Neural strength of visual attention gauged by motion adaptation

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Single-cell and neuroimaging studies reveal that attention focused on a visual object markedly amplifies neural activity produced by features of the attended object. In a psychophysical study, we found that visual attention could modulate the strength of weak motion signals to the point that the perceived direction of motion, putatively registered early in visual processing, was powerfully altered. This strong influence of attention on early motion processing, beside complementing neurophysiological evidence for attentional modulation early in the visual pathway, can be measured in terms of equivalent motion energy, and thus provides a useful metric for quantifying attention's effects.

From everyday experience, we intuitively know that visual attention enables us to select from a cluttered visual scene only those objects or events of immediate relevance. In the case of vision, it is well established that attention modulates neural activity in several areas within visual cortex[1–3], including V1, the earliest cortical stage[4–7]. This attentional modulation seems to involve a boost in the gain of responses of cells to their preferred stimuli, not a sharpening of their stimulus selectivity[8–11]. Neuroimaging experiments in humans point to comparable attentional effects: brain activity evoked by visual stimuli is enhanced when attention is focused on those stimuli[12].

Although it is straightforward to gauge attention's influence on cognitive and perceptual performance, it is less clear how to specify the gain in neural response presumably underlying attention's influence. We have developed a psychophysical strategy that quantifies attentional gain in the case of visual motion perception, thereby, permitting meaningful comparisons between perception and physiology. Specifically, our strategy used the same metric—motion coherence level—to reveal a striking equivalence of attention's effects measured psychophysically and physiologically.

To probe the visual system's response to motion, we used the motion aftereffect (MAE). The MAE is the illusory motion of a stationary test pattern viewed following prolonged adaptation to a moving stimulus: the test pattern temporarily appears to move in the direction opposite that of the adapting motion. It is already well known that attention can modulate the duration[13] and the perceived strength[14] of the MAE. In our study, we used bivectorial motion stimuli composed of two superimposed fields of drifting random dots (**Fig. 1**). A viewer of these stimuli clearly sees two fields of dots transparently moving across one another. The MAE direction generated by these bivectorial motion fields has a single direction corresponding to the vector sum of the MAEs generated by the separate component motions of the inducing stimulus[15,16]. Thus, varying the strength of one of the components systematically changes the direction of the MAE. If attention to a given direction of motion indeed increases gain in direction-selective neurons[8], then attention alone should be able to induce changes in the perceived direction of the MAE. Specif-

ically, attending to one of the component motions in a bivectorial motion field should shift the direction of the MAE closer to a direction opposite that of the attended motion. Our first experiment tested this prediction.

The 'adapting' dots (**Fig. 1a**) drifted continuously at 100% coherence during adaptation, whereas the 'attentional' dots alternated between 0% coherence and brief periods of weak, coherent motion inserted randomly throughout adaptation (**Fig. 1b**; see Methods). Detecting these motion inserts constituted the attentional task during 'active attention' trials. Passive trials involved observing the same stimuli without performing the detection task. Following adaptation to these two motion vectors, observers indicated the direction of the resulting MAE. As the 'adapting' motion (arbitrarily assigned a direction of 0°) was far stronger than the weak 'attentional' motion, MAE direction should generally have been close to opposite the direction of the adapting motion (180°). Depending on which of the 8 'attentional' motion directions was combined with the adapting motion, small systematic deviations in MAE direction should follow a sinusoidal pattern oscillating around 180° (**Fig. 1c**). The amplitude of the sinusoid would depend on the weights of the vectors, with stronger attentional-motion components producing larger amplitudes. If attention boosted the neuronal response to an attended motion, then active conditions would yield a larger-amplitude sinusoid than passive conditions. In other words, the deviations in MAE direction opposite the adapting motion would be enhanced by active attention[17].

RESULTS

The best-fitting sinusoids provided good descriptions of the active and passive data, with active conditions producing greater deviations in MAE direction (**Fig. 2a**). For the passive conditions, MAE direction did not differ much from the direction opposite that of the adapting dots (180°). Nonetheless, the MAE direction was modulated sinusoidally, indicating that the motion inserts, although weak, were sufficient to influence the bivectorial MAE. The difference between the active and passive conditions was the MAE component attributable to attention *per se* (**Fig. 2b**). Maximum MAE deviation (20°) predictably occurred with attentional
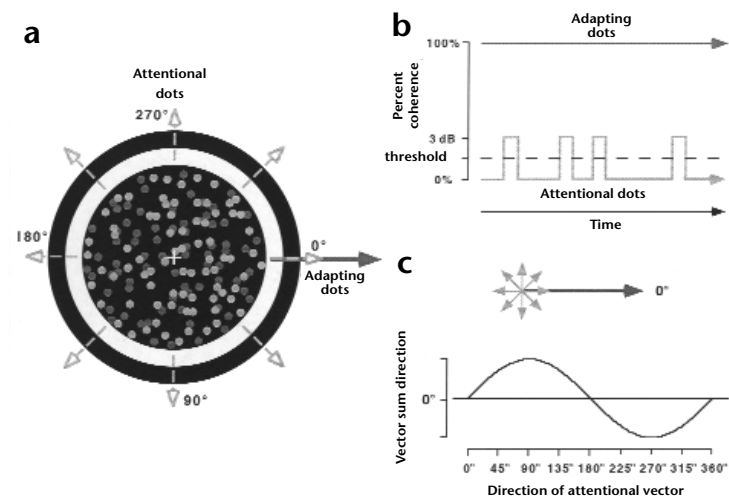
Fig. 1. Bivectorial motion adaptation. (**a**) Schematic diagram of the bivectorial motion display used in these experiments. On a given trial, the lighter colored 'attentional' dots moved in one of eight directions with respect to the darker 'adapting' dots. The adapting dots were arbitrarily assigned a direction of 0°, although between trials, both motions were randomly shifted by 0°, 90°, 180° or 270° to balance the effect of motion adaptation. (**b**) Adapting dots drifted continuously at 100% coherence throughout the adaptation period. Attentional dots alternated intermittently between incoherent motion and brief bursts of weak, coherent motion gauged with respect to each observer's threshold and randomly inserted during adaptation. There were 8 motion inserts during the initial adaptation period (32 s) and 3 during the periods of readaptation (16 s). Detecting these transitions from incoherent motion to weak, coherent motion was the attentional task during active attention trials. (**c**) Vector representation of the motion stimuli. Pairing the strong 'adapting' motion vector with each of the eight weak 'attentional' motion vectors would ideally produce resultant MAE directions that fit a sinusoidal pattern oscillating about the direction of the adapting motion, or 180°. The amplitude of the sinusoid that best fit the data conveniently measures the magnitude of the attentional motion vectors. If active attention to weak motion indeed boosted its effective strength[8], the sinusoid describing the active attention data would have a greater amplitude than that describing the passive attention data.

motion directions of 90° and 270°, where the two motion vectors were orthogonal. Frequency and phase were 1.08 and –8.59°, respectively, close to the ideal values of 1 cycle of modulation with 0° phase lag.

One might wonder why the MAE directions deviated at all from 180°, as the attentional motion was presented only intermittently and weakly. Other evidence, however, implies that brief bursts of motion on the order of a second can produce significant adaptation in cortical motion mechanisms, as revealed by MAEs[14] and by elevations of motion-coherence thresholds[18]. Moreover, because of storage, the adaptation produced by intermittent, weak motion bursts persists and accumulates until it is tapped by a static test figure[19,20].

We also performed a modified version of the experiment in which the pattern of the weak, attentional motion was the inverse of that shown in Fig. 1b. Weak, coherent motion was present throughout most of the adaptation period, with eight randomly inserted one-second periods of incoherent motion. During active attentional viewing, observers tried to detect these brief interruptions in the

weak, coherent motion; during passive viewing, they fixated the stimulus without performing the detection task. In both conditions, the resulting MAEs were deflected farther from 180° than is shown in Fig. 2a, because weak, coherent motion was present for most of the adaptation period. However, the difference between passive and active conditions was similar, with an attentional boost of magnitude comparable to that observed in experiment 1.

Equivalent motion strength

These results imply that attention boosts the cortical response to weak motion signals. Experiment 2 quantified the size of this effect in terms of equivalent motion strength. MAE direction following adaptation to bivectorial motion fields was measured as in experiment 1, but with passive viewing only. Over trials, we varied the coherence level of the intermittent motion inserts (from 0 to 100% coherence, in steps of 25%) to find the motion-signal strength, under passive viewing, producing the same magnitude of MAE deflection measured in the active conditions of experiment 1. Only attentional directions of 90° and 270° were tested.

Results from this experiment mirrored those from the passive conditions of experiment 1, with brief, weak motion inserts shifting the direction of the MAE by about 5° relative to that obtained when inserts were absent (**Fig. 3**). Thus, we could determine the increase in signal strength of motion inserts needed to shift MAE direction by 20°, the shift produced by active attention to the weak motion inserts in experiment 1. From the regression equation, we computed that a coherence level of 71% would produce a 20° shift in MAE direction. This coherence level was approximately threefold stronger than that actually present in the weak, attended motion stimulus employed in experiment 1.

Variable attentional load

It is reasonable to expect that the degree of attentional modulation would vary with the difficulty of the task: relatively easy tasks should require less attention and, therefore, should engender weaker attentional modulation. In the case of the MAE, then, reducing attentional demands should attenuate the shift in perceived MAE direction produced by actively attending to the weak motion inserts. Experiment 3 tested this prediction by varying the coherence of the brief motion inserts over four levels, equal-
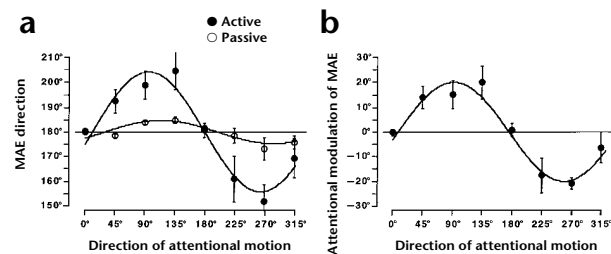

Fig. 2. Results from experiment 1. (**a**) Motion aftereffect directions obtained from pairing eight attentional motions with the adapting motion. Data from active and passive trials are plotted separately. The amplitudes of the best-fitting sinusoids are 24.27° and 4.63°, respectively. (**b**) The magnitude of attentional modulation of direction of motion aftereffect. Data show differences between active and passive trials for each of the eight attentional directions. The best-fitting sinusoid has an amplitude of 20.09°. All data points in this and the following figures show the averages for four observers; error bars indicate ± 1 s.e.
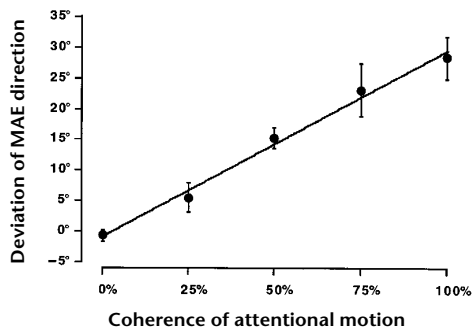
Fig. 3. Experiment 2: motion aftereffect direction as a function of coherence strength of the attentional motions. Data obtained with 90° and 270° attentional motions were pooled and expressed as deviations from 180°. The slope of the regression line is 0.37.

ly logarithmically spaced with respect to each observer's coherence motion threshold. We also tested using 0 and 100% coherence. MAE direction was measured following both active trials, where observers were required to detect brief pulses of coherent motion, and passive trials, where observers simply watched the adaptation display. As expected, stronger motion inserts produced greater deviations in MAE direction. Once again, attention amplified the effectiveness of these motion inserts, especially when those inserts were weak (**Fig. 4**).

Why was attention less effective for stronger coherent motion? One could argue that this was simply a ceiling effect, with MAE deviation reaching a maximum at about 20°. However, in a related experiment, we found that manipulating luminance contrast to vary the conspicuousness of weak attentional motion also modulated the attentional MAE effect: more conspicuous attentional motion produced smaller MAE deviations. We are inclined, therefore, to believe that motion inserts more difficult to detect call for greater attentional vigilance during adaptation, consistent with the proposal that selective attention is most pronounced on tasks involving high perceptual load[21,22]. Not surprisingly, the attentional effect was also small for motion inserts with little or no coherent motion signal. Attention is regarded as a process by which given features are selected for more detailed analysis[23]. If motion inserts were below the perceptual threshold, then there would be no motion signal for attention to operate upon.

Discussion

Attention boosts the strength of weak, coherent motion, amplifying its contribution to the perceived direction of the MAE. By measuring perceived MAE direction while varying the strength of the motion adaptation signal, we estimated that the effect of attention was approximately equivalent to a 0.5-log unit increment in the actual signal strength of weak, coherent motion. How does this value translate into amplified neural responses? We can estimate the equivalent increase in neural responsiveness by determining the magnitude of increase in response produced by an increment of this magnitude in motion signal strength. To derive this estimate, we used published data on responses of neurons in primate area MT, an important stage in motion processing. Of course, individual neurons vary considerably in their response gains, but on average, a 0.5 log-unit signal increment doubles a neuron's firing rate[24]. So, under the conditions of our experiments, focused attention on weak, coherent motion was roughly equivalent to a 100% increase in neural firing rate.

A percentage increase of this order is certainly large, but not unexpected. Our protocol involved competing stimuli within the same spatial location. This configuration is generally associated with the larger attentional modulations reported in the neurophysiological literature, both in motion processing areas MT and MST[8,10] and in other visual areas[1,11]. Neurons in areas MT and MST, for example, roughly double their responses when a moving stimulus within the receptive field is the focus of attention[10]. Also, the random insertion of weak, coherent motion demands constant attentional vigilance throughout the adaptation period, which could further enhance attention's potency[25].

Our experiments, by requiring selection of one motion from two competing motions within the same spatial location, tap into feature-based attentional processes. Despite its potency in amplifying suprathreshold stimuli, attention cannot fabricate coherent motion when it is not present in the stimulus, as demonstrated by attention's failure to confer adaptation power to a 0% motion signal. Feature-based attention is grounded in sensory input: if no feature is detected, it cannot be amplified. This limitation is adaptive, for otherwise an observer's expectations could override sensory signals. We need to see what is actually present in the world, not what we think might be there.

Methods

Four observers, including one author (DA), participated in these experiments. Stimuli were programmed using Matlab (Math Works, Natick, Massachusetts) software in conjunction with the Psychophysics Toolbox[26]. A 6.7° aperture contained two sets of random dot patterns and a central fixation cross. These were surrounded by a bullseye pattern to elicit stronger MAEs[27]. The two sets of dots differed in luminance to facilitate their segregation into two transparent planes (see below). To adapt neurons selective for a given direction, the darker, 'adapting' dots (8.3 cd per m^2; $n = 100$) drifted smoothly at 2.5° per s in that direction throughout the adaptation period. The lighter, 'attentional 'dots (16.6 cd per m^2; $n = 100$) moved completely incoherently except for 1-s periods of weak, coherent motion inserted randomly throughout the adaptation period. These dots were the focus of the attentional task described below.

Observers adapted to the superimposed motions of attentional and adapting dots in the following sequence: an initial adaptation period (32 s) was followed by 3 additional readaptation periods (16 s each) and a subsequent 60-s pause. After each adaptation period, the dots ceased moving and the observer indicated the MAE direction using a mouse cursor. To indicate the forthcoming attentional condition, adaptation
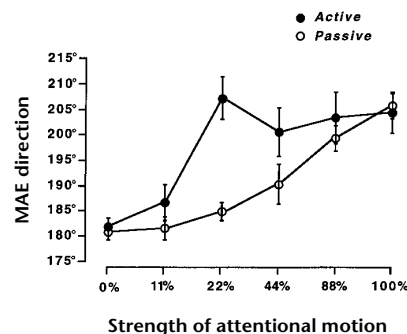

Fig. 4. Experiment 3: motion aftereffect direction as a function of coherence strength of the attentional motion inserts, shown for active and passive conditions. Average coherence threshold for observers was 11%. Thus the average coherence levels for the four motion strengths were 11%, 22%, 44% and 88% (percent coherence).

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sequences began with appearance of the word 'active' or 'passive' on the video screen. In passive trials, the observer simply fixated the central cross without trying to detect weak motion inserts. On active-attention trials, an arrow cued the direction of the weak motion. While fixating the central cross, the observer monitored the incoherent sheet of dots for brief insertions of weak, coherent motion in the cued direction, clicking the mouse button whenever an insert was detected. There were eight discrete motion inserts during the initial adaptation period and four inserts during the readaptation periods.

Observers had to detect and respond to the motion insert during its 1-s presentation. In this way, task vigilance could be measured and a performance criterion was set for data to be included. Observers had to detect at least six motion inserts during initial adaptation (three during readaptation), with no more than two misses or false alarms (one during readaptation). If performance during an adaptation sequence failed the criterion, the data were rejected and the whole sequence was repeated at the end of the session.

On a given adaptation sequence, the adapting dots were first arbitrarily assigned a direction of 0°. The motion inserts for the attentional dots were randomly assigned one of 8 directions, either 0°, 45°, 90°, 135°, 180°, 225°, 270° or 315°. Then, a direction (0°, 90°, 180° or 270°) was added to both motions to balance the effects of adaptation over trials. For each observer and for each of the eight directions, coherence levels for the motion inserts were standardized at a value double the detection threshold as determined by QUEST[28]. Threshold measurements were made in the presence of the adapting dots. All conditions were presented in completely randomized orders.

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