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KEEPING POSTDICTION SIMPLE

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Abstract

Postdiction effects are phenomena in which a stimulus influences the appearance of events taking place before it. In metacontrast masking, for instance, a masking stimulus can render a target stimulus shown before the mask invisible. This and other postdiction effects have been considered incompatible with a simple explanation according to which (i) our perceptual experiences are delayed for only the time it takes for a distal stimulus to reach our sensory receptors and for our neural mechanisms to process it, and (ii) the order in which the processing of stimuli is completed corresponds with the apparent temporal order of stimuli. As a result, the theories that account for more than a single postdiction effect reject at least one of these theses. This paper presents a new framework for the timing of experiences—the non-linear latency difference view—in which the three most discussed postdiction effects—apparent motion, the flash-lag effect, and metacontrast masking—can be accounted for while simultaneously holding theses (i) and (ii). This view is grounded in the local reentrant processes, which are known to have a crucial role in perception. Accordingly, the non-linear latency difference view is both more parsimonious and more empirically plausible than the competing theories, all of which remain largely silent about the neural implementation of the mechanisms they postulate.

1 Introduction

An attractively simple view on the timing of perceptual experience consists of two theses. The first, *the thesis of minimal delay*, states that our perceptual experiences are near-instantaneous, meaning that they are delayed for only the length of time it takes a distal stimulus to reach our sensory receptors and for our neural mechanisms to process this particular stimulus. The second thesis, *the thesis of temporal isomorphism*, holds that the time in which an event is experienced to occur is isomorphic with the time in which the neural processes that realize the experience of the event occur—e.g., if stimulus A is processed before stimulus B, we also experience them in this order. Because the temporal properties of experiences mirror the temporal properties of the neural processes that underlie these experiences, temporal properties such as time-order do not need to be represented separately.[1] Thus, in this view, the order in which the processing of stimuli is completed corresponds to the experienced temporal order of stimuli—our experience is an "online … phenomenon, coming about as soon as a stimulus reaches its 'perceptual end point'" (Eagleman & Sejnowski, 2000, p. 2036).

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[1] The views that subscribe to the thesis of temporal isomorphism have been referred to as the "time as its own representation" views (Kiverstein & Arstila, 2013), which emphasize that time does not need to be represented separately. Another term, *the braintime view* (Arstila, 2015a; Johnston & Nishida, 2001; Yarrow & Arnold, 2015), emphasizes how experienced temporal properties are determined by the temporal properties of neural events.

These two theses are consistent with many empirically oriented theories of perception. The most prominent theory of the timing of experiences to explicitly subscribe to them is the Paillard-Fraisse hypothesis (Aschersleben & Prinz, 1995, 1997). Additionally, this hypothesis holds that the timing of experiences is determined by the latency differences that arise early in the neural processing of a stimulus; temporal differences due to the cortical processing of sensory signals are considered largely marginal. The hypothesis correctly suggests that simultaneous taps on the nose and toe are not experienced as simultaneous because the sensory signal from the toe takes much longer to reach the brain than the sensory signal from the nose. The Paillard-Fraisse hypothesis has also figured in the debates concerning the flash-lag illusion, where it is known as the latency difference hypothesis, the simple differential latency hypothesis, and the simple differential lag model (Arnold, Ong, & Roseboom, 2009; Chappell & Hine, 2004; Eagleman & Sejnowski, 2007; Whitney, Murakami, & Cavanagh, 2000; Whitney & Murakami, 1998). Below, I refer to this position as *the simple latency difference view.*[2]

The simple latency difference view has been considered incompatible with the postdiction effects. These are phenomena in which a stimulus (S_2) presented at t_2 influences how we experience a stimulus (S_1) or the events taking place before S_2, at t_1.[3] The postdiction effects have been employed in two kinds of arguments against the simple latency difference view. First, as will be discussed shortly, it is argued that the view cannot account for the postdiction effects. Since this view remains the best-developed view on the timing of experiences that subscribes to the two theses, the explanations for the postdiction effects often also reject at least one of the theses. Second, the postdiction effects challenge the simple latency difference view by questioning the assumption that some kind of perceptual endpoint exists. This assumption is implied by the thesis of temporal isomorphism, as it holds that the order of the completion of the sensory processing caused by stimuli determines the experienced order of stimuli. The simple latency difference view therefore rests on the often discarded assumption of Cartesian materialism (Dennett & Kinsbourne, 1992).

The objective of this paper is to present a new general framework for the timing of perceptual experiences, one that subscribes to the thesis of minimal delay and the thesis of temporal isomorphism and yet can explain the postdiction effects. In what follows, I will begin by briefly considering why the simple latency difference view cannot account for the three best-known and most studied postdiction effects, namely apparent motion, the flash-lag effect, and metacontrast masking. I will then continue by describing the alternative view—the non-

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[2] Robert Efron's notion of simultaneity center subscribes to the theses too, but differs from the Paillard-Fraisse hypothesis by taking into account the cortical latencies (Efron, 1963). For a recent assessment of the prospects of explaining simultaneity and temporal order judgments by holding these theses, see (Yarrow & Arnold, 2015; Yarrow, Jahn, Durant, & Arnold, 2011). Together with *the thesis of instantaneous contents*, which maintains that the contents of our experiences are confined to an instant (i.e., the doctrine of specious present is incorrect), the thesis of minimal delay and the thesis of temporal isomorphism form what I call the simple view on the temporal properties of experiences (Arstila, 2015b).

[3] The postdiction effects are sometimes called temporal illusions. Although they illustrate the appearance versus reality distinction, this term is misleading, as the effects do not demonstrate that temporal properties per se (e.g., simultaneity and duration of stimuli) are misperceived. Instead, the temporally interesting feature of these cases depends on our view concerning the "normal" order of neural processing and the timing of experiences.

linear latency difference view—in section three. Finally, in section four, I will explain how the postdiction effects can be accounted for in this framework.

2 Postdiction effects and the simple latency difference view

The postdiction effect that has drawn the most attention from philosophers is that of *apparent motion* (e.g. Arstila, 2015c; Dainton, 2008b; Grush, 2005b, 2008; Hoerl, 2012). This phenomenon refers to an illusion of movement brought about by two spatially separate and stationary stimuli shown in short asynchrony. The illusory movement is reported to take place between the locations of the two stimuli. The apparent motion phenomenon requires that both stimuli are shown in suitable spatial and temporal organization (Gepshtein & Kubovy, 2007). If the interstimulus interval is too short, the two stimuli (in this case, flashes of light) are experienced as simultaneous; when the interval is too long, the flashes are experienced as separate and succeeding each other. Apparent motion challenges the simple latency difference view because the subjects report seeing the movement before the second stimulus is experienced. This is puzzling because the processing of direction of motion, necessary for any movement, can begin only after the locations of both stimuli have been determined. That is, it seems that the processing of the second stimulus must have proceeded quite far before the motion processing begins. Thus, contrary to the reports, the simple latency difference view implies that the second stimulus is experienced before the motion.

The metacontrast masking effect refers to cases in which a target stimulus (S_1) is followed by a masking stimulus (S_2), and the latter reduces the visibility of the former. With a stimulus onset asynchrony (SOA) of around 40-50 milliseconds and suitable stimuli (e.g., the internal contour of the mask matches the external contour of the target), the mask can render the target invisible. Most theories account for the effect by explaining how the processing of the mask catches up with the processing of the target (for reviews, see Bachmann & Francis, 2014; Breitmeyer & Ögmen, 2006). The simple latency difference view cannot appeal to such an explanation, however: If S_1 and S_2 are equally luminous, there should be no latency differences. Consequently, S_1 should be processed and experienced before S_2. Nevertheless, according to subjects' reports, this is not the case.

The flash-lag effect, described as early as the 1930's (Metzger, 1932), is possibly the most researched timing error phenomenon of the past two decades. In the "normal" version of the experiment, subjects are presented with a continuously moving stimulus and, at some later point, a brief flash is presented in alignment with the moving stimulus. Although aligned, subjects report that the flash lags the moving stimulus—at the time the flash is seen, the moving stimulus is seen to have already passed the point of the flash. In *the flash-initiated condition* of the flash-lag effect, the flash and the moving stimulus are presented at the same time. Again, the flash appears to lag the moving stimulus. Notably, the onset location of the moving stimulus is misperceived to the direction of movement. This phenomenon was first studied systematically by Friedrich Fröhlich (1923), and is therefore also known as the Fröhlich effect. In *the flash-terminated condition*, the movement stops with the flash. In this case, the flash is not perceived as lagging, which suggests that the flash-lag effect is not due to motion extrapolation. In *the flash-reversed condition*, the direction of movement changes at the time of the flash. Here too, the flash lags the moving stimulus, but this time in the new direction of movement. This illustrates that the flash-lag effect is a postdiction effect—the localization of the moving stimulus is influenced by its trajectory up to 80 milliseconds after the flash (Eagleman & Sejnowski, 2000, 2007). In addition to these spatial conditions, the flash-lag effect also occurs when the color or luminance dimension of a stimulus changes (Sheth, Nijhawan, & Shimojo, 2000).

The simple latency difference view cannot explain the flash-lag effect for three reasons. First, the view postulates that the lag results from the flash having a longer latency than the moving stimulus. However, the measured latency difference for moving and stationary stimuli in the primary visual cortex is between 10 and 20 milliseconds, which is too little to account for the fact that the flash lags the moving stimulus by as much as 45-80 milliseconds (Arnold et al., 2009; Eagleman & Sejnowski, 2000; Krekelberg & Lappe, 2001). This concurs with results showing that the flash-lag effect also occurs in the absence of magnocellular visual pathway activation, which accounts for the latency difference between moving and stationary stimuli (Chappell & Mullen, 2010). Second, the simple latency difference view postulates that the two stimuli differ as regards their latency and not as regards spatial properties. Therefore, the onset location of the moving stimulus should be perceived correctly in the Fröhlich effect. This is contrary to what subjects report (Eagleman & Sejnowski, 2000; Fröhlich, 1923). The third explanatory shortcoming of the simple latency difference view is the following: In the Fröhlich effect, the motion begins at the same time as the flash, and hence there is no prior history of movement. Accordingly, the moving stimuli "should suffer the same initial processing delay as the flashed stimulus" (Rao, Eagleman, & Sejnowski, 2001, p. 1245) and the flash-lag effect should not occur. Nevertheless, it does occur. This problem appears to be particularly difficult to reconcile with the fact that the flash lags the moving stimulus even in cases in which the motion is induced by two stimuli with an SOA of 53 milliseconds—that is, the flash has a considerable lead compared to the (apparently) moving stimuli, and yet the flash is perceived to lag (Eagleman & Sejnowski, 2007).

While the simple latency difference view cannot account for the mentioned postdiction effects, there is, of course, no shortage of other theories which strive to do so.[4] However, many of the suggested theories explain only one effect (or one version of an effect) and do not provide a general explanation for all the effects.[5] Nonetheless, the mentioned postdiction effects are

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[4] For reviews on metacontrast masking, see (Bachmann & Francis, 2014; Breitmeyer & Ögmen, 2006), on the flash-lag effect, see (Hubbard, 2014), and on apparent motion, see (Arstila, 2015c; Gepshtein & Kubovy, 2007; Ivry & Cohen, 1990; Larsen et al., 1983).

[5] To give a few examples, the motion extrapolation view (Nijhawan, 1994) explains the usual flash-lag effect, but not the flash-terminated or flash-reversed conditions (nor other postdiction effects). Whitney and Cavanagh (2000), in turn, argue that latency differences could explain all three versions of the effect, but not the Fröhlich effect, which they consider separate from the flash-lag effect. Concurring, Müsseler and Aschersleben (1998) give an attention-shifting explanation for the Fröhlich effect. Given that attention follows the moving stimulus in the usual flash-lag effect, it is not apparent how attention-shifting could explain the flash-lag effect. It should be mentioned that although attentional mechanisms have also been suggested to account for the flash-lag effect (Baldo, Kihara, Namba, & Klein, 2002; Baldo & Klein, 1995; Sarich, Chappell, & Burgess, 2007), it is likely that these mechanisms merely modulate the effect, since "the computations that give rise to the flash-lag effect are independent of attentional deployment" (Khurana, Watanabe, & Nijhawan, 2000, p. 675). The effect of attention on the Fröhlich effect was also very limited (Müsseler & Aschersleben, 1998, experiment 4).

often considered to be somehow related. For example, Kirshfeld and Kammer (1999) argue that the Fröhlich effect is due to metacontrast masking and cue-induced focal attention. Zenz and Cai's results (2008) agree that masking is present in the Fröhlich effect, although it cannot account for the whole effect. Müsseler and Aschersleben (1998), on the other hand, claim that the attentional switching account could explain both the Fröhlich effect and metacontrast masking. Kahneman (1967) and Fisicaro, Bernstein, and Narkiewicz (1977), in turn, argue that apparent motion and metacontrast masking are intimately related and that the two effects have the same influence on the perceptual delay (Didner & Sperling, 1980).

It therefore seems well justified to seek a possible common basis for different postdiction effects instead of putting forward specific explanations for single effects (or versions of effects). That being said, even if some underlying cause for the postdiction effects exists, it does not follow that the suggested explanations for the particular postdiction effects should be refuted altogether. On the contrary, although a common basis for the postdiction effects would imply that many of the suggested factors do not cause the effects in the first place, these factors might still modulate the magnitude of the effects. For example, it has been suggested that the flash-lag effect is modulated, but not caused, by the latency differences (Arnold et al., 2009) and trajectory of the moving stimulus before the flash (Chappell & Hine, 2004).

The more general theoretical frameworks that provide a unified explanation for the mentioned postdiction effects come in three classes. The first class of theories rejects the thesis of minimal delay and instead maintains that our perceptual experiences are delayed longer than the latencies of the neural processing dictate. During this additional time, the specific pre-experiential content that has already been determined can be revised before one is conscious of it (Bachmann, 1994, 1997; Dainton, 2008a, 2010). The second class of explanations rejects the thesis of temporal isomorphism and maintains that the experienced time of an event is represented by specific temporal markers, not by the time of neural processing. In this way, the apparent time of an experienced event can differ from the time when the neural correlates of the experience occur (Dennett & Kinsbourne, 1992; Grush, 2005a, 2007; Paul, 2010). Finally, the third option is to discard both theses. That is, to hold that perception is delayed longer than the thesis of minimal delay states and that the time of representing must be separated from the represented time. Such an explanation also provides a framework in which various postdiction effects can be accounted for (Eagleman & Sejnowski, 2000, 2007).

These three classes of theories thus account for the postdiction effects by rejecting at least one of the theses that underlie the simple latency view. This causes them to have problems of their own, however. For example, the idea of an added delay is not empirically supported in light of the known timing of perceptual processes (Arstila, 2015c; Grush, 2005a), and the notion of temporal markers remains underdeveloped and possibly at odds with the empirical evidence (Arnold, 2010; Arstila, 2015b). Adding to the shortcomings of these competing theories, by and large all positions remain silent on how the mechanisms they postulate could be neurally implemented. However, it is not my purpose here to focus on these shortcomings. Instead, in what follows, I will illustrate how the postdiction effects can be accounted for even when one subscribes to both the thesis of minimal delay and the thesis of temporal isomorphism.

3 The non-linear latency difference view

The unified framework for the timing of perceptual experiences (and for the mentioned postdiction effects) that I want to put forward, *the non-linear latency difference view*, makes the following claims:

(i) The termination of reentrant processing in the primary visual cortex forms the perceptual endpoint
(ii) the feedforward sweep and the reentrant processing interact at the perceptual endpoint
(iii) the thesis of temporal isomorphism is correct
(iv) the thesis of minimal delay is correct

The first claim concerns the issue of what could constitute the hypothesized perceptual endpoint. In general, there are three possibilities. The first appeals to the fact that different features of the stimuli are processed in different areas of the visual cortex. According to this alternative, we become conscious of a feature once the processing related to it is completed in the area specialized to process that feature. Accordingly, Semir Zeki's theory of micro-consciousness maintains that we become conscious of colors when the processing in V4 is completed, and become conscious of motion when the processing in V5 is completed (Zeki & Bartels, 1999; Zeki, 2003, 2007). Whereas this alternative relies on feedforward processing from the primary visual cortex (V1) to later cortical areas, the two other alternatives define the perceptual endpoint in terms of reentrant processing. Both of them hold that the perceptual endpoint is reached when the reentrant processing that originates from the later cortical areas reaches the primary visual cortex. They differ with regard to the nature of the reentrant processing: the perceptual endpoint can be defined either in terms of local reentrant processing, which originates within the visual cortex, or in terms of global reentrant processing, which originates from the higher cortical areas, namely the frontal lobe.

The following discussion focuses on the local reentrant processing and assumes it as that which determines the perceptual endpoint for two reasons. First, as will be illustrated in section 4, by doing so the three mentioned postdiction effects can be explained in a unified framework. Second, treating the local reentrant processing as some sort of general perceptual stage is justified because it has been shown that the local reentrant processing is required for the processing of elemental features such as figure-ground perception (Lamme, Zipser, & Spekreijse, 2002), surface segmentation (Scholte, Jolij, Fahrenfort, & Lamme, 2008) and responses related to gratings (Shapley, 2004). Likewise, motion perception depends on the local reentrant processing—if the reentrant activation from V5 (the cortical area that processes visual motion in humans) to V1 is disrupted, we do not have a perception of motion regardless of V5 activation (Pascual-Leone & Walsh, 2001; Silvanto, Cowey, Lavie, & Walsh, 2005). This means that the role of feedback processing is more fundamental in perception than that of merely modulating the properties of V1 neurons. Accordingly, most neurophysiological theories of consciousness postulate that the local reentrant processing is necessary for visual perception to occur (e.g., Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Kouider, 2009; Lamme, 2006).

It is, however, important to highlight the fact that the views concerning the function of the two types of reentrant processes differ. In Victor Lamme's theory (2004, 2006), the local reentrant processing brings about phenomenally conscious states, and this is what Ned Block calls phenomenality (2007, 2011). Similarly, Boehler et al. (2008) hold that this processing correlates with visual awareness. In the global workspace theory, however, the local recurrent processes amount to unconscious perception (Dehaene et al., 2006; Dehaene & Changeux, 2011). This means that the explanation of the postdiction effects based on the local reentrant processing concerns either unconscious or conscious perception. This difference is irrelevant for our purposes, however, because both parties agree that the global reentrant processing is related to cognitive access to the sensory qualities, which have been processed within the local reentrant processing. Hence, if the local reentrant processing can account for the postdiction effects (or at least the three discussed here), the latter processes do not concern the issues at hand—even if the local reentrant loops only designate the unconscious perceptual endpoint, the timing differences due to the local reentrant processing are generally mirrored in the later processing stages.

The reasoning above does not exclude the (likely) possibility that other factors modulate the three mentioned postdiction effects as well. Nevertheless, assuming that the local reentrant processing can account for the effects, the influence of other factors is conditional—the effects occur even when the top-down effects, such as attentional factors that are known to be crucial for global reentrant processing, are fixed. As taking such processing into account would unnecessarily complicate the matters at hand (e.g., to properly address these issues would require one to separate, at least theoretically, the experienced timing of events from the judged timing of events), the discussion on the global reentrant processing will be largely ignored at this time.

As for the claims laid out at the beginning of this section, the first does not differ between the non-linear latency difference view and the simple latency difference view, even though Eagleman and Sejnowski (2000) refer to Zeki’s theory in their discussion of the idea of perceptual endpoint in relation to the simple latency difference view. Nonetheless, the simple latency view is not exclusive to the stage at which a conscious perception occurs, as it was assumed that the relative timing of perception was settled before reaching the endpoint or awareness of stimuli. Accordingly, if it is assumed that the latency differences due to cortical processing are minor and the feedforward activation of the primary visual cortex does not influence reentrant activation, all three possibilities are compatible with the simple latency difference view.

According to the second claim, the feedforward sweep and the reentrant processing interact at the perceptual endpoint. This happens when the area of the perceptual endpoint triggered by the reentrant processing is activated by the feedforward processing originating from the retina at roughly the same time. Since the processing at the endpoint reflects what we perceive, our perception of the first presented stimulus (the cause of the reentrant processing) can be influenced by the latter presented stimulus (the cause of the feedforward processing). Because such an effect is not due to differences in processing speed, this means that the linearity of the neural processing can be violated. This possibility separates the non-linear latency difference view from the simple latency difference view.

The result of the interaction (the percept) depends on the properties of the stimuli and processes involved. As regards the postdiction effects, there are two particularly important events which may possibly occur. First, the feedforward sweep can disrupt at least some of the processes dependent on the local reentrant activation. Whether or not this occurs depends on the processes involved and the strength of both sensory signals in the primary visual cortex. Figure-ground separation is one example in which such disruptive processing has been thought to occur (Lamme et al., 2002). Second, the feedforward processing and the reentrant processing may fuse or combine together. That is, rather than one simply replacing or disrupting the processing of the other, the outcome can be a combination of both. Here the relative strength of both activations is also crucial for the outcome, meaning that the stronger activation will have more presence in the outcome. The processes involved are also relevant. For example, perhaps the figure-ground processing does not allow contours to belong to both figure and ground at the same time.

This second possible occurrence is rarely mentioned, possibly because most studies (e.g., Lamme's research) often use stimuli which either do not cause conflicts, or the conflicts cause masking effects. Yet, this alternative is not without empirical support. One particularly convincing case comes from a transcranial magnetic stimulation (TMS) study concerning motion perception: In accordance with the known sizes of the receptive fields of neurons in V1 and V5, a suprathreshold TMS pulse to V1 results in small and stationary phosphenes, whereas a suprathreshold TMS pulse to V5 results in large and moving phosphenes. However, when the suprathreshold TMS pulse to V5 is followed by a suitable TMS pulse to V1, subjects experience phosphenes that share the features of those induced by both V1 and V5 TMS pulses. In this context, 'suitable' means that the time course of TMS to V1 matches with the time course of reentrant processing from V5 to V1 and that the pulse is subthreshold (i.e., it alone would neither cause phosphenes nor disrupt the reentrant processing). In other words, while it is well established that the reentrant processing originating from V5 modulates activation in V1, and that this is necessary for motion perception to occur, this activation does not determine our perceptions. Instead, our perception of motion is also influenced by V1 activation that is concurrent with but independent of the V5 modulated activation in V1 (Silvanto et al., 2005).

An overlooked aspect of the described TMS study on motion perception is that it demonstrates that a visual percept does not need a specific reentrant process to occur. After all, the reentrant processing brings about the perception of things (V1-type of features in phosphenes) other than those that caused the reentrant processing in the first place (V5 activation). Although such a claim appears to disagree with, say, Lamme's view (in which the reentrant processing relates to a sustained neural activation in V1), this may simply be an apparent disagreement because Lamme has not commented on the situation at hand. Thus, this aspect can be understood to expand upon Lamme's neurobiological theory of consciousness.

An important consequence of the aforementioned aspect is that the apparent timing of the events that cause the feedforward sweep could be influenced by the possible reentrant activation of prior events. Indeed, if the reentrant processing makes us perceive things and the feedforward sweep and the local reentrant processing together can determine our perceptual contents, then if the feedforward sweep combines with this activation, the sensory signals related to the feedforward sweep should be perceived faster than instances in which they are not combined with any preceding reentrant processing. This intriguing effect as regards the timing of experiences is not due to priming effects, prior entry, or acceleration of the processing of the latter stimulus, but rather to "skipping" cortical feedforward and reentrant processing altogether—reentrant activation related to S_1 causes one to perceive S_2. Arguably, the temporal difference between the accelerated vs. non-accelerated perception should be approximately equal to the time it takes to complete one cortical feedforward-reentrant loop (e.g., in motion processing, it would be around 50 milliseconds).[6]

Of the four claims of the non-linear latency difference view, the final two are those that it shares with the simple latency difference view. The thesis of temporal isomorphism forces the non-linear latency difference view to explain the apparent temporal properties of perceptual states in terms of the temporal properties of the activation of the perceptual endpoint. The order in which neural signals reach the perceptual endpoint corresponds with the order in which events are perceived; if signals reach the perceptual endpoint at the same time, they are perceived simultaneously.[7] Due to the thesis of minimal delay, in turn, the feedforward sweep and the local recurrent processing do not include any extra delays.

Neither of these theses is necessitated by the first two claims. Instead, the main reason to accept them is that doing so is more economical that rejecting one or both of them, as the latter would require us to postulate additional mechanisms related to the timing of experiences. Besides, as argued above, the main reason to reject one or both of the theses is the assessment that the postdiction effects cannot be explained if both of them are subscribed to. Thus, if the effects can be accounted for while simultaneously holding the two theses, there is no particularly pressing reason to reject the theses.

The next section illustrates how the postdiction effects can be explained in the framework of the non-linear latency difference view. Before turning to that task, one worry needs to be addressed: In subscribing to the idea of a concrete perceptual endpoint, one is obliged to deal with the issue of whether or not subjects' reports of postdiction effects are true—of whether or not there is a definable boundary between pre-perceptual and post-perceptual states as maintained by Cartesian materialism. Daniel Dennett and Marcel Kinsbourne's (1992) argument against such an idea regarding perceptual experiences well-known. In short, they claim that in cases of apparent motion and metacontrast masking (i.e., short timescale phenomena lasting a few hundred milliseconds) we cannot settle the question of whether subjects experienced what they reported (Stalinesque revision) or merely remembered incorrectly and misreported their experiences (Orwellian revision). Dennett and Kinsbourne claim that this is because both revisions result in the same report and because psychophysical studies do not differentiate between these revisions. Thus, the difference between them is irrelevant. Cartesian materialism is therefore called into question because there is no fact of the matter whether or not reports about experiences are correct—there is no way to verify whether or not the boundary between pre-perceptual and post-perceptual states was crossed. Contrary to Dennett and Kinsbourne, however, psychophysical and neuroimaging studies suggest that the difference between Orwellian revision and Stalinesque revision is

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[6] Another empirically verifiable prediction concerns the perceived saliency of stimulus: if two stimuli (S_1 and S_2) are presented in a way that the reentrant activation related to S_1 is concurrent with the feedforward activation related to S_2, the sum total of activation in the perceptual endpoint is larger than it would be if S_2 were shown in isolation. Accordingly, in this case, S_2 should appear brighter than it would be if presented in isolation. If the first possible interaction only disrupts some particular processes and not the local reentrant activation of V1 in general, then this possible interaction results in the same outcome as well.

[7] Although I will not defend this view here, I also maintain that equal duration of the neural signals at the perceptual endpoint corresponds to equal durations in perception.

observable in the cases of apparent motion (Arstila, 2015c), illusory line motion (Christie & Barresi, 2002) and metacontrast masking (Breitmeyer, Ogmen, & Chen, 2004; Todd, 2009). Moreover, these studies suggest that it is Stalinesque revision that takes place most often, and thus provide independent support for theories which hold that reports of the postdiction effects are largely truthful (e.g., the non-linear latency difference view).

4 The non-linear latency difference view and postdiction effects

4.1 Metacontrast masking

Many of the most prominent current theories of metacontrast masking explain the effect by means of reentrant processing (e.g., Bridgeman, 1980; Lamme et al., 2002; Ro, Breitmeyer, Burton, Singhal, & Lane, 2003). These theories come in two forms, or groups. The difference between them concerns the scope of the phenomena explained and the nature of the reentrant processing involved.

The first group of theories is concerned with metacontrast masking and object substitution masking (e.g., Di Lollo, Enns, & Rensink, 2000; Enns & Lollo, 1997, 2000; Visser & Enns, 2001). Given that accounting for the latter necessitates global reentrant processing, these theories challenge the non-linear latency difference view. There are, however, good reasons to think that metacontrast masking and object substitution are due to different processes. For example, unlike metacontrast masking, object substitution masking is not sensitive to local spatial factors significant for surface segmentation. Their differences are also reflected in timing. The metacontrast masking effect is strongest with SOAs of around 50 milliseconds (which corresponds to the timing of one local reentrant processing loop), while the object substitution effect occurs with SOAs between 100-300 milliseconds. Moreover, in metacontrast masking, the processing of the target is disrupted at 110-140 milliseconds (Fahrenfort, Scholte, & Lamme, 2007), whereas it continues for more than 200 milliseconds in object substitution masking (Woodman & Luck, 2003). Finally, while attentional factors modulate the metacontrast masking but are not the main cause of it (e.g., Boyer & Ro, 2007; Ramachandran & Cobb, 1995; Shelley-Tremblay & Mack, 1999; Tata, 2002), object substitution masking is explained in terms of the target being replaced by the mask due to attentional factors (Brehaut, Enns, & Lollo, 1999; Giesbrecht & Lollo, 1998; Visser & Enns, 2001). Given these differences, it is more reasonable to think that the two phenomena are due to many different processes rather than one single process.

The previous lends credibility to the second group of theories, which is exclusively concerned with metacontrast masking. These theories maintain that that the masking is a result of early surface segmentation or figure-ground organization processes that, in turn, depend on the local reentrant processing (Fahrenfort et al., 2007; Lamme et al., 2002). In more detail, these theories argue that the local reentrant processing caused by the target (S_1) arrives at the perceptual endpoint around the same time as the feedforward sweep caused by the mask (S_2), allowing the two to interact. In the masking situation, the feedforward sweep disrupts the figure-ground segmentation (which depends on local reentrant processing), and consequently the perception of S_1 is also disrupted (Fahrenfort et al., 2007).

The explanation for metacontrast masking provided by the non-linear latency difference view agrees with that provided by the second group of theories to the extent that the masking is caused by the local reentrant processes interacting with the feedforward sweep. Despite this notable agreement, there is one important difference though: The non-linear latency difference view predicts that the mask should be perceived faster when it is preceded by a target versus when it is not, whereas the second group of theories is neutral as regards this issue.

Ingrid Scharlau and Odmar Neumann have addressed the question concerning the apparent timing of the mask, and their results support the prediction made by the non-linear latency difference view (Neumann & Scharlau, 2007b; Scharlau & Neumann, 2003a, 2003b). Talis Bachmann (1994, 1997) likewise reports that the target accelerates the perception of the mask. Furthermore, in accordance with the non-linear latency difference view, Scharlau and Neumann's results show that the target accelerates the perception of the mask by roughly 30-60 milliseconds under various experimental conditions (Neumann & Scharlau, 2007a; Scharlau & Neumann, 2003a, 2003b). Finally, the target does not accelerate the perception of the mask if the target precedes the mask by less than 28 milliseconds (Scharlau & Neumann, 2003b). This also concurs with the predictions of the non-linear latency view since such short SOAs means that the reentrant processing and the feedforward sweep do not reach the perceptual endpoint at the same time, and the interaction between them does not occur.[8]

One may wonder how the target can accelerate the perception of the mask if the figure-ground separation dependent on the local reentrant processing related to the target is disrupted. One likely possibility is that the figure-ground separation is linked to border ownership, and the perceived contours can only belong to one object at a time (e.g., Kellman & Shipley, 1991; Nakayama, Shimojo, & Silverman, 1989; Sajda & Finkel, 1995; Shipley & Kellman, 1992). In other words, resolving the border ownership concerns the formation of perceptual units by specifying the figure-ground organization, and it is this organization which local reentrant processing is thought to bring about. Accordingly, rather than understanding metacontrast masking as simply a phenomenon in which local reentrant processing and figure-ground separation are disrupted altogether, it could also be understood as a phenomenon in which the figure-ground separation is disrupted only as regards the target stimulus. This means that the figure-ground separation and the local reentrant processing are not disrupted altogether: the mask "captures" the processes related to the border of the target, and the figure-ground separation continues in the sense that the border is interpreted as belonging to the mask. As a result, the mask is perceived faster than it would be if it were in isolation (i.e., if the target was not shown). This way of expressing the phenomenon is in agreement with Breitmeyer and Ögmen's (2006) description of masking as a failure to attain a perceptual synthesis of the target.

It is worth emphasizing, however, that the non-linear latency difference view's prediction concerning the advanced perception of the mask is due to the capture of the local

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[8] A target that precedes the mask by 136-510 milliseconds can accelerate perception of the mask by 60-110 milliseconds, depending on the judgment type used in the experiment (Scharlau, Ansorge, & Horstmann, 2006). Because such facilitation occurs in situations involving transient attention, and because the attentional modulation is postulated to play a role in metacontrast masking experiments involving longer SOAs (Neumann & Scharlau, 2007b), these results can be interpreted to illustrate an additional (modulating) factor which quickens perception of the mask.

reentrant processing and not to the process of figure-ground separation per se—this highlights its difference from other theories that aim to explain metacontrast masking by appealing to the local reentrant processes. Consequently, even if the target and mask are not retinotopically similar enough to cause competition as regards border ownership—even if the figure-ground separation proceeds normally and the mask is ineffective—the target should accelerate perception of the mask (assuming they are shown in the same location). This implication of the non-linear latency view also receives support from empirical results (e.g., Scharlau & Neumann, 2003a).

4.2 The flash-lag effect

In order to explain the flash-lag effect within the framework of the non-linear latency difference view, it is enough to focus on only three stimuli: the flash (F), the moving stimulus at the time of flash (M_1), and the moving stimulus in its later location (M_2). The timing of M_2 is specified so that the feedforward sweep it causes can interact with the reentrant processing related to M_1.

Let us begin with the Fröhlich effect in which the flash and the moving stimulus onset at the same time (t_0) but the flash appears to lag the moving stimulus. As the shortcomings of the simple latency difference view illustrate, the Fröhlich effect invites explanation of two aspects. The temporal aspect concerns the fact that the flash (presented at t_0) is perceived to occur at the same time as the stimulus matching the location of the moving stimulus presented at $_{t0+x}$. The spatial aspect concerns the fact that the onset location of the movement is misperceived.

The non-linear latency difference view explains the Fröhlich effect as follows. When the reentrant processing related to F terminates at the perceptual endpoint, the activation caused by the preceding feedforward sweep related to F has already begun to decay. Since there is no "competing" stimulus for F, no other process replaces or disrupts the decaying activation, the reentrant processing brings about the perception of F. The situation is different with regard to the moving stimulus: When the reentrant processing related to M_1 terminates at the perceptual endpoint, the feedforward sweep from the retina related to M_2 has already arrived. Because the activation caused by the latter is more salient than the already decayed activation caused by the feedforward sweep related to M_1, the M_2 related processing "captures" the reentrant processing related to M_1. The inhibition of the decaying activation caused by M_1 is arguably strengthened by the masking effects that are present in the Fröhlich effect (Kirschfeld & Kammer, 1999; Zenz & Cai, 2008) and known to be caused by a stimulus that is perceived to move (Schwiedrzik, Alink, Kohler, Singer, & Muckli, 2007; Yantis & Nakama, 1998).

The consequence of M_2‘s capture of the local reentrant processing initiated by M_1 is that we perceive M_2 and not M_1. Hence, the onset location of the movement is misperceived. Moreover, similar to the perceptual latency priming that takes place in metacontrast masking, the "captured" reentrant processing speeds up perception of the stimulus which is shown later (M_2). Accordingly, we perceive M_2 at the same time as F (as we would perceive M_1 if no competing stimuli were shown). That is, the moving stimulus is perceived in its later location at the time we perceive the flash—the flash appears to lag the moving stimulus. Thus, the given account can explain both the spatial and temporal aspects of the Fröhlich effect.

The other variations of the flash-lag effect can be explained in a similar fashion: it takes some time to process the moving stimulus at some location, and the related reentrant processing also takes some time to terminate at the primary visual cortex. Exactly how long this takes is not important; what matters is that, during this processing, the sensory signal concerning the stimulus at its later location also reaches the neighboring areas in the primary visual cortex. Accordingly, in all cases (whether the motion continues regularly, or is reversed or terminated) the perception of the moving stimulus at the time of the flash reflects the location of the moving stimulus after the flash. Whereas the simple latency difference view appeals to the latency difference between the moving stimulus and stationary stimulus, the provided explanation does not do so. Hence, this explanation is not refuted by the fact that the measured latency differences between the stationary stimulus and the moving stimulus is smaller than the measured lag. Furthermore, this explanation can also be extended to cases in which the color and luminance of the stimulus changes rather than its location (Sheth et al., 2000), which supports the idea that the neural circuits underlying the effect are not limited to motion processing.

In addition to accounting for the general characteristics of the different variations of the flash-lag effect, the non-linear latency difference view can also account for the more detailed empirical results. To begin with, because it is the events taking place after the flash that are relevant according to this view, the spatial magnitude of the flash-lag effect should increase with the velocity of the moving stimulus after the flash. The velocity before the flash should not make any real difference. This is indeed the case (Brenner & Smeets, 2000; Krekelberg & Lappe, 2000, 2001; Whitney et al., 2000). Second, the temporal magnitude should remain the same and the temporal advancement of the moving stimulus should roughly match the duration of one local reentrant loop. Assuming that the feedforward sweep from the primary visual cortex to V5 takes roughly the same amount of time as the reentrant processing between the two areas, we can estimate that the flash should lag around 50 milliseconds. This is exactly what Whitney, Murakami and Cavanagh found (Whitney et al., 2000). Eagleman and Sejnowski argue for a slightly longer duration, but even in their studies the main effect appears to occur within the first 50 milliseconds (2000, fig. 2).

Finally, in addition to the previous spatio-temporal implications of the non-linear latency difference view, the view also implies a phenomenon that is difficult to reconcile with the current competing explanations of the flash-lag effect. This phenomenon results from the fact that the non-linear latency difference view explains the flash-lag effect by appealing to the masking of decaying feedforward activation of M_1 at the perceptual endpoint and M_2 capturing the reentrant processing related to M_1. Accordingly, if the activation caused by the feedforward sweep related to M_1 remains equal in strength to the feedforward sweep related to M_2, the masking should not occur because neither activation is more salient than the other. (Unlike in the metacontrast masking, M_1 and M_2 do not share the same possible borders.) As a result, M_1 and M_2 should be perceived at the same time, together with F. One way to test this is to make M_1 more luminous than M_2, so that the decayed activation of M_1 would match the non-decayed activation of M_2. In effect, this is what Kirschfeld and Kammer (1999, p. 3705) did when they illuminated the moving stimulus (line) with an additional flash at its onset in a Fröhlich effect type of experiment. Concurring with the implication of the non-linear latency difference view, the results showed that "a single object—the line—is seen in two different positions at the same time."[9]

4.3 Apparent motion

As with other postdiction effects, the non-linear latency difference view aims to explain apparent motion by means of the local reentrant processing. Although the theories of apparent motion have not been grounded on local reentrant processing in general (with the exception of Arstila, 2015c), such processing has been established to determine whether apparent motion is perceived or not (Sterzer, Haynes, & Rees, 2006; Wibral, Bledowski, Kohler, Singer, & Muckli, 2009). For example, when subjects experience motion in apparent motion experiments, there is a continuous representation of motion in the primary visual cortex caused by and controlled by the prior activation of V5 (Larsen, Madsen, Lund, & Bundesen, 2006; Sterzer et al., 2006). Given that these studies show that the local reentrant processing from V5 to the primary visual cortex determines whether or not motion is experienced, they provide direct support for the non-linear latency difference view.

Nevertheless, a puzzle remains concerning the temporal nature of the phenomenon: how can we experience motion before the second stimulus, given that the motion processing requires information about the location of the second stimulus? We can begin to unravel this puzzle by noting that, for the purpose of motion processing, it is enough if the retinotopic location of the second stimuli is determined. In practice, this means that the (apparent) motion processing can begin at the same time as the beginning of the processing of the second stimulus—already in the retina. The second step is to overcome the fact that the measured latency difference between moving and stationary stimuli in the primary visual cortex is only around 20 milliseconds, which would leave very little time for motion to be experienced before the second stimulus. This can be addressed by acknowledging that the non-linear latency difference view allows for the cortical processing of motion to proceed faster than the processing of the other visual features. Moreover, the view also allows for V5 to be activated by the processes that bypass the primary visual cortex. After all, the non-linear latency difference view does not take a stance on the cause of the activation of the later cortical areas. Neither possibility is merely a hypothetical—for instance, V5 has been shown to receive visual inputs that do not come through V1 (Sincich, Park, Wohlgemuth, & Horton, 2004). Since such information bypasses V1, a moving stimulus can activate V5 at roughly the same time as V1, or even sooner (Ffytche, Guy, & Zeki, 1995). This means that V5 is activated much earlier than any other area of the visual cortex specialized in the processing of particular features; when V5 is activated, other areas still need to receive an input from V1. Consequently, the processing of visual motion can happen faster than the processing of motionless stimuli.

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[9] This explanation concurs with results that the illusory location and the correct location of a moving stimulus can be perceived at the same time with a suitable TMS pulse (Wu & Shimojo, 2010). Arguably, this is due to the strengthening of the saliency of the activation related to the correct location. See also (Kanai & Verstraten, 2006), in whose study the flash and moving stimulus were adjacent, which in turn resulted in both M_1 and M_2 being seen together with F. This can be explained by postulating that the reentrant processing related to F also increases the saliency of the decayed activation of M_1, which in turn has the consequence that M_1 is perceived as well.

Crucially for the non-linear latency difference view, such direct activation of V5 due to processes that bypass V1 also occurs with stimuli similar to those used in the apparent motion experiments (Azzopardi & Hock, 2011; Blythe, Bromley, Kennard, & Ruddock, 1986). This suggests that, in the apparent motion experiments, the cortical motion processing can begin even before the sensory signals resulting in the perception of the second stimulus reach the cortex. Given that the apparent motion stimuli can induce V5 activation, which in turn activates the primary visual cortex by means of reentrant processing in a mere 20 milliseconds after the activation of V5 (Larsen et al., 2006; Muckli, Kohler, Kriegeskorte, & Singer, 2005; Wibral et al., 2009), there is ample time for us to perceive (apparent) motion before the processing related to the perception of the second stimulus is completed.

Although the non-linear latency difference view can therefore account for apparent motion, and do so in a way that is well substantiated by the empirical evidence, it may appear to be in disagreement with results showing how apparent motion results from two computationally distinct systems. Such disagreement is only superficial, however, because even though the two systems (the short-range and long-range motion systems) are computationally different (Braddick, Ruddock, Morgan, & Marr, 1980; Larsen, Farrell, & Bundesen, 1983), their differences concern the early stages of the processing. Indeed, both induce vivid perceptions of motion which can appear so alike that we cannot identify which system is behind the perception (Ivry & Cohen, 1990). This finding agrees with the previous discussion according to which the experiences of motion require activation in V5—a requirement that both systems fulfill (Kaneoke & Bundou, 1997). Thus, although the early processing underlying the short- and long-range motion system is distinct, their latter processing appears to converge at V5. Given that the non-linear latency difference view is concerned with V5 and the local reentrant processes thereafter, it is not contradicted by the existence of two mechanisms underlying the early processing related to the apparent motion.

5 Concluding remarks

Arguably, the simplest position regarding the timing of perceptual experiences subscribes to the thesis of minimal delay—the idea that perceptions are delayed for only the amount of time it takes for distal stimulus to reach our sensory receptors and for our sensory systems to process the stimulus—and the thesis of temporal isomorphism—the idea that the time when an event is perceived to occur is isomorphic with the time when the neural processes underlying the perception occur. This position is often rejected, however, because it has been considered incompatible with the postdiction effects. Accordingly, the general theories of the postdiction effects reject one or both theses, e.g., by postulating extra delays in perception or by separating the apparent time of perception and the time when perception is realized by neural processes. Neither course of action is necessary, however, once it is recognized that these explanatory shortcomings concern only the simple latency difference view and not all theories that hold the two theses.

The non-linear latency difference view presented in this paper maintains that the visual perceptual endpoint is determined by the local reentrant processing that terminates in the primary visual cortex, and that this processing can make us perceive stimulus features that are not the cause of the processing in the first place. Given that this accounts for the postdiction effects, there is no need to complicate the view by adding extra delays in the neural processing or by separating the moment when something is experienced to occur from the moment when the neural processes realize the experiences. Therefore, this explanation is compatible with both the thesis of minimal delay and the thesis of temporal isomorphism.[10]

One of the strengths of the non-linear latency difference view is its basis in empirical findings independent of the motives that spurred its creation in the first place. In particular, it is firmly established that local reentrant processing is involved in perception and forms some kind of perceptual stage. Moreover, the view's framing of metacontrast masking does not differ much from some previous suggestions, and the role of local reentrant processing in cases of apparent motion is also well established. In a sense, the non-linear latency difference view expands upon previous explanations for these two phenomena by bringing them together into a single framework that includes temporal considerations as regards the timing of perception. Furthermore, it extends this explanatory framework to the flash-lag effect, which thus far has not been explained by means of reentrant processing.[11] As regards all three post-diction effects, the view can also account for more detailed results (e.g., how the target quickens perception of the mask even when the masking is unsuccessful, and how in some cases of the flash-lag effect the moving stimulus is perceived as being in two places at the same time). Given these facts, the non-linear latency difference view is both more parsimonious and more empirically plausible than the competing views. These competing views need to postulate new mechanisms to account for the postdiction effects, and yet they have remained silent on how these mechanisms could be neurally implemented.

One caveat should be mentioned, however. Similar to the discussed competing theories, the non-linear latency difference view is ambitious in the scope of the postdiction effects it tries to account for and in arguing for a shared basis for the effects. Such an approach highlights the common characteristics between different effects and downplays their differences. Accordingly, it is to be expected that the non-linear latency difference view provides only a partial explanation for each postdiction effect because modulatory effects can influence separate effects differently (as they do, for example, with short- and long-range apparent motion). Nevertheless, given that the non-linear latency difference view agrees with many empirical findings and is based on well-established conceptions on how the visual system functions, it is unlikely to be more erroneous than the other explanations that aim to provide a single explanation for many different phenomena.

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[10] Given that the non-linear latency difference view holds that pre-perceptual states are tampered with, and that our reports and memories of what we experienced are correct, it is a version of the theories maintaining Stalinesque revisions in perception.

[11] Eagleman and Sejnowski (2007, p. 10) have suggested that "a final understanding [of the flash-lag effect] may require the inclusion of feedback". Their discussion on the reentrant processes is restricted to only few paragraphs, however, and rather than elaborating on the possible role of the feedback processing, their main claim appears to be that further studies on the matter "should be revealing." Moreover, since their own explanation for the flash-lag effect (see section 2) is not based on reentrant processing, it is reasonable to conclude that they do not explain the flash-lag effect by means of reentrant processing either. Finally, it should also be noted that their discussion ignores altogether the timing issues related to these processes.

References

Arnold, D. H. (2010). Relative timing and perceptual asynchrony. In R. Nijhawan & B. Khurana (Eds.), *Space and time in perception and action* (pp. 254–277). Cambridge, UK: Cambridge University Press.

Arnold, D. H., Ong, Y., & Roseboom, W. (2009). Simple differential latencies modulate, but do not cause the flash-lag effect. *Journal of Vision*, *9*, 1–8. http://doi.org/10.1167/9.5.4.Introduction

Arstila, V. (2015a). Defense of the brain time view. *Frontiers in Psychology*, *6*(September), 4–7. http://doi.org/10.3389/fpsyg.2015.01350

Arstila, V. (2015b). The Time of Experience and the Experience of Time. In B. Mölder, V. Arstila, & P. Øhrstrøm (Eds.), *Philosophy and Psychology of Time* (pp. xx–xx). Dordrecht, The Netherlands: Springer.

Arstila, V. (2015c). Theories of apparent motion. *Phenomenology and the Cognitive Sciences*, *xx*(xx). http://doi.org/10.1007/s11097-015-9418-y

Aschersleben, G., & Prinz, W. (1995). Synchronizing actions with events: the role of sensory information. *Perception & Psychophysics*, *57*(3), 305–317. http://doi.org/10.3758/BF03213056

Aschersleben, G., & Prinz, W. (1997). Delayed auditory feedback in synchronization. *Journal of Motor Behavior*, *29*(1), 35–46.

Azzopardi, P., & Hock, H. S. (2011). Illusory motion perception in blindsight. *Proceedings of the National Academy of Sciences*, *108*(2), 876–81.

Bachmann, T. (1994). *Psychophysiology of visual masking: The fine structure of conscious experience*. Commack, NY: Nova Science Publishers, Inc.

Bachmann, T. (1997). Visibility of brief images: the dual-process approach. *Consciousness and Cognition*, *6*(4), 491–518. http://doi.org/10.1006/ccog.1997.0320

Bachmann, T., & Francis, G. (2014). *Visual Masking Studying Perception, Attention, and Consciousness*. Oxford, UK: Academic Press.

Baldo, M. V. C., Kihara, A. H., Namba, J., & Klein, S. A. (2002). Evidence for an attentional component of the perceptual misalignment between moving and flashing stimuli. *Perception*, *31*, 17–30.

Baldo, M. V. C., & Klein, S. A. (1995). Extrapolation or attention shift? *Nature*, *378*(6557), 565–566.

Block, N. (2007). Consciousness, accessibility, and the mesh between psychology and neuroscience. *The Behavioral and Brain Sciences*, *30*(5-6), 481–99; discussion 499–548.

Block, N. (2011). Perceptual consciousness overflows cognitive access. *Trends in Cognitive Sciences*, *15*(12), 567–575.

Blythe, I. M., Bromley, J. M., Kennard, C., & Ruddock, K. H. (1986). Visual discrimination of target displacement remains after damage to the striate cortex in humans. *Nature*, *320*, 619–621.

Boehler, C., Schoenfeld, M., Heinze, H.-J., & Hopf, J.-M. (2008). Rapid recurrent processing gates awareness in primary visual cortex. *Proceedings of the National Academy of Sciences*, *105*(25), 8742–8747.

Boyer, J. L., & Ro, T. (2007). Attention attenuates metacontrast masking. *Cognition*, *104*, 135–149.

Braddick, O. J., Ruddock, K., Morgan, M. J., & Marr, D. (1980). Low-Level and High-Level Processes in Apparent Motion [and Discussion]. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *290*(1038), 137–151. http://doi.org/10.1098/rstb.1980.0087

Brehaut, J. C., Enns, J. T., & Lollo, V. Di. (1999). Visual masking plays two roles in the attentional blink. *Perception & Psychophysics*, *61*(7), 1436–1448.

Breitmeyer, B. G., Ogmen, H., & Chen, J. (2004). Unconscious priming by color and form: different processes and levels. *Consciousness and Cognition*, *13*(1), 138–57.

Breitmeyer, B. G., & Ögmen, H. (2006). *Visual masking: Time slices through conscious and unconscious vision*. Oxford: Oxford University Press.

Brenner, E., & Smeets, J. B. J. (2000). Motion extrapolation is not responsible for the flash-lag effect. *Vision Research*, *40*(13), 1645–8.

Bridgeman, B. (1980). Temporal response characteristics of cells in monkey striate cortex measured with metacontrast masking and brightness discrimination. *Brain Research*, *196*(2), 347–364.

Chappell, M., & Hine, T. (2004). Events before the flash Do influence the flash-lag magnitude. *Vision Research*, *44*(3), 235–239. http://doi.org/10.1016/j.visres.2003.09.021

Chappell, M., & Mullen, K. T. (2010). The Magnocellular visual pathway and the flash-lag illusion. *Journal of Vision*, *10*(11), 1–10. http://doi.org/10.1167/10.11.24.Introduction

Christie, J., & Barresi, J. (2002). Using Illusory Line Motion to Differentiate Misrepresentation (Stalinesque) and Misremembering (Orwellian) Accounts of Consciousness. *Consciousness and Cognition*, *11*(2), 347–365. http://doi.org/10.1006/ccog.2001.0539

Dainton, B. (2008a). Sensing Change. *Philosophical Issues, 18*, 362–84.

Dainton, B. (2008b). The Experience of Time and Change. *Philosophy, 3/4*, 619–638.

Dainton, B. (2010). Temporal consciousness; Supplement: Interpreting temporal illusions. In *Stanford Encyclopedia of Philosophy*.

Dehaene, S., & Changeux, J.-P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, *70*(2), 200–27.

Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in Cognitive Sciences*, *10*(5), 204–11.

Dennett, D. C., & Kinsbourne, M. (1992). Time and the observer. *Behavioral and Brain Sciences*, *15*(2), 183–247.

Di Lollo, V., Enns, J. T., & Rensink, R. A. (2000). Competition for Consciousness Among Visual Events: The Psychophysics of Reentrant Visual Processes. *Journal of Experimental Psychology: General*, *129*(4), 481–507.

Didner, R., & Sperling, G. (1980). Perceptual delay: a consequence of metacontrast and apparent motion. *Journal of Experimental Psychology: Human Perception and Performance*, *6*(2), 235–243.

Eagleman, D. M., & Sejnowski, T. J. (2000). Motion integration and postdiction in visual awareness. *Science*, *287*(5460), 2036–2038.

Eagleman, D. M., & Sejnowski, T. J. (2007). Motion signals bias localization judgments: A unified explanation for the flash-lag, flash-drag, flash-jump, and Frohlich illusions. *Journal of Vision*, *7*(4), 1–12.

Efron, R. (1963). The effect of handedness on the perception of simultaneity and temporal order. *Brain*, *86*, 261–284.

Enns, J. T., & Lollo, V. Di. (1997). Object Substitution: A New Form of Masking in Unattended Visual Locations. *Psychological Science*, *8*(2), 135–140.

Enns, J. T., & Lollo, V. Di. (2000). What's new in visual masking? *Trends in Cognitive Sciences*, *4*(9), 345–352.

Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. F. (2007). Masking disrupts reentrant processing in human visual cortex. *Journal of Cognitive Neuroscience, 19*(9), 1488–97.

Ffytche, D. H., Guy, C. N., & Zeki, S. (1995). The parallel visual motion inputs into areas V1 and V5 of human cerebral cortex. *Brain*, *118*, 1375–94.

Fisicaro, S. A., Bernstein, I. H., & Narkiewicz, P. (1977). Apparent movement and metacontrast suppression: A decisional analysis. *Perception & Psychophysics*, *22*(6), 517–525. http://doi.org/10.3758/BF03198757

Fröhlich, F. W. (1923). Über die Messung der Empfindungszeit [Measuring the time of sensation]. *Zeitschrift Für Sinnesphysiologie*, *54*, 58–78.

Gepshtein, S., & Kubovy, M. (2007). The lawful perception of apparent motion. *Journal of Vision*, *7(8)*(9), 1–15.

Giesbrecht, B., & Lollo, V. Di. (1998). Beyond the attentional blink: visual masking by object substitution. *Journal of Experimental Psychology: Human Perception and Performance*, *24*(5), 1454–1466.

Grush, R. (2005a). Brain time and phenomenological time. In A. Brook & K. Akins (Eds.), *Cognition and the brain: The philosophy and neuroscience movement* (pp. 160–207). Cambridge, MA: Cambridge University Press.

Grush, R. (2005b). Internal models and the construction of time: generalizing from state estimation to trajectory estimation to address temporal features of perception, including temporal illusions. *Journal of Neural Engineering*, *2*(3), S209–18.

Grush, R. (2007). Time and experience. In T. Müller (Ed.), *Philosophie der Zeit* (pp. 1–18). Frankfurt: Klosterman.

Grush, R. (2008). Temporal representation and dynamics. *New Ideas in Psychology*, *26*(2), 146–157.

Hoerl, C. (2012). Seeing Motion and Apparent Motion. *European Journal of Philosophy*, pp. 1–27. http://doi.org/10.1111/j.1468-0378.2012.00565.x

Hubbard, T. L. (2014). The flash-lag effect and related mislocalizations: findings, properties, and theories. *Psychological Bulletin*, *140*(1), 308–38. http://doi.org/10.1037/a0032899

Ivry, R. B., & Cohen, A. (1990). Dissociation of short- and long-range apparent motion in visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *16*(2), 317–31.

Johnston, A., & Nishida, S. (2001). Time perception: brain time or event time? *Current Biology*, *11*(11), R427–R430.

Kahneman, D. (1967). An onset-onset law for one case of apparent motion and metacontrast. *Perception & Psychophysics*, *2*, 577–584. http://doi.org/10.3758/BF03210272

Kanai, R., & Verstraten, F. A. J. (2006). Visual transients reveal the veridical position of a moving object. *Perception*, *35*(4), 453–460. http://doi.org/10.1068/p5443

Kaneoke, Y., & Bundou, C. A. M. (1997). Human cortical area responding to stimuli in apparent motion. *Neuroreport*, *8*(3), 677–682.

Kellman, P. J., & Shipley, T. F. (1991). A theory of visual interpolation in object perception. *Cognitive Psychology*, *23*, 141–221. http://doi.org/10.1016/0010-0285(91)90009-D

Khurana, B., Watanabe, K., & Nijhawan, R. (2000). The role of attention in motion extrapolation: Are moving objects “corrected” or flashed objects attentionally delayed? *Perception*, *29*(6), 675–692.

Kirschfeld, K., & Kammer, T. (1999). The Fröhlich effect: a consequence of the interaction of visual focal attention and metacontrast. *Vision Research*, *39*, 3702–3709.

Kiverstein, J., & Arstila, V. (2013). Time in Mind. In A. Bardon & H. Dyke (Eds.), *Blackwell companion to the philosophy of time* (pp. 444–469). Oxford: Wiley-Blackwell.

Kouider, S. (2009). Neurobiological Theories of Consciousness. In *Encyclopedia of Consciousness* (pp. 87–100). NY: Elsevier.

Krekelberg, B., & Lappe, M. (2000). A model of the perceived relative positions of moving objects based upon a slow averaging process. *Vision Research*, *40*(2), 201–15.

Krekelberg, B., & Lappe, M. (2001). Neuronal latencies and the position of moving objects. *Trends in Neurosciences*, *24*(6), 335–339.

Lamme, V. A. F. (2004). Separate neural definitions of visual consciousness and visual attention; a case for phenomenal awareness. *Neural Networks*, *17*, 861–872.

Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, *10*(11), 494–501.

Lamme, V. A. F., Zipser, K., & Spekreijse, H. (2002). Masking interrupts figure-ground signals in V1. *Journal of Cognitive Neuroscience*, *14*(7), 1044–1053. http://doi.org/10.1167/1.3.32

Larsen, A., Farrell, J., & Bundesen, C. (1983). Short-and long-range processes in visual apparent movement. *Psychological Research*, *45*, 11–18.

Larsen, A., Madsen, K. H., Lund, T. E., & Bundesen, C. (2006). Images of illusory motion in primary visual cortex. *Journal of Cognitive Neuroscience*, *18*(7), 1174–1180.

Metzger, W. (1932). Versuch einer gemeinsamen Theorie der Phänomene Fröhlichs und Hazeloffs und Kritik ihrer Verfahren zur Messung der Empfindungszeit [An attempt toward a common theory of the phenomena of Fröhlich and Hazeloff and a criticism of their methods to measure sen. *Psychologische Forschung*, *16*(1), 176–200.

Muckli, L., Kohler, A., Kriegeskorte, N., & Singer, W. (2005). Primary visual cortex activity along the apparent-motion trace reflects illusory perception. *PLoS Biology*, *3*(8), e265.

Müsseler, J., & Aschersleben, G. (1998). Localizing the first position of a moving stimulus: the Fröhlich effect and an attention-shifting explanation. *Perception & Psychophysics*, *60*(4), 683–95.

Nakayama, K., Shimojo, S., & Silverman, G. (1989). Stereoscopic depth: its relation to image segmentation, grouping, and the recognition of occluded objects. *Perception*, *18*, 55–68.

Neumann, O., & Scharlau, I. (2007a). Experiments on the Fehrer-Raab effect and the “Weather Station Model” of visual backward masking. *Psychological Research*, *71*(6), 667–77. http://doi.org/10.1007/s00426-006-0055-5

Neumann, O., & Scharlau, I. (2007b). Visual attention and the mechanism of metacontrast. *Psychological Research*, *71*(6), 626–33. http://doi.org/10.1007/s00426-006-0061-7

Nijhawan, R. (1994). Motion extrapolation in catching. *Nature*, *370*(6487), 256–257. http://doi.org/10.1038/370256b0

Pascual-Leone, A., & Walsh, V. (2001). Fast Backprojections from the Motion to the Primary Visual Area Necessary for Visual Awareness. *Science*, *292*, 510–512.

Paul, L. A. (2010). Temporal Experience. *Journal of Philosophy*, *CVII*(7), 333–359.

Ramachandran, V., & Cobb, S. (1995). Visual attention modulates metacontrast masking. *Nature*, *373*(5), 66–68.

Rao, R. P., Eagleman, D. M., & Sejnowski, T. J. (2001). Optimal smoothing in visual motion perception. *Neural Computation*, *13*(6), 1243–53.

Ro, T., Breitmeyer, B. G., Burton, P., Singhal, N. S., & Lane, D. (2003). Feedback Contributions to Visual Awareness in Human Occipital Cortex. *Current Biology*, *11*, 1038–1041.

Sajda, P., & Finkel, L. H. (1995). Intermediate-level visual representations and the construction of surface perception. *Journal of Cognitive Neuroscience, 7*(2), 267–91. http://doi.org/10.1162/jocn.1995.7.2.267

Sarich, D., Chappell, M., & Burgess, C. (2007). Dividing attention in the flash-lag illusion. *Vision Research*, *47*(4), 544–547.

Scharlau, I., Ansorge, U., & Horstmann, G. (2006). Latency facilitation in temporal-order judgments: time course of facilitation as a function of judgment type. *Acta Psychologica, 122*(2), 129–59. http://doi.org/10.1016/j.actpsy.2005.10.006

Scharlau, I., & Neumann, O. (2003a). Perceptual latency priming by masked and unmasked stimuli: Evidence for an attentional interpretation. *Psychological Research*, *67*, 184–196.

Scharlau, I., & Neumann, O. (2003b). Temporal parameters and time course of perceptual latency priming. *Acta Psychologica*, *113*(2), 185–203. http://doi.org/10.1016/S0001-6918(02)00157-9

Scholte, H. S., Jolij, J., Fahrenfort, J. J., & Lamme, V. A. F. (2008). Feedforward and Recurrent Processing in Scene Segmentation: Electroencephalography and Functional Magnetic Resonance Imaging. *Journal of Cognitive Neuroscience, 20*(11), 2097–2109.

Schwiedrzik, C. M., Alink, A., Kohler, A., Singer, W., & Muckli, L. (2007). A spatio-temporal interaction on the apparent motion trace. *Vision Research, 47*(28), 3424–33.

Shapley, R. (2004). A new view of the primary visual cortex. *Neural Networks*, *17*(5-6), 615–623.

Shelley-Tremblay, J., & Mack, A. (1999). Metacontrast masking and attention. *Psychological Science*, *10*(6), 508–515.

Sheth, B. R., Nijhawan, R., & Shimojo, S. (2000). Changing objects lead briefly flashed ones. *Nature Neuroscience*, *3*(5), 489–495.

Shipley, T. F., & Kellman, P. J. (1992). Perception of partly occluded objects and illusory figures: Evidence for an identity hypothesis. *Journal of Experimental Psychology: Human Perception and Performance*, *18*(1), 106–120. http://doi.org/10.1037//0096-1523.18.1.106

Silvanto, J., Cowey, A., Lavie, N., & Walsh, V. (2005). Striate cortex (V1) activity gates awareness of motion. *Nature Neuroscience, 8*(2), 143–144.

Sincich, L. C., Park, K. F., Wohlgemuth, M. J., & Horton, J. C. (2004). Bypassing V1: a direct geniculate input to area MT. *Nature Neuroscience*, *7*(10), 1123–8.

Sterzer, P., Haynes, J.-D. D., & Rees, G. (2006). Primary visual cortex activation on the path of apparent motion is mediated by feedback from hMT+/V5. *NeuroImage*, *32*(3), 1308–16.

Tata, M. S. (2002). Attend to it now or lose it forever: selective attention, metacontrast masking, and object substitution. *Perception & Psychophysics*, *64*(7), 1028–38.

Todd, S. J. (2009). A difference that makes a difference: Passing through Dennett's stalinesque/orwellian impasse. *The British Journal for the Philosophy of Science*, *60*(3), 497–520.

Whitney, D., & Cavanagh, P. (2000). The Position of Moving Objects. *Science*, *289*, 1107a.

Whitney, D., & Murakami, I. (1998). Latency difference, not spatial extrapolation. *Nature Neuroscience*, *1*(2), 656–657.

Whitney, D., Murakami, I., & Cavanagh, P. (2000). Illusory spatial offset of a flash relative to a moving stimulus is caused by differential latencies for moving and flashed stimuli. *Vision Research*, *40*(2), 137–49.

Wibral, M., Bledowski, C., Kohler, A., Singer, W., & Muckli, L. (2009). The timing of feedback to early visual cortex in the perception of long-range apparent motion. *Cerebral Cortex*, *19*(7), 1567–82.

Visser, T. A. W., & Enns, J. T. (2001). The role of attention in temporal integration. *Perception*, *30*(2), 135–145. http://doi.org/10.1068/p3089

Woodman, G. F., & Luck, S. J. (2003). Dissociations among attention, perception, and awareness during object-substitution masking. *Psychological Science*, *14*, 605–611. http://doi.org/10.1046/j.0956-7976.2003.psci_1472.x

Wu, D.-A., & Shimojo, S. (2010). TMS reveals the correct location of flashes in motion-mislocalization illusions. *Journal of Vision*. http://doi.org/10.1167/2.7.26

Yantis, S., & Nakama, T. (1998). Visual interactions in the path of apparent motion. *Nature Neuroscience*, *1*(6), 508–512.

Yarrow, K., & Arnold, D. H. (2015). The Timing of Experiences: How Far Can We Get with Simple Brain-time Models? In B. Mölder, V. Arstila, & P. Øhrstrøm (Eds.), *Philosophy and Psychology of Time*. Dordrecht, The Netherlands: Springer.

Yarrow, K., Jahn, N., Durant, S., & Arnold, D. H. (2011). Shifts of criteria or neural timing? The assumptions underlying timing perception studies. *Consciousness and Cognition*, *20*(4), 1518–1531. http://doi.org/10.1016/j.concog.2011.07.003

Zeki, S. (2003). The disunity of consciousness. *Trends in Cognitive Sciences*, *7*(5), 214–218.

Zeki, S. (2007). A theory of micro-consciousness. *The Blackwell Companion to Consciousness*.

Zeki, S., & Bartels, A. (1999). Toward a theory of visual consciousness. *Consciousness and Cognition*, *8*(2), 225–59.

Zenz, M., & Cai, R. (2008). The effect of metacontrast masking on the Fröhlich effect. *Journal of Vision*, *8*(6), 15–16. http://doi.org/10.1167/8.6.133