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Spatially localized motion aftereffect disappears faster from awareness when selectively attended to according to its direction

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ABSTRACT

In searching for the target-afterimage patch among spatially separate alternatives of color-afterimages the target fades from awareness before its competitors (Bachmann, T., & Murd, C. (2010). Covert spatial attention in search for the location of a color-afterimage patch speeds up its decay from awareness: Introducing a method useful for the study of neural correlates of visual awareness. *Vision Research* 50, 1048–1053). In an analogous study presented here we show that a similar effect is obtained when a target spatial location specified according to the direction of motion aftereffect within it is searched by covert top-down attention. The adverse effect of selective attention on the duration of awareness of sensory qualiae known earlier to be present for color and periodic spatial contrast is extended also to sensory channels carrying motion information.

1. Introduction

The facilitative effect of attention on a vast variety of perceptual experiences and responses is well documented, including the enhancing effect on motion perception (Allen & Ledgeway, 2003; Dobkins, Rezec, & Krekelberg, 2007; Itti, Rees, & Tsotsos, 2005; Posner, 2004; Rezec, Krekelberg, & Dobkins, 2004). This includes facilitation of the motion aftereffect (MAE) when inducing stimuli are attended, compared to when they are unattended (Cavanagh, 1992; Chaudhuri, 1990). However, there are exceptions to this rule. It has been found that voluntary covert attention to afterimages of color and afterimages of spatially modulated contrast tends to speed up their decay from awareness (Bachmann & Murd, 2010; Lou, 2001; Suzuki & Grabowecki, 2003; van Boxtel, Tsuchiya, & Koch, 2010; Wede & Francis, 2007). These findings support the growing understanding that mechanisms of attention and conscious awareness are not the same and may even have mutually opposite effects (Baars, 1997; Brascamp, van Boxtel, Knapen, & Blake, 2010; Koch & Tsuchiya, 2007; Lamme, 2003; Tsuchiya & Koch, 2009; van Boxtel et al., 2010; Van Gaal & Fahrenfort, 2008).

In a recent study we showed that when subjects searched for a color-afterimage patch among the mutually distant, competing color-afterimage patches, the duration of the target patch decreased compared to the selectively unattended patches (Bachmann & Murd, 2010). While up to now the demonstrations of the adverse effects of selective attention on afterimages have used static stimuli conditions, we wonder whether this adverse effect might be extended also to dynamic displays and aftereffects used in an experimental design analogous to that of Bachmann and Murd (2010). The answer to this question is not obvious. First, selective attention to inducing motion stimuli *increases* MAE duration (Cavanagh, 1992; Chaudhuri, 1990), which is not consistent with the effects on afterimage duration when inducers of the color-afterimages are attended to (e.g., Suzuki & Grabowecki, 2003; Wede & Francis, 2007). Second, general literature on motion detection and MAE does not have very good clues to what might be expected when the post-adaptation attentional effects on MAE are explored (Derrington, Allen, & Delicato, 2004; Mather, Verstraten, & Anstis, 1998). Third, it is not obvious whether, in principle, selective attention should necessarily have adverse effects on all types of afterimages. Furthermore, mechanisms of motion sensing and awareness are multilevel, with the effects of independent variables on these levels being often independent and uncorrelated or non-additively interacting. For example, the relative contribution of and accessibility to first- and second-order motion analysing mechanisms is varying with positional uncertainty and awareness, independence of coding spatial position and motion direction of the moving stimulus has been observed, attentional effects on motion perception depend on stimuli parameters, the relation of the effects of attention and awareness can depend on whether low-level phase-sensitive mechanisms are tapped or higher-level phase-insensitive mechanisms are involved, and the data on awareness and attention involvement in these effects is often inconsistent (Allen & Ledgeway, 2003; Brascamp et al., 2010; Bulakowski, Kolde-

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wyn, & Whitney, 2007; Lu, Liu, & Dosher, 2000; Whitney & Bressler, 2007). Before it is substantiated to go into the details about whether the putative attentional effects on MAE depend on first- or second-order mechanisms, mainly through position coding channels or directly via motion direction coding channels, etc., our main aim now is to ascertain whether the adverse effect of selective attention on MAE can be found in principle.

To minimize the possible sensory confounding factors, it is important to verify whether the opposite effect of attention on afterimage experience in case of MAE would hold in the conditions where there are no competing feature-signals from the same or a closely neighboring receptive field, but the spatial areas including explicitly perceived MAE are mutually distant. The corresponding hypothesis motivated by the findings from Bachmann and Murd (2010) states that post-adaptation selective attention to spatially localized MAE-area decreases the average duration of this aftereffect compared to the MAE created by the inducing stimuli with different directions of motion located in the alternative, spatially remote areas. We explore the effects with a search task where targets are defined at the moment when the motion in the inducing stimuli is stopped and MAE is about to be perceived.

Similarly to some of the aims Bachmann and Murd (2010) had, the present study is also useful for the development of new experimental methods for studying neural correlates of the contents of visual perceptual consciousness (awareness) (NCC). The typical strategy in these studies is to combine some psychophysical experimental method where target stimuli awareness is a dependent variable (e.g., as is the case with binocular rivalry, visual masking, motion induced blindness, attentional blink) and combine this method with brain imaging (e.g., fMRI, MEG, EEG). This permits to see what and how in the conscious brain is involved in producing consciousness-level subjective representation of the target stimulus. As the motion-sensitive visual areas (e.g., V5) are well localizable by brain imaging, variations in the duration of MAE awareness vis-à-vis variation in the activity of V5 and some putative related cerebral locations should help better study neural correlates of consciousness deconfounded from attention. So the default purpose of the present study is to present another method that conforms to the suggested useful criteria of NCC research as well.

2. Experiment

2.1. Methods

2.1.1. Subjects

Six subjects (four females, two males, age range 19–27) with normal or corrected-to-normal visual acuity participated. Informed consent was obtained and signed.

2.1.2. Stimuli and procedure

In each trial four disc-shaped areas, equidistant from a small central fixation cross were used for presenting the adapting and testing stimuli (Fig. 1a). Within these areas, achromatic sine-wave gratings were presented; in the adapting phase of each trial the grating moved orthogonally to its isoluminance vectors and the movement directions were mutually different. Four possible different directions of movement were used: up, down, rightward, leftward. Four directions and four possible locations allowed using 24 different stimulation sets. Movement directions were assigned to the disc-shaped motion areas randomly. The diameter size of each area subtended about 3.5° as estimated from the viewer's point of view; the distance of the center of each area from fixation was about 4° of the visual angle. The space-average luminance of the stimuli was set at 63 cd/m^2. The gratings had spatial frequency equal to 2.86 cycles/deg. The adapting stimuli appeared in combinations of four different motion directions that, when switched off, were followed by opposite-direction MAE spatially projected onto four static test gratings presented in the same disc-shaped areas where the adapting gratings-in-motion had been presented.

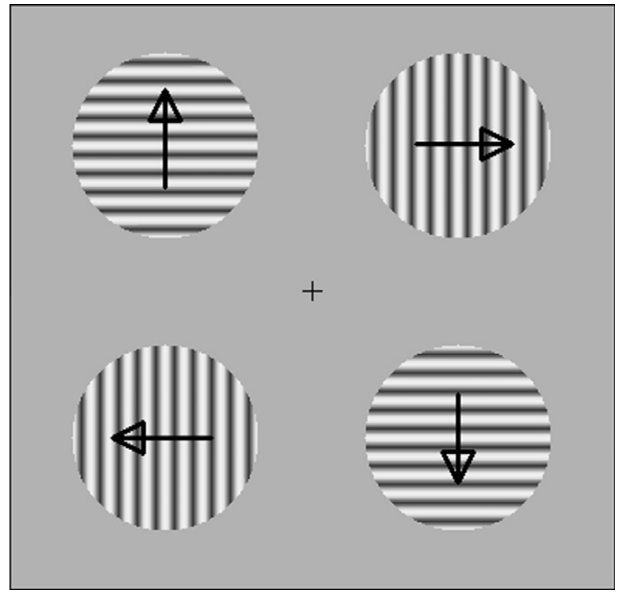

Fig. 1a. An example of four areas of adaptation including gratings moving in four alternative directions (black arrows for illustration purposes, not seen in experimental displays). The disc-shaped areas including the moving adapting stimuli were centered around central fixation. Subjects keep fixating the central small cross area while the adapting gratings-in-motion are presented for 24 s.

Each trial started with a blank grey field (luminance 65 cd/m^2), followed by the presentation of four simultaneously displayed dics filled with moving gratings for 24 s; after motion offset static gratings were presented in the discs. Subjects were asked to keep their gaze fixated at the central fixation cross during the trial.

Experiment was carried out in two sessions, with their order counterbalanced between subjects. One session was specified as target-aftereffect search where subjects had to report whether the target aftereffect (which direction was indicated by an arrow presented at the fixation after motion offset; see Fig. 1b for an example) faded as the first one among the four alternatives or not (condition Search); the other session consisted in monitoring the aftereffects for the relative temporal delay of the aftereffect fading, with subjects having to report which direction-specified aftereffect faded as the first among the four alternatives (condition Monitoring). Before main experiment each subject performed three training trials in order to familiarize with the general procedure and aftereffect experiences.

Between trials, a short resting pause was inserted. Each subject performed 90 trials, 45 in both conditions (Monitoring, Search). The motion direction and location combinations for each trial were selected randomly from the 24 possible combinations.

The principal dependent measure was proportion of trials where each direction of motion aftereffect was reported as 'faded first' compared to any other motion aftereffect in that trial.

2.2. Results

For each subject, proportion of trials where some MAE of a definite motion direction disappeared before other sensed MAE directions in the rest of the areas, was calculated. Repeated Measures ANOVA had factors condition (Search, Monitoring) and direction (four levels). The main hypothesis was supported by the significant

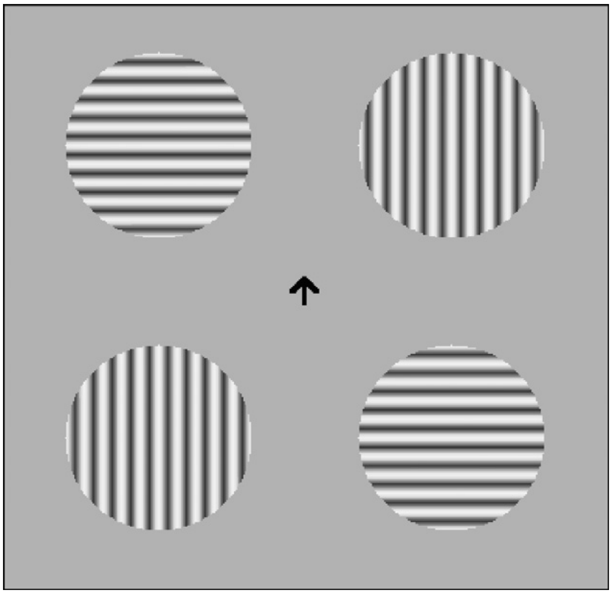

Fig. 1b. An example of a screen used in the Search condition. The cue arrow with target-MAE direction appears at the fixation, indicating the direction of motion that has to be covertly localized in one of the four areas in order to report whether MAE with this direction in its area faded from experience before any other MAE in other areas.

main effect of the task [$F(1,5) = 41.30$, $p < 0.0013$] showing that when subjects attended to a cued MAE direction, it faded earlier than apparent motion in other MAE areas with other directions, compared to when subjects monitored the four simultaneous MAE display areas for detecting which direction MAE faded as the first. The effect of direction appeared as a tendency [$F(3,15) = 2.91$, $p < 0.069$], referring to the fact that the likelihood of fading as the first was different for different directions. Particularly, in searching for target-directional MAE, up- and downward directed motion AEs tended to disappear as first more often than right- or leftward directed motion AEs. In the Monitoring conditions there were no differences between MAE directions [$F(3,15) = 5.54$, $p = 0.653$]. Naturally to expect, interaction between task condition and MAE direction was significant [$F(3,15) = 3.32$, $p < 0.049$], supporting the tendency of the effect of selective attention to appear relatively stronger for upward and downward MAE experiences. Fig. 2 shows percentages of trials where each of the MAE directions localized in spatially separated areas faded before other MAE directions localized in other areas, depicted separately for each motion direction.

Because two different tasks used in this study had equal probability distributions of the possible perceptual events, but not the same type of actual probability value distributions for response alternatives, it was advisable to carry out statistical analysis for the significance of the difference between the theoretically expected value of randomly produced response "disappeared before others" (0.25) and the actual value of the proportion of "disappeared before others", responses, drawn for each direction separately. This analysis (single sample *t*-test comparing the actual empirical value against theoretical 0.25) showed no significant effects in the Monitoring condition, but significant effects in search condition for downward and upward MAE ($M = 55.86$ [SE = 5.58] was significantly different from the theoretical $M = 25.0$ [$t = 5.53$, $p < 0.002$] for downward MAE; $M = 60.28$ [SE = 5.79] was significantly different from the theoretical $M = 25.0$ [$t = 6.09$, $p < 0.0017$] for upward MAE). With other directions of MAE, there was no effect of attention that would contradict our principal results; simply the trend in the expected direction is observable as a slight tendency in the graph (see Fig. 2).

The results taken together provide support for the restricting effect of selective covert spatial attention on the duration of MAE in the conditions where competing sensory signals from the alternative directional motion cues were presented from the spatially remote receptive fields.

3. Discussion

In the present study we extended the earlier results showing that selective attending to a critical color of a negative chromatic afterimage suppresses its visible duration compared to when the same quality afterimage is ignored by attention (Bachmann & Murd, 2010) and showed an analogous effect to be the case also in the domain of motion aftereffects. For the first time the adverse effect of selective covert attention on MAE studied in the conditions of visual search from mutually distant spatial areas was found. Contrary to the facilitative effects on MAE when adapting stimuli are attended (Cavanagh, 1992; Chaudhuri, 1990; Dobkins

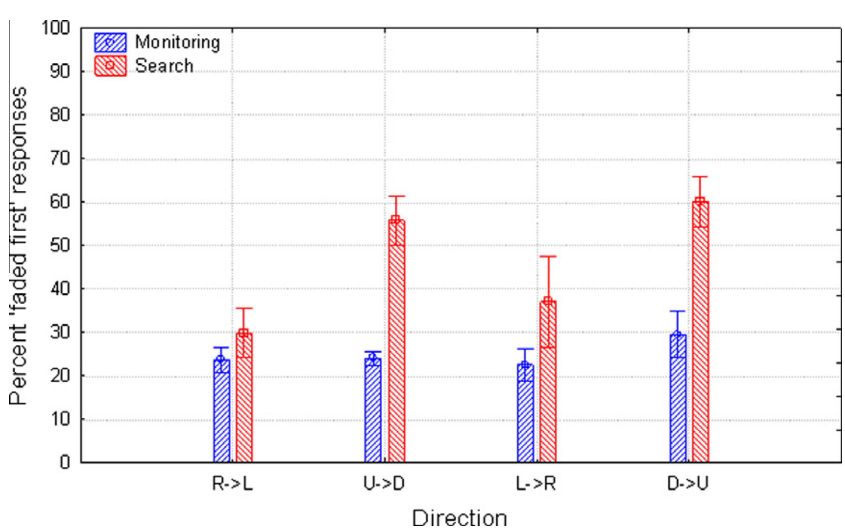

Fig. 2. The diagram showing the percentage of responses indicating that the MAE of this particular direction faded from experience before any other localized MAE in other areas. Task 1 – Search; Task 2 – Monitoring. Directions of searched or monitored MAEs: R → L – leftwards motion, U → D – downwards motion, L → R – rightwards motion, D → U – upwards motion.

et al., 2007; Rezec et al., 2004) and contrary to the expectation that attention increases MAE (Huk, Ress, & Heeger, 2004), attention to the "pure" motion sensing during the episode when external sensory input communicating motion cues is absent restricts MAE duration. This happens provided the MAE direction matches the direction looked for with the aid of top-down attentional influence. Thus, the list of the qualiae associated with adverse effects of attention on direct sensory awareness has been extended. Selective spatial attention mechanisms involved in pre-specified sensory object search and driven in the top-down manner can function as working against the sustained sensory awareness of a critical selected sensory feature. Additional support for the notion of non-equivalence of attention and awareness is provided (Baars, 1997; Koch & Tsuchiya, 2007; Lamme, 2003; Tsuchiya & Koch, 2009; Van Gaal & Fahrenfort, 2008; Wilimzig, Tsuchiya, Fahle, Einhäuser, & Koch, 2008).

3.1. On the possibility of response bias

It could be argued that our results might be confounded by a response bias. For example, when unexperienced observers are asked to report whether or not the MAE of the cued direction disappears the earliest, observers may tend to confirm it readily. To check for this possibility we ran an additional experimental condition with subjects asked to report whether the MAE with cued direction faded as the last. If the bias effect would be the cause of the "attentional" effects, this new condition should have produced opposite results – cued direction should have been reported as lasting the longest. The effect of the searched direction was absent in this condition, showing no support for the bias effect [$F(3, 15) = 0.65$, $p = 0.594$].

3.2. Possible levels of the attentional effect on MAE

An influential experiments-based set of theories explaining MAE assume it to be the result of direction-selective imbalance in motion-sensing channels as a result of directionally selective adaptation (Huk et al., 2004; Morgan, Chubb, & Solomon, 2006). The balance point of an opponent mechanism implementing the interaction between various directionally tuned channels is changed by directionally selective adaptation and as a result the autochthonous activity of the neurons in the disinhibited channel leads to MAE with opposite direction to the one that has been adapted. What can be the reason why selective top-down attention to the "unleashed" direction speeds up its activity compared to when attention is distributed or randomly changed between the alternative MAE locations? When we realistically assume that attention to a feature enhances the activity of the neural units responsible for its perception, its inhibitory effect on the opponent units should also increase. Consequently, the MAE in the neurons tuned to other, competing receptive fields signalling different directions of motion should *decrease*, but as our results show, it actually does not decrease. On the other hand, if we assume that top-down attention leads to "fatiguing" or exhaustion of firing resources of the neurons it influences and if this effect is relatively stronger compared to the lateral-inhibitory effect on the competing units, then our results can be reasonably explained. This also means that the origins of our effect belong to the top-down effects rather than to some low level lateral effects.

From the two recently acknowledged attentional systems, the dorsal fronto-parietal system is considered as the basis for top-down attention, with the ventral system thought to mediate bottom-up attentional effects (Corbetta & Shulman, 2002). In our experimental task target selection was cued in a top-down manner and it is therefore tempting to relate our results to the effects of the dorsal attentional system. The dorsal system is present bilaterally in both hemispheres while the ventral system is dominantly present in the right hemisphere (Corbetta & Shulman, 2002; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006). All this together with the well known fact that spatial neglect tends to cover left visual field suggested us look for the possible effects of laterality in our data. This is in order to get some additional clues for interpretation. In the Search condition, the proportion of responses indicating that target faded as the first was higher for the left visual field targets compared to the right visual field targets ($M = 51.55$ [SD = 8.58] vs. $M = 38.02$ [SD = 9.50], respectively; [$t = 3.20$, $p < 0.024$]). At first this may seem to point at the ventral system involvement. However, there are a couple of problems with this interpretation. First, we found that in the Monitoring condition without pre-cued top-down attention there was nevertheless a strong tendency in the same direction as was the effect in the Search condition ($M = 62.96$ [SD = 13.74] vs. $M = 37.04$ [SD = 13.74], [$t = 2.31$, $p = 0.069$]). This problem can be overcome if we remind that both attentional systems sustain their relative share of typical activity also in the resting state without explicit attentional cueing (Fox et al., 2006). However, the second problem is more difficult. Recently it was found that there is a left visual field stimulation advantage in activating the attentional systems (Siman-Tov et al., 2007). Importantly, this bias is present universally – in the ipsilateral as well as contralateral hemispheres for the dorsal system, in the ventral system of the right hemisphere, and also throughout most of the hierarchy of visual processing beginning with the subcortical levels. Thus, it is difficult at present to relate our results unequivocally to some specific attentional system, especially when bearing in mind that these systems strongly interact (Fox et al., 2006).

When attention is tested by visual crowding, upper hemifield stimulation poses more serious problems for attentional resolution compared to lower hemifield stimulation (He, Cavanagh, & Intriligator, 1996). Knowing the mechanism responsible for this effect could aid interpretation of our results, provided that our data also would show analogous effects. An additional analysis showed no effect of whether stimuli were presented in the upper or lower hemifields (for Monitoring, $t = -1.34$, $p = 0.237$; for Search, $t = -0.88$, $p = 0.418$).

3.3. Possible motion analysing mechanisms involved in the attentional effects

MAE can be caused both by first-order and second-order motion displays and by implicit as well as explicitly perceived stimulation (Seiffert, Sommers, Dale, & Tootell, 2003; Whitney & Bressler, 2007). As we used luminance based motion regimens and did not manipulate first- vs. second-order effects purposely, it is impossible to draw any firm conclusions about the relative involvement of first-order and second-order motion mechanisms in the adverse attentional effect on MAE. As both of these mechanisms were shown to be susceptible to attentional effects in earlier studies (e.g., Allen & Ledgeway, 2003), both may be involved also in the effects found here. Moreover, the adaptation process based on first-order motion signals may influence activity or state of the higher-level motion analysing mechanisms sensitive to both the first-order motion and second-order motion. Based on the highly similar neural activity patterns accompanying MAE from first- and second-order motion and recorded from all principal areas involved in motion perception (Seiffert et al., 2003) we would like to speculate that the adverse attentional effect found here is a general one, relevant for the unified motion detection system.

In order to try to specify the motion perception mechanisms implied in the emergence of the effect found in this study it is advisable to see what the known effects of decreasing MAE duration are. For example, MAE-durations decrease with speed of the adapting stimulus (e.g., Seiffert et al., 2003; van de Grind, Lankheet, & Tao, 2003). It is therefore reasonable to expect that the adverse effect of attention on MAE duration is related to the motion analysing mechanisms sensitive to the speed of motion. Among the mechanisms of implicit and explicit motion perception the ones that influence perceived velocity of motion in MAE are the attention-related ones that increase perceived velocity, provided attentional tracking of the high-level, awareness related motion (Cavanagh, 1992). Consequently, it is possible that selectively attending to one of the spatial areas including MAE increases the apparent speed of the attended motion feature and by this, as a secondary effect, decreases MAE duration. This possibility should be studied in future experiments, with the prediction that attended MAE areas may appear having relatively higher speed of illusory motion.

Speed of motion contributes to MAE also in terms of influencing the interaction of directionally selective mechanisms in determining the perceived direction of motion in MAE (Alais, Verstraten, & Burr, 2005). This is relevant also because our attentional instruction was specified by the direction of the target-MAE and the selectivity of the speeded-up decay was based on motion direction. These considerations additionally and indirectly support the putative involvement of the inhibition of the MAE through covert manipulation of the apparent speed by attention.

If these speculations prove to be valid by later experiments, we will have to accept that in addition to the facilitative and neutral effects of speed of motion (e.g., Kreegipuu, Murd, & Allik, 2006; Murd, Kreegipuu, & Allik, 2009) on the perception some effects can be just the opposite – the inhibitory or restrictive ones.

Our findings seem to even more complicate the picture of awareness- and attention related interactions in visual perception in general and motion perception in particular. On the one hand we know that awareness of the adapting stimuli augments MAE (Blake, Tadin, Sobel, Raissian, & Chong, 2006; Whitney & Bressler, 2007) and attention to the adapting stimuli prolongs MAE (Cavanagh, 1992; Chaudhuri, 1990).[1] On the other hand we see that attention to MAE inhibits it (data from the present work). And to make the picture even more varied, Brascamp et al. (2010) found evidence of response enhancement accompanying both attention and awareness, both in the phase-sensitive neural channels characteristic of early processing stages and in the phase-insensitive channels typical of higher cortical areas. Importantly, the effects of attention and awareness on phase-insensitive responses were positively correlated, but no correlation between the effects on phase-sensitive responses was found. Thus there appear to be independent signatures of attention and awareness in early visual areas, but a convergence of their effects at more advanced processing stages. At first sight this seems to suggest that our results are due to interactions in early visual areas where attention and awareness effects are independent. However, the absence of *positive* correlation does not mean that there cannot be *negative* correlation between attention and awareness effects. This means that the adverse effect of attention on the duration of visual awareness of MAE may be mediated by higher levels, but the effect is negative. Thus, we are on square one again and future experiments should reveal whether early level or higher-level mechanisms are producing our effects, or their interaction.

Future experiments should also explain why the effect is significantly present with vertical motion vectors, but very weak, if present at all with lateral motion vectors. The solution to this problem may not be so straightforward because in terms of the factors related to the aperture problem and the relative share of component motion and pattern motion mechanisms the concept of motion vectors appears ambiguous. Our present experimental design was not sufficient in order to control for the relative effects of these factors. In subsequent studies our present approach could be developed by purposely manipulating the relative impact of component motion and pattern motion in attended and unattended stimulation. Based on a recent finding by Tsuchiya and Braun (2007) who found stronger effects of attention on pattern motion compared to component motion, the subsequent combination of our present paradigm with that of Tsuchiya and Braun might help more firmly relate the adverse effect of attention on motion awareness to higher order cortical mechanisms.

On the other hand, because the adverse effect of attention on the sensory aftereffect tends to be universal (by behaving analogously for static color cues, periodic spatial contrast, and motion cues), it is possible that considering one or another motion analysing mechanism and carrying out special experiments for this purpose may not help to understand the basic nature of this effect at all. Indeed, there is enough strong evidence that visual attention conforms exactly to the predictions of a single, integrated resource similarly acting upon sensory evidence widely varying in terms of specific contents (Pastukhov, Fischer, & Braun, 2009).

4. Conclusions

In the present study we showed that selective covert attention tends to speed up the decay of MAE when it is used in visual object-search among spatially distant objects specified in the subjective, phenomenal domain of motion perception. This effect in its robust form appears with MAE along vertical motion vectors. We therefore extended the examples where selective attention has an adverse effect on sensory phenomenology also to the perceived motion domain. Likewise to what was found with color and spatial periodic contrast stimuli, this paradigm can be productively used in future studies of the neural correlates of visual awareness free from the attentional confound and in the conditions where temporal uncertainty of the emergence, persistence and decay of the critical subjective experience can be much better controlled and evaluated when compared to the traditional methods of masking, sensory (iconic) memory, temporal order judgment, attentional blink and several others.

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[1] In a small informal experiment, we also asked subjects to selectively attend to one of the moving gratings during induction in order to test whether this would selectively prolong MAE similarly to what was found in earlier studies with afterimages. The result was negative: MAE at the locus that was attended during induction did not decay later compared to MAE in the unattended loci ($M = 24.44$, $SD = 25.63$, $t = 0.589$, $p = 0.615$). Even if selective attention to an inducer would have prolonged MAE at that locus, this potential effect may have been cancelled during the evaluation episode because in order to perform the task subjects may have selectively attended to the corresponding afterimage and thus, conversely, decreased its duration. We lack any good theory to predict whether facilitation or inhibition should have won over in this situation. As a corollary, this finding cautions us about studying inducer-attention effects on afterimages in the conditions where critical stimuli occupy the same location during induction and test phases. Unless one separates the effects of attention during induction and perception of aftereffects, one may get the results confounding the two factors.

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