



## Changes in fMRI BOLD dynamics reflect anticipation to moving objects



W. Schellekens<sup>a,\*</sup>, N.F. Ramsey<sup>a</sup>, R.J.A. van Wezel<sup>b,c</sup>, M. Raemaekers<sup>a</sup>

<sup>a</sup> Brain Center Rudolf Magnus, Department of Neurology, UMC Utrecht, Utrecht, The Netherlands

<sup>b</sup> Department of Biophysics, Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, Nijmegen, The Netherlands

<sup>c</sup> Biomedical Signals and Systems, MIRA, University of Twente, Enschede, The Netherlands

### ABSTRACT

The human brain is thought to respond differently to novel versus predictable neural input. In human visual cortex, neural response amplitude to visual input might be determined by the degree of predictability. We investigated how fMRI BOLD responses in human early visual cortex reflect the anticipation of a single moving bar's trajectory. We found that BOLD signals decreased linearly from onset to offset of the stimulus trajectory. Moreover, decreased amplitudes of BOLD responses coincided with an increased initial dip as the stimulus moved along its trajectory. Importantly, motion anticipation effects were absent, when motion coherence was disrupted by means of stimulus contrast reversals. These results show that human early visual cortex anticipates the trajectory of a coherently moving object at the initial stages of visual motion processing. The results can be explained by suppression of predictable input, plausibly underlying the formation of stable visual percepts.

### 1. Introduction

Over the last decades, it has been suggested that the human brain actively predicts input, rather than passively waiting for it. Mechanisms like 'predictive coding' pose that predictions are made for all sensory input, possibly using Bayesian statistics (Mumford, 1992; Rao and Ballard, 1999). Several studies have shown signs of prediction-based mechanisms in the brain, with novel or unpredictable input resulting in relatively enhanced neural activity (Alink et al., 2010; Wacongne et al., 2012). Additionally, elevated BOLD-signals have been reported in early visual cortex at the trailing edge of moving random dot patterns, where novel dots enter the stimulus area (Maloney et al., 2014; Raemaekers et al., 2009; Schellekens et al., 2014, 2013; Wang et al., 2014). The latter results may suggest that the visual system may encode novelty of a moving stimulus through anticipation of its trajectory. However, these motion novelty effects have specifically been demonstrated using random dot kinematograms that constantly generate motion input all across a static area of the visual field. The continuous presence of motion energy at the same portions of the visual field complicates the interpretation of previous reports with respect to motion anticipation. If visual cortex genuinely anticipates motion trajectories, encoding of stimulus novelty is therefore expected for single object motion as well.

In this study, we address two essential questions regarding motion input prediction in the human brain. For one, what is the spatial extent over which predictive mechanisms operate given the trajectory of a single moving object? If effects are only found directly near motion trailing/leading edges or any particular visual field eccentricity, they

could be due to classical receptive field effects (Dumoulin and Wandell, 2008; Swindale, 2000) as opposed to predictive multi-sensor integration of motion input. In the latter case, a gradual change in neural activity along the entire motion trajectory is expected. A second issue concerns the hierarchical level at which predictive processing of visual motion occurs (Mijović et al., 2013). If predictive motion integration is primarily a low-level bottom up process, then effects of motion anticipation should be diminished when low-level motion coherence (first-order motion) is disrupted, even if some high-level motion coherence (second-order motion) still persists (Ashida et al., 2007; Smith et al., 1998). If on the other hand predictive motion integration occurs at a later stage in visual motion processing, the presence of either low- or high-level motion coherence might be sufficient. Modifying the coherence of a moving stimulus could thereby reveal clues on the processing level at which the visual system anticipates an object's movement.

The current study investigates changes in BOLD responses along motion trajectories of a single moving bar. Based on previous findings, we expect BOLD responses to decrease in accordance with the predictability of a motion stimulus. In the first experiment using a fluently moving bar, we show that the BOLD responses are not merely enhanced at the trajectory onset and suppressed at the trajectory offset, but also gradually decrease in a linear fashion across the entire motion trajectory. In the remaining 2 experiments we show that a similar motion anticipation pattern is present for apparent motion only if low-level motion coherence is preserved.

\* Correspondence to: Str. 4.205, Postbus 85060, 3508 AB, Utrecht, The Netherlands.  
E-mail address: [w.schellekens@umcutrecht.nl](mailto:w.schellekens@umcutrecht.nl) (W. Schellekens).

## 2. Material and methods

### 2.1. Subjects

Twelve healthy volunteers (mean age=24, female=6) were recruited from the Utrecht University. All participants gave written informed consent before entering the study. The protocol was approved by the local ethics committee of the University Medical Center Utrecht, in accordance with the Declaration of Helsinki (2013).

### 2.2. Scan protocol

Scanning was performed on a 7T Philips Achieva scanner (Philips Healthcare, Best, Netherlands) with a 32-channel receive head coil (Nova Medical, MA, USA). Functional MRI (fMRI) measurements were obtained using an EPI-sequence with the following parameters: SENSE factor=2.2, TR=1500 ms, TE=25 ms, flip angle=80°, coronal orientation, interleaved slice acquisition, FOV (AP, FH, LR)=35.2×152×152 mm<sup>3</sup>. The acquired matrix had the following dimensions: 22×96×96, voxel size: 1.6×1.583×1.583 mm<sup>3</sup>. The functional images were acquired from the posterior 35 mm of the brain, covering the occipital lobe, and slices were angulated orthogonal to the calcarine sulcus. Additionally, a T1-weighted image of the whole brain (1.00×0.98×0.98 mm<sup>3</sup>, FOV=190×256×256) and a proton density image of equal dimensions were acquired at the end of the functional sessions.

### 2.3. Stimuli and experimental design

Stimuli were presented with a projector on a rear projection screen that was placed in the bore of the scanner. Stimuli were programmed using C++ software (Stroustrup, 1983, Bell Laboratories, USA), and their onset was triggered by the scanner. All stimuli were projected on a gray

background and the mean luminance was held constant at 42.2 cd/m<sup>2</sup>. During the presentation of all stimuli, a red fixation dot with a radius of 0.075° visual angle (VA) was projected on the center of the screen. Participants were instructed to remain focused on the fixation dot during all experiments. The experiments consisted of a retinotopic mapping and 3 different moving bar stimuli.

#### 2.3.1. Retinotopic mapping

The mapping stimulus was a moving bar-shaped checkerboard pattern (height: 15° VA; width: 1.875° VA), that reversed contrast every 125 ms (8 Hz). This mapping stimulus assessed the visual field in Cartesian coordinates and covered the area in visual space, where the motion stimulus was to be presented (i.e. the 15° horizontal×15° vertical VA area at central view). Coordinates on the horizontal axis were mapped with a vertically oriented bar (Fig. 1A) that made 4 cycles: twice moving rightward and twice moving leftward. Coordinates along the vertical axis were assessed with a similar contrast reversing checkerboard bar, which was oriented horizontally and moved upwards and downwards for 2 cycles each (Fig. 1B). The bidirectional mapping of the visual field, allowed for a nullification of the shape of the BOLD response (Buxton et al., 2004), possibly biasing cortical visual field representations. The mapping of both horizontal and vertical coordinates was performed in a single run, resulting in 400 functional images.

#### 2.3.2. Motion stimuli

We presented 3 different stimuli to investigate the effect of stimulus novelty of single moving objects on BOLD activity in early visual cortex. The first motion stimulus was a fluently moving bar stimulus to assess the presence of motion anticipation effects within BOLD responses. The latter 2 experiments, using coherent and incoherent stepwise motion, were conducted to investigate the hierarchical level at which motion prediction occurs.

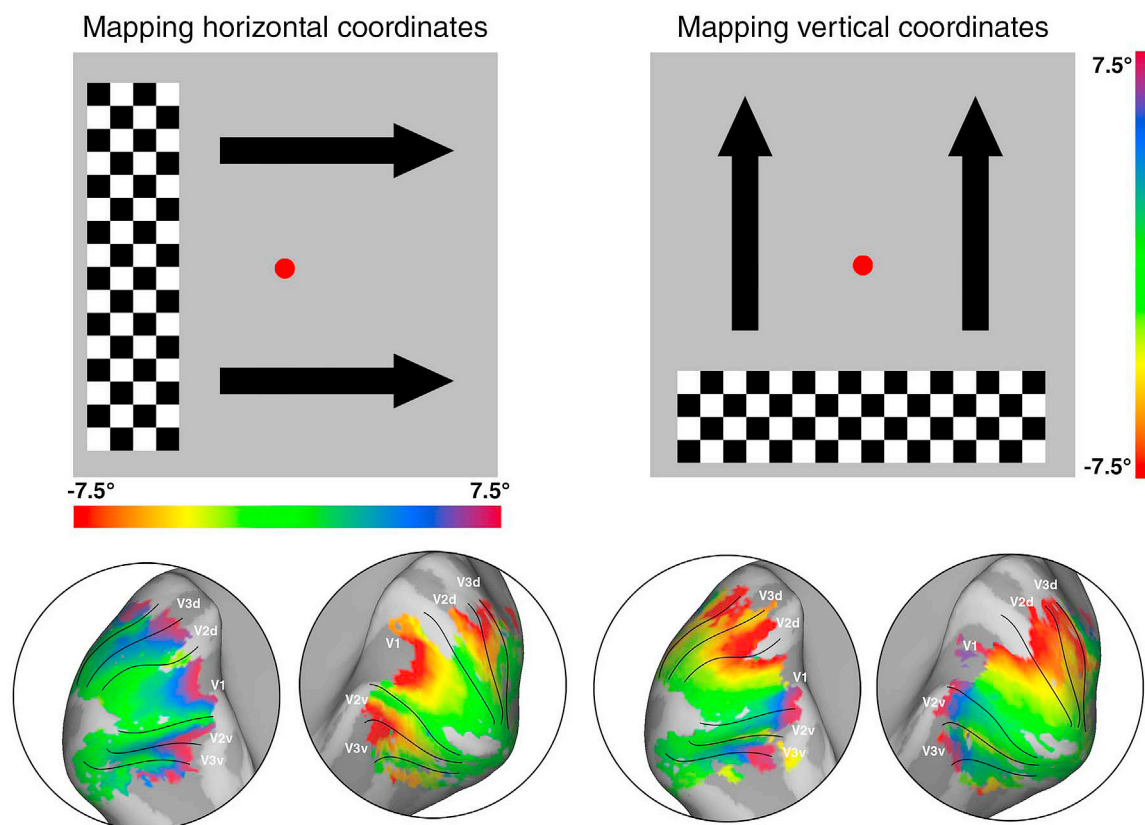


Fig. 1. Retinotopic mapping Cartesian coordinates The figure displays a schematic of the mapping stimulus for horizontal (left) and vertical (right) coordinates. Results of 1 participant in both hemispheres are shown in the bottom row. Colors correspond to the color bar of the visual field maps.

For all stimuli, a bar (length:  $15^\circ$  VA; width:  $0.65^\circ$  VA) moved across the mapped visual field in one of four directions: right, left, up, or down. When the motion direction was right- or leftward, the bar was vertically oriented, whereas its orientation was horizontal for up- and downward motion directions (Fig. 2A). Each cycle of the moving bar (i.e. presentation from start to end location) was alternated with a 12 second rest period, allowing the BOLD responses to return to baseline. During the rest period, only the gray background, fixation dot and attention task were visible. All 3 motion experiments were presented once to each participant, during which each motion direction was repeated 5 times, resulting in 20 trials, and 240 functional images per stimulus condition, and 720 functional images in total. There was a circular aperture (equal color as the background) around the fixation dot ( $0.3^\circ$  VA), which allowed the fixation dot and attention task (see below) to be visible at all times.

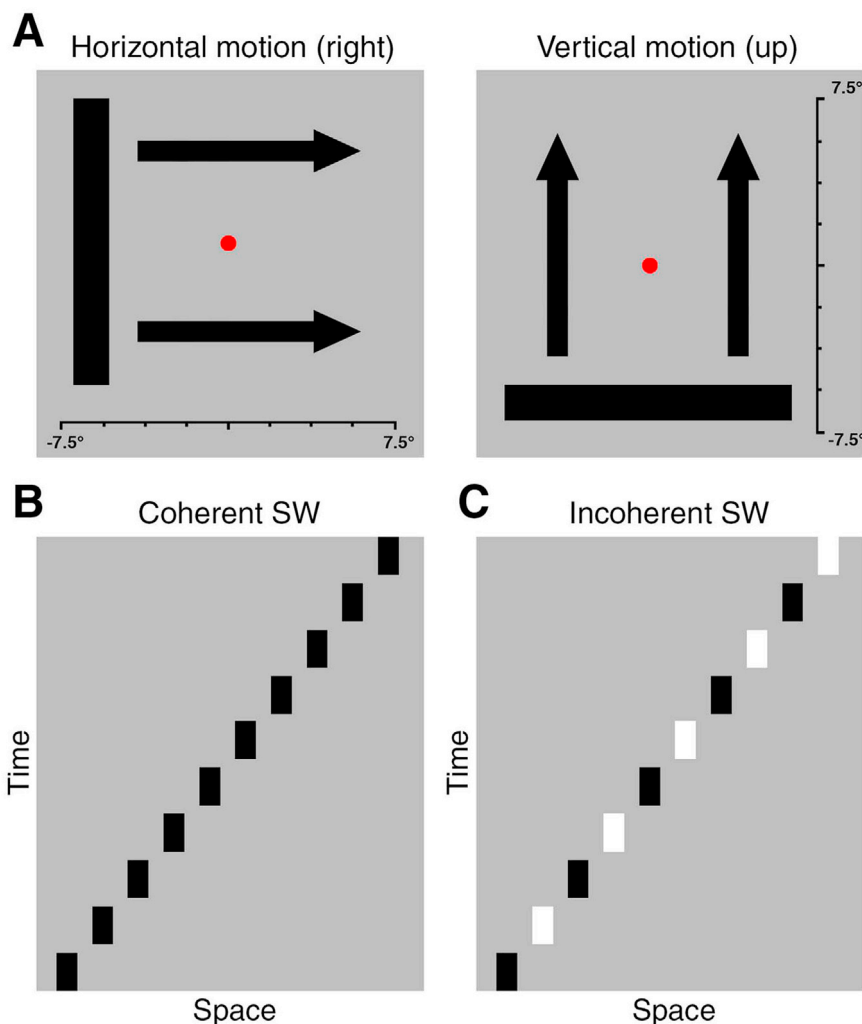
During fluent motion, a black bar ( $21 \text{ cd/m}^2$ ) moved fluently along the full motion trajectory ( $15^\circ$  VA) with velocity of  $3.3^\circ/\text{s}$ . The moving bar gradually appeared and disappeared at the edges of the mapped visual field (Movie 1). During coherent stepwise motion, the bar was consecutively presented at 20 equally spaced locations ( $0.75^\circ$  VA apart) across the mapped visual field for 300 ms per location (Fig. 2B, Movie 2). The stimulus progression across the visual field in 20 discrete and consecutive steps creates an apparent motion trace. Since apparent

motion contours are known to produce responses similar to fluent motion (Muckli et al., 2005), similar response patterns are expected compared to the fluently moving bar. During incoherent stepwise motion, the bar was also presented at 20 equally spaced and consecutive locations for 300 ms per location. However, the bar switched between black and white contrast ( $21 \text{ cd/m}^2$  and  $84 \text{ cd/m}^2$  respectively) at every consecutive location (Fig. 2C, Movie 3). This stimulus exhibited a form of low-level motion incoherence (i.e. on the basis of contrast), while population receptive fields are visually stimulated in similar fashion compared to coherent stepwise motion, which still resulted in high-level motion coherence (i.e. from the viewer's perspective).

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### 2.3.3. Attention task

To ascertain that participants fixated on the center of the screen, an attention task was presented on top of the fixation dot. The attention task consisted of a white cross that was briefly presented (300 ms) on top of the fixation dot every 1000 ms. For 25% of the cross projections, 3/4th of the cross was omitted, resulting in the projection of a white bar either on the left, right, top or bottom of the fixation dot (i.e. attention cue). Participants were instructed to respond to the attention cue with a button press, using a button box with 4 buttons (left, right, top and bottom



**Fig. 2.** Stimulus design figure displays a schematic of the different bar stimuli. (A) Fluent motion. A black bar moved along the horizontal (rightward and leftward motion) or vertical axis (upward and downward motion). The orientation of the bar was orthogonal to the motion direction. (B) Coherent stepwise motion. The experiment is presented as a space-time plot, showing the sequential presentation of a black bar at discrete locations across the stimulus area. (C) Incoherent stepwise motion. Bar stimulus was presented at discrete and sequential locations across the stimulus area. However, the bar contrast switched between black and white at every other location.

buttons). For a correct response, the corresponding button needed to be pressed. Any other button was an incorrect response. A missed response was reported, whenever the participant failed to press a button before the next attention cue was presented on screen.

#### 2.4. Statistical analysis

The T1-weighted anatomical image was divided by the proton density image to correct for macroscopic field inhomogeneities (Van de Moortele et al., 2009). The corrected T1-weighted image was loaded in CARET (Van Essen et al., 2001) and a surface was constructed per hemisphere, corresponding to gray matter layer 4 (on average 1.6 nodes per mm<sup>2</sup>). The functional volumes were preprocessed (including slice time correction and realignment) using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/>). The preprocessed functional images were mapped to the reconstructed surfaces using a Gaussian mapping algorithm. This procedure resulted in a timeseries for each node on the reconstructed surface. Additionally, the timeseries were filtered using a high-pass filter with a cut-off at  $7.1 \times 10^{-3}$  Hz.

##### 2.4.1. Retinotopic mapping

The mapping stimulus was analyzed with a phase-encoded design matrix. Every factor in the design matrix represented the cyclic BOLD activation of the moving checkerboard pattern, which lasted 7500 ms every 60,000 ms for both the mapping of the horizontal and vertical axes of the stimulus area. For every node in the surface, Pearson correlation coefficients were calculated between the nodes timeseries and each factor in the design matrix. A node's peak correlations during the mapping of the horizontal and vertical axes determined the node's receptive field location in Cartesian coordinates. The mapping results were also used to draw ROIs on the surfaces, encompassing the visual areas V1, V2 and V3. For analysis of the motion stimuli, only nodes were included that were situated in early visual cortical areas (i.e. V1, V2, V3), and were significantly activated during the horizontal and vertical mapping stimuli ( $T \geq 4.51$ ).

##### 2.4.2. Motion experiments

All 3 motion experiments were analyzed identically. The trajectory of the moving bar (fluent and stepwise) was divided in 10 equally spaced steps. Responses were averaged across the cortical surface area of the bar for each of the 10 steps. This procedure resulted in 10 locations in each fieldmap for which BOLD responses were analyzed, as the bar made a sweep across the visual field. Note that this procedure is the same for opposite motion directions (e.g. rightward and leftward), but that fieldmap locations are flipped 90° for the other 2 opposite motion directions (upward and downward). Additionally, the onset of the BOLD signal was corrected for the lag of the stimulus, since the moving bar was positioned at any of the 10 fieldmap locations at different points in time.

The amplitude of the BOLD response was estimated using a linear regression and a design matrix that contained factors representing BOLD activation during the different motion directions. Subsequently, BOLD amplitudes were to be compared among the 10 visual field locations along the bar's trajectory. To compensate for eccentricity dependent variations in contrast and motion sensitivity (Arnold et al., 2007; Schellekens et al., 2013), BOLD amplitudes were subtracted from those induced by a bar with opposite motion direction. In the case of absence of anticipation effects, the difference in activity for opposing motion directions should be roughly 0 for each fieldmap position along the bar's trajectory. However, if the bar's movement is anticipated, then the difference in activity for opposing motion directions should decrease along the trajectory, becoming negative halfway the motion trajectory. We determined the slope of this activity decrease (separate for right-leftward and up-downward) by fitting a first order polynomial using a simple linear regression. A Student's *T*-test was used to determine whether the slope differed significantly from 0. Additionally, paired samples *T*-tests were used to test if the slopes differed for horizontal (i.e. right-leftward)

and vertical (i.e. up-downward) motion, or differed between stimulus conditions. A multivariate repeated measures test was used on the average correct responses of the attention task to assess differences in attention task performance between motion experiments. The number of incorrect and missed responses of the attention task were averaged in 3 bins corresponding to the location of the bar stimulus at the time of the attention cue: onset, middle and offset of the motion trajectory. Then, we used a multivariate repeated measures test to investigate if there was an effect of stimulus position on the number of incorrect or missed responses to an attention cue.

### 3. Results

#### 3.1. Fluent motion

During fluent motion a bar moved fluently at constant velocity across the cortically mapped visual field either along the horizontal (i.e. leftward/rightward) or vertical axis (i.e. upward/downward). We consistently found that the BOLD amplitude was highest near the onset of a motion trajectory and lowest near the offset. This pattern was distinguishable across all field maps of early visual cortex (Fig. 3). The BOLD amplitudes of opposite motion directions, measured at different portions of the visual field, were subtracted to cancel out any local eccentricity effects in measured responses following stimulation by the bar stimulus. We found that for all presented motion directions, a fluently moving bar resulted in a gradual decrease in BOLD amplitudes along the full motion trajectory. Differences between opposite motion directions were mostly absent near the middle of motion trajectories, where traveled distances of opposite moving bars were equal (Fig. 4A). A simple linear regression analysis showed that the effect of decreasing BOLD signals as function of traveled distance was significant ( $T_{(11)} = -5.560$ ,  $p < .001$ ), and did not differ between bars moving along the horizontal or vertical axis ( $T_{(11)} = .554$ ,  $p = .591$ ). This result shows that BOLD amplitudes in human early visual cortex elicited by a fluently moving stimulus depend on the traveled distance of the stimulus.

#### 3.2. Coherent and incoherent stepwise motion

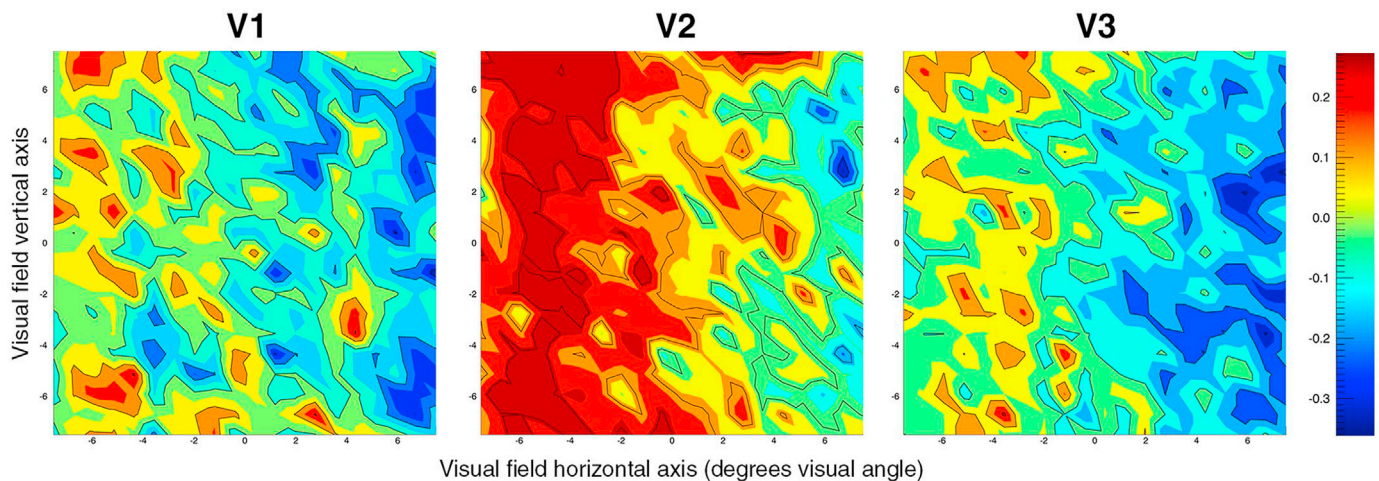
During stepwise motion, a bar was presented for 300 ms at 20 equally spaced locations across the range of the obtained fieldmap. Therefore, the bar progressed linearly along its trajectory in noticeably discrete steps, which created an apparent motion trace. For coherent stepwise motion, we found a similar pattern of results as for fluent motion. Estimated BOLD amplitudes were enhanced near the onset as compared to the offset of the motion trajectory. Subtraction of opposite motion directions resulted in a comparable gradual signal decrease across the motion trajectory (Fig. 4B), of which the slope differed significantly from zero ( $T_{(11)} = -5.004$ ,  $p < .001$ ).

However for incoherent stepwise motion, where the bar contrast changed at every discrete step, we did not observe the activity decrease along the bar's trajectory (Fig. 4C) with the slope not differing significantly from 0 ( $T_{(11)} = -.487$ ,  $p = .636$ ). Consequently, we found a significant difference between the slopes (Fig. 5) of coherent and incoherent stepwise motion ( $T_{(11)} = 7.243$ ,  $p < .001$ ), but not between fluent motion and coherent stepwise motion ( $T_{(11)} = 1.983$ ,  $p = .073$ ). These results show that enhanced BOLD activity at the motion trajectory onset and its gradual decrease towards the trajectory's offset depend on low-level coherence of a moving stimulus.

#### 3.3. Change in shape of the BOLD response along the trajectory

We found that estimated BOLD amplitudes steadily decreased from onset to offset of motion trajectories during coherently moving bar stimuli. Upon closer inspection, we observed that the entire shape of the BOLD signal transforms along the trajectory of the fluent moving bar. At the onset of a motion trajectory, the BOLD signal does not exhibit an





**Fig. 3.** Contour plot fluent motion Figure displays the amplitude during a fluently moving bar stimulus (corrected for stimulus lag) across representations of the full stimulus area in V1, V2 and V3. Results were averaged across all motion directions, and rotated to align onset and offset of the motion trajectory corresponding to rightward motion (i.e. vertically oriented bar moving from left to right). All visual areas show enhanced BOLD activity on the left side of the stimulus area, i.e. near the onset of the bar stimulus trajectory. BOLD amplitudes decrease for visual field representations towards the offset (right side stimulus area) of the motion trajectory. Effects were found along the full length of the bar stimulus, i.e. from top to bottom of the visual field representations.

initial dip. However, as the bar progressed along its trajectory, an initial dip with increasing size becomes apparent (Fig. 6). To quantify this finding, we estimated the peak of the initial dip at 10 equally sized bins covering the full motion trajectory by taking the lowest percentage of BOLD signal change during the first 3 functional images of each bin (corrected for stimulus lag), and subtracted opposite motion directions to compensate for local confounding eccentricity effects. Using a simple linear regression, we found a mean increase in initial dip across subjects of  $m = .030$  ( $sd = .018$ ) percentage of BOLD signal change per degree visual angle. The regression coefficients that represent the change in initial dip along the motion trajectory differed significantly from zero across subjects ( $T_{(11)} = 5.614$ ,  $p < .001$ ), indicating that the initial dip significantly increased in amplitude over the course of the bar's trajectory. This finding indicates that not only the amplitude but also the initial dip of BOLD responses contains information on neural signal integration, and motion predictability in particular.

### 3.4. Attention task

An attention task was present on top of the fixation dot to ascertain that participants focused on the center of the screen. On average, 80% of the presented attention cues were followed by a correct button press, and did not differ between experiments ( $F_{(2,10)} = 3.864$ ,  $p = .057$ ). The average number of incorrect button presses was 0.5%, while 19.5% of attention cues were not accompanied by any button press and counted as missed responses. Additionally, we did not find that the position of the moving bar (onset, middle or offset of the motion trajectory) had an effect on the amount of incorrect or missed responses ( $F_{(2,10)} = 2.650$ ,  $p = .119$ ). The results from the attention task show that participants had been able to fixate properly on the center of the screen during all experiments, and that none of the experiments had a significant influence on attention task performance.

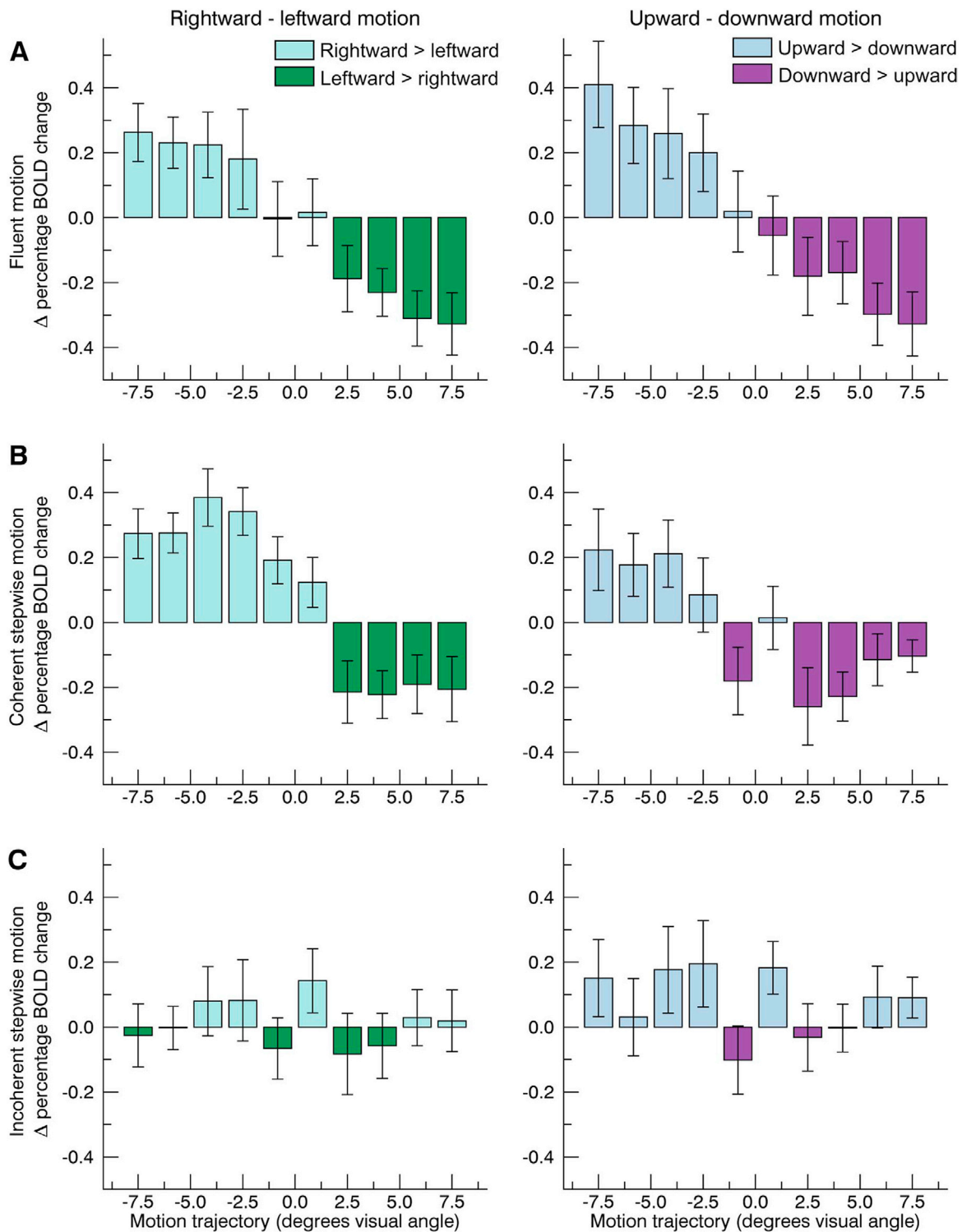
## 4. Discussion

We investigated if human early visual cortex anticipates the motion trajectory of a single moving stimulus. We hypothesized that fMRI BOLD responses would gradually decrease in correspondence to the increased predictability with respect to the motion stimulus. We have found that BOLD signals were enhanced at the onset relative to the end of a moving bar's trajectory. Furthermore, the BOLD amplitude decreased gradually along the motion trajectory and was also accompanied by a gradual

change in amplitude of the initial dip. Additionally, we demonstrated that the changes in BOLD signal were in fact dependent on low-level stimulus features. When a black bar was presented at 20 discrete steps (i.e. stepwise, or apparent motion), BOLD responses exhibited a similar pattern, related to motion prediction, compared to a fluently moving bar. However, when the contrast of the bar switched between black and white at each discrete motion location, prediction effects completely disappeared.

In the current study, we present clear evidence that BOLD responses to a single moving object decrease along the motion trajectory. This finding is in line with previously reported BOLD signal enhancements at the onset of motion paths (or motion trailing edge) using various random dot kinematograms (Maloney et al., 2014; Raemaekers et al., 2009; Schellekens et al., 2014, 2013; Wang et al., 2014). Classical receptive field (RF) effects could theoretically induce directional motion biases, as visual motion input at the onset of a motion trajectory may stimulate the center of a neuron's RF without first stimulating the neuron's surround, which might theoretically enhance neural transients (Allman et al., 1985; Borg-Graham et al., 1998). However, the spatial extent at which the signal decrease occurs makes it unlikely that classical RF effects are underlying current findings. The BOLD signal decreased across the full motion trajectory (i.e.  $15^\circ$  visual angle), which clearly exceeds classical (population) receptive field sizes in human early visual cortex, ranging from approximately  $1^\circ$  visual angle in V1 to  $3^\circ$  visual angle in V3 at the outermost eccentricities of the current stimulus area (Dumoulin and Wandell, 2008; Smith et al., 2001). Classical RF effects may well contribute to signal enhancement directly near the onset of a motion trajectory, but offer no plausible explanation for the gradual decrease in BOLD signal over the range of  $15^\circ$  visual angle.

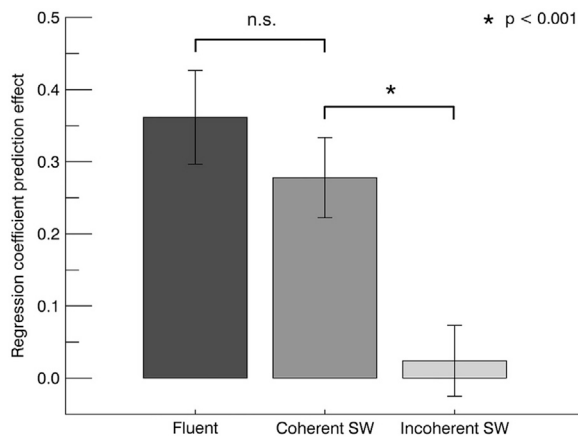
If the BOLD signal changes along the trajectory of a moving bar are not explained by classical RF effects, then by what other mechanism? There are several mechanisms that may affect visual motion processing through extraclassical (i.e. contextual) RF effects. First, there is the possibility of overt/covert shifts in spatial attention, which have been reported to alter BOLD activity in visual cortex (Corbetta et al., 1998; Jack et al., 2006; Melcher and Morrone, 2003; Tootell et al., 1998). Attention could be drawn involuntarily to the trajectory onset, where a moving bar first appears. Shifts in spatial attention could, therefore, explain the elevated BOLD signals directly at the trajectory onset of a moving bar. However, in previous studies we showed that elevated BOLD activity at motion onset was not correlated with the direction of microsaccades (Raemaekers et al., 2009), and also not attenuated during the



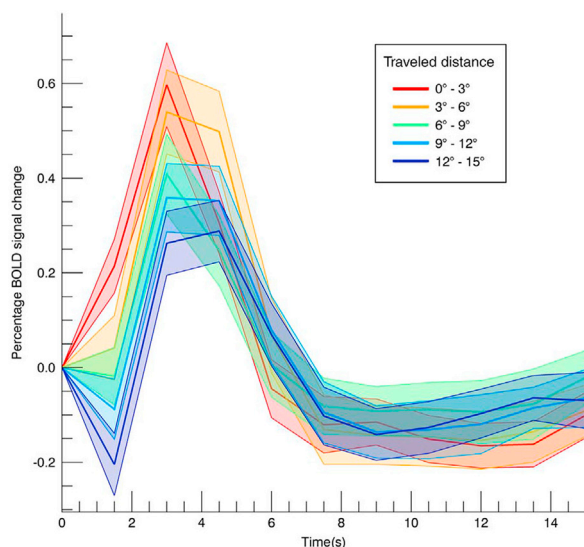
**Fig. 4.** Subtraction BOLD-amplitude opposite motion directions Figure displays subtracted BOLD amplitudes (mean amplitude of V1, V2 and V3) from opposite motion directions. Different coloring of the bars in the bar plots, shows which motion direction resulted in larger BOLD amplitudes across the visual field. During fluent motion (A), BOLD amplitudes were largest when the bar stimulus was near the onset of the motion path (e.g. rightward motion left hemifield). Differences between opposite motion directions decrease to zero near the middle of the motion trajectory. The same pattern was found for coherent stepwise bar motion (B). However, during incoherent stepwise bar motion (C), differences between opposite motion directions all reside around the zero difference line, showing no effect of motion novelty. Error bars denote the standard error across subjects.

presentation of multiple motion stimuli (Schellekens et al., 2015), thereby dismissing shifts in overt/covert spatial attention towards a stimulus onset as a viable explanation for current results. Furthermore, shifts in spatial attention offer no real explanation for the gradual signal decrease across the full length of motion trajectories. Subjects were engaged in a demanding attention task at central fixation, of which

performance was good with 80% correct responses and did not differ between motion experiments. Moreover, the number of incorrect and missed responses did not appear to be affected by the location of the moving bar within the stimulus area. These results are not in favor of spatial attention shifts as an explanation for the presence or absence of the gradual signal decrease along the motion trajectory. The second



**Fig. 5.** Regression coefficients motion prediction The regression coefficients are shown derived from the regression of a linear decreasing function with the subtraction of BOLD amplitudes from opposite motion directions. The larger the regression coefficient, the larger was the motion novelty effect (i.e. enhanced BOLD amplitudes for novel visual motion). Error bars denote the standard error across subjects.



**Fig. 6.** BOLD signal fluent motion The figure shows separate BOLD curves (mean V1, V2, V3) for different distances that the fluently moving bar had traveled (colors). Note that all curves are shifted in time (horizontal axis) to correct for stimulus lag. When the bar was still close to the onset of its trajectory (i.e. shortest traveled distance; red curve), there is no initial dip and the amplitude is largest of all curves. However, when the bar had traveled the maximum distance (blue curve), there was a large initial dip and the BOLD amplitude is lowest of all curves. Both the BOLD amplitude and initial dip changed gradually as the bar stimulus moved along its trajectory. Areas of lighter shade represent standard error across subjects.

extraclassical RF effect relates to motion (de)blurring. Cortical motion signals may be summated over space and time (Amano et al., 2009; Webb et al., 2007). The temporal summation is thought to be quite slow leading to a blurred representation of motion trajectories (Burr, 1980; Geisler, 1999), which might subsequently be nullified by deblurring mechanisms (Arnold et al., 2007; Hammett et al., 1998; Wallis and Arnold, 2009). Despite the fact that these motion processing mechanisms could in theory affect neuronal activity across the entire motion trajectory, they offer no satisfactory explanation for the gradual decrease in BOLD activity. Stimulus characteristics did not change along the trajectory, meaning that motion vector averages or blurred representations should be roughly equal along the entire motion path. Instead, the gradual decrease in BOLD signal is most likely caused by extraclassical RF effects related to prediction mechanisms (Friston, 2010; Rao and Ballard, 1999), resulting

in the suppression of predicted neural input. We postulate that neural activity induced by a moving stimulus is increasingly suppressed along its trajectory, as predictability of future fieldmap positions increases with increased traveled distance of the stimulus. This notion of predictive motion processing is in accordance with other reports of decreases in neural activity for predictable visual input (Alink et al., 2010; den Ouden et al., 2010), and might possibly even relate to certain other (psycho-physical) findings, such as the dissimilarity in stimulus detection between motion leading and trailing edges (Roach et al., 2011; Schwiedrzik et al., 2007).

It is not only the amplitude, but also the initial dip of the BOLD response that changes along a motion trajectory. When the bar stimulus was near the onset of its motion trajectory, BOLD responses did not exhibit an initial dip. However, an initial dip emerged and increased in size as the bar stimulus moved closer towards the end of its trajectory. The initial dip is thought to reflect the immediate decrease in oxyhemoglobin, following oxygen consumption as a result of neuronal activity (Thompson et al., 2003; Yacoub et al., 2001). However, it appears counterintuitive that initial oxygen consumption in response to the signaling of a motion stimulus would increase as the stimulus keeps moving, while stimulus characteristics remain unchanged. Rather, the currently observed changes in initial dip support recent views that the neurovascular coupling is not solely determined by metabolic demands (Carmignoto and Gómez-Gonzalo, 2010; Petzold and Murthy, 2011). Several studies have reported that glial cells effect the neurovascular coupling by directly influencing synaptic activity in both excitatory and inhibitory ways (Fellin et al., 2006; Figley and Stroman, 2011). Astrocytes can cause a heterosynaptic depression of unstimulated neighboring synaptic pathways through the release of adenosine. In light of predictive coding mechanisms, astrocytes may contribute to the inhibition of predictable visual input, putatively resulting in an increased initial dip for increased levels of predictability of neural input. We argue that these results indicate that, at least under some conditions, the initial dip is associated with a neuronal mechanism, perhaps inhibition. A neuronal account, directly associated with specific stimulus features, could perhaps also contribute to the question why the initial dip is not always detected in fMRI BOLD studies (Hu and Yacoub, 2012; Silva et al., 2000).

The observed pattern of results indicates that the predictive mechanism is part of a low-level bottom-up mechanism. While fluent and apparent coherent motion produce similar motion anticipation patterns, confirming assertions of a similar neural basis underlying both types of visual motion processing (Goebel et al., 1998; Muckli et al., 2005), the BOLD activity pattern related to motion anticipation disappears during incoherent stepwise motion. Reverse-phi phenomena could possibly have contributed to the disruption of motion coherence during the presented contrast switches (Bours et al., 2009; Mo and Koch, 2003). Incoherent stepwise motion might have stimulated low-level first-order motion detectors that are sensitive to the opposite direction as the actual stimulus progression, as well as second-order motion detectors that are sensitive to the same direction as the stimulus progression (Fleet and Langley, 1995). This contrasts the coherently moving stimuli, where both first- and second-order stimulated motion detectors would have the same direction sensitivity as the motion direction, indicating that the occurrence of motion prediction effects is dependent on low-level motion stimulus coherence. Also note that population RFs were stimulated in the same consecutive order during coherent and incoherent stepwise motion, ensuring that the second-order motion trace, which was predictable from the participant's point of view, was equal for both stepwise motion stimuli. The observed mechanism is, thus, dependent on low, but not high-level anticipatory or otherwise perceptual processes. Arguably the simplest neurophysiological mechanism that can account for the observed findings is that coherently stimulated motion detectors in early visual cortex induce a temporary hyperpolarization of cell membranes at fieldmap locations in the direction of motion, which attenuates neural responses to contrast changes when the stimulus arrives at its anticipated location. Such anticipatory inhibition might occur through (lateral) long



range horizontal connections and possibly glial cells as well.

In summary, we present evidence that human early visual cortical areas V1, V2, and V3 anticipate the trajectory of a single moving bar stimulus. Relatively enhanced BOLD responses were measured near the onset of the motion trajectory, which linearly decreased as the bar stimulus moved towards the end of the motion trajectory. This effect was accompanied by an increase of an initial dip in the BOLD response. These findings can be attributed to the anticipation of a coherently moving object. We propose that early visual cortex actively predicts upcoming motion input by means of predictive coding suppression mechanisms.

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