

Modulating Irrelevant Motion Perception by Varying Attentional Load in an Unrelated Task

Geraint Rees,* Christopher D. Frith, Nilli Lavie

Lavie's theory of attention proposes that the processing load in a relevant task determines the extent to which irrelevant distractors are processed. This theory was tested by asking participants in a study to perform linguistic tasks of low or high load while ignoring irrelevant visual motion in the periphery of the display. Although task and distractor were unrelated, both functional imaging of motion-related activity in cortical area V5 and psychophysical measures of the motion aftereffect showed reduced motion processing during high load in the linguistic task. These findings fulfill the prediction that perception of irrelevant distractors depends on the relevant processing load.

To what extent does perception depend on attention? This issue has been a central question in attention theory over the past 40 years, yet it remains unresolved. Two contrasting positions have emerged. Some studies have suggested the importance of attention for perception, showing that unattended stimuli apparently receive very little processing (1). Other studies, however, have implied that unattended stimuli can be perceived and have some effect on behavior as measured by indirect methods (for example, reaction times and evoked potentials) (2). Here, we combine functional imaging and psychophysics to test a theory that resolves the long-standing controversy between these two established positions.

Lavie's theory (3) proposes that capacity for perception is limited but that, within those limits, perception proceeds automatically. Thus, although we may not be able to perceive everything, we are unable to stop perceiving whatever we can. The extent to which a target task exhausts available capacity thus determines the extent to which irrelevant distracting stimuli will be processed. If the processing load of the target task exhausts available capacity, irrelevant stimuli will not be perceived. However, if the target-processing load is low, attention will inevitably spill over to the processing of irrelevant distractors (4). The extent to which irrelevant stimuli are excluded from perception does not thus depend simply on participants' intentions to ignore them. Irrelevant stimuli are excluded from perception only when the processing load of a task engages full attention under conditions of high load (5).

We sought to investigate this theory by studying the perception of irrelevant visual

motion during performance of a task requiring linguistic judgments on single words. Although both of these tasks require visual input, they are thought to rely on completely different psychological processes. Yet, if both depend on a common source of attention, as the load theory suggests, then they should be strongly interdependent. Specifically, we predicted that participants would fail to ignore irrelevant visual motion as long as processing load in the linguistic task was low but that higher load in the linguistic task would prevent perception of the irrelevant motion. Despite participants' wishes to ignore the motion distractors in all conditions, they would only succeed in doing so under conditions of high load in another task that exhausted their attentional capacity.

Visual motion was used as a distracting stimulus as it is known to activate a distinct area of the brain, V5, whose location has been reliably identified in previous functional-imaging studies (6, 7). Activation of V5 by a moving stimulus should therefore allow determination of whether processing of irrelevant visual motion has occurred. Previous functional-imaging, psychophys-

ical, and single-cell electrophysiological studies have all suggested that motion perception may depend to some extent on attention (8–12). However, none of these studies have provided a critical test for our claim that the crucial factor determining when participants can ignore motion distractors is the attentional load in an unrelated task. Every previous study has compared explicit attention to motion with explicit ignoring of motion. Any difference in motion-related brain activity between these two conditions can be attributed to an enhancement of perception with deliberate attention to the moving stimulus, rather than successful ignoring of motion in the unattended condition. These previous studies therefore cannot provide any clear answer to the principal issue in attention theory: whether irrelevant distractors can be excluded from perception. Here, we test the load theory by characterizing changes in selective processing of a motion stimulus that is always irrelevant, while varying the attentional load of an unrelated target task.

For the irrelevant motion stimulus, we used an optic flow field with a full field of dots moving radially toward the screen edge. This type of motion may be particularly difficult to ignore because of its biological relevance (13). Irrelevant motion processing was characterized by measurement of brain activity in motion-related areas during changes in the demands of an imposed (and unrelated) linguistic task. Participants viewed a display with two different components. In the periphery of the display were scattered white dots. We assessed motion perception by comparing conditions under which these dots moved with conditions under which the dots were static (14). Participants were asked to ignore the white dots throughout and were told that the dots were always irrelevant to the experiment and might produce unpleas-

Table 1. Areas where evoked activity during visual motion (compared with the no-motion conditions) was significantly greater under conditions of low load (compared with high load) (19, 20). Only areas that are also active during the comparison of visual motion (irrespective of load) and rest (fixation) are shown (20), to ensure that only areas concerned with the processing of visual motion are considered. Only areas that reach $P < 0.05$ after correction for multiple comparisons are reported, except in V5, where a threshold of $P < 0.001$ uncorrected was used (because of our previous anatomical hypothesis for this area).

Area	Talairach coordinates	Z score
Left V5 complex	-44 -64 4	6.69
Right V5 complex	42 -66 -8	3.40
Right V1-V2	26 -96 -8	5.67
Superior colliculus	-2 -26 -2	5.02
Left fusiform	-40 -74 -14	5.52
Left lingual gyrus	-8 -80 -12	5.14
Right premotor cortex	10 2 68	5.06
Left superior parietal lobule	-26 -64 32	4.79
Right superior frontal gyrus	8 58 26	5.62

G. Rees and C. D. Frith, Wellcome Department of Cognitive Neurology, Institute of Neurology, 12 Queen Square, London WC1N 3BG, UK.

N. Lavie, Department of Psychology, University College London, Gower Street, London WC1E 6BT, UK.

*To whom correspondence should be addressed. E-mail: g.rees@fil.ion.ucl.ac.uk

ant motion aftereffects if they were not ignored. In the center of the display, single words were presented successively in a blank ellipse that separated them from the dots (15). Participants were asked to focus on these words and, during low-load conditions, press a key whenever a word was printed in uppercase letters. Under high-load conditions, they saw the same letter strings but were now asked to press the button whenever they saw a bisyllabic word. Each participant performed both high- and low-load tasks, with and without irrelevant visual motion, while undergoing functional magnetic resonance imaging (fMRI) (16). We confirmed that processing load was manipulated appropriately by recording participants' responses in the linguistic task (17).

The critical test of our hypothesis is whether evoked activity related to irrelevant visual motion (compared with no motion) is smaller under conditions of high processing load (compared with low load). This pattern of modulation is represented by the interaction term in the factorial design of the experiment. We therefore constructed the statistical parametric map that reflects this interaction between processing load and visual motion, using statistical parametric mapping (SPM) (18, 19). Data from all six participants were analyzed as a group to identify areas activated in common across all participants. This analysis identified several areas (Table 1) in which the effect of visual motion (compared with no motion) was greater under conditions of low load (compared with high load). Our discussion will be limited to those areas at or before V5 in the pathway for the processing of visual motion (6, 7, 20).

Robust bilateral modulation of V5 complex activity, related to visual motion by load in the target task, was identified (Fig. 1) (21). This interaction of motion and load is in accord with our experimental hypothesis. Under conditions of low load, the moving dots produced strong activation compared with the static dots (and baseline fixation), suggesting motion perception. However, under conditions of high load, there was no increase in activity associated with the moving dots. Thus, under conditions of high load, we infer that distracting visual motion was not processed, whereas under low-load conditions it was processed. In other words, despite our instructions to participants to always ignore the dots, their perception of irrelevant visual motion was in fact determined by the experimental manipulation of load in an unrelated task and not by their intentions alone.

We tested this result further in a second experiment that was adapted from

Chaudhuri's psychophysical procedure (8) to make it suitable for testing the load theory. Prolonged exposure to visual motion, followed by viewing of a static stimulus, produces an illusory perception of opposing motion in the static display that fades over time. This motion aftereffect is contingent on V5 activity (22) and has been shown to be sensitive to attention (8, 9). The duration of this aftereffect can therefore serve as a behavioral probe for the extent of irrelevant visual motion processing in our task, allowing a convergent test of our load hypothesis. The pattern of evoked activity observed in V5 complex suggests that the motion aftereffect should be substantially reduced under high-load conditions of the linguistic task. Four participants viewed displays identical to those used in the functional-imaging experiment while performing either the high- or

low-load task. The surround was always moving and was followed by a static full field of dots that produced a vivid motion aftereffect, where the static dots appeared to radially contract. This motion aftereffect was significantly shorter under conditions of high load than under conditions of low load for all participants (23). This result is consistent with both our theoretical predictions and our observation in the fMRI study that motion-specific responses were suppressed with high load in the linguistic task.

In the functional-imaging data, a number of other areas, predominantly visual, showed a significant modulation of motion-related activity by processing load in addition to V5. Our results suggest that the effects of processing load become manifest at multiple levels of the sensorimotor network, including very early visual areas.

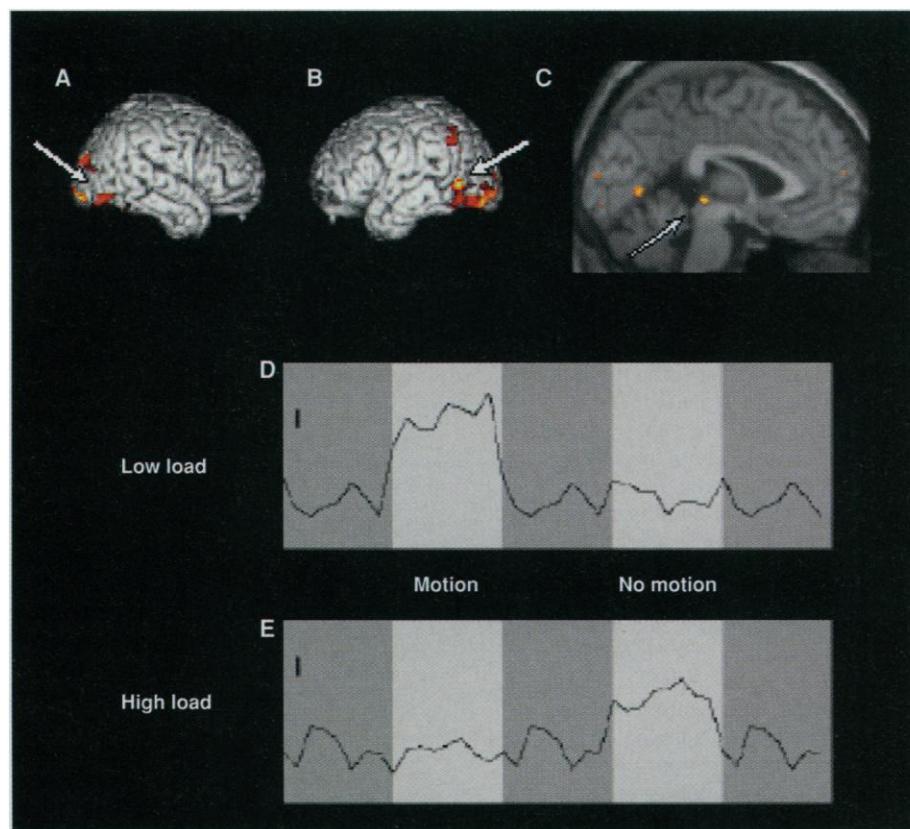


Fig. 1. (A and B) Lateral views of the right and left hemispheres of a T1-weighted volume-rendered anatomical image that conforms to the stereotactic space of Talairach and Tournoux. Superimposed in red are the areas from Table 1 where brain activity in the group of participants showed the predicted interaction between the effects of visual motion and linguistic-processing load. The locations of the right and left V5 complex activity described in the text and Table 1 are indicated by the arrows. (C) A sagittal slice through the same canonical anatomical image, on which is superimposed the location of activity in the SC (arrow) that is due to the interaction of visual motion and linguistic-processing load. (D and E) Mean activity over all participants and replications of each experimental condition taken from the left V5 complex area described in Table 1. Activity during baseline periods (dark gray shading) is shown alternating with that during experimental conditions (light gray shading). The order in which the conditions are displayed is illustrative and does not correspond to that used in the experiment (because order of conditions was counterbalanced across participants). The statistical comparisons reported in Table 1 and the text refer to the comparison of the experimental conditions (light gray). The scale bar represents a value of 0.1% BOLD signal change.

Differential activation was seen at the V1-V2 border on the right and at a lower significance on the left. Reciprocal connections between V1-V2 and V5 have been demonstrated by reversible cooling of V5 and neuroanatomical studies in monkey (24). Changes in neural responses in early visual cortex that are due to attention have previously been shown in monkey (25, 26); our results show that early visual areas in humans are also sensitive to the effects of attention. Modulation of motion-related activity by attentional load was also seen in the superior colliculus (SC) (Fig. 1). This pattern of evoked responses is compatible with an ablation study in monkey that demonstrated that the impairment in visual discrimination after a lesion in the SC is manifest only when the unaffected part of the visual field contained a competing item (27). Our data suggest that the SC is sensitive to attentional load (rather than just low-level visual competition between stimuli), because we modulated motion-related activity in the SC in our study by varying the processing requirements in a target task without adding more visual stimuli. Thus, there is greater competition for attention with either an increased number of items or with more processing for the same items (4, 26). Moreover, the SC has direct reciprocal anatomical connections with V5, and both the SC and the striate cortex contribute to visual function and motion-specific neural response properties in V5 (28). It is interesting, therefore, that we observe modulation of motion processing by load in an unrelated cognitive task in both the geniculostriate (V1-V2) and retinotectal (SC) pathways by which motion-related signals can reach V5. Although the SC has been implicated in oculomotor control, eye movements do not provide a plausible explanation for our findings (29).

In conclusion, our results demonstrate the use of functional imaging to test a cognitive theory of attention. Specifically, we have proposed a resolution to the longstanding issue of whether perception of irrelevant stimuli depends on attention. Our results show that participants' intentions to avoid irrelevant distractors are not always sufficient for ignoring them. As long as the target task imposes only a low load on attention, irrelevant stimuli such as motion will still be perceived. However, this irrelevant perception is strongly reduced if the load of the unrelated task is increased. Selective perception is therefore possible only under conditions of high load. Under such conditions, even the perception of biologically significant stim-

uli such as optic flow can be reduced by a demanding but entirely unrelated task.

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4. The concept of perceptual load entails increasing the number of items in a display or increasing the processing requirement for the same number of items. For further discussion, see (3).
5. A review of previous behavioral studies of attention supported these claims (3). Results compatible with selective perception were typically obtained in situations of high attentional load, and results compatible with nonselective perception were typically obtained in situations of low load.
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13. Optic flow is continuously used in judgments about motion direction in the environment (for example, an expanding field indicates approaching the source of the expansion) [J. J. Gibson, *The Perception of the Visual World* (Houghton Mifflin, Boston, MA, 1950); *Scand. J. Psychol.* **18**, 161 (1977)].
14. This component of the display comprised 400 single white dots, each subtending 0.1° scattered randomly outside a central ellipse in a display 17° across. When the display was moving, each dot moved radially outward at a constant velocity of $\sim 5^\circ$ per second. As dots left the edge of the display, new dots were added at the periphery of the central ellipse surrounding the words to ensure that the dot density of the display remained constant.
15. High-frequency, five-letter nouns were presented in the center of the display, surrounded by a blank ellipse to distinguish the words from the peripheral display. Each word subtended $\sim 1.4^\circ$, and the ellipse subtended $\sim 2.7^\circ$ (vertical) by 4.1° (horizontal). Each word was presented for 750 ms, followed by a blank interval of 250 ms. During each experimental epoch, there were eight targets and 24 foils. The words were identical for each participant in high- and low-load conditions, although their order within an epoch was randomized. The position of targets within an epoch was constrained to be matching in both high- and low-load conditions. The condition order and stimulus materials were counterbalanced across participants.
16. Informed consent was obtained from six participants (five females and one male; mean age, 24.5 years; age range, 22 to 29 years; five right handed and one left handed). All participants used their dominant hand to respond. A Siemens VISION system operating at 2 T was used to acquire both T1 anatomical and gradient-echo, echo-planar T2* weighted image volumes with blood oxygenation level-dependent (BOLD) contrast. The experiment began with the acquisition of a T1 weighted anatomical image from each participant. Functional imaging was then performed in four separate runs; a total of 280 functional volumes per participant were acquired. Each functional-image volume com-
17. Behavioral data were unavailable from two participants for technical reasons. Participants detected significantly more targets during the low-load condition compared with the high-load condition (80% versus 63%; $t = 3.7$, $P < 0.05$). Participants also made more false positive errors in the high-load condition than in the low-load condition (2.0 errors per block versus 0.9 errors per block; $t = 3.1$, $P = 0.052$). The processing load was thus effectively manipulated by the two tasks.
18. K. J. Friston, A. P. Holmes, J. Ashburner, J.-B. Poline, SPM96 (<http://www.fil.ion.ucl.ac.uk/spm/>).
19. The imaging time series was realigned, spatially normalized to the stereotaxic space of Talairach and Tournoux, and smoothed with a Gaussian kernel of 8 mm full width at half maximum [J. Talairach and P. Tournoux, *Co-Planar Stereotaxic Atlas of the Human Brain* (Thieme, New York, 1988); K. J. Friston et al., *Hum. Brain Map.* **3**, 165 (1995); K. J. Friston et al., *ibid.* **2**, 189 (1995); K. J. Friston et al., *NeuroImage* **2**, 157 (1995); K. J. Friston et al., *Magn. Reson. Med.* **35**, 346 (1996)]. Condition-specific effects were estimated with the General Linear Model with a delayed boxcar wave form. Low-frequency sine and cosine waves modeled and removed participant-specific low-frequency drifts in signal [A. P. Holmes et al., *NeuroImage* **5**, S480 (1997)], and global changes in activity were removed by proportional scaling. The statistical contrast between the condition-specific effects (low load and motion compared with low load and no motion) and (high load and motion compared with high load no motion) represents the interaction term of interest and was used to create an SPM{t}, which was transformed into an SPM{Z} and thresholded at a Z value of 3.09 (corresponding to $P < 0.001$ uncorrected for multiple comparisons). Masking with the contrast between motion conditions and baseline fixation (20) was used to restrict our analysis to areas activated by visual stimulation. Resultant areas of activation were characterized in terms of their peak heights. In cortical area V5, because of our prior hypothesis, we reported activations above a threshold corresponding to $P < 0.001$ uncorrected. However, outside this area, we made a correction (on the basis of the theory of random Gaussian fields) for multiple comparisons across the whole brain volume examined and reported only areas of activity above a threshold corresponding to $P < 0.05$ corrected.
20. We confined our interaction analysis to the subset of voxels that showed significant activation when the motion conditions (irrespective of load) were compared with fixation. This masking procedure does not alter the Z scores or affect statistical inference for the interaction term but represents a way of limiting our interpretation of the data to areas plausibly activated by visual stimulation.
21. To account for the variability in position in human V5 (7), we sought activations within the stereotaxic coordinates defined by Watson et al., plus or minus half the width of the smoothing kernel. We tested whether the right and left hemisphere activations identified were significantly different from each other by comparing the participant-specific effect sizes for conditions of high and low perceptual load. This is formally equivalent to testing for a (load \times motion \times hemisphere) interaction and was not significant ($t = 0.832$, $P > 0.4$).

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23. For each participant, the mean motion aftereffect durations (with standard deviation given in parentheses) for seven repetitions of low- and high-load conditions, respectively, were 9.3 s (2.0) and 6.4 s (1.0) ($t = 3.26$, $P = 0.01$; one-tailed throughout), 3.4 s (0.9) and 2.5 s (0.4) ($t = 2.74$, $P = 0.02$), 13.73 s (2.2) and 11.7 s (1.8) ($t = 1.92$, $P = 0.05$), and 14.9 s (1.6) and 11.4 s (0.9) ($t = 5.02$, $P = 0.002$). Thus, there was a significant decrease in the motion aftereffect duration under high-load conditions in every participant.
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29. A number of factors make this explanation unlikely. Typically, eye movements do not occur with radial optic flow stimuli [see (17) for a full discussion and experimental evidence]. The optic flow display was widely separated from the single words, which were presented foveally for a brief duration, factors that would be further expected to minimize eye movements. Nevertheless, we elected to formally measure eye movements during the experimental paradigm. Technical limitations impede accurate recording of electro-oculography (EOG) while functional images are acquired, so we measured EOG in a single participant performing the experimental paradigm within the experimental apparatus but without acquisition of functional images. The measurement was calibrated and sensitive to saccadic movements of about 1°. During the experimental conditions, no significant eye movements were detected.
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Spatial Pattern Formation in an Insect Host-Parasitoid System

John L. Maron* and Susan Harrison

Spatial models in ecology predict that populations may form patchy distributions within continuous habitats, through strong predator-prey or host-parasitoid interactions combined with limited dispersal. Empirical support of these models is provided. Parasitoids emanating from a population outbreak of tussock moths (*Orgyia vetusta*) suppressed the growth of nearby experimental populations of the moth, while experimental populations farther away were able to grow. This result explains the observed localized nature of tussock moth outbreaks and illustrates how population distributions can be regulated by dynamic spatial processes.

Population ecology has recently seen a surge of interest in spatial phenomena such as limited dispersal, localized species interactions, and habitat geometry. The realization that spatial context may be key to understanding many ecological interactions has been fueled by a profusion of models, and in some cases, a vigorous interplay between theory and empirical research (1). For example, metapopulation models are beginning to enjoy success at predicting the behavior of populations in fragmented habitats. But one well-developed branch of spatial theory has still received little empirical attention: the set of models, many of them based on reaction-diffusion equations, that generate the counterintuitive prediction that patchy distributions in population density can arise even within continuous habitats (2). Such models combine strong predator-prey interactions (the "reaction") with limited dispersal ("diffusion"). Predators are assumed to control their prey, to disperse farther than do their prey,

and to have a partly random element to their dispersal. Under these conditions, the abundant predators supported by a dense patch of prey will spill over at the edges of the prey patch, producing a peripheral zone with a high predator-to-prey ratio that prevents the prey patch from spreading.

These reaction-diffusion (or "activator-inhibitor") models are formally analogous to models of spatial pattern formation in cellular and developmental biology (3), as well as in physics. Computer simulations known as cellular automata have recently made the study of spatial pattern formation more detailed and accessible, compared with purely mathematical formulations (4). If widely applicable, such models force empirical ecologists to rethink their assumption that species' distributions are usually controlled by extrinsic factors such as climate or competition. We show that theory on spatial pattern formation can explain the observed behavior of a natural insect population.

We have been studying a population of western tussock moths (*Orgyia vetusta*, Lymantriidae) (5, 6) that attains high local densities which are spatially stable through time (7, 8). Outbreaks of moths remain spatially restricted despite the widespread and continuous availability of their abundant host plants. Unlike in

some plant-insect herbivore systems, differences in host plant quality or phenology do not explain the patchiness in tussock moth population density (7–9). Rather, poor dispersal of flightless female tussock moths together with low rates of aerial ballooning by young larvae are partly responsible for the restricted nature of tussock moth outbreaks (7–9). Tussock moth larvae are attacked by several generalist predators (10), and larvae, pupae, and eggs are subjected to heavy parasitism by a variety of parasitoids that are local specialists on the moth (11).

Low mobility by the tussock moth and heavy parasitism by its mobile parasitoids suggest that the mechanisms portrayed in models of spatial pattern formation may be operating. Under this hypothesis, rates of parasitism on tussock moths should be highest immediately outside the outbreak and should decline at distances greater than the parasitoids typically disperse. As predicted, recent experiments showed that parasitism was substantially higher on eggs and larvae placed 100 to 600 m from the edge of the outbreak than on those placed within it. Moreover, parasitism increased to 200 m from the edge of the outbreak and then declined (11). These results, plus recent simulation and analytical modeling of our system (12), provide tantalizing evidence for intrinsic spatial pattern formation in this host-parasitoid system. However, a crucial unanswered question is whether distance-dependent parasitism is strong and consistent enough to suppress incipient new outbreaks near the margins of the existing one.

In our experiment, we created new tussock moth outbreaks on lupine bushes at distances of 0 to 700 m from the edge of the outbreak observed the previous year (1996). Because earlier work suggested a possible role for ants and spiders as important larval and pupal predators (8, 10), we simultaneously tested the role of ground-dwelling generalist predators. In February and March 1997, we established two transects emanating from the edge of the

J. L. Maron, Department of Botany, Box 355325, University of Washington, Seattle, WA 98195, USA.
S. Harrison, Division of Environmental Studies, University of California at Davis, Davis, CA 95616, USA.

*To whom correspondence should be addressed. E-mail: jlmaron@ucdavis.edu. Present address: University of California Bodega Marine Laboratory, Box 247, Bodega Bay, CA 94923, USA.