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Priming reveals attentional modulation of human motion sensitivity

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Abstract

Although recent fMRI and single unit recording studies have shown that attention modulates neural activity in motion sensitive areas of extrastriate cortex, these approaches cannot reveal qualitative or quantitative effects of attention on perception of motion. To investigate this, we asked observers to select one of two orthogonal directions in a brief, transparent dot display (prime) and then measured their sensitivity to global directional motion in a second uni-directional dot display (probe) presented a short time later. When probe direction matched the attended prime direction, sensitivity was degraded. But, when probe direction matched the ignored prime direction, sensitivity was enhanced, even though both components were of equal physical strength. Sensitivity was unchanged for directions opposite to either previously seen direction. Neither sensory adaptation nor opponent direction mechanisms can account for these data. Rather, processes initiated by visual selection must underlie these dramatic changes in motion sensitivity. © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Recently, Treue and Maunsell [1] demonstrated that neural activity of a proportion of single units in MT/MST in the behaving monkey are modulated by attentional state. In humans, attention to motion stimuli produces high levels of activity in human area V5 as measured using fMRI, whereas viewing the same moving stimuli but attending to other stationary stimuli does not [2]. However, neither existing single unit nor fMRI data can reveal what the qualitative effects of attention on motion sensitivity (i.e. gains vs. losses) might be. Since a subset of single units in the study by Treue and Maunsell [1] were not modulated by attention, these, or non-attentional units in other unstudied areas, could mediate behavioural thresholds [3]. In single unit studies, as in fMRI studies, one cannot assume that attentionally induced increments or decrements in neural activity in a single brain area are evidence for

enhancements or losses, respectively, in perceptual sensitivity since the effect of that activity (excitatory vs. inhibitory) on other neural mechanisms in the same or different areas cannot be determined. Moreover, behavioural studies demonstrating that attention enhances the magnitude of the motion aftereffect, i.e. an illusory perception of motion in a stationary stimulus after prolonged viewing of a moving stimulus [4,5], fail to describe how attention (both selecting and ignoring) might affect visual sensitivity to motion. Our goal was to determine whether changes in attentional state in the absence of any changes in physical stimulation could alter subsequent sensitivity to visual motion.

We assessed sensitivity using partially-coherent, dynamic, random dot displays [6]. In these displays, a percentage of dots move in a single, coherent (signal) direction whilst remaining dots move in random directions. Phenomenally, such displays with a low percentage of coherent dots appear like a 'snowstorm' with an obvious global direction that corresponds to the physical signal direction. Such displays have been used effectively to quantify motion sensitivity in behaving

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monkeys [7] and humans [8,9,6], by determining the minimum percent coherence needed for just accurate signal identification, a quantity referred to as the motion coherence threshold. In monkey, this behavioural threshold corresponds closely to the percentage coherence needed to raise activity levels (just above baseline) of single motion direction sensitive units in Area MT of the dorsal extrastriate pathway [3]. Monkeys with lesions in this area (and nearby MST) [7] or humans with lesions in homologous V5 [10,11] cannot judge global motion in such dot displays normally, indicating that these areas are especially important for the perception of motion. Since perception of coherent motion in dynamic dot displays appears to depend on V5 and since this area is sensitive to attentional states, we asked whether attention could modulate motion coherence threshold of normal human adults.

2. Methods

Using a dual-task priming procedure, we asked observers to view dynamic dot displays presented in two brief episodes, a prime and a probe, separated by a short interval. Observers made two responses at the end of each trial, one to the prime and then one to the probe. Fig. 1 illustrates a sample trial.

On most trials, the prime had two obvious, fully-coherent, and orthogonal directions (upward or down-

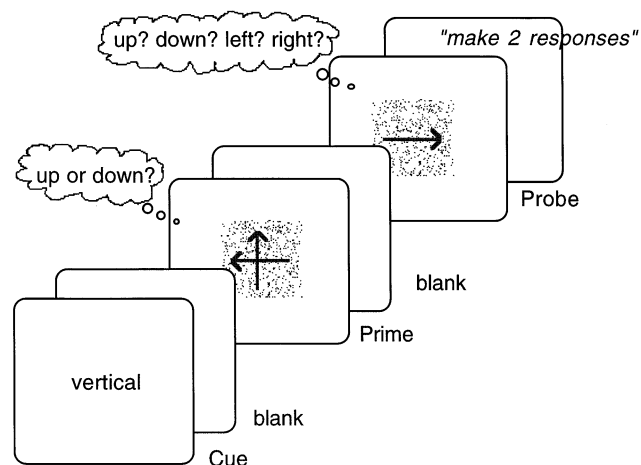


Fig. 1. An example trial. After pressing a button, the observer viewed a cue, a prime, and a probe, presented successively with blank intervals between. The prime (600 ms) was a dynamic dot display with half the dots moving in a vertical direction and half in a horizontal direction and appeared as two, transparent sheets of dots. The probe (96 ms) was a similar dot display except the percentage of coherent dots was varied from trial to trial. 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.

ward and leftward or rightward) and appeared as two transparent sheets of dots. This was created by moving half the dots in one direction and half in another. The probe always had only one global direction (upward, downward, leftward, or rightward) and its coherence was varied from trial to trial so that sensitivity to the probe direction could be measured. On each trial, the observer was first presented with a word, 'horizontal' or 'vertical', that instructed him or her to select motion in the specified axis from the subsequently presented prime. The cued direction is referred to as the target and the non-cued direction as the distractor. The observer was also required to identify the global direction in the probe, reporting both prime target and probe directions at the end of the trial. On some trials in the same session, the prime was composed of 50% of dots moving in one direction and 50% of dots remaining stationary, producing a stimulus that appeared to have only a single global direction. A cue was still provided and was consistent with the movement axis in the prime. These single-direction prime conditions allowed us to gauge the effect of target selection difficulty and more closely resemble conventional adaptation procedures. Two groups of eight naive observers were tested; each group was tested with a different interval between prime offset and probe onset. We conducted a second experiment identical to the first except that the transparent moving dot arrays in the prime were replaced with symbolic arrows; either two orthogonal, superimposed arrows or a single arrow. The cues, probes and nature of the tasks remained the same, allowing us to determine if selection of a directional response, rather than a visual motion direction, determined our results. For each experiment, coherence threshold for each prime-probe direction combination was the interpolated 50% correct point on the psychometric function for the four-alternative forced choice probe direction identification task.

Our priming procedure bears close resemblance to sensory adaptation experiments in that both use successive presentations of the same or similar stimuli. In a previous adaptation experiment, one of us reported that if observers passively view a moving dot array (adapting pattern) for a prolonged period, motion coherence threshold for a subsequently presented test display is markedly elevated if test and adapting directions match (same-direction effect) [12,13]. Subsequent experiments have shown that similar sized same-direction effects can be produced with very brief exposures (less than half a second) to adapting motion [14]. This same-direction effect was expected in the current experiment, but would it occur for both directions (attended and ignored) physically present in the prime (i.e. adapting stimulus)? Sensory adaptation explanations of same-direction effects and related effects (e.g. motion aftereffect) generally postulate that low level stimulus-driven

neural fatigue or inhibition of direction selective mechanisms is responsible for sensitivity loss or illusory motion [15,16]. If such processes determined motion sensitivity in our experiment, then threshold elevations should be found for probes matched to either prime target or prime distractor since each component provides the same degree of physical stimulation. Sensory adaptation explanations for same-direction effects further predict the same magnitude of sensitivity loss for single versus dual direction primes because the number of dots moving in the target direction is equal in both cases and, in dual direction primes, distractor directions were always orthogonal and therefore likely to be processed by independent mechanisms [17,12]. Previous work indicating that attention enhances the magnitude of the motion aftereffect [4,5] makes no prediction about the effect of ignored stimuli on sensitivity and predicts the same outcome for attended directions for single and dual direction trials.

The questions central to our experiment is how and why might attentional selection of motion influence subsequent motion sensitivity? By attention we mean a neural process that can select a perceptual input (e.g. the target direction) to control behaviour from competing perceptual inputs (e.g. the distractor direction). Priming procedures such as the one described here are widely used to study attention because they assume that task dependent neural processes engaged during selection of information from the prime persist during the presentation of the probe, affecting its processing. In the current experiment, persistent attentional activity provoked by the prime task makes two predictions. First, sensitivity to probe directions matched to the target versus distractor should be qualitatively different since one is attended and the other ignored. Same-direction effects predict that attended primes should produce direction selective inhibition of motion processing. Since numerous studies have shown that ignored stimuli produce internal representations that are capable of influencing subsequent perceptual processes and that these effects are invariably opposite to those produced by attended stimuli (e.g. [18]), attention models predict that the ignored direction (distractor) should facilitate perception of subsequent probes which match it in direction. Second, same-direction sensitivity losses should be greater in the dual versus single direction prime conditions because the selection of the target in the former should engage selection mechanisms more. Sensory adaptation or low level competition of direction analysers make neither prediction.

2.1. Observers

Twenty naive undergraduates (mean age = 22 years) participated in the experiment for course credit. Informed consent was obtained prior to participation.

2.2. Stimuli, apparatus and procedure

Dynamic random dot stimuli, generated using conventional algorithms were displayed centrally on a high resolution (Apple) monitor placed 90 cm from the observer. Each motion display consisted of a series of stationary dot arrays (frames) 30 ms in duration, with no interval between successive frames. Both prime and probe patterns were 2.5 degrees square and consisted of 100 white dots on a black field. Trials began with a small white fixation dot. After the observer pressed a button, a cue word appeared for 660 ms followed by a 660 ms blank interval. All primes (motion and arrows displays) lasted 600 ms and motion primes were composed of 20 successive frames. After a blank interval of either 200 or 390 ms, a 3-frame (96 ms) motion display (probe) was presented. It always contained a single signal direction with a coherence of either 5, 15, 25, 35 or 45%. Each subject completed a session of 240 trials, consisting of 160 trials with dual direction primes and 80 trials with single direction primes. Each of the four possible probe directions were equally likely to occur so that primes did not predict probes in any way. For dual direction conditions, each combination of relative target, distractor and probe direction and probe coherence was presented eight times. For single direction probes, each percent coherence was presented four times for matched and opposite target-probe combinations and eight times each for orthogonal target-probe combinations (baseline). For 16 observers, motion, as described above, was present in the prime stimuli: for half of these the duration of the prime-probe interval was 200 ms and for the remaining half this interval was 390 ms. Four observers had symbolic arrows as primes (with a 200 ms interval). Percent correct direction identification on the four alternative forced choice probe task for each percent coherence was averaged for observers for each condition and the 50% correct point interpolated and reported here as threshold. Only trials in which the target direction was correctly identified (92% or greater for all observers) were used in the calculation of test threshold because only on these trials could we be certain that attention was allocated to the target.

3. Results

The outcome of our experiment (Fig. 2) provides clear evidence that selective attention modulates motion sensitivity. First, for dual direction primes, group thresholds for probes matched to the target versus distractor were dramatically different. An analysis of variance on proportion correct data (using interval duration as a between factor and priming condition and percent coherence as within factors) showed that differ-

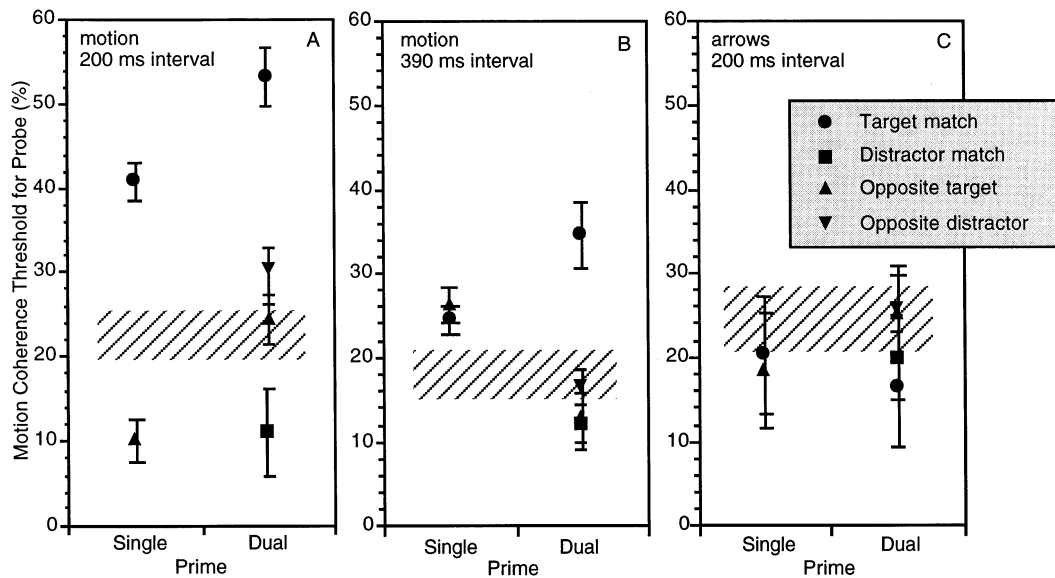


Fig. 2. Group motion thresholds are shown for probes presented after single and dual direction motion primes (panels A and B) or symbolic arrow primes (panel C). The duration of the interval between prime offset and probe onset is indicated in each panel. Data obtained when the cued (target) direction 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 (distractor) 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.

ences between these conditions was highly significant, $F(1, 14) = 27.9$, $P < 0.001$. Thresholds were elevated above baseline levels when the probe and prime target matched in direction (circles) but were lowered below baseline when the probe and prime distractor matched (squares). (Since a previous study showed that probes orthogonal to single direction primes had no effect on probe threshold, [14], we used this condition as the baseline against which sensitivity losses and gains could be judged.) These results show that simply changing the cue word and therefore the attentional state of the observer was sufficient to produce changes in coherence threshold for subsequent stimuli from as low as 12% coherence when the ignored direction matched the probe to over 50% coherence when the attended direction matched the probe. Although low-level sensory adaptation would have predicted sensitivity loss for probes matched to either target or distractor components of the prime, these effects were not found.

Second, for both prime-probe intervals (panels A and B), thresholds were elevated to a greater extent above baseline for attended dual direction primes than for attended single direction primes, supporting an attention basis for the effect. An ANOVA on proportion correct data using interval duration as a between factor and prime condition (attended dual direction primes vs. attended single direction primes) showed a highly significant effect of condition, $F(1, 14) = 10.58$, $P < 0.001$. With the longer (390 ms) interval, threshold

elevation above baseline for attended single direction primes was marginal but for attended dual direction primes, large, significant threshold elevations were still evident ($P < 0.01$, as revealed from planned post hoc comparisons from a large overall ANOVA of proportion correct data). This suggests that active selection from competing information produces greater persistence of attentional effects.

Another important feature of the data are the results with probes that were opposite in direction to either target (triangles) or distractor (inverted triangles). Motion opponency models often invoked in adaptation explanations of the motion aftereffect [15] predict a sensitisation effect for these conditions. Although we observed thresholds to fall below baseline for single direction primes (for the brief prime-probe interval only) consistent with previous work, there was no such facilitation of coherence threshold for probes opposite in direction to either component of dual-direction primes.

The results of the control experiment using symbolic arrows, rather than motion, in the prime (panel C) provide strong evidence that the effects reported above are due to motion priming, not priming of directional responses or semantic codes. A lack of difference in the dual versus single arrow prime conditions illustrates that increasing selection difficulty in the task, per se, cannot account for the increase in the size of the threshold elevation found with dual versus single direction motion primes.

4. Discussion

These experiments indicate clearly that selective attention modulates visual global motion perception. Attention to one direction causes a loss in sensitivity to that direction in a subsequent event, whereas actively ignoring a direction increases sensitivity for that direction, if it occurs within 200 ms. Such attentional effects are distinct from facilitatory effects resulting from symbolic, predictive cues that reduce directional uncertainty and task difficulty [19,20]. None of the prime stimuli used here were predictive of test direction. Direction uncertainty and task difficulty were the same in all conditions and therefore cannot serve to account for our results.

Our data may be explained as follows. Initially both directions of motion are analysed. Very rapidly, however, the firing rates of cells encoding the selected motion direction increase, while those of the distractor are inhibited [1]. Upon stimulus offset, previously attended information used to initiate explicit behaviour, is suppressed. Numerous authors have argued that such suppression is necessary to prevent perseveration of action [21,22] and to enable sequential behaviour. In the present case we consider that change in an object's direction of motion is more salient than continuation along a trajectory, therefore mechanisms to reduce sensitivity to already coded motion information makes function sense. Why then is sensitivity to the ignored direction enhanced and sensitivity to the directions not present in the prime unaffected? The neural activity encoding the physically present motion in the ignored direction is reduced by inhibitory selection mechanisms. The activity of neural mechanisms coding the other two directions remains unchanged because these neural units are not activated by a physical stimulus and consequently receive no such selection-based inhibition. The smaller level of activity in units coding the ignored direction means that the former cannot compete successfully for control of the observer's response. Thus they do not receive any subsequent inhibitory feedback to prevent perseverative processing. However, the small residual activity of neurons encoding the ignored direction of motion is sufficient to facilitate subsequent motion perception which is reliant on the cells tuned to the same direction of motion. This would result in a sensitization for previously ignored stimuli.

Although low level sensory adaptation has long been viewed as the mechanism for alterations in sensitivity commonly observed after prior exposure to salient stimuli, our data indicate clearly that attentional processes, such as those suggested here, more likely mediate such

effects. Moreover, our demonstration of attentional modulation of human visual motion sensitivity has important implications for the interpretation of brain imaging and single unit recording studies.

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