blank intervals between. The prime (600 ms) was a dynamic dot display with half the dots moving in a vertical direction and half in a horizontal direction, which appeared as two transparent sheets of dots. The probe (96 ms) was a similar dot display except that the percentage of coherently dots was varied from trial to trial. The interval between the two stimuli was 200 ms. There were two tasks: identify the direction in the prime moving in the axis specified by the cue ('vertical' or 'horizontal') and identify the global direction in the probe. By changing only the cue word, the effect of attentional selection on correct identification of movement direction in the probe could be assessed without changing stimulation to motion analysers. In a control experiment, only arrows (no RDKs) were presented in the prime.

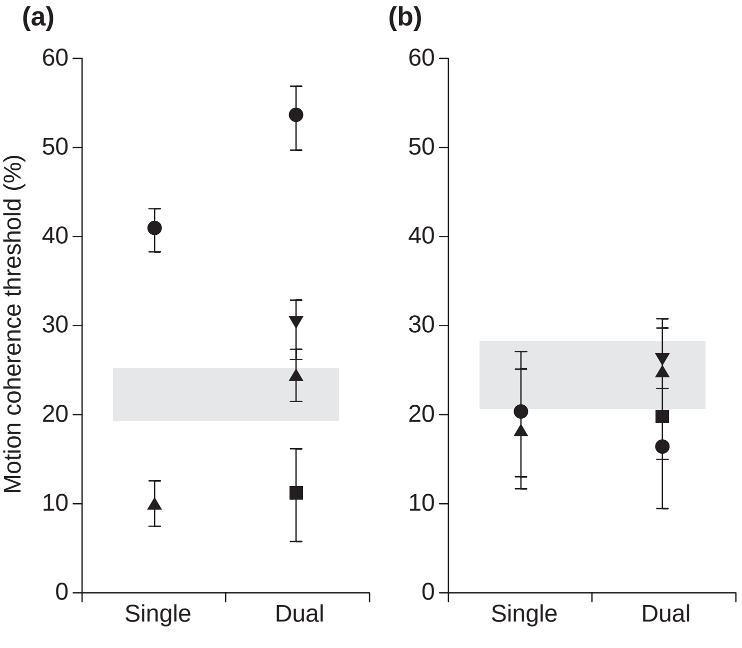

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Fig. 4. Group mean motion coherence thresholds obtained in the priming experiment[42]. Thresholds (% coherence) are shown for partially coherent probes presented after **(a)** single and dual direction coherent motion primes, or **(b)** symbolic arrow primes consisting of one or two arrows. Data obtained when the cued (target) direction in the prime matched (circles) or was opposite (triangles) to that of the probe is shown for all conditions. For dual direction primes, group thresholds obtained when the non-cued (distracter) prime direction was matched (squares) or opposite (inverted triangles) to that of the probe are also shown. Vertical lines represent ±1 standard error of estimate (s.e.e.). The hatched area indicates mean baseline threshold ±1 s.e.e.

the observer was first presented with a cue word ('horizontal' or 'vertical'), then the transparent prime (600 ms), a brief interval, and then a 40 ms probe stimulus. The task was to report the direction of the motion component identified by the cue and then to report the probe direction. By simply changing the cue word, the to-be-attended and to-be-ignored component in the prime could be switched without any change to the motion stimuli. The prime task allowed us to monitor how attention was being allocated during the prime presentation on each trial. Performance on the probe task was only analysed on prime-correct trials. To determine whether priming effects were due to semantic priming or directional words, we repeated the whole experiment using symbolic arrows in the prime rather than RDKs. The probe task and responses required were the same as before but there was no motion in the prime.

With RDK primes (but not with arrow primes), we found evidence of attentional control over motion coherence thresholds. We found that thresholds were significantly higher when the probe direction matched the attended direction than when the probe direction matched the ignored component (Fig. 4). The stimuli in these two conditions are identical; only the behavioural relevance of the prime components is different. Yet, thresholds for the probes were altered from 54% in the attend-match compared with 11% in the ignore-match condition. Furthermore, when the attended and test directions matched, coherence thresholds were significantly higher with dual direction primes than with single direction primes. Because attentional selection is more difficult with dual primes (yet physical stimulation in the to-be-attended prime direction was the same), the larger threshold elevations found in the dual prime condition indicate that attentional processes play a primary role in changes in global motion sensitivity produced by motion priming. An interesting side note is that sensitivity for a direction opposite to the attended prime direction was not different from baseline, indicating that priming effects occur after any motion opponency is computed. This experiment indicates clearly that attention to one direction causes a loss in sensitivity to that direction in a subsequent event, whereas actively ignoring a direction enhances sensitivity for that direction. These effects are opposite to more typical negative priming effects (where ignoring an item causes reduced subsequent processing)[43]. However, if we consider that changes in an object's motion are more salient than continuation along a trajectory, mechanisms to reduce sensitivity to already coded information make sense.

Effects of prior information on motion perception have also been reported by Ball and Sekuler[45,46]. In one study, they presented successively two similar circular grey patches. One contained low contrast coherently moving dots and the other did not. The task was to indicate the interval containing the moving dots. In one condition, only one (predictable) motion direction occurred and in the other, two unpredictable directions were presented. Observers were more accurate in the predictable condition, suggesting that a task-dependent process could have been deployed to monitor motion detection channels selective for a specific direction of motion. Both these cueing and our priming studies indicate that task-relevant information affects motion sensitivity.

Gogel and Sharkey[47] asked whether attention could modulate a stimulus interaction effect in motion. When an object is oscillated vertically whilst a second object is oscillated horizontally, the perceived direction of the first will be distorted so that it appears to move along an oblique trajectory, away from the horizontal object's path. Their experiment exploited this stimulus interaction effect (see Fig. 5) and demonstrated that attention can dramatically determine object motion interactions. Such phenomena merit more study, especially in light of Treue and Maunsell's[38] study that used stimuli similar to the inducers used here. Unfortunately Gogel and Sharkey did not measure attention, nor make its selective allocation task-relevant. Because the primary task was to judge the direction of the target, how attention may have been allocated to inducing stimuli in this situation is somewhat unclear and limits interpretation of these nevertheless interesting results.

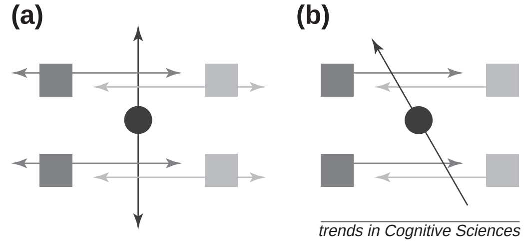

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Fig. 5. A motion interaction effect that depends on attention. (a) The stimuli used by Gogel and Sharkey[47]. 'Inducer' squares oscillated horizontally whilst the target circle oscillated vertically. At the start of each trial, two of the inducers were blue, appeared on, say, the left and began moving in tandem with, in this case, a rightward motion. The other two were red, appeared on the opposite side, and began moving in tandem in the opposite direction. The observer was instructed to attend to the red or blue objects only and to report the perceived direction of the vertically moving target. **(b)** A typical percept experienced during rightward motion of the attended (darker) inducers. The path of the circle is perceived as oblique with the direction of motion repulsed from that of the attended squares. Attending to the lighter squares is reported to cause the circle to appear to be moving in an upward and rightward direction. Although the stimuli were identical in both instructional conditions, the perceived orientation of the target's path was determined by the to-be-attended inducer motion.

Illusory motion perception

Research on attentional control over illusory motion perception has been directed primarily at the motion aftereffect (MAE) and the illusory line motion (ILM) effect. A major problem with exploiting these illusions to study attention is that the neural sites and mechanisms mediating them remain elusive[48], making interpretation of attention effects also elusive. Nevertheless, the results are clear: attending to objects makes stimuli related to them more likely to produce illusory motion experiences.

The MAE is the illusory perception of motion in one direction of a stationary or directionally ambiguous pattern after prolonged viewing of (adaptation to) a similar pattern moving in the opposite direction. Although Wohlgemuth's often-sited 1911 report[49] describes how the illusion is unaffected by other concurrent and distracting tasks performed during adaptation, it is now clear that the observer's attentional state during motion adaptation has a modulating effect on the illusion[41,50–54]. In the first demonstration of this, Chaudhuri[50] manipulated the task required of observers during adaptation (see Fig. 6). His results showed clearly that the magnitude of the MAE depended on attending the moving adapting stimulus. Another similar study manipulated the linguistic load in a secondary task during motion adaptation[41] and reported that pulling attention away from the motion adaptation stimulus reduced the MAE and was accompanied by reductions in activity levels in hMT+ as measured using fMRI.

Attention effects on motion aftereffect have also been studied using bi-directional adaptation patterns, such as transparent moving dot arrays[51–53] and plaids[54]. In most of these studies, observers are instructed to attend to motion in one direction or the other, or to passively view the bi-directional display. With no specific instructions, a single direction MAE in the direction opposite to the vectorial sum of the two component directions is typically reported[55]. With instruction to attend to a single surface, motion aftereffects are consistent with (i.e. opposite to) the attended adaptation direction[51–54]. A shortcoming of these studies is that attention was not measured. Manipulating attention by instructions to 'attend' to one stimulus or another (or neither), without simultaneously requiring the observer to *use* the to-be-attended information in any task makes the behavioural relevance of the assumed attention mechanism obscure. Such studies cannot ascertain attentional compliance on a trial by trial basis, are susceptible to demand characteristics, and give no indication of the attentional load required to follow the instruction set. They are further complicated by use of a 'passive' viewing baseline in which observers may be attending alternately to both motion surfaces.

However, taken together, the MAE studies clearly indicate that attention can modulate the mental representations of motion. An open question is whether attention acts late in processing by modulating conscious awareness of a data-driven, post-adaptation illusory motion signal, or influences the effects of prolonged exposure to motion on early motion analysers (e.g. via fatigue or inhibitory processes). As the MAE itself probably reflects the summation of effects at multiple sites in the motion-processing system[48], understanding where attention is influencing motion processing to result in MAE modulation remains unclear.

Illusory line motion (ILM), (also called the shooting-line illusion or the motion-induction effect), is the illusory perception that a line is being lengthened away from a visual focal point when it is, in fact, presented at full length[56]. Experimental study of this illusion has typically involved presenting one or more focal points on an empty field, and then presenting a line. Observers are asked typically to report the direction of illusory motion in the line and to rate its magnitude. This powerful motion illusion appears to depend on the spatial location of attention prior to the line's presentation. If two focal points are presented and the line is positioned as if to connect them, the perceived direction of motion can be manipulated by cueing spatial attention to one point or the other[57]. There are two main theories to explain the effect: the gradient model[56] and an object impletion model[57]. The gradient model assumes that attention is focused spatially, producing a graded speeding of visual signals that falls off with distance from

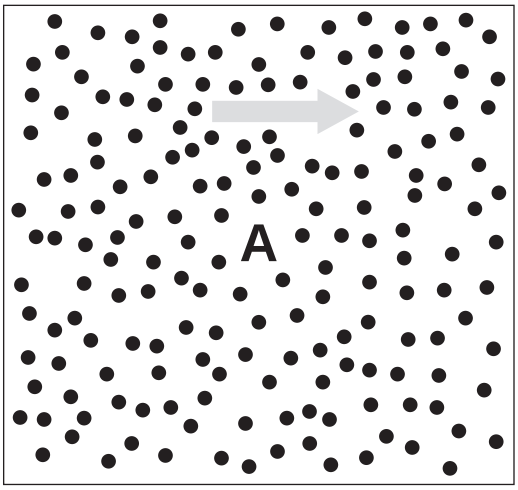

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Fig. 6. The stimuli used by Chaudhuri[50] to study attentional modulation of the motion aftereffect. The adaptation stimulus was a 60 s coherently moving random-dot array with a small letter presented at fixation. The test display was a similar but stationary dot array. During adaptation the letter changed four times per second, only occasionally becoming a number. In the two critical conditions observers were told either to ignore the changing central letter or to press a button whenever a number appeared. The duration of the MAE was reduced when viewers engaged in the number detection task compared with when they were told to ignore the alphanumeric stimuli. In other conditions, observers were required to report occasional colour changes in the dot array during adaptation. This task did not affect MAE duration, suggesting that simply engaging in a task during adaptation could not account for the MAE reductions seen in the letter task.

the attended location. Differences in the arrival time of visual signals to motion analysers is thought to give rise to the illusion of motion[56,58]. Thus in this model, attentional modulation of processing is thought to occur prior to processing by motion analysers, placing it at potentially very early stages of processing. Support for this is that the illusion can be nulled by manipulating the line's luminance gradient[59].

The object impletion model[57] proposes that mechanisms of long-range apparent motion are used to link the representations of the attended focal stimulus and the line, creating a single albeit changing object representation. Support for this idea is that ILM can be produced from multiple sites simultaneously[60], a finding that is inconsistent with 'spotlight' metaphors of spatial attention. Probably both gradient effects of spatial attention (giving rise to first-order motion signals) and object linking processes giving rise to object-level motion signals contribute to this illusion. As with the MAE studies, clear interpretation of the effects of attention on the line motion illusion awaits greater understanding of the illusion itself.

Outstanding questions

- If attentional modulation of motion is object-based, then would attentional motion priming effects be absent when primes and test objects are distinctly different objects?
- Does the repulsion effect seen in Gogel and Sharkey's study[47] represent an object-based motion interaction? If inducers and target were perceptually grouped as belonging to the same object versus different object, would repulsion effects still be produced?
- Would ILM effects be found with texture- or motion-defined stimuli that do not produce luminance change when presented? Impletion models suggest that they should but (simple) gradient models do not.
- Would attention to a moving object for the purpose of gaining non-motion information (e.g. the object's colour or shape) still produce attentional modulation of motion-processing areas? Beauchamp *et al.*'s study[37] suggests that it would, but behavioural studies using motion priming or MAE are needed to reveal the magnitude and quality of perceptual effects of such object-based attention.

Why should attention modulate motion perception?

Both neuroscience and behavioural data indicate that attention influences motion processing, especially at the object-relevant level of processing. Why might this occur and how do such interactions integrate with attentional processes more generally? Perhaps some answers can be found in object-oriented attention theories. Because a significant amount of human action is directed at physical objects, it has been sensibly proposed that the perceptual and attentional mechanisms of the brain are organized to promote rapid perception and awareness of *objects*[61,62]. Object-oriented theories of perception posit that attention acts to facilitate processing of visual (and other sense modality) information descriptive of task-relevant objects and, at the same time, inhibits processing of information descriptive of distracting objects. The idea is that brain deals in the currency of object representations, not disembodied stimulus features.

A convenient metaphor for understanding object representations and their relationship to stimulus features is the 'object file'[63]. An 'object file' is a hypothetical, complex, whole-object representation that contains descriptors of the object's various features, like notes in a file folder. In most expressions of this idea, it is proposed that low-level visual sub-systems analyse various aspects of the visual array, contributing information called 'tags' about the features (e.g. location, colour, shape, motion) of the selected object. Attention is required to create the 'file' by binding the 'tags' sharing similar spatiotemporal locations.

How might the brain implement this? Duncan[62] proposed that within each brain system attentional mechanisms operate in a competitive manner (preferentially processing task-relevant information at the expense of distractor information) and that such activity is co-ordinated among different brain systems. With successive iterations of task-relevant competition, different brain networks settle on perceptual promotion of the *same* object, ignoring the *same* distractors. In visual processing, the co-ordinated competitive activity of neural networks may be seen as the 'file' binding together the features derived from different visual modules. It suggests that competitive, task-relevant activity should occur with each module, including, of course, the motion module. Such ideas provide a rationale for why task-relevant modulation of neural activity seems to occur within the visual motion modules of the brain.

In the natural world, dramatic changes in visual stimuli can occur without coherent object representations being disrupted. Substantial object motion or deformation, observer head or eye motion, cast shadows, or the temporary presence of occluding objects can occur without evoking the perception that an object has vanished. For example, if you view a person's fist which is then made into an open hand, you do not experience the arrival of a new object, but rather sense the transformation of an 'old' object. How is this accomplished? One suggestion is that the feature tags in the 'object file' (or activity of neural networks) are checked against current sensory input on a regular and frequent basis. If the correlation between just stored and current information is reasonably high but not perfect, then the object file (or network configuration) is simply updated and the same object is perceived as present, albeit in its moved or modified state. If, on the other hand, the correlation is low, then the old file is scrapped, a new file is constructed, and the appearance of a new object is experienced. Clearly stimuli in motion benefit from a high correlation between just stored and current sensory information. Motion may thus provide an important sensory signal for maintaining and updating, as opposed to destroying, existing object files. Selective activation of visual motion processing in object-specified terms should facilitate object file maintenance. Thus, object-oriented theories of attention provide a rationale for why motion processing, at least at object-relevant levels, may be modulated by attention.

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Do the eyes have it? Cues to the direction of social attention

Stephen R.H. Langton, Roger J. Watt and Vicki Bruce

The face communicates an impressive amount of visual information. We use it to identify its owner, how they are feeling and to help us understand what they are saying. Models of face processing have considered how we extract such meaning from the face but have ignored another important signal – eye gaze. In this article we begin by reviewing evidence from recent neurophysiological studies that suggests that the eyes constitute a special stimulus in at least two senses. First, the structure of the eyes is such that it provides us with a particularly powerful signal to the direction of another person's gaze, and second, we may have evolved neural mechanisms devoted to gaze processing. As a result, gaze direction is analysed rapidly and automatically, and is able to trigger reflexive shifts of an observer's visual attention. However, understanding where another individual is directing their attention involves more than simply analysing their gaze direction. We go on to describe research with adult participants, children and non-human primates that suggests that other cues such as head orientation and pointing gestures make significant contributions to the computation of another's direction of attention.

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Since the early 1980s, considerable progress has been made in understanding the perceptual, cognitive and neurological processes involved in deriving various different kinds of meaning from the human face[1,2]. For example, we now have a much better understanding of the operations involved in recognizing a familiar face, categorizing the emotional expression carried by the face, and of how we are able to use the configuration of the lips, teeth and tongue to help us interpret what the owner of a face is saying to us (see Ref. 2 for a review). In their influential model of face processing, Bruce and Young[3] proposed that these three types of meaning – identity, expression and facial speech – are extracted in parallel by functionally independent processing systems, a suggestion for which there is now converging empirical support[4] (although see Refs 5,6 for some complications).

However, in common with other cognitive models of face processing, Bruce and Young's account neglected a number of additional facial movements that convey important meaning and make substantial contributions to interpersonal communication. One such signal – gaze – has been widely studied by social psychologists who have long known that it is used in functions such as the regulation of turn-taking in conversation, expressing intimacy, and exercising social control[7]. Despite this knowledge, interest in the perceptual and cognitive processes underlying the analysis of gaze and gaze direction has only emerged in recent years, particularly stimulated, perhaps, by the work of Perrett[8,9] and Baron-Cohen[10,11].

Perrett and his colleagues have proposed a model based on neurophysiological research, which we outline later in this

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