

# Inferring the direction of implied motion depends on visual awareness

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**Visual awareness of an event, object, or scene is, by essence, an integrated experience, whereby different visual features composing an object (e.g., orientation, color, shape) appear as a unified percept and are processed as a whole. Here, we tested in human observers whether perceptual integration of static motion cues depends on awareness by measuring the capacity to infer the direction of motion implied by a static visible or invisible image under continuous flash suppression. Using measures of directional adaptation, we found that visible but not invisible implied motion adaptors biased the perception of real motion probes. In a control experiment, we found that invisible adaptors implying motion primed the perception of subsequent probes when they were identical (i.e., repetition priming), but not when they only shared the same direction (i.e., direction priming). Furthermore, using a model of visual processing, we argue that repetition priming effects are likely to arise as early as in the primary visual cortex. We conclude that although invisible images implying motion undergo some form of nonconscious processing, visual awareness is necessary to make inferences about motion direction.**

## Introduction

The visual system constantly draws indirect inferences about properties that are not explicitly defined in terms of physical signals. A striking example is our capacity to infer motion features from static pictures implying movement (e.g., an athlete running rightward, see Freyd, 1983). This capacity involves the analysis of static cues such as figure-ground segregation (Roelfsema, Lamme, Spekreijse, & Bosch, 2002), motion streaks (Burr & Ross, 2002; Geisler, 1999), body posture (Jellema & Perrett, 2003), and their integration

within the context of the scene. Although such stimuli do not carry explicit motion information (i.e., there is no continuous variation of luminance over time), they are known to activate brain areas involved during real motion processing such as MT/V5 (Kourtzi & Kanwisher, 2000; Lorteije et al., 2006; Peuskens, Vanrie, Verfaillie, & Orban, 2005; Senior et al., 2000; Williams & Wright, 2009; but see Lorteije et al., 2011, for potential low-level confounds). Furthermore, exposure to implied motion adaptors is known to induce repulsory shifts in the perceived position of subsequent static probes (Pavan, Cuturi, Maniglia, Casco, & Campana, 2011) and in the perceived direction of subsequent real-motion probes (Winawer, Huk, & Boroditsky, 2008). Such a shift in the perception of motion direction (i.e., directional adaptation) is supposed to result from a decrease in the responsiveness of directionally selective neurons coding for real motion (Barlow & Hill, 1963). Thus, it has been proposed that the same subset of neurons encode both implied and real motion information. Interestingly, it is known that motion information is encoded even when rendered invisible by binocular rivalry (Wiesenfelder & Blake, 1991), continuous flash suppression (Kaunitz, Fracasso, & Melcher, 2011; Maruya, Watanabe, & Watanabe, 2008), or crowding (Aghdaee, 2005; Faivre, Berthet, & Kouider, 2012; Rajimehr, Vaziri-Pashkam, Afraz, & Esteky, 2004; Whitney, 2005). These results suggest that one can infer the direction of real motion even though it is not accessible to awareness. Here, we aimed at testing whether a similar inference can be made regarding the direction of implied motion.

Much more processing is required to infer the direction of implied motion than of real motion, since the former involves the encoding of complex features and their integration into one unified perceptual representation, while the latter simply involves the

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detection of luminance (or contrast, in case of second order motion) changes over time. Considering the complexity of the features defining the direction of implied motion, we tested whether they could induce directional adaptation when rendered invisible by continuous flash suppression.

The integration of different physical features into one unified perceptual representation is commonly considered to depend on conscious processes (Baars, 2005; Dehaene & Changeux, 2011; Dehaene & Naccache, 2001). Accordingly, it has been proposed that visual awareness intrinsically relates to the capacity of the brain to integrate different aspects of incoming signals into a unified percept (Tononi, 2008). By contrast, integrative capacities are not held to be as potent for signals that are not accessed consciously. Building upon these assumptions, Koch and Tononi (2011) proposed that a system able to process the intricate elements of a complex visual scene as a whole may be considered as conscious. Recently, this tentative operational test for visual awareness has been challenged by two studies suggesting that semantic relations between an object and its background can be processed in the absence of awareness (Mudrik, Breska, Lamy, & Deouell, 2011; Mudrik & Koch, 2013). Here, we further investigated the relevance of this test for visual awareness by measuring whether human observers could infer the direction of invisible implied motion stimuli.

## Experimental procedures

### Participants

Healthy paid volunteers with normal or corrected-to-normal visual acuity were recruited from the California Institute of Technology student population (age range: 18–30). Five participants were included in Experiment 1, 15 in Experiment 2 (divided to three equal groups assigned to Experiments 2a, b, c), and 21 in Experiment 3 (10 in Experiment 3a, 11 in Experiment 3b). Subjects were naïve to the purpose of these experiments and gave informed written consent. All experiments conformed to institutional guidelines for experiments with human participants and to the Declaration of Helsinki.

### Apparatus

Stimuli were presented using Matlab and the Psychophysics toolbox (Brainard, 1997; Pelli, 1997). Participants' heads were stabilized using a chinrest located 57 cm away from a 19-in. CRT screen

(resolution  $1024 \times 768$ ; refresh rate 100 Hz). A mirror stereoscope was used to present images separately to each eye.

### Stimuli

Stimuli were derived from the ones used by Winawer et al. (2008). They consisted of 80 pictures of people, animals, or vehicles moving leftward or rightward. All of them were equated in terms of luminance histogram and spatial frequency using the SHINE toolbox (Willenbockel et al., 2010).

### Continuous flash suppression

A frame ( $9.9^\circ \times 9.9^\circ$ ) composed of textured black and white bars ( $0.6^\circ$  width) was presented to each eye against a gray background ( $6.15 \text{ cd.m}^{-2}$ ) to facilitate stable binocular fusion. Trials were self-paced and started after participants indicated that a fixation dot presented to the dominant eye ( $0.2^\circ$  diameter) was centered within a circle presented to the nondominant eye ( $1.2^\circ$  diameter). Continuous flash suppression (CFS) patterns consisted of arrays of 600 randomly generated disks (diameters from  $0.1^\circ$  to  $1.2^\circ$ ) of different shades of gray. They were flashed at an effective frame rate of 10 Hz to the dominant eye.

### Procedure for Experiment 1

Experiment 1 measured directional adaptation from visible implied motion stimuli. The experiment was divided into six blocks of 24 trials and lasted around 1 hr. On each trial, while the dominant eye received a static homogeneous gray background, the nondominant eye was presented with a sequence of adaptors (i.e., implied motion pictures;  $9.3^\circ \times 9.3^\circ$ ) during 20 s in the first trial of each block or 6 s in other trials (i.e., top-up adaptation procedure). Each adaptor was presented for 500 ms with no interstimulus interval (ISI), so that a sequence contained either 40 adaptors (first trial of each block) or 12 adaptors (other trials), with no repetition within a sequence. The direction of implied motion was constant within a block. The sequence of adaptors was followed by a probe presented for 1 s, consisting of a set of 100 dots randomly distributed within a  $9.3^\circ \times 9.3^\circ$  area (dot diameter =  $0.1^\circ$ , Michelson contrast = 0.23). On each frame, a fraction of dots was translated horizontally towards the right or the left, with a speed of  $10.3^\circ \cdot \text{s}^{-1}$  (i.e., real motion). A new set of dots was reselected for coherent motion on each frame, so that the trajectory of single dots could not be followed over the probe's

duration. All other dots disappeared and randomly reappeared at any other location within the test window. The proportion of moving dots defined motion coherence from 0% to 100% in each direction. Three levels of motion coherence were selected for each subject, based on a motion sensitivity measure preceding the experiment (see below). Motion coherence and motion direction changed randomly from trial to trial. Participants were instructed to indicate the motion direction as accurately as possible using the left or right arrow of the keyboard, with no constraint on reaction time. Finally, using the same keys, they had to guess whether the adaptors implied leftward or rightward motion (objective visibility measure).

### Motion sensitivity measure

Prior to the adaptation phase of Experiments 1 and 2, the motion sensitivity of each participant was measured, using the random-dot display described above with motion coherence ranging from 5% to 65%. The maximal motion coherence for a participant was defined as the average of the absolute coherence values that gave rise to asymptotic performance (e.g., 99% and 1% of trials perceived as moving in each direction). In the adaptation phase, random dots were displayed with 100%, 50%, and 25% of the maximal motion coherence for each direction, resulting in six different probes. Defining motion coherence for each participant allowed us to account for subject's variability in terms of motion sensitivity and to therefore optimally sample the psychometric response. Across participants, the average of the maximal motion coherence in Experiment 1 was 11.6% ( $SE = 1.9\%$ ), and no systematic directional bias was found.

### Procedure for Experiment 2a

Experiments 2a and 2b measured directional adaptation for invisible implied motion stimuli. The procedure was identical to that of Experiment 1 except for the following changes. First, instead of a gray background, the dominant eye received a stream of CFS patterns, decreasing the visibility of the implied motion stimulus presented to the nondominant eye (see Figure 1 and Tsuchiya & Koch, 2005). Second, before the objective visibility task, participants were asked to report their subjective percept of the adaptor using a four-alternative forced choice task by indicating whether they had no perceptual experience of the implied motion adaptors, a brief glimpse, an almost clear percept, or a perfectly clear percept (subjective visibility measure, see Ramsy & Overgaard, 2004). The use of objective and subjective visibility measures

allowed for a reliable estimation of awareness at the single trial level (see below). Across participants, the average of the maximal motion coherence was 17.6% ( $SE = 5.0$ ).

### Procedure for Experiment 2b

The procedure was identical to the procedure of Experiment 2a, except that the direction of adaptors changed randomly within a block, and all adaptors were presented for 6 s. Across participants, the average of the maximal motion coherence was 11.7% ( $SE = 2.4$ ).

### Procedure for Experiment 2c

Experiment 2c measured directional adaptation for invisible directional arrows. The procedure was identical to the invisible condition in Experiment 2b, except that the implied motion adaptors were replaced by  $4^\circ \times 4^\circ$  directional arrows ( $>$  or  $<$ ). Edges of the arrow were blurred by blurring the image with a Gaussian filter ( $\sigma = 0.055^\circ$ ). In order to prevent the arrow from breaking CFS, the Michelson contrast was ramped up linearly from zero to a maximum value of 0.22 during the first 500 ms of stimulus display. Across participants, the average of the maximal motion coherence was 12.0% ( $SE = 1.35\%$ ).

### Procedure for Experiment 3a

Experiment 3a measured repetition priming from invisible implied motion stimuli. The procedure was identical to the one of Experiment 2b, except for the following changes. Rather than a random-dot display, we used an implied motion picture as a probe, which could be either identical to the adaptor (congruent condition) or any picture of the stimulus set implying a motion of opposite direction (noncongruent condition). The size of the probe was  $7.5^\circ \times 7.5^\circ$ , which is 80% of the size of the adaptor. Participants were instructed to indicate as fast as possible the motion direction implied in the probe. Visibility (i.e., presence or absence of CFS) was manipulated in a within-subject design, with the invisible condition always preceding the visible condition.

### Procedure for Experiment 3b

Experiment 3b measured direction priming from invisible implied motion stimuli. The procedure was identical to the one of Experiment 3a, except for the following changes. We randomly split the stimulus set

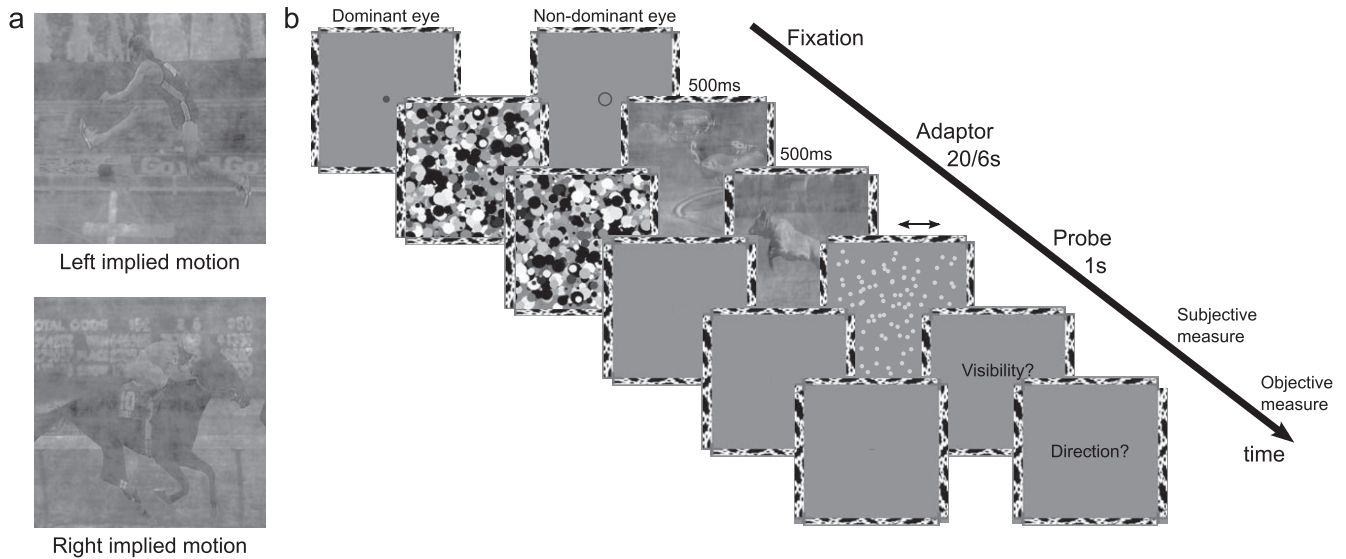


Figure 1. (a) Examples of left and right implied motion stimuli. (b) Experimental procedure for Experiment 2a. While the nondominant eye was stimulated by the adaptors (here a series of static pictures that implied leftward motion), the dominant eye received a stream of salient patterns. After 20 s (first trial of each block) or 6 s (other trials) of such display, participants had to report whether they perceived a random-dot probe as moving rightward or leftward. Subsequently, they were presented with a question asking if they had no perceptual experience, a brief glimpse, an almost clear image, or a perfectly clear image of the implied motion adaptor (*subjective measure*). Finally, they had to indicate the direction of motion implied by the adaptor (*objective measure*).

into two equal subsets containing 40 stimuli, one for the adaptors and the other for the probes. Thus, an adaptor was never seen as a probe throughout the experiment and vice versa. In the congruent condition, the adaptor and the probe were different pictures with the same implied motion direction (e.g., a horse running leftward followed by a cyclist riding leftward), while in the incongruent condition, the adaptor and the probe were different pictures with the opposite implied motion direction (e.g., a car driving leftward followed by a man running rightward). Finally, a prime never appeared as a probe, in order to avoid potential instances of conscious stimulus-response mapping (Damian, 2001).

## Data analysis

In Experiments 1 and 2a, b, c, which involved measures of directional adaptation, the shape of the psychometric function was derived using a two-parameter logistic function in which the upper limit was fixed at one (i.e., for leftward motion at maximal motion coherence) and the lower limit was constrained to approach zero (i.e., for rightward motion at maximal motion coherence).<sup>1</sup>

The midpoint of the logistic function was used as a measure for the point of subjective equality (PSE). The negative slope of the function at the midpoint was taken as a measure for the discriminability of motion direction. In the invisible condition of Experiments 2a,

b, c and 3a, b we discarded trials in which performance on the objective visibility task was beyond 65% in a given subjective visibility category and a given participant. In Experiments 3a and 3b, involving measures of reaction times (repetition and direction priming respectively), we excluded trials for which the reaction time on the probe was faster than 300 ms or slower than 1500 ms (corresponding respectively to 4.4% and 3.9% of total trials) (Whelan, 2010). Kolmogorov-Smirnov test showed that reaction times averaged across participants and experimental conditions did not significantly deviate from a normal distribution (Experiment 3a:  $D = 0.09$ ,  $p = 0.90$ ; Experiment 3b:  $D = 0.10$ ,  $p = 0.78$ ). Unless specified, statistic tests were two sided. Statistical analysis was performed using R (R Foundation for Statistical Computing, Vienna, Austria).

## Image analysis

We estimated the physical similarity between adaptors and probes in Experiment 3 using a model of early visual processing (Serre & Riesenhuber, 2004) adapted from Kietzmann, Swisher, König, and Tong (2012). First, we mimicked the decrease of spatial resolution with eccentricity in the visual field by a foveation procedure using the Space Variant Imaging System Toolbox (Kortum & Geisler, 1996). Stimuli were low-pass filtered and down sampled in order to produce a quadratic decrease of spatial resolution with eccentric-



	No experience	Brief glimpse	Almost clear experience	Very clear experience
Exp. 2a	73.1 ± 11.3	23.5 ± 8.3	3.3 ± 0.7	9.2 ± 3.7
Exp. 2b	75.5 ± 9.6	16.5 ± 5.2	8.9 ± 5.1	5.2 ± 2.9
Exp. 2c	67.6 ± 7.11	22.2 ± 4.7	8.5 ± 3.3	12.7 ± 7.5
Exp. 3a visible	1.9 ± 0.4	21.6 ± 11.4	23.7 ± 12.7	78.4 ± 11.6
Exp. 3a invisible	71.2 ± 8.2	16.2 ± 4.8	7.6 ± 2.7	11.1 ± 5.8
Exp. 3b visible	1.5 ± 0.05	12.3 ± 6.1	26.7 ± 10.8	69.7 ± 10.8
Exp. 3b invisible	47.6 ± 11.4	26.7 ± 6.3	24.3 ± 8.0	9.4 ± 1.6

Table 1. Average proportion of trials for each category of the subjective perceptual awareness scale ± SEM. Note that proportion of trials do not sum up to 100% as not every subject has trials in all four categories.

ity (50% resolution at 1.5° of eccentricity from the center of the stimulus). Then, we filtered the foveated stimuli with a set of two-dimensional Gabor functions modeling parafoveal simple cells from monkey primary visual cortex (Schiller, Finlay, & Volman, 1976). We used 17 receptive field sizes with  $\sigma$  ranging from 2.8° to 19.3° and four angular orientations of 0,  $\pi/4$ ,  $\pi/2$ , and  $3\pi/4$ . The output of the model was used to create correlation matrices reflecting low-level similarities between the adaptors and the probes used in Experiments 3a (repetition priming) and 3b (direction priming). From Experiment 3a, 40 stimuli implying leftward motion were analyzed, half of them being derived from rightward motion stimuli using a horizontal mirror transformation. This resulted in a  $40 \times 40$  symmetric matrix of cross-correlation coefficients. Hence, only the low-level similarity between stimuli was estimated, without any confound with the direction of implied motion. From Experiment 3b, 20 adaptors implying leftward motion and 20 adaptors implying rightward motion were analyzed, in comparison to 20 probes implying leftward motion and 20 probes implying rightward motion. Hence, we compared the similarity between adaptors and probes implying the same versus different motion direction, without any confound of identity present in Experiment 3a.

## Results

Experiment 1 measured directional adaptation for visible implied motion stimuli. The direction of visible implied motion adaptors was discriminated with an accuracy of 98.1% ( $SE = 1.4\%$ ), and the motion direction of random-dot probes (real motion) averaged over all coherence values was discriminated with an accuracy of 75.8% ( $SE = 3.8\%$ ). Analysis of the psychometric function revealed that the point of subjective equality (PSE) for the random-dot probe was globally shifted towards the left (33% of normalized motion coherences), revealing a perceptual or response bias for rightward motion. Surprisingly, this bias is of relatively large magnitude and was not found when

measuring motion sensitivity prior to the main experiment (see Experimental procedures). This suggests that it is likely to originate from nonspecific phenomena occurring during the procedure, which remain to be explored (e.g., attentional or training effects, implied motion default value in all stimuli).

Importantly though, this bias is orthogonal to the measure of directional adaptation, which is the central aspect of our study. Accordingly, we found a difference in PSE after exposure to rightward versus leftward implied motion (one-sided Wilcoxon signed rank test: PSE shift = 38.8% of motion coherence,  $W = 0$ ,  $p = 0.03$ , where  $W$  denotes the absolute value of the sum of the signed ranks), revealing a directional adaptation effect (Figure 2). No difference in terms of motion discriminability reflected by the slope of the psychometric function was found (Wilcoxon signed rank test: slope difference = 1.32,  $W = 5$ ,  $p = 0.6$ ). These results replicate the finding that fully visible implied motion cues induce directional adaptation effects (Winawer et al., 2008).

We then tested whether directional adaptation could be induced by invisible implicit motion inducers. In Experiment 2a, after sorting trials following both objective and subjective criteria (see Experimental procedures and Tables 1, 2), performance on the objective visibility task fell to 51.9% ( $SE = 2.0\%$ ), which was not significantly different from chance level (Wilcoxon signed rank test with continuity correction:  $W = 9$ ,  $p = 0.81$ ). As in Experiment 1, the motion direction of random-dot probes was discriminated far above chance (74.1%,  $SE = 2.9\%$ ). Also as in Experiment 1, analysis of the psychometric function revealed a perceptual bias for rightward motion (average PSE = 19% of normalized coherence). Yet, the direction of implied motion had no influence on the perception of the random-dot probe, nor in terms of PSE (Wilcoxon signed rank test: PSE shift = 5.1,  $W = 7$ ,  $p = 1$ ), nor in terms of discriminability (Wilcoxon signed rank test: slope difference = 0.2,  $W = 7$ ,  $p = 1$ ) (Figure 3a). We conclude that under these conditions, invisible implied motion stimuli did not elicit a directional adaptation effect. It is of note that similar results were obtained when analyses were run exclu-

	No experience	Brief glimpse	Almost clear experience	Very clear experience
Exp. 2a	52.7 ± 2.0	69.5 ± 11.4	100 ± 0	100 ± 0
Exp. 2b	54.1 ± 3.3	58.4 ± 11.0	91.7 ± 8.3	100 ± 0
Exp. 2c	53.1 ± 2.5	88.0 ± 5.5	100 ± 0	100 ± 0
Exp. 3a visible	83.3 ± 16.7	76.6 ± 21.7	98.7 ± 1.3	94.9 ± 1.6
Exp. 3a invisible	52.7 ± 2.1	68.7 ± 7.2	97.4 ± 2.0	98.2 ± 1.1
Exp. 3b visible	100 ± 0	95.3 ± 2.9	98.2 ± 1.7	98.4 ± 0.06
Exp. 3b invisible	48.8 ± 5.5	61.1 ± 6.0	80.2 ± 8.2	63.7 ± 15.1

Table 2. Average accuracy in percent on the objective visibility task for each category of the perceptual awareness scale ± SEM. In the invisible conditions, in order to take into account the variability of accuracy depending on subjective states of perceptual awareness (e.g., see high SEM in the “brief glimpse” category), we further analyzed trials in which objective accuracy was below 65% within each category of the perceptual awareness scale.

sively on trials associated with “no experience” on the perceptual awareness scale ( $p$  values > 0.7). The absence of directional adaptation from invisible implied motion could have either stemmed from the lack of implied motion detection in the absence or awareness or from the use of a block design, in which the direction of implied motion was constant within a block of 24 consecutive trials lasting 20 s (first trial) or 6 s (other trials). Accordingly, visibility of a stimulus during a single trial may have influenced the processing of stimuli presented in subsequent trials and triggered the development of strategies we could not control for.

To account for this possibility, we conducted Experiment 2b, in which the direction of implied motion was interleaved randomly within a block (see Experimental procedures). After sorting trials following both objective and subjective criteria (see Experimental procedures and Tables 1, 2), performance on the objective visibility task fell to 53.4% ( $SE = 3.6\%$ ), which was not significantly different from chance (Wilcoxon signed rank test with continuity correction:

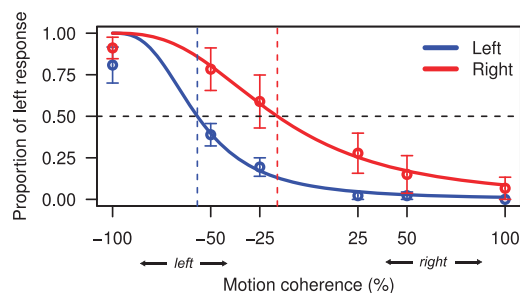


Figure 2. Experiment 1—Proportion of perceived leftward motion as a function of motion coherence, after exposure to leftward (blue) or rightward (red) implied fully visible static motion adaptors. Percentages indicate normalized motion coherences, which is the proportion of absolute coherence values giving rise to asymptotic performance (see Experimental procedures). Vertical lines stand for the perceptual point of equality (i.e., a hypothetical probe categorized as moving leftward with a probability of 0.5). Error bars correspond to the standard error of the mean (SEM).

$W = 11, p = 0.42$ ). The motion direction of random-dot probes was discriminated accurately 77.4% ( $SE = 4.6\%$ ). As in Experiment 2a, analysis of the psychometric function revealed a perceptual bias for rightward motion (average PSE = 20% of normalized coherence), independent of the direction of implied motion (Wilcoxon signed rank test with continuity correction: PSE shift = 6.9,  $W = 5, p = 0.63$ ). No influence of implied motion on the discriminability of the random-dot probe was found (Wilcoxon signed rank test: slope difference = 1.36,  $W = 6, p = 0.81$ ) (Figure 3b). It is of note that similar results were obtained when analyses were run exclusively on trials associated with “no experience” on the perceptual awareness scale ( $p$  values > 0.9). Experiment 2b accordingly suggests that invisible implied motion stimuli did not elicit directional adaptation.

One explanation for the absence of significant results is that the direction of implied motion cannot be inferred for invisible adaptors, most likely due to the complexity of the spatial structure carrying this information. We therefore designed follow-up Experiment 2c, in which the adaptors consisted of simple directional arrows. Such stimuli are known to be processed when rendered invisible with metacontrast masking (Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003) and visual crowding (Faivre & Kouider, 2011a), although to our knowledge no evidence exists regarding CFS. After sorting trials following both objective and subjective criteria (see Experimental procedures and Tables 1, 2), performance on the objective visibility task fell to 53.0% ( $SE = 2.5\%$ ), which was not significantly different from chance (Wilcoxon signed rank test with continuity correction:  $W = 9, p = 0.20$ ). The motion direction of random-dot probes was discriminated above chance 78.4% ( $SE = 4.1\%$ ). Here again, analysis of the psychometric function revealed a perceptual bias for rightward motion (average PSE = 13% of normalized coherence) independent from the direction of implied motion (Wilcoxon signed rank: PSE shift = 3.8%,  $W = 5, p = 0.63$ ). The discriminability of the random-dot

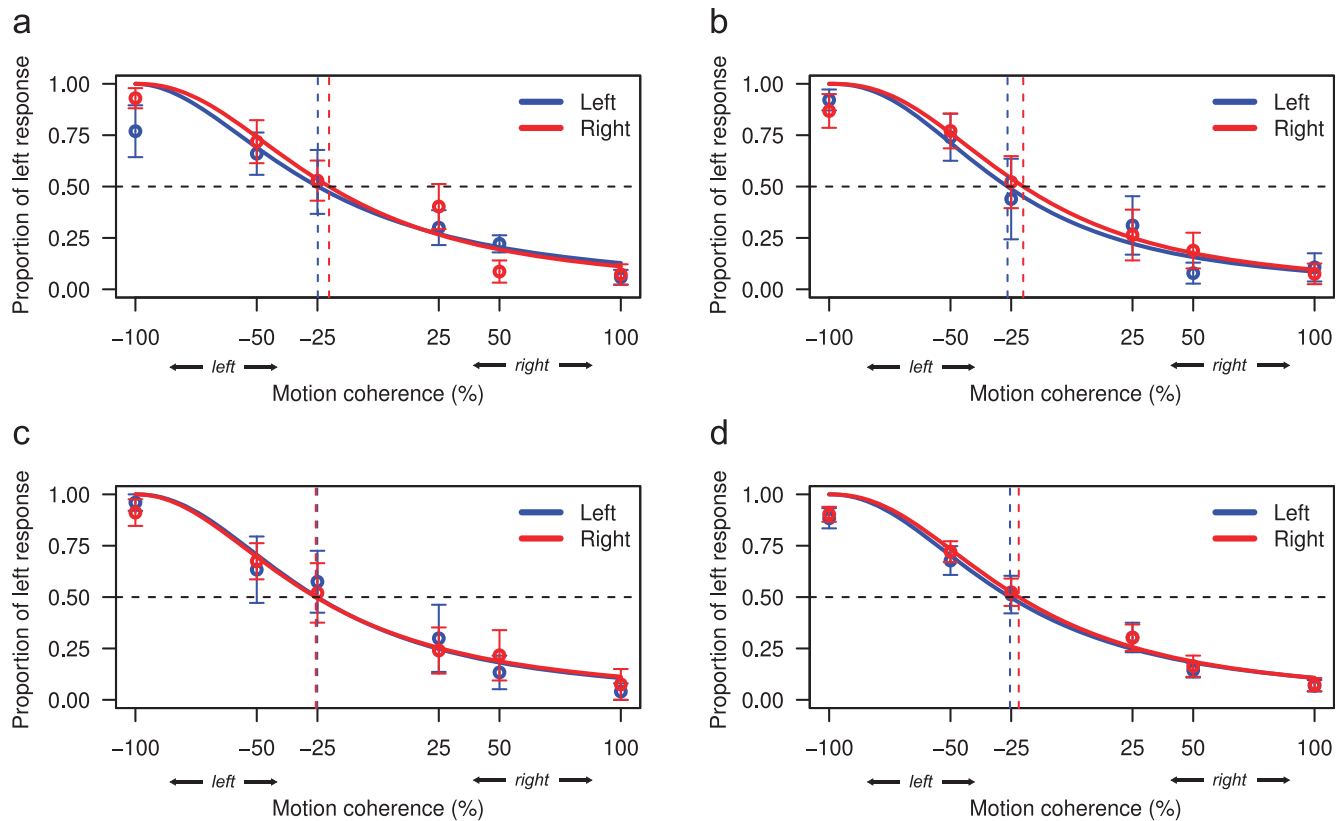


Figure 3. Proportion of perceived leftward motion as a function of motion coherence, after exposure to invisible leftward (blue) or rightward (red) adaptors. (a) Implied motion stimuli presented in a block (Experiment 2a) or (b) in a random design (Experiment 2b). (c) Directional arrow stimuli presented in a random design (Experiment 2c). (d) Data from Experiments 2a, b, c grouped together. Percentages indicate normalized motion coherences, which is the proportion of absolute coherence values giving rise to asymptotic performance (see Experimental procedures). Vertical lines stand for the perceptual point of equality (i.e., a hypothetical probe categorized as moving leftward with a probability of 0.5). Error bars correspond to SEM.

probe did not change according to the direction of implied motion (Wilcoxon signed rank: slope difference = 4.0,  $W = 10$ ,  $p = 0.63$ ) (Figure 3c). It is of note that similar results were obtained when analyses were run exclusively on trials associated with “no experience” on the perceptual awareness scale ( $p$  values > 0.4). In order to examine the possibility that Experiments 2a, b, c lacked statistical power, we analyzed the psychometric functions of all participants grouped together. Despite a triple amount of data points, we did not find a shift in terms of PSE (Wilcoxon signed rank: PSE shift = 7.0%,  $W = 46$ ,  $p = 0.45$ ) nor in terms of discriminability (Wilcoxon signed rank: slope difference = 0.9,  $W = 63$ ,  $p = 0.89$ ) (Figure 3d).

Taken together, Experiments 2a, b, c demonstrate that static directional stimuli did not elicit a directional adaptation effect. In the following experiments, we tested whether implied motion stimuli could be processed nonconsciously to a lower extent by relying on measures of priming at two different levels of visual processing. Priming reflects the fact that the processing of a probe stimulus is more efficient (i.e., typically

faster) when preceded by a related compared to a nonrelated prime stimulus (Henson, 2003; Schacter, Dobbins, & Schnyer, 2004). By varying the nature of the relation between the prime and the probe, we estimated the level of processing undergone by the implied motion prime with and without awareness. In Experiment 3a, a related pair consisted of a prime and a probe sharing a relation of identity: They depicted the exact same implied motion picture. In Experiment 3b, a related pair consisted of a prime and a probe sharing a relation of directionality: They consisted in different implied motion images with the same direction of implied motion. In both experiments, an unrelated pair consisted of a prime and a probe representing two distinct implied motion images of opposite direction. In all cases, the size of the probe was reduced to 80% the size of the prime in order to decrease low-level confounds.

In the visible condition of Experiment 3a (repetition priming), considering that both subjective and objective reports indicated high visibility for every participants (see Tables 1, 2), we kept all trials for further analyses.

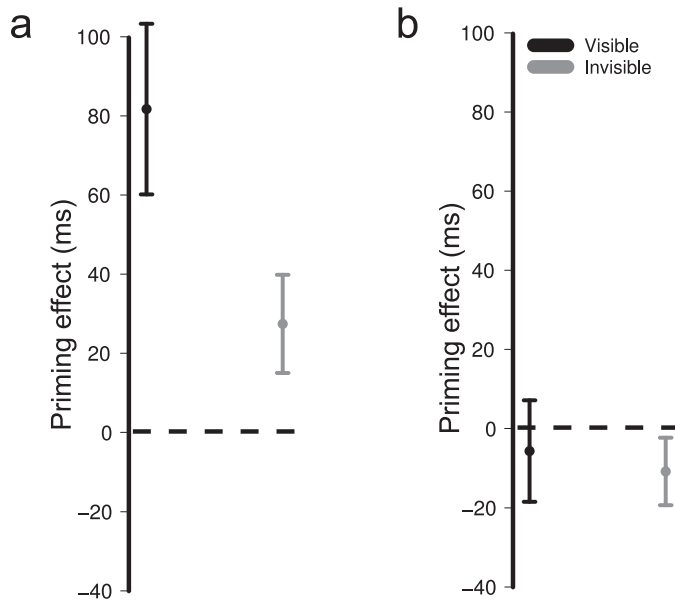


Figure 4. (a) Repetition priming effects and (b) direction priming effects in Experiments 3a and 3b, in the visible (black) and invisible (gray) condition. Error bars correspond to SEM.

The direction of the implied motion probe was discriminated accurately (94.2%,  $SE = 1.9\%$ ). Analyses of reaction times revealed a repetition priming effect, reflecting the fact that observers categorized the direction of the probe faster when it was preceded by an identical adaptor compared to an adaptor implying motion in the opposite direction, paired  $t$  test: 86 ms,  $t(9) = 3.85$ ,  $p = 0.004$  (Figure 4a). In the invisible condition, after sorting trials following both objective and subjective criteria (see Experimental procedures and Tables 1, 2), performance on the objective visibility task in the invisible condition fell to 54.1% ( $SE = 2.2\%$ ), which was marginally significant, one-sample  $t$  test:  $t(9) = 2.24$ ,  $p = 0.052$ . The direction of the implied motion probe was discriminated accurately (91.0%,  $SE = 1.4\%$ ). As in the visible condition, we found a repetition priming effect, paired  $t$  test: 30 ms,  $t(9) = 2.37$ ,  $p = 0.042$ . It remains possible that this priming effect resulted from residual visibility of the adaptor, as performance on the objective visibility task was slightly above chance level. This possibility was undermined by two aspects of our results. First, the amplitude of priming did not correlate with visibility, as revealed by a linear regression analysis (adjusted  $R^2 = 0.097$ ,  $p = 0.20$ ). Second, the priming effect was marginally below significance when measured on trials associated with “no experience” on the perceptual awareness scale,  $t(9) = 2.14$ ,  $p = 0.06$ . Yet, as it is often reported, the priming effect in the invisible condition was of lower amplitude than in the visible condition, paired  $t$  test, difference = 56 ms,  $t(9) = 2.95$ ,  $p = 0.02$ .

In the visible condition of Experiment 3b (direction priming), all trials were included for further analyses since subjective and objective reports indicated high visibility in every participants (see Tables 1, 2). The direction of the implied motion probe was discriminated accurately (92.5%,  $SE = 1.4\%$ ). Analyses of reaction times revealed no direction priming effect, paired  $t$  test:  $-9$  ms,  $t(10) = -0.86$ ,  $p = 0.41$  (Figure 4b). In the invisible condition, after sorting trials following both objective and subjective criteria (see Experimental procedures and Tables 1, 2), performance on the objective visibility task in the invisible condition fell to 52.5% ( $SE = 1.6\%$ ), which was not significantly different from chance, one sample  $t$  test:  $t(10) = 1.53$ ,  $p = 0.15$ . The direction of the implied motion probe was discriminated accurately (92.8%,  $SE = 1.5\%$ ). Analyses of reaction times revealed no direction priming effect, paired  $t$  test:  $-14$  ms,  $t(10) = -1.29$ ,  $p = 0.23$ ; priming remained nonsignificant when measured on trials associated with “no experience” on the perceptual awareness scale, with  $p > 0.6$ . Furthermore, there was no difference in terms of high-level priming effect between the visible and invisible conditions, paired  $t$  test:  $-5$  ms,  $t(10) = -0.35$ ,  $p = 0.73$ . These results suggest that irrespective of visibility, an adaptor implying motion does not speed up the categorization of a perceptually different probe implying motion in the same direction. Post-hoc analyses revealed significant differences between the amplitude of repetition (Experiment 3a) and direction priming effects (Experiment 3b), both in the visible, Welch two-sample  $t$  test  $t(18.0) = 2.65$ ,  $p = 0.016$ , and invisible conditions, Welch two-sample  $t$  test  $t(12.8) = 3.85$ ,  $p = 0.002$ . We concluded from Experiment 3 that weak repetition priming but no direction priming arises from invisible implied motion stimuli.

It is usually assumed that size differences between probes and adaptors are sufficient to rule out potential low-level origins of repetition priming effects, typically at the level of the primary visual cortex. However, it is known that processing in the primary visual cortex (V1) supports scale-invariant properties (Teichert, Wachtler, Michler, Gail, & Eckhorn, 2007). We ran a simple, but physiologically compatible, model of spatial processing in V1 (Serre & Riesenhuber, 2004) in order to estimate the similarity within pairs of stimuli sharing a relation of identity (see Experiment 3a) or directionality (i.e., see Experiment 3b) as a function of the size ratio between the two members of the pair (see Experimental procedures and Figure 5a). Measures of similarity were obtained by cross-correlating the output coefficients provided by the model between the two members of related versus nonrelated pairs. For identity relations, we found that the similarity between related pairs (0.983,  $SD = 0.036$ ) was significantly higher than for non-related pairs (0.974,  $SD = 0.0006$ ),  $t(78) = 15.7$ ,  $p <$



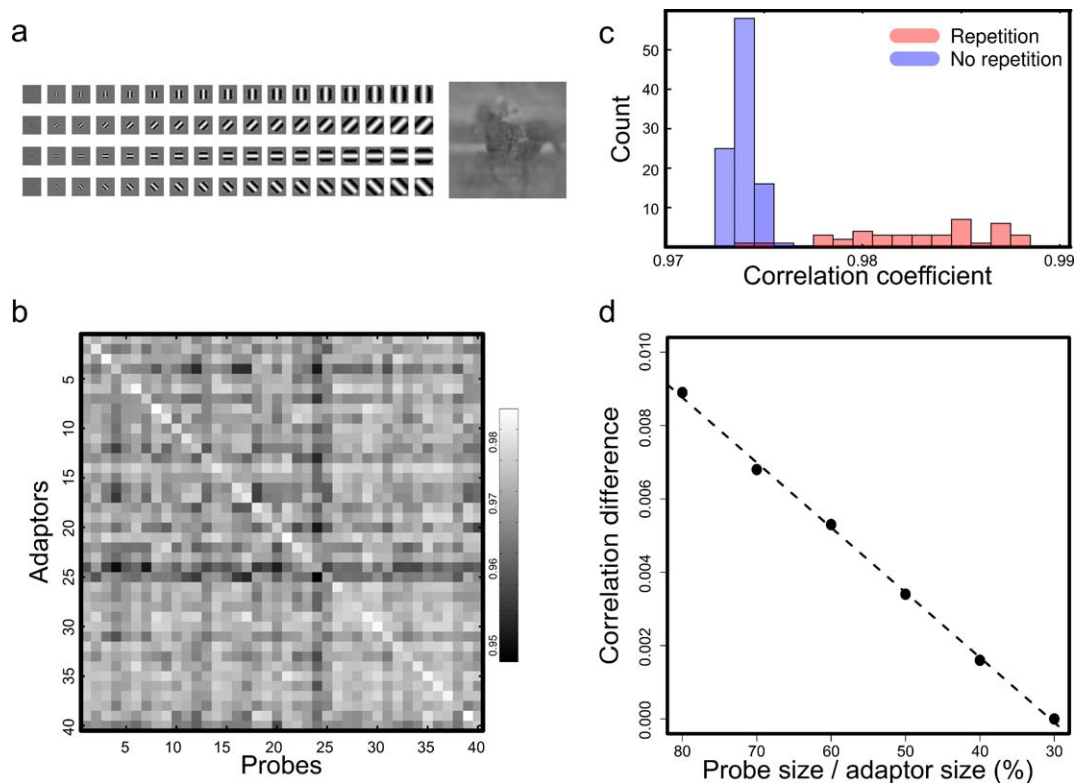


Figure 5. Primate V1 filtering model applied to the stimuli used in Experiment 3a. (a) Gabor filters (17 receptive field sizes, four orientations) applied on the foveated implied motion stimuli (here, a horse running leftward). (b) Matrix of cross-correlation coefficients between a subset of 40 probes and adaptors implying rightward motion, with a size ratio of 80%. The diagonal of the matrix shows higher correlation coefficients for repeated versus nonrepeated pairs of adaptors and probes. (c) Histogram of correlation coefficients for repeated (pink) versus nonrepeated (blue) pairs of adaptors and probes. (d) Difference of correlation coefficients between repeated versus nonrepeated pairs of adaptors and probes as a function of their size ratios. The dashed line represents the linear variation between the two factors.

0.001, despite the decreased size of the probes in respects to the primes (Figures 5b, c). In addition, we found that the difference of similarity between related and nonrelated pairs decreased linearly with the size ratio ( $R^2 = 0.998$ ,  $p < 0.001$ ) (Figure 5d). Our analyses suggest that the similarity between related and non-related pairs disappears for a size ratio of 30%, similarity difference = 0.009,  $t(78) = -0.6$ ,  $p = 0.55$ . The same analysis performed on the directionality relations revealed no similarity difference between related pairs (0.9735,  $SD = 0.0011$ ) and nonrelated pairs (0.9732,  $SD = 0.0014$ ),  $t(38) = 0.74$ ,  $p = 0.47$  (Figures 6a, b). These similarity measures shed light on the discrepancy we encountered between Experiments 3a and 3b. It is quite possible that the repetition priming we found in Experiment 3a does not reflect the encoding of motion direction but simply a perceptual facilitation at the level of V1. By contrast, in case adaptors and probes do not share any similarity at the level of V1 (Experiment 3b), no such facilitation takes place. The fact that directionality priming was not observed independently of stimulus visibility (i.e., with or without CFS) is

surprising and suggests that inferring the direction of implied motion primes involves high-level post-perceptual processes which are irrelevant to disambiguate the direction of implied motion probes.

## Discussion

While the processing of translational motion (Kaunitz et al., 2011; Maruya et al., 2008) and spiral motion (Kaunitz et al., 2011) under CFS is now well documented, the case of invisible implied motion remained thus far uncovered. With a series of experiments involving measures of directional adaptation and priming, we found that when invisible, the direction of implied motion did not bias the perception of subsequent stimuli depicting real motion (Experiments 2a, b) or implied motion (Experiments 3a, b; yet such a bias was also not found for visible stimuli). We consider three explanations for our findings.

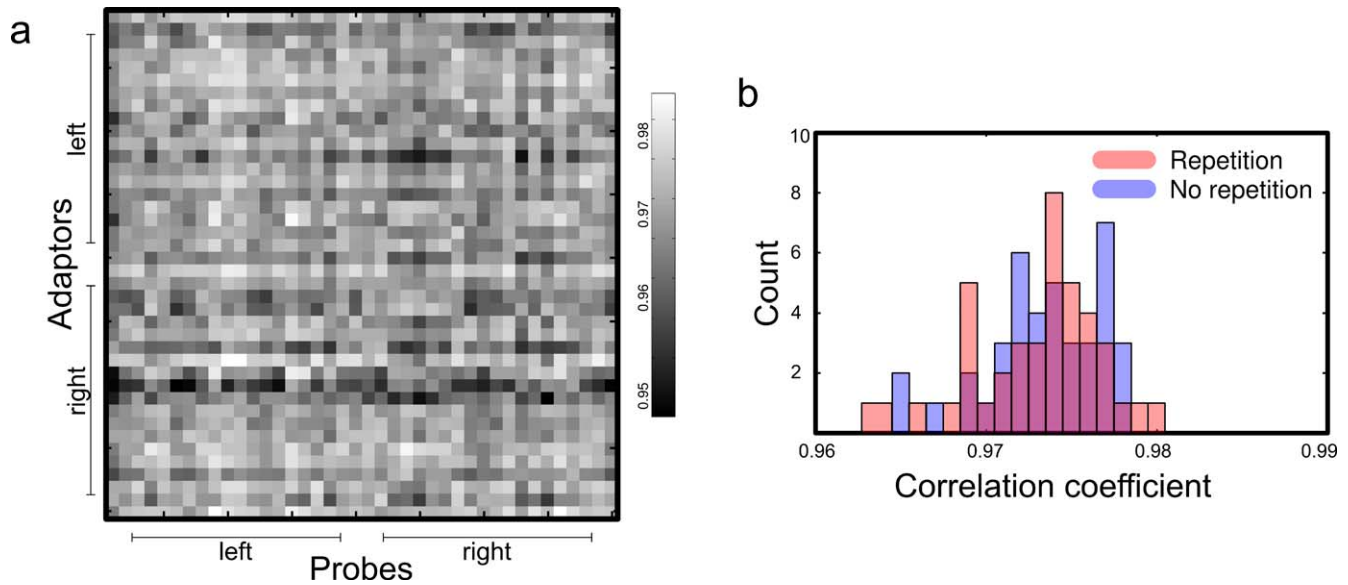


Figure 6. Primate V1 filtering model applied to the stimuli used in Experiment 3b. (a) Matrix of cross-correlation coefficients between two distinct subsets of 40 probes and 40 adaptors, with a size ratio of 80%. In each subset, half of the stimuli implied rightward motion, and the other half leftward motion. (b) Histogram of correlation coefficients for repeated (pink) versus nonrepeated (blue) pairs of adaptors and probes.

The first explanation is a non-specific decrease of signal strength induced by CFS. According to this hypothesis, the direction of implied motion can be inferred in the absence of awareness, but directional adaptation effects are too weak to be detected. This issue is inherent to the contrastive study of consciousness and is present in several studies reporting negative findings under nonconscious processing (e.g., Amihai, Deouell, & Bentin, 2011; de Zilva, Vu, Newell, & Pearson, 2013; Kang, Blake, & Woodman, 2011; Moradi, Koch & Shimojo, 2005). We consider this explanation unlikely for two reasons. The first one is that invisible implied motion stimuli were found to induce repetition priming effects, suggesting that their processing was detectable at a lower level (Experiment 3a). The second one is that CFS has a relatively low impact on motion processing. In case of real motion, CFS was found to reduce by half the magnitude of adaptation effects compared to a visible condition (Kaunitz et al., 2011; Maruya et al., 2008). Plus, we recently found that CFS had no impact on the magnitude of adaptation effects from apparent motion (Faivre & Koch, 2014). Similarly, crowding was found to reduce such adaptation effects by only 10% (Rajimehr et al., 2004). Thus, in case CFS impacted the processing of implied motion similarly to what was observed for real or apparent motion, one would expect an adaptation effect reduced to (at most) half the magnitude of what we found in the visible condition (i.e., that is roughly a 18% PSE shift). The possibility that this effect could be missed due to lack of statistical

power is unlikely, as we also found a null effect when analyzing the psychometric functions of all participants grouped together (Experiments 2a, b, c).

The second explanation of our results is that CFS may have specifically disrupted the processing of implied motion, preventing the multiple features conveying the information of directionality to be completely analyzed, and integrated into a unified percept. Inferring the direction of implied motion is likely to involve several processing steps at different levels of the visual pathways. As opposed to motion streaks that may possibly be detected automatically in early retinotopic areas (Apthorp et al., 2010), the segmentation of a figure from its background and the encoding of complex information like body posture or semantic categories are known to involve feedback neural activity (Lamme, Zipser, & Spekreijse, 2002) and higher level visual areas (e.g., anterior temporal lobe, see Jellema & Perrett, 2003; superior temporal sulcus, see Kourtzi & Kanwisher, 2000) which may require activation by visible stimuli (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Lamme, 2006). Yet it has been recently described that CFS decreases visual activity as early as the primary visual cortex (Yuval-Greenberg & Heeger, 2013) and potentially disrupts processing in the ventral visual pathways (Almeida, Mahon, Nakayama, & Caramazza, 2008; but see Hesselmann & Malach, 2011). Consequently CFS may allow for a basic encoding of the implied motion stimulus but disrupts the subsequent and more complex steps necessary for the information of directionality to

be inferred (see Lin & He, 2009, for the extent of nonconscious processing under interocular suppression).

This potential limit of nonconscious processing of implied motion is compatible with the priming effects we found in Experiment 3, which occurred when adaptors and probes shared the same identity but not the same direction. The similarity measures we performed suggest that repetition priming effects may arise as early as the primary visual cortex. Thus, the low-level similarity between primes and probes may be sufficient to explain nonconscious repetition priming, which challenges previous behavioral studies using it as an evidence for high-level visual processes in the absence of awareness (e.g., Barbot & Kouider, 2012; Faivre et al., 2012; Stein, Peelen, & Sterzer, 2012). Furthermore, the fact that the amplitude of repetition priming was higher in visible than invisible conditions suggests that CFS decreases the coding efficiency in these early visual areas (Yuval-Greenberg & Heeger, 2013). Our analysis suggests that experimentalists aiming at ruling out low-level confounds during repetition priming should use adaptors and probes with a size ratio of 30% or less. In order to generalize our results and probe the limit of bottom-up processes during nonconscious processing of implied motion, it would be relevant to compare different approaches impeding visual awareness (e.g., visual masking, see Kouider & Dehaene, 2007; visual crowding, see Faivre et al., 2012; Faivre & Kouider, 2011; Kouider, Berthet, & Faivre, 2011, and for a methodological comparison between visual crowding, visual masking, and continuous flash suppression).

A third possible explanation for our results relates to the dual origin of adaptation to implied motion. It has been proposed that directional adaptation effects arise from bottom-up, automatic shifts in the perception of the real-motion probes. This view is supported by the fact that the amplitude of adaptation decreases when a brief delay is inserted between the adaptor and the probe and is not correlated with participants' prior knowledge of the implied motion phenomenon (Winawer et al., 2008). However, it remains possible that directional adaptation effects also require top-down strategic processes that do not take place in the absence of awareness (see Kiefer, 2007, for a review). Electroencephalography showed that the response latency in the occipital lobe is  $\sim 100$  ms longer following exposure to implied versus real motion, consistent with a feedback projection following extended perceptual processing in high-level brain areas (Lorteije et al., 2006). Within the dual-stream visual processing framework (Milner & Goodale, 1993, 2008), implied motion may involve first posture-dependent neurons in the ventral visual pathway, which in turn activate motion sensitive

neurons in the dorsal visual pathway (Giese & Poggio, 2003). Along this line, it has been shown that imagery of motion induces directional adaptation effects on real-motion probes, suggesting that top-down processes in the absence of sensory stimulation can exert specific influence on sensory neurons (Winawer, Huk, & Boroditsky, 2010). Furthermore, a recent study found evidence for cross-modal adaptation effects, in which motion implied in the auditory modality by ascending or descending scales produced a motion aftereffect in the visual modality (Hedger, Nusbaum, Lescop, Wallisch, & Hoeckner, 2013). Top-down influences may decrease over time, which would account for the negative correlation between adaptation and stimulus onset asynchrony, and be completely implicit, which would explain why previous knowledge of the implied motion phenomenon is not a predictor of the effect amplitude (Winawer et al., 2008). The fact that we did not find any directional adaptation effects with simple arrow adaptors argues in favor of top-down limitation, rather than a limit in visual processing under CFS (see Experiment 2c). It is of note that the bottom-up and top-down reasons mentioned above are not mutually exclusive. Whether the absence of adaptation to invisible implied motion arises from limitations in the bottom-up encoding of the stimulus, top-down post-perceptual processes, or a combination of the two, our results are in contrast to the ability of the visual system to detect high-level semantic incongruities within natural yet perceptual invisible scenes (Mudrik et al., 2011; Mudrik & Koch, 2013). This suggests that different limits of processing and perceptual integration apply to different visual signals. Although natural scenes depicting implied motion or semantic incongruities are relevant to study spatial integration, deciphering the low-level mechanisms at play with and without awareness may benefit from the use of simpler stimuli, such as Gabor plaids, in which on Gabor patch with vertical motion superimposed to another one with horizontal motion is perceived as an integrated oblique drift (e.g., Adelson & Movshon, 1982). To conclude, while the theoretical framework relating awareness to information integration is appealing (Tononi, 2008), one still has to investigate the continuum of integrative capacities and its link with perceptual awareness. The goal is to define the criteria about which types of integration require and which do not require awareness. As those criteria are likely to be numerous and complex, we believe that measures comparing systematically different classes of sensory signals under different methods preventing perceptual awareness are required.

*Keywords:* awareness, consciousness, implied motion, continuous flash suppression, priming



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## Footnote

<sup>1</sup>Similar results were obtained using a four-parameter logistic function with no constrain on the upper and lower limits.

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