

Pessi Lyyra

The Scope and Limits of Implicit Visual Change Detection



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The Scope and Limits of Implicit Visual Change Detection

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Editors

Timo Suutama

Department of Education, University of Jyväskylä

Pekka Olsbo, Harri Hirvi

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ABSTRACT

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Tiivistelmä: Visuaalisten muutosten esitietoinen havaitseminen

Humans are naturally adept at noticing unexpected changes, such as an appearance, a disappearance, or a movement of an item, in their visual environment. However, this ordinary high capacity visual change detection is eliminated to almost chance level, if the change occurs together with a global distracting stimulus. Conscious change detection under these circumstances requires effortful serial search, guided by top-down focal attention. This phenomenon, dubbed “change blindness”, was initially taken to suggest that, by its nature, implicit visual perception is simplistic, scarce, short-lived and superfluous, and thus unable to guide conscious visual change detection. Recent studies of change blindness, however, have revealed that, already before conscious reportability, changed items can be registered, localized, or even identified. Despite this evidence, the full scope of implicit visual change detection and its effect on its explicit counterpart remain poorly understood. These issues were further investigated by measuring event-related potentials and change detection performance using different change conditions in the change blindness paradigm. The results confirmed that changes are implicitly processed at many, starting from the first, stages of visual perception. At later stages of processing, stimulus specific electrophysiological responses related to face perception revealed that complex representations of presented changes can be formed at the implicit level. Interestingly, stronger traces of implicit change detection were not necessarily correlated with enhanced change detection performance, emphasizing the role of top-down focal attention in explicit change detection. Nevertheless, stimuli with social and threat-related relevance enhanced detection rates even without the contribution of top-down focal attention, suggesting a limited bottom-up influence on change detection for biologically relevant stimuli. These results deepen and broaden the views on what kind of information about visual changes can be nonconsciously extracted, and how this information can make changes better or worse detected.

Keywords: change blindness, change detection, event-related potentials, visual awareness, consciousness, social perception, emotion perception

Author's address

Pessi Lyyra
Department of Psychology
P.O. Box 35
FI-40014
University of Jyväskylä
pessi.lyyra@jyu.fi

Supervisors

Piia Astikainen
Department of Psychology
University of Jyväskylä

Heikki Lyytinen
Department of Psychology
University of Jyväskylä

Antti Revonsuo
School of Humanities and Informatics
University of Skövde, Sweden

Reviewers

Ronald Rensink
Department of Psychology
University of British Columbia

Mika Koivisto
Centre for Cognitive Neuroscience
University of Turku

Opponent

Mika Koivisto
Centre for Cognitive Neuroscience
University of Turku

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My personal interest in the topic of this dissertation spawned in a conference in Copenhagen in 2003, where change blindness figured strongly in the presentations of both Kevin O'Regan and Alva Noë. They both used it to defend a radical view of consciousness, already made famous a couple of years earlier in their seminal article in *The Behavioral and Brain Sciences*, according to which the massive unnoticed changes in change blindness are not represented by the unconscious mind – and not able to guide conscious change detection. Their theory seemed outrageous to me, but at the same time intriguing and indismissible. Shortly, I was offered an opportunity to empirically test the presuppositions of this theory using change blindness at my home university, which eventually developed into this research project. All the research reported in this dissertation still revolves around the same original question of how far the unnoticed changes are processed before breaking through to visual awareness.

First, I wish to thank my supervisor Piia Astikainen for the opportunity to venture into this path under her dedicated guidance. The other people who have influenced this project the most are the co-authors of the articles, Prof. Jari Hietanen, Dr. Jan Wikgren, and Dr. Timo Ruusuvirta, to whom all I want to express my gratitude. Invaluable comments on the dissertation were also kindly offered by Dr. Mika Koivisto, Ass. Prof. Ronald Rensink, and my supervisors, Prof. Antti Revonsuo and Prof. Heikki Lyytinen. Special thanks to Lauri Viljanto for technical support, and my beloved aunt Anna-Liisa Lyyra for help with statistical analyses. Many thanks also to all the students involved in this research project for help, ideas and inspiration.

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- III Lyyra, P., Mäkelä, H., Hietanen, J.K., & Astikainen, P. (2014). Implicit binding of facial features during change blindness. *PLoS One*, 9, e87682.
- IV Lyyra, P., Hietanen, J.K., & Astikainen, P. Anger superiority effect for change detection and change blindness. Manuscript.

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1 INTRODUCTION: VISUAL CHANGE DETECTION AND CHANGE BLINDNESS

Despite a more than century-long research tradition, many aspects of non-conscious visual perception remain poorly understood (Merikle, Smilek, & Eastwood, 2001). The aim of the studies on this topic has been to establish the existence of non-conscious processing, and the methods used rarely allow investigation of its interaction with conscious visual processing. Still fewer methods allow non-conscious stimuli to reach consciousness (Eastwood & Smilek, 2005). Probably the most intriguing question about non-conscious visual perception is, then, how its content can break through to become the content of conscious visual awareness (Kiefer et al., 2011).

The most influential contemporary views of consciousness maintain that compared to conscious processing, operating with limited serial resources, nonconscious processing is parallel, domain-specific and vastly efficient, with ample content (Baars, 1988; Baars, 1997; Block, 2011; Dehaene & Naccache, 2001). On this view, attention selects one of the competing implicit contents for further conscious processing. However, this view does not address so much the relationship between these two modes of processing as the differences between them. It describes consciousness as the tip of the iceberg but does not specify which facet of the iceberg the tip is going to be.

Another popular view emphasizes that the content of visual consciousness is detailed only within the sphere of attention, and that otherwise visual perception is sparse and operates with low-level features (Dennett, 1991; O'Regan & Noë, 2001; Rensink, 2000a, 2002; Treisman, 1998; Treisman & Gelade, 1980). This view, however, explicitly states that implicit processing has very limited chances of influencing explicit processing due to its incomplete, short-lived nature, and that the workings of top-down attention dictate the contents of visual consciousness. Perhaps the most important source of evidence for this view comes from the recent studies on visual change detection.

The purpose of the visual system is to pick up signals from the immediate environment, essential for the thriving of the individual. In addition to bright

lights and colors, the human visual brain is particularly tuned to sudden motion and unexpected changes in the visual environment (Abrams & Christ, 2003; Franconeri & Simons, 2003). For obvious evolutionary reasons, an object suddenly appearing, disappearing, or changing color or form is irresistible to the brain. From the experiential viewpoint, we immediately become conscious of any such change. In everyday life, we can rely on large enough changes not escaping our attention, or at least this is what we are inclined to think (Levin, Momen, Drivdahl, & Simons, 2000). A natural way to explain this is that the visual system implicitly processes the whole visual scene in detail, and summons attention to the locus of a salient event, forcing us to become conscious of the change (Jensen, Yao, Street, & Simons, 2011; Parker, 1978; Zelinsky, 2001).

Despite appearances, the change detection system is not infallible. The research reported below concentrate on the efficacy – and lack thereof – of the visual change detection system. Changes in the visual environment can occur without us noticing them consciously. Recent studies of change detection have been informative about within what kind of limitations we can rely on this system. Most notably, the recently discovered phenomenon dubbed *change blindness* has revolutionized our view about the vulnerability of the visual change detection system (Henderson & Hollingworth, 1999; Jensen et al., 2011; Rensink, 2002; for reviews, see Simons, 2000b; Simons & Levin, 1997, 2003; Simons & Rensink, 2005). Change blindness refers to the phenomenon that, when appropriately interfered with, the change detection system can fail, and massive changes can go unnoticed for several seconds. Once detected, the change becomes impossible to ignore, and the viewers incredulous about missing it.

Thanks to its anomalous nature, change blindness has been seen as potentially informative about the functioning of the visual system. Indeed, it does carry a methodological advantage for studying both conscious and nonconscious visual perception. In studies of the latter, it is only if the implicitly presented stimuli are allowed eventually to reach consciousness that they can be used to study the function they have in this process (Eastwood & Smilek, 2005; Merikle et al., 2001). Change blindness allows to do just this: it offers a prolonged period of non-conscious presentation for a stimulus change, eventually resulting in the observer becoming conscious of the stimulus. In change blindness studies, ample evidence of implicit visual processing of changes has also been provided. Nevertheless, the questions still remain as to what kind of information is implicitly extracted from unnoticed changes and whether the nature of this information can influence attention and contribute to their reaching the level of consciousness. The following research aimed to shed new light on this issue.

1.1 Visual change detection

1.1.1 The type of change relevant for visual change detection

The concept of *change* is at worst a vague, all encompassing concept. In a sense, everything can be viewed as consisting of change, both in the world and even more so in the constant fluctuations of the visual stream. Such meanings of change are useless for empirical psychology, and therefore the relevant meaning has to be pinned down to suit its purposes (Rensink, 2002). One way to do this is by contrasting change with neighbouring concepts such as *difference* and *motion*.

Difference can involve many objects, but change involves a difference in time in one and the same element in the visual scene. At the same time, change involves (a relative) continuity of identity of the changing element or some of its parts. Motion could be defined as the relatively continuous change of position of a coherent object across time, whereas change concerns discontinuous changes of position or changes of static features like color or form. From the viewpoint of vision research, motion detection and change detection form distinct domains of interest. Nevertheless, they are interrelated phenomena, and the connection between change and motion detection at the neurocognitive level is potentially important for understanding change detection.

Here, by changes, I refer to substantial unexpected changes across two similar static views in some elementary part of them, such as an object or one of its prominent features appearing, disappearing, or changing in form or color. The changes in the experiments described below may involve sudden substantial changes introduced together with an interruption of stimulation. These changes are such that, under ordinary circumstances, they would become explicitly detected immediately and effortlessly. Here, explicit means that a voluntary behavioural report can be given about the change, whereas implicit refers to detection observed by indirect behavioural and neural means in the absence of the ability of voluntary report. The advantage of change blindness studies lies in the fact that the blindness effect can be maximized by the researcher in proportion to the size of the changes.

1.1.2 Two mechanisms of explicit visual change detection

Two mechanisms have been proposed for explicit change detection in the human visual system (see, e.g., Kanai & Verstraten, 2004; Rensink, O'Regan, & Clark, 1997). A sudden change in the visual field automatically captures attention, leading to its immediate conscious detection. It has been found that the abrupt appearance of an object captures attention in a stimulus-driven manner even when not the target of visual search (Cosman & Vecera, 2009; Yantis, 1993; Yantis & Jonides, 1990). This phenomenon, known as *attentional capture* (see, Simons, 2000a for a review), is even greater when the item is

actively searched for, in terms of attention in the “diffused attention mode” (Yantis & Jonides, 1990) or in “the search mode of attention” (Fernandez-Duque, Grossi, Thornton, & Neville, 2003). This kind of immediate, bottom-up driven system constitutes the first and foremost form of human change detection. It is said to work with high-capacity parallel resources, and its operations seem to vary with the deployment of attention (Folk, Remington, & Johnston, 1992) or even along differences between individuals (Huang, Mo, & Li, 2012; Lechak & Leber, 2011).

Attentional capture can occur either implicitly, when inferred from indirect measurements, or explicitly when the sudden content becomes automatically the content of conscious visual awareness (Simons, 2000a). Ordinary change detection can be viewed as an instance of explicit attentional capture.

It has been proposed that, at the cognitive level, change detection is related to the motion transients created by the changes (Rensink et al., 1997). Motion captures attention in a similar bottom-up way (Abrams & Christ, 2003; Franconeri & Simons, 2003). Some studies of bottom-up change detection have suggested a single brain mechanism for change and motion detection (Franconeri & Simons, 2003; Hillstrom & Yantis, 1994; Shulman, Ollinger, Linenweber, Petersen, & Corbetta, 2001; Shulman et al., 2001). Detection occurs primarily in monocular subcortical structures (Kanai & Verstraten, 2004; Phillips & Singer, 1974b). Such subcortical areas most often linked to change detection and shifts of attention include the pulvinar nucleus of the thalamus (Michael & Buron, 2005) and the superior colliculus (SC) (Cavanaugh & Wurtz, 2004). These areas may thus represent the first areas to react to changes with or without awareness of the change by the observer. However, the motion-specific cortical area of the occipital brain MT/V5 also participates in the process (Lechak & Leber, 2011). It has been proposed that the SC-pulvinar-MT/V5 is an effective combined change and motion detector system in the primate brain (Rokszi et al., 2010).

The second form of human change detection is related to focal attention. This type of change detection acts in a serial manner on a few objects at a time, but the comparison processes span long periods of time (Hughes, Caplovitz, Loucks, & Fendrich, 2012). It is suggested to consist of a number of the following suboperations: 1) initial encoding of the scene, what items are present and where, 2) initial parallel comparison of items across the two scenes, 3) gaze/attention shift to change location, 4) focused encoding of the prechange item at the change location, 5) focused encoding of the post-change item at the change location, 6) comparison of pre- and post-change items, and 7) consolidation in working memory and conscious recognition of the discrepancy (Jensen et al., 2011; Kiefer et al., 2011; Parker, 1978; Zelinsky, 2001). Some form of initial change detection is necessary for visual processing to proceed from stage 2 to stage 3.

Another way to distinguish between different types of change detection is by their level of information processing. Sometimes change detection is simply

registration by the brain or the individual of something changing in a visual stimulus (Turatto & Bridgeman, 2005). This could happen either as a simple reaction to the changing stimulus or as detection of change *as a change*. Either one of these could correspond to initial change detection between stages 2 and 3. The difference between these modes of change detection can be investigated by eliminating the physical effects of the changes, and if the changes still leave some physiological trace, this can be interpreted as something related to the change as a change, not the changing physical features per se (see, e.g., Kimura, Katayama, & Murohashi, 2005). For the phenomenon of change blindness, the point is not so much concealing the changing features but rather the transient experience of change within the sphere of experience. Some have suggested that the relevant aspect of change is its element of novelty, and it has been shown that the greater the novelty value of the change, the more relevant it is for the visual system (Mazza, Turatto, & Sarlo, 2005).

Subjectively, participants are able to report initial feelings of something changing in the visual field before conscious recognition or localization of the change (Busch, Frund, & Herrmann, 2010; Howe & Webb, 2014; Rensink, 2004). This is often referred to as “sensing” rather than detecting the change. It is not quite clear at which stage of visual processing this type of change processing can take place. Presumably, it occurs at preattentive stages of change detection, possibly already between stages 2 and 3 of the above model.

Changes may further be localized (up to stage 3 in the above model) or identified (up to stage 7) (Busch, Dürschmid, & Herrmann, 2010; Turatto & Bridgeman, 2005). There is no specific stage of visual processing at which detection has to become explicit: implicit processing can extend up to stage 6 (Laloyaux, Destrebecqz, & Cleeremans, 2006), while explicit may start at least from stage 2 (Rensink, 2000a; Turatto & Bridgeman, 2005). The distinct types and levels of change detection should be kept apart, as they are relevant for the instructions given to the participants in a change detection study (Hughes et al., 2012). Registration of the changes may be best measured by indirect means as a physiological response to changes. At the level of conscious change detection, participants may respond to changes as changes, or they may try to locate or recognize them.

Sometimes change detection is further divided into incidental and intentional change detection (Levin & Simons, 1997; Rich & Gillam, 2000; Simons, 2000b). The intentional type is the form in which changes are actively searched for, and this is the relevant form for the present purposes. The incidental approach involves passive viewing or a primary attentional task, and therefore resembles more the inattentive blindness (Mack & Rock, 1998) or the visual mismatch negativity paradigms (Kimura, Schroger, & Czigler, 2011; Pazo-Alvarez, Cadaveira, & Amenedo, 2003; Winkler & Czigler, 2012).

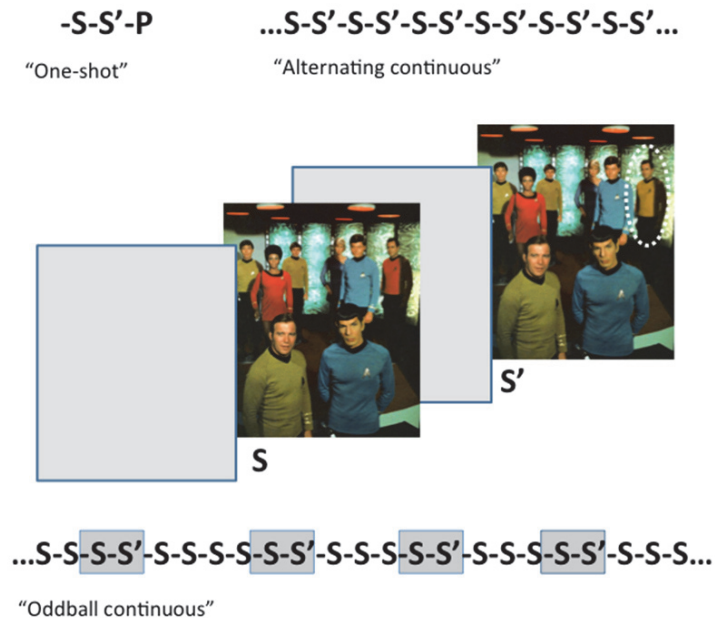
1.2 Change blindness: the phenomenon

Automatic explicit change detection, as described above, is very effective under ordinary, natural circumstances. It has been suggested that people even tend to overestimate their ability at detecting changes (Levin et al., 2000; Scholl, Simons, & Levin, 2004). Namely, it has been shown by a number of experimental cognitive psychologists during the past few decades that if disrupted in an appropriate manner, this system exhibits surprising proneness to failure. There is evidence from studies of attentional capture that high perceptual load itself decreases the attentional capture created by motion, or the abrupt appearance or disappearance of items in visual scenes (Cosman & Vecera, 2009, 2010a, 2010b). If the attention load is increased by a difficult primary task, massive events may go unnoticed, a phenomenon dubbed as “inattention blindness” (Mack & Rock, 1998).

Another effective way to weaken automatic visual change detection is to simultaneously introduce a global disturbing event together with the change, even when viewers are searching for changes. This phenomenon has been dubbed “change blindness”. Change blindness-inducing events include eye-blinks (O’Regan, Deubel, Clark, & Rensink, 2000) and eye-movements (Grimes, 1996), a sudden flash of light or brief blank interval, usually called a *flicker* (Rensink et al., 1997), or some other global transient stimulus, e.g. a *mud splash* (O’Regan, Rensink, & Clark, 1999). Less common ways to induce this condition include introducing colors to a grey-scale image or a change in luminance simultaneously with the change (Arrington, Levin, & Varakin, 2006). Also, if the change occurs in a sufficiently gradual manner, it does not capture attention in the ordinary way (Simons, Franconeri, & Reimer, 2000). Changes go unnoticed if the change in an image presented to one eye occurs when the presentation of the image is shifted to the other eye without interruption, suggestive of a monocular level origin in the brain for automatic change detection (Phillips & Singer, 1974b).

In laboratory settings, change blindness is most frequently induced using the flicker paradigm, originally developed to mimic the blurring effect of a saccade on the retinal image (Rensink et al., 1997). In this paradigm, an image is presented followed by a brief blank interval, after which a modified version of it is presented. The two basic ways of using the paradigm are the *one-shot* and *continuous* flicker paradigms (see Fig 1). In the one-shot paradigm, the original and modified images are presented in a sequence, after which a probe for change perception is presented. In the continuous paradigm, either the original and modified image alternate in a sequence of multiple presentations, or the modified image is interspersed infrequently, usually in a pseudorandom manner between the frequent unmodified ones (oddball paradigm). The stimulus sequence can be restricted to a limited number of change presentations (for example 3-10) (Niedeggen, Wichmann, & Stoerig, 2001), called here a *semi-continuous* flicker paradigm.

FIGURE 1 The basic versions of the change blindness flicker paradigm.



S and S' represent an example of an image pair in embedded in stimulus sequences. "S" refers to the original image and "S'" to its modified version, and the white rectangle to the blank screen between them. "P" refers to a forced-choice response probe for change detection in the one-shot paradigm. The dotted white ellipse indicates the site of modification in S'.

However, there are some limitations to the occurrence of change blindness. In interruptions of stimulation, attentional capture ceases to occur when the interruption is prolonged to 67–80 ms (Pashler, 1988; Phillips & Singer, 1974a; Rensink et al., 1997). This aspect of change blindness is not well understood, and it may be related to motion transients created by abrupt onsets or offsets of changing stimuli. Interestingly, the above duration corresponds to that of critical flicker fusion frequency in vision driven by the rod cells (15 Hz or 67 ms) (Sharpe & Stockman, 1999). For cone cell-mediated vision, the critical flicker fusion frequency is 50–60 Hz, and hence it would be interesting to study whether change blindness could be induced by isoluminant color changes with shorter interval durations than the changes commonly used with luminance differences, and whether these two change types are processed by different neural mechanisms.

Another limitation of change blindness is that the change should not occur for immediate objects of interest (Kelley, Chun, & Chua, 2003; Rensink et al., 1997), and be rather in the background than the foreground of the visual scene (Mazza, Turatto, & Umiltà, 2005; Turatto, Angrilli, Mazza, Umiltà, & Driver, 2002). Among other things, large changes (Smilek, Eastwood, & Merikle, 2000), changes in socially relevant vs. socially neutral objects (Amado, Yildirim, &

Iyilikci, 2011; Bracco & Chiorri, 2009; David, Laloyaux, Devue, & Cleermans, 2006; Humphreys, Hodsoll, & Campbell, 2005; Kikuchi, Senju, Tojo, Osanai, & Hasegawa, 2009; Ro, Russell, & Lavie, 2001; Wilford & Wells, 2010), and items related to vs. not related to expertise are detected more easily (Werner & Thies, 2000). Clearly, the detection facilitated in these cases is due to enhanced attention allocation to objects of central interest that leads to more efficient detection of changes in these objects. Therefore, it has been suggested that enhanced detection of changes, for example, in socially relevant objects is due to the greater top-down attention allocated to these objects than other objects (Bracco & Chiorri, 2009; Kikuchi et al., 2009), although others have claimed that the effect may be stimulus-driven, owing to its biological relevance (Ro et al., 2001).

It has also been frequently shown that spatial cues attenuate change blindness (Becker, Pashler, & Anstis, 2000; Scholl, 2000; Tse, Sheinberg, & Logothetis, 2003), the effect extending even to change detection in the opposite hemifield (Tse et al., 2003). Interestingly, however, their facilitatory effect can be short-lived, spanning only a few hundred milliseconds after which it is diminished (Smith & Schenk, 2008). Also semantic cues help in overcoming change blindness (Caudek & Domini, 2012). The effect of such cues is probably attentional as well. Others have suggested that previous unnoticed changes may serve as spatial cues guiding spatial attention implicitly to the location of the change, leading eventually to explicit change detection (Niedeggen et al., 2001). Additional support for this view is lent by studies showing more efficient detection of changes presented in locations of previously detected changes (Rensink, 2000b; Vergeer, von Schmid, & van Lier, 2006), and those showing search bias towards the previously detected change location, even if the change is presented elsewhere in the display, resulting in aggravation of change blindness (Takahashi & Watanabe, 2008). Inhibition of return, the property of visual search of preferring novel and neglecting the previous search locations, exaggerates change blindness (Smith & Schenk, 2010), which suggests that these different ways of disrupting detection do not act in an on/off manner but rather have a cumulative effect. Furthermore, the context properties of the image can have an alleviating, probably attentional cueing effect on change blindness (Kelley et al., 2003).

Corresponding phenomena for change blindness have been found for the auditory (Gregg & Samuel, 2008; Pavani & Turatto, 2008; Vitevitch, 2003), tactile (Auvray, Gallace, Hartcher-O'Brien, Tan, & Spence, 2008; Gallace & Spence, 2008; Gallace, Zeeden, Roder, & Spence, 2010; Pritchett, Gallace, & Spence, 2011) and olfactory (Pritchett et al., 2011; Sela & Sobel, 2010) modalities. However, here I focus on change *blindness*. The properties and limitations perceived for visual change blindness may differ from corresponding phenomena in other sensory modalities, e.g. (Pavani & Turatto, 2008), and they may work across different modalities (Auvray, Gallace, Tan, & Spence, 2007; Auvray et al., 2008; Gallace, Auvray, Tan, & Spence, 2006; Gallace & Spence, 2008). Future studies are needed to explore these effects.

1.3 Theories of change blindness

The findings on change blindness rapidly drew interest from cognitive psychologists and inspired new radical views of human visual perception and change detection developed to accommodate this newly found anomalous phenomenon. The most radical proposition was the so-called no-representation theory (O'Regan & Noë, 2001). Basically, it proposes that representations of the changed features of unnoticed do not exist; outside of the focus of attention, the representation of the world as scarce and simplistic as necessary for successful action guided by the senses. This view was taken to support the recent paradigms of cognitive science, active and embodied views of visual perception replacing those based on information processing and visual representations (e.g., Noë, 2004). The no-representation theory was popular for some time, various alternative ways of explaining change blindness have since been proposed:

1. No representation
2. Change amnesia
3. Overwriting
4. Search complication
5. Feature combination
6. First impressions
7. Comparison failure
8. Retrieval/ Access failure

According to the change amnesia account, change detection in the change blindness condition proceeds via top-down resources with only spatial layout and scene gist as guides, since detection cannot rely on stored detailed information about the scene, as it has faded before the next presentation cycle (Alston & Wright, 2002; Horowitz & Wolfe, 1998; Wolfe, 1999). However, it is implausible that with the shortest intervals – less than 100 ms – the information has faded, since this is well within the span of visual sensory memory (Coltheart, 1980; Di Lollo, 1980). This is not so much a problem for the very similar overwriting view, holding that although the representation of the original image could be preserved across the interval, it is overwritten (or masked) by the content of the changed stimulus – unless protected from masking in attentional memory (Rensink, 2000a, 2002; Rensink et al., 1997). Without memory traces of both scenes, implicit comparison between them is impossible. This view is also reminiscent of the view presented in Tse (2004), suggesting that change blindness is due to elimination of the operation of the motion detector system, since the global flash resets the parallelly updated salience map needed to guide visual search. A study comparing the overwriting view against this “search complication” view claimed to support the former on the basis that the effect of a spatial cue was diminished when presented

simultaneously with the second view compared to cues presented during the blank interval (Becker et al., 2000).

The more hypothetical feature combination view states that the changed and unchanged features of an object become fused into one representation in visual memory, rendering change detection through comparison of two views impossible (Levin & Simons, 1997). This view is not currently supported by subjective or objective data.

The first impressions account states that the information about the first view dominates that about the second, and thus even when detectable, in practice the change is actively repressed (Levin & Simons, 1997). While support for this quasi-Freudian view has come from real-life or motion picture studies of change blindness with high ecological validity, these studies differ from other change blindness studies in that the task is not to actively search for changes, and in which respect, therefore, they come close to inattentive blindness studies.

More plausible explanatory models are provided by the comparison, retrieval and access failure accounts. In these models, although more or less detailed information about the changes can be implicitly extracted from the pre- and post-change scenes, these two scenes cannot be compared with each other (stage 6) (Scott-Brown, Baker, & Orbach, 2000), or can be compared but not consolidated into visual working memory for conscious access or retrieval (stage 7). Studies reporting preserved information across interruptions are compatible with these models (e.g., Hollingworth, 2001, 2003). One plausible option is that there is more than a single cause for change blindness, such as both representation and comparison failures (Varakin, Levin, & Collins, 2007), or that the cause of change blindness may depend on how change blindness is induced. For example, the first impressions view may hold in real life social interaction, or the overwriting view may hold for short interruptions and the amnesia view for longer ones.

The essential question for evaluating different theories of change blindness, and the role of implicit change detection in recovery from change blindness, is in what kind of information survives across interruptions (Irwin, 1991; Irwin, 1996). Recent suggestions for what kind of information is retained and integrated across interruptions include, in addition to the content of focal attention, the semantic gist of the scene (Oliva & Torralba, 2006; Sampanes, Tseng, & Bridgeman, 2008), a spatial layout with a "salience map" (Itti & Koch, 2000) and "object files" (Irwin, 1996) containing essential information about some of the perceived objects. Some other suggestions for retained transsaccadic information include spatial position and object form (Deubel, Schneider, & Bridgeman, 2002). It has been suggested, however, that although the content of transsaccadic memory survives across interruptions and guides visual search, it does not accumulate with repetitive stimulation (Irwin & Zelinsky, 2002). However, others have suggested that detailed information can be accumulated in a long-term memory store (e.g., Hollingworth, 2001, 2003). Disentangling the different types of memory at play and their role in the

development of explicit change detection is another important challenge for future change blindness studies.

1.4 Implicit change detection

Each theoretical position entails different views about implicit change detection and its relation to explicit change detection. On the no-representation view, implicit change detection can have no role in the development of explicit change detection, since implicit change detection is deemed not to exist. The change amnesia view, comparison failure and other views could incorporate some role for bottom-up operations in the development of explicit change detection, as long as they allow implicit information about changes affect attention. Elucidating the nature and function of implicit change detection in the development of its explicit counterpart is an essential task in evaluating the validity of the various theoretical positions.

Behavioral studies (Aivar, Hayhoe, Chizk, & Mruczek, 2005; Fernandez-Duque et al., 2003; Fernandez-Duque & Thornton, 2000b; Hayhoe, Bensinger, & Ballard, 1998; Henderson & Hollingworth, 2003; Hollingworth, 2001; Hollingworth, Williams, & Henderson, 2001; Laloyaux et al., 2006; Thornton & Fernandez-Duque, 2000; Thornton & Fernandez-Duque, 2002) have demonstrated the existence of implicit change detection. In gaze-tracking studies, it has been found that gaze lingers at the site of change after its presentation for a significantly longer time compared to other locations, indicating change registration and localization at some level (Hayhoe et al., 1998; Hollingworth et al., 2001). This also accords with the observation that changes may even be fixated at the moment of change (Caplovitz, Fendrich, & Hughes, 2008), and that change detection is highly task-dependent (Triesch, Ballard, Hayhoe, & Sullivan, 2003).

More controversy has revolved around self-report studies using behavioral measures such as forced choice and reaction times. In forced-choice experiments, orientation of the changing object were guessed above chance levels (Fernandez-Duque & Thornton, 2003; Thornton & Fernandez-Duque, 2000), as was their location (Fernandez-Duque & Thornton, 2000a; Smilek et al., 2000; Watanabe, 2003), while response times have been longer for change blindness than for no-change conditions (Koivisto & Revonsuo, 2003). Such implicit change detection during change blindness has been contested time and time again, as explicable by reference to residues of explicit awareness, compromised by lack of confidence, and to the conservative response criteria of explicit change detection (Mitroff & Simons, 2002; Mitroff, Simons, & Franconeri, 2002). However, the results have stood in an experiment claiming to have taken these criticisms into account (Laloyaux et al., 2006).

Further evidence has been provided in neural studies of change blindness. Initially, brain-level studies of change blindness by electrophysiological and brain imaging methods concentrated on explicit change detection. Usually, this

was contrasted with brain activity during the change blindness period or no change condition (Beck, Rees, Frith, & Lavie, 2001; Eimer & Mazza, 2005; Huettel, Guzelde, & McCarthy, 2001; Koivisto & Revonsuo, 2003; Turatto et al., 2002; Turatto & Bridgeman, 2005). Some of these studies also compared change blindness to the no change condition, finding indications of neural traces of implicit change detection. Other neural studies have reported that enhanced electrophysiological pre-stimulus activation immediately preceding the onset of change is predictive of successful change detection (Koivisto & Revonsuo, 2005; Pourtois, De Pretto, Hauert, & Vuilleumier, 2006), while similar evidence has been reported in change blindness studies using EEG to measure brain frequency differences before successful and unsuccessful detection (Darriba, Pazo-Alvarez, Capilla, & Amenedo, 2012). Increasingly, the focus has shifted towards implicit change detection.

In the present research, the focus is exclusively on implicit change detection. To date, evidence of implicit change detection by the brain has been obtained from brain imaging (Beck et al., 2001; Pessoa & Ungerleider, 2004) and electrophysiological studies (Busch, 2013; Eimer & Mazza, 2005; Fernandez-Duque et al., 2003; Khittl, Bauer, & Walla, 2009; Kimura, Katayama, & Ohira, 2008; Niedeggen et al., 2001; Schankin & Wascher, 2007, 2008). Neural studies of implicit change detection in the change blindness condition and their relevant methodological details and results are collected in Tables 1–3. A table of brain stimulation studies, in which stimulation have been observed to affect change detection rates (Beck, Muggleton, Walsh, & Lavie, 2006; Cavanaugh & Wurtz, 2004; Tseng et al., 2010; Turatto, Sandrini, & Miniussi, 2004), is also included (Table 3). Brain stimulation studies can be indirectly informative about implicit mechanisms of change detection, assuming that explicit detection builds on bottom-up influences from preceding implicit processes.

TABLE 1 Electrophysiological studies reporting specific activation associated with unnoticed changes.

Study	Paradigm	Stimuli	Stimulus/ Interval (ms)	Latency (ms)	Electrode sites	Polarity
Niedeggen et al., 2001	Semi-cont.	Alpha-numeric symbols	1500/200	400-700 500-700	Central- Parietal	Positive
Fernandez-Duque et al., 2003	Cont.	Natural scenes	500/300	240-300	Anterior	Positive
Eimer & Mazza, 2005	1-shot	Faces	200/500	30-80 90-130	Global	Positive
Schankin & Wascher, 2007	1-shot	Colored dots	200/50 200/30	N2pc (220-260)	PO7/8	Negative
Kimura et al., 2008	1-shot	Colored circles	100/400	160-180	Fronto- Central	Positive
Schankin & Wascher, 2008	1-shot	Array of colored dots	400/100	N2pc (245-295)	PO7/8	Negative
Khittl et al., 2009	1-shot	Faces	900/500	0-100	Global	Negative
Busch, 2013	1-shot	Objects	700/250	200-700	Global	Negative

TABLE 2 Brain imaging studies reporting specific activation associated with unnoticed changes.

Studies	Method	Paradigm	Stimuli	Stimulus/ Interval (ms)	Location
Beck et al., 2001	fMRI	1-shot	Alphabetical letters	500/500	fusiform gyrus (R), lingual gyrus (R), rIFG,
Pessoa et al., 2004	fMRI	1-shot	Simple bars	500/6000	parahippocampal gyrus, IPS, posterior occipital cortex, SEF, rIFG, right cerebellum

Abbreviations: fMRI = functional magnetic resonance imaging, rIFG = right inferior frontal gyrus, IPS = intraparietal sulcus, R = right hemisphere, SEF = supplementary eye field.

TABLE 3 Brain stimulation studies reporting modulation of development of explicit change detection.

Studies	Method	Paradigm	Stimuli	Stimulus/ Interval (ms)	Location	Type of TMS	Effect
Turatto et al., 2004	TMS	1-shot	Faces + Letters	200/300	DLPFC	rTMS	Increase in CB
Beck et al., 2006	TMS	1-shot (1/3)	Faces	200/100	PPC (R)	rTMS	Increase in CB
Tseng et al., 2009	TMS	1-shot	Faces	200/100	PPC (R)	rTMS	Increase in CB
Cavanaugh et al., 2004	SCS	1-shot	Moving dots	750-1500/ 150	SC	-	Decrease in CB

Abbreviations: DLPFC = dorsolateral prefrontal cortex, PPC = posterior parietal cortex, TMS = transcranial magnetic stimulation, SC = superior colliculus, SCS = superior colliculus stimulation.

The brain imaging studies have revealed the participation of sensory stimulus-related areas (fusiform, lingual and parahippocampal gyri) and the fronto-parietal attentional network (SEF, rIFG) in implicit processing of changes, with wider and amplified processing (DLPFC, PPC) in conscious detection of changes (Beck et al., 2001; Pessoa & Ungerleider, 2004). The functioning of the same areas in change detection has been the target in the brain stimulation studies (Table 3). The electrophysiological data have revealed very early processing (Eimer & Mazza, 2005; Khittl et al., 2009), change processing as changes (Fernandez-Duque et al., 2003; cf., Gregg & Snyder, 2012; Kimura et al., 2008), and change localization (Schankin & Wascher, 2007, 2008) at the implicit level. The results are fairly compatible but have not been systematically linked with each other.

Despite these findings, the theories of change blindness remain at the cognitive level, and the brain data have not been taken into account in theory formation at this level. Currently, no neural theories specifically of change blindness exist. Only a few neural theories of consciousness have taken a stand on the change blindness phenomenon (Campana & Tallon-Baudry, 2013; Lamme, 2003), but even these have not incorporated the results of the neural studies of change blindness. As is evident from these tables, brain studies of implicit change detection have not yielded systematic patterns of brain responses for implicit changes. Another reason may be that electrophysiological studies have failed to link the results to established components associated with known functions, with some prominent exceptions related to change localization (Schankin & Wascher, 2007, 2008).

1.5 The purpose of the research

The general purpose of the present research was to provide further evidence that implicit change detection exists during change blindness and, most importantly, provide new understanding of what this implicit change detection may consist. At the time of conducting the first experiments, the most important questions concerned the existence and nature of implicit visual change detection. Does implicit processing exist in the first place? A further question was, At what stages of visual processing does implicit change detection operate (Studies I and II)? What kinds of memory systems harbor the implicit representations of changed objects and their properties (Study II)? Does it operate at the level of single features (Study I) or can combinations of features be detected implicitly (Studies III and IV)? This was studied together with the question whether the social or emotional meaning of the changed items are implicitly registered during change blindness.

Another question concerned the function of visual implicit change detection. What is the relation between implicit and explicit change detection? At the behavioural level, the most important question was whether explicit change detections operate independently of implicit change detection, or whether implicit change detection somehow precedes and guides explicit change detection (Studies II-IV). Lastly and more specifically, it was investigated whether the biological relevance of the changes contributes to behavioural recovery from change blindness (Studies III and IV).

The results of the studies also serve to impose constraints on different views of change blindness, thus helping in evaluating them. These views, in turn, help us in refining our views on the interplay between attention, non-conscious and conscious visual perception and on the development of explicit visual change detection.

2 METHODS

As the purpose of this research was to study implicit change detection, indirect electrophysiological measures were used to measure the effects of changes with the subjects unaware of those changes. The primary method was to measure event-related potentials of the electroencephalogram (EEG) elicited by changes in the change blindness condition.

EEG is a measure of residual voltage differences over the scalp, reflecting subcranial cortical processes, supposedly of the summated postsynaptic potentials of vertically oriented cortical pyramidal cells, making up local field potentials consisting of electrophysiological activity of hundreds of thousands or millions of neurons (Luck, 2005). Event-related potentials are relatively systematic fluctuations in the bipolar amplitude of the EEG, time-locked to an event such as the onset of a visual stimulus, resulting in a characteristic, positive or negative EEG waveform, when averaged over multiple event occurrences. The temporal resolution of event-related potentials is extremely high, and is therefore well suited to investigation of fast-occurring neural phenomena such as implicit visual processing. Also, there is a long tradition of ERP studies with different types of stimuli content, such as facial stimuli, and established components related to this type of perception (e.g., the N170 component for perception of facial structure (Bentin, Allison, Puce, Perez, & McCarthy, 1996)). Previous electrophysiological studies of implicit change detection applying this method have mostly done pioneering work, as introduced above. However, a couple of studies have managed to measure modulations of previously known electrophysiological responses in the change blindness condition (Schankin & Wascher, 2007, 2008), characteristic of an ideal ERP study (Picton et al., 2000). For the last three of the present ERP studies, a general strategy was adopted of searching for information processing related to established ERP components, so that the potential modulations could be interpreted in the light of the information processing functions associated with these components.

2.1 Participants

Participants were healthy adult humans (12-22 persons per experiment) with no self-reported sensory or other neurological problems, and with normal or corrected-to-normal vision. The experiments were run in laboratory settings. During the recordings, they were seated comfortably in an electrically shielded and acoustically attenuated chamber equipped with a video screen, on which the visual stimuli were displayed.

All experiments were approved by the local ethical committee and conducted according to the the Code of Ethics of the World Medical Association (Declaration of Helsinki). A written informed consent was obtained from all participants, and the subjects were rewarded with movie tickets for their participation.

2.2 Stimuli and procedure

The images were presented on 17" CRT display according to the flicker paradigm.

The stimuli were flicker images in which an original and a modified version of it separated by a brief blank screen were presented. The images were designed so that the size of the change was made as large as possible to maximize the possibility of observing implicit ERP effects. For this reason and also to make the studies correspond to most behavioral studies of change blindness, images of natural scenes were used. In the first two studies using these stimuli, effects of changes in general were looked for, and so did not control for the type or location of the change, and the original and modified images were counterbalanced across participants. In the latter two studies using facial stimuli, specific effects related to change types were looked for, and hence the type and location of the changes were controlled for.

As described above, in a couple of electrophysiological studies of change blindness, fast registrations of changes, as early as 30-130 ms after stimulus onset, as indicated by ERPs, were observed during the change blindness period. However, given the methodological procedure of those experiments, the effects of different task preparation in distinct experimental conditions could not be excluded as potential confounding factors. The experiment in Study I was devised to confirm the early registration of changes during change blindness while avoiding this confounding factor. For this purpose, a novel version of the flicker paradigm was developed to avoid the effect of task preparation: the changes were presented in a single continuous sequence, and also in a pseudo-random order to avoid the possibility of predicting the occurrences of the changes when recording ERPs. The stimuli were pictures of complex natural scenes differing from each other in one substantial respect: an object appearing,

disappearing, changing identity, position or colour, thus corresponding well to behavioral studies of change blindness.

In the first two studies, the continuous oddball paradigm was used (see Figure 1). The latter two used a semi-continuous oddball paradigm. The oddball paradigm is used for two main reasons. Compared to the conventional alternating paradigm, the oddball paradigm carries a few advantages. First, it increases the novelty and deviance value of the change, and it is required to elicit novelty or deviance-related electrophysiological responses, such as vMMN (e.g., Winkler & Czigler, 2012). Second, it can be ensured that the participants are not aware of the moments of occurrence of the changes. As a continuous mode of presentation, it also prevents systematic selection of trials with different preparation in the change blindness and no-change conditions.

2.3 Behavioral measures

At the behavioral level, change detection performance was measured. The dependent measure was the number of change presentation cycles required for explicit report of change detection. Explicit detection was typically reported by a button press. The task was a change detection task in an intentional search paradigm in each experiment, but the level of change detection required for change report varied from study to study. In the first study, recognition of the change was required, in the second experiment the presence of the change, not necessarily with recognition. In the third and fourth experiments, the task was localizing the change (right vs. left). If the response criterion was a strict one (identification of the change), one presentation cycle preceding the report was excluded from the analyses to prevent initial explicit change detection from contaminating the data from the preceding change blindness period. In studies of change blindness, a sensing or initial localization of the change is suggested to precede one occurrence of change before explicit change identification (Busch, Durschmid, & Herrmann, 2010; Chun & Nakayama, 2000; Niedeggen et al., 2001; Schankin & Wascher, 2007, 2008).

In Study III, eye-movements were monitored with an SMRI® gaze tracking device. However, the results on eye-movements are not reported here.

2.4 Electrophysiological measures

An electroencephalogram (EEG) was recorded from 4–29 electrodes according to the international 10-20 system. An average or linked mastoid reference was used, and the EEG signals amplified, filtered and digitized at a rate of 500–1000 Hz, depending on the experiment. The relevant methodological details of the electrophysiological measurements in each experiment are summarized in Table 4.

It was decided not to restrict eye-movements in these studies. Constraining eye-movements has been suggested to result at worst in data on active inhibition of eye-movements rather than responses to visual stimulation (Smith, Jackson, & Rorden, 2005), and it has also been shown to affect change detection performance in the flicker paradigm (Hollingworth, Schrock, & Henderson, 2001). In this way, the studies were designed to better correspond to the existing behavioural studies of implicit change detection and avoid any compromising effects of covert visual spatial attention or inhibition of eye-movements on responses to changes. However, eye-movements can be a potential confounding factor for ERPs. To counter this, strict muscular artifact rejection was applied, and independent component analysis (ICA) (Jung et al., 2000) or Gratton & Coles algorithm (Gratton, Coles, & Donchin, 1983) was used to identify and correct for artifacts caused by excessive muscular activation relating to blinks and eye-movements.

2.5 ERP extraction and data analysis

ERPs were averaged and corrected against a -50-(-)150 ms pre-stimulus baseline. For each participant, mean or peak ERP amplitudes were measured from time windows based on the grand average ERPs obtained for each change condition, stimulus type and electrode location. The resulting values for each subject were analyzed with a repeated measures analysis of variance (ANOVA). Paired t-tests were used to further explore significant ANOVA effects. Point-by-point paired t-tests were used to further study the temporal properties of the ERP responses when appropriate.

Individual data on change detection performance averaged for each change and change-type condition were subjected to a repeated measures analysis of variance (ANOVA), with further pairwise comparisons, as done for the ERP amplitudes. Change detection required either sensing, localization or identification of the change (see section 1.1 for the differences between these).

The relevant methodological details that varied from study to study are collected in Table 4.

TABLE 4 Relevant methodological details of Studies I-IV.

Study	I	II	III	IV
Experimental manipulation	Change/No change	Change/No change Length of interval	Change/No Change Change type (face/nonface)	Change/No change Change type (angry/happy /neutral facial expression)
Paradigm	Continuous oddball	Continuous oddball	Semi-continuous oddball	Semi-continuous oddball
Task	Identification of change	Sensing change	Locating change	Locating change
Stimuli	Natural scenes	Natural scenes	Schematic or scrambled faces	Schematic faces with emotional expressions
Inter-stimulus interval	100 ms	100 ms/ 500 ms	250 ms	400/800 ms
ERP time windows (ms)	60-100	vMMN (250-300)	P1 (90-120) N170 (150-170) vMMN (250-300)	P1 (90-120) N170 (150-170) EPN (250-350)

3 OVERVIEW OF THE ORIGINAL STUDIES

3.1 Study I: Early registration of unnoticed changes

In study I, it was investigated how fast the brain can register implicitly presented changes. A very rapid change-related response of 30–100 ms post-stimulus has been reported in two earlier studies (Eimer & Mazza, 2005; Khittl et al., 2009). However, in the first of these, the authors were not able to affirm that the responses were genuinely change-related, and in the second one the authors did not address the result in the limited discussion of their short format report. Eimer & Mazza compared responses to unnoticed changes with responses to in the no-change condition in the one-shot flicker paradigm, and proposed that the result may be due to different preparation conditions between the stimulus sequences, with more instances of weak preparation in the change blindness condition than no-change condition, and that the early ERP effect more likely reflects pre- than poststimulus differences. It was sought to eliminate the differences between sequences by combining the oddball paradigm with the traditional continuous flicker paradigm (see above), so as to render the occurrences of changes impossible to predict during the change blindness period. Since responses to consequently presented images in the same sequence were compared, the level of preparation in responses to images in both the no-change and change blindness conditions should have been the same. It was hypothesized that changes could elicit similar differential global positivities at early latencies as in Eimer & Mazza (2005) despite the elimination of systematic preparation effects.

12 healthy adult humans participated in the study. The participants performed a change detection task in the continuous change blindness paradigm with 10 series of stimulus sequences with complex stimuli. Stimuli were images of complex natural scenes differing from each other in one respect: an object appearing, disappearing, or changing identity, position or colour. Ten blocks of stimuli were presented, each block containing 50 trials where standard and deviant stimuli of 500 ms duration were separated by a blank interval

(inter-stimulus interval, ISI) of 100 ms. Change detection performance and ERPs were measured for each stimulus interval condition.

It was found that the brain responded to changes very rapidly, well before the first 100 ms after stimulus onset at all midline electrode sites (Fz, Cz, Pz, Oz). The study confirmed that such early registration of changes is possible even when the potential confounding factor of preparation effect is eliminated, as in all the aforementioned studies, the ERP differences were observed as a global positivity from frontal to occipital sites. The short latency of the change registration process strongly suggests that registration occurs in the first stages of visual processing. It was also found that differential processing was more marked at the fronto-parietal electrode sites than the occipital ones, and suggested that this may reflect different kind of processing at the frontal and occipital sites. The registration of changes may thus not be confined to the occipital visual stream, but other systems may participate in these processes already at these early latencies. However, with only a few electrodes, it was not possible to determine the neural sources of these responses.

3.2 Study II: Fleeting, superfluous sensory memory traces of implicitly presented changes

The small number of electrodes used in Study I left open the question of whether visual responses associated with rare changes would become observable with a larger electrode montage and with an electrode reference that can better render visible ERP responses occurring posteriorly than the mastoid reference used in the first study. In Study II, it was thus studied further the event-related potentials (ERPs) to visual oddball stimuli using the change blindness paradigm. The effects of different ISIs (100 ms and 500 ms) were explored. Stimuli were similar pictures of complex natural scenes as in Study I. Change detection rates and ERPs, especially sensory memory-related visual mismatch negativity (vMMN), responding to preattentively presented infrequent changes requiring no behavioural response, were measured. The hypothesis was that the change blindness levels would be high with both interval durations (Rensink et al., 1997). Furthermore, it was hypothesized that a marker of implicit change detection (visual mismatch negativity, vMMN) would be observed in the oddball paradigm, and that lengthening the ISIs might reduced the vMMN owing to fading of the visual sensory memory trace of the previous scene, as has been observed in previous studies of vMMN (Astikainen, Lillstrang, & Ruusuvirta, 2008).

16 healthy adult humans performed a change detection task similar to Study I, with the exception that two durations of blank interval were used: a short (100 ms) and a long one (500 ms). The task was to sense the changes, not recognize as in Study I (see section 1.1). The electroencephalogram (EEG) was

recorded with a larger montage (29 channels) than in Study I (only 4 channels) to observe vMMN.

It was observed that in the short-interval condition, a marker of implicit change detection, the short-term sensory memory-dependent vMMN of the event-related potentials was modulated by implicitly presented changes. With the longer blank interval, the response was absent or at least attenuated. However, both interval durations induced considerable change blindness, although detection was slightly more efficient with the short interval, as observed in previous studies (Phillips & Singer, 1974a; Rensink et al., 1997). The presence and absence of the vMMN response seemed thus to be relatively independent of the occurrence of change blindness, and does not seem to contribute to the development of explicit detection of the changes in a substantial manner.

3.3 Study III: Implicit detection of changes in complex facial configuration

Study III ventured in a relatively unexplored direction in the quest for implicit change detection in change blindness studies. The purpose of the study was to find evidence of implicit change detection in the organization of complex stimuli in the change blindness paradigm (Rensink, 2013). Social stimuli are often complex, and their significance is often carried by the complex structure of simple features. Faces are perhaps the clearest example of this. Faces require at the very least a representation of eyes and a mouth to be recognized as a face, and specific cortical and subcortical neural systems have been suggested to exist for processing this kind of configural information in the visual environment (Haxby, Hoffman, & Gobbini, 2000; Johnson, 2005). The use of facial configurations as stimuli has affected neural measures outside awareness (Jiang & He, 2006; Jiang et al., 2009). Also, changes in faces have been shown to be more efficiently detected than nonfacial stimuli (Kikuchi et al., 2009; Ro et al., 2001). In these studies, the more efficient detection of the socially relevant stimuli was explained by an attentional bias to this kind of stimuli, called henceforth 'the social bias of attention hypothesis'. The rationale for the Study III was that implicitly presented changes in the structure of facial stimuli could elicit differential processing in the electrophysiological measures related to facial structure also in the change blindness condition.

22 healthy adult humans performed a change detection task in a semi-continuous oddball flicker paradigm. Change detection performance and ERPs to stimuli representing schematic faces with emotional expressions – neutral, happiness and anger – were measured in a flicker paradigm. Stimuli were schematic facial stimuli and scrambled versions of these, made of the same set of elementary components (see Figure 2).

FIGURE 2 Stimulus and change types in Study III.



All the change alternatives possible occurred: schematic to scrambled, scrambled to schematic, schematic to schematic and scrambled to scrambled (Figure 2). The hypothesis was that the features of complex social stimuli can be bound together preattentively outside of awareness, as observed in studies using continuous flash suppression (Jiang & He, 2006; Jiang et al., 2009). The measures for the binding together of facial features were change detection performance and, especially, the N170 ERP response, associated with perception of the structural configuration of facial features in a face (Bentin et al., 1996). The main finding of this study was that already during change blindness, the N170 component at the T6 electrode site on the right hemisphere was modulated by the changes. Scrambled features changing to schematic faces led to pronounced N170 responses, and the deformation of a schematic face led to decreased N170 responses. The bidirectional modulation of the N170 component indicates that changes in the complex organization of facial features are detected and bound to coherent wholes even outside of awareness.

At the behavioural level, changes affecting the complex configuration of a face, whether formation or deformation of a face, were detected much more efficiently than those that did not. This suggests that changes in the presence of a facial configuration are relevant for human change detection in general. Moreover, and compatible with the social bias of the attention hypothesis, changes in facial expressions were detected more readily than those in scrambled features. However, such a discrepancy was not present for the formation and deformation of faces in the stimuli. The social bias of the attention hypothesis would predict that changes in originally intact faces would be detected more efficiently. As the formation of a face was detected as efficiently as the deformation of a face, this suggests that the appearance of a new face may be more relevant for the change detection system than the disappearance of a face.

3.4 Study IV: Enhanced detection and brain responses for threatening changes

Study IV was a follow-up to Study III, focusing on whether, in addition to the social relevance carried by facial stimuli, their emotional content is also registered implicitly by the brain. An influential theory states that there are at least two distinct systems for detecting emotionally significant, especially threat-related stimuli: one for biologically important stimuli, such as snakes and spiders, and another for social ones such as angry faces (Öhman, 1986, 2009).

The latter is a part of the social dominance-submissiveness system of us as primates, in which perception of threatening states of conspecifics is the key. In support of this theory, the “anger superiority effect” has been invoked; according to this effect, people detect angry faces among neutral or happy ones faster than happy ones among neutral or angry ones, as shown in the visual search paradigm (Hansen & Hansen, 1988).

The purpose was to show that the anger superiority effect should emerge in the change blindness paradigm as well as in the visual search paradigm. The authors who first reported on the anger superiority effect, Hansen & Hansen (1988), also theorized that some kind of implicit detection of threat-related stimuli captures the attention and speeds up visual search for them. Based on the implicit face perception shown previously by us (Study III) and others (Jiang et al., 2009) and the dominance-submissiveness theory, the hypothesis was that electrophysiological responses related to perception of threatening stimuli, such as the early posterior negativity (EPN, see (Schupp et al., 2004; Schupp, Flaisch, Stockburger, & Junghofer, 2006)) of event-related potentials, modulated by the emotional relevance of the stimuli, could also be modulated already during change blindness. Such a result would indicate that such complex information as that related to emotional expression on facial stimuli could be implicitly extracted.

16 healthy adult humans performed a change detection task in a semi-continuous oddball flicker paradigm. Change detection performance and ERPs to stimuli representing schematic faces with emotional expressions of happiness or anger, were measured in a flicker paradigm. Two initial frequently presented views, a happy crowd and a threatening crowd were used. Changes consisted of one face in a crowd changing expression. A threatening change was one face changed to angry in an otherwise happy crowd, and a non-threatening change was one face in an angry crowd changed into a happy one, as depicted in Figure 3.

FIGURE 3 Stimuli and change types in Study IV.



It was found that the emotional valence of stimuli, especially negative stimuli, does affect change blindness: a change towards threatening emotional content speeded up the recovery from change blindness. The second hypothesis was that responses to different emotional stimuli differ electrophysiologically from one another also before awareness of the differences. This was shown by the modulation of the EPN of the ERPs as a function of the emotional expression present in the changing schematic face.

Since it is possible that the background may affect visual search so that an angry crowd may compromise the efficiency of the search (Frischen, Eastwood, & Smilek, 2008), the better detection rates for threatening changes may actually be due to the greater distracting effect of the threatening than non-threatening context on search of the non-threatening changes. Therefore, an additional experiment with 12 healthy participants was run. The experiment was closely similar to the first one with the major difference that the context was made similar for both change conditions by using a crowd of four faces with neutral expressions. Changes were expression changes from neutral to happy or angry. The results replicated the behavioral results of the first experiment: threatening changes were detected more efficiently than the non-threatening changes. Furthermore, emotional changes elicited differential EPN amplitudes. However, the EPN did not vary as a function of the emotional content of the change, indicating that also the context plays an important role in determining the emotional relevance of the change.

Together with the results of Study III, these results showed for the first time the possibility of detecting changes involving conjunctions of features that can carry biologically determined social and emotional relevance. Moreover, the emotional content seemed to have a significant effect on the change detection rate: changes to threatening expressions among positive ones were detected more efficiently than vice versa, in accordance with the results of the corresponding studies using the visual search paradigm. These results suggest that such complex information as emotional content can be extracted from the changing stimuli and retained across the interruptions. Also, biologically relevant emotional information such as threat may have a slight advantage in a change detection task.

4 DISCUSSION

During this research project, novel evidence was obtained for the existence of implicit change detection in the change blindness condition. Moreover, the nature of implicit change detection was further elucidated. Traces of implicit change detection were found at different levels of visual processing, and content-specific ERP differences were observed, indicating that the brain is able to respond not only to the occurrence of changes, but also to the specific content of implicitly presented change. Interestingly, this was associated with slightly enhanced change detection, especially where the changed contents had biological relevance. However, the strength of the neural traces of the undetected changes did not necessarily determine the detection of change at the behavioural level. These results yield a fairly complex picture of the nature of implicit change detection and especially of its role in the emergence of explicit change detection in the change blindness condition.

More specifically, it was found that implicit processing of changes can be extremely rapid, suggesting registration of the changed features take place during the first stages of visual processing. The results of Study II also showed that changed visual content elicits differential processing compared to unchanged content at the later stages (of visual processing). Change-related electrophysiological responses (vMMN) associated with the workings of sensory memory (Maekawa, Tobimatsu, Ogata, Onitsuka, & Kanba, 2009) were observed, showing decay in time together with a roughly equal change blindness effect.

Information on the social and emotional significance carried by the changed configurations is nonconsciously extracted, which was observed as enhanced performance at the behavioural level and as traces of differential electrophysiological activation at the cortical neural level. This means that implicit representations do not exclusively reside in the realm of primitive features but that some biologically relevant configurations are at least coarsely represented without awareness.

Moreover, the enhanced behavioural detection could not be explained as the biased allocation of attention, as it was associated solely with the

biological relevance of the content of the change. Similarly, the change processing in the facial configuration could not be due to low-level features, since the non-facial stimuli were made up of a physically identical set of features to the facial stimuli.

Together, the results of this series of experiments help deepen our understanding of the nature of implicit change detection. Although the scope of these experiments is limited, the results nevertheless extend the existing evidence of implicit change detection, which challenges some theoretical views of change blindness (the no representation theory) and can be used to update others. Together with previous evidence, the results can be used to formulate a preliminary model of the extent and functions of implicit change processing. I will approach formulating such a model by discussing the results from the point of view of the structure of implicit representations, the memory systems involved in their processing, and their effect on guiding attention and conscious processing.

4.1 The types of implicit representations of change

Evidence of implicit change detection have been provided in change blindness studies from many stages of processing. In particular, they suggest the involvement of both spatial attention-related (Fernandez-Duque & Thornton, 2003; Hayhoe et al., 1998; Schankin & Wascher, 2007, 2008), and sensory memory-related systems (Study II; Hollingworth et al., 2001; Hollingworth & Henderson, 2002; Varakin & Levin, 2006).

The contribution of the present research lies in deepening, and perhaps complicating, this view. Contrary to previous studies using one-shot paradigms, the present studies also showed that implicit change detection occurred for a considerable time before change detection, since the change blindness period in these studies was longer than in the one-shot paradigm. These results thus reflect implicit change detection that well precedes explicit change detection.

The results of Study I corroborated the hypothesis that changes in an image affect the earliest stages of visual processing. Interestingly, such changes elicit global differential processing, which is strongest at the fronto-central electrode sites. This effect may reflect operation not only of the visual sensory areas but also of other areas, a finding not easily interpreted in light of the canonical visual ERP literature. Not many studies have reported activation in areas other than the occipital ones in response to visual stimulation in general, especially at these early latencies. However, the few appropriately targeted studies have revealed widespread activation elicited by visual stimuli at frontoparietal sites at latencies earlier than 30 ms, preceding that of sensory areas in the cueing paradigm (Foxye & Simpson, 2002; Saron, Schroeder, Foxye, & Vaughan, 2001). The authors interpreted this as activation of the faster dorsal stream related to operations of spatial attention shifts compared to the slower

sensory ventral pathway. Activated areas include dorsal areas MT/V5, and the lateral prefrontal cortex together with the parietal and frontal eye fields. These areas have been shown to be activated as soon as the visual signal enters the cortical level of the processing stream (Bullier, 2001). These areas related to attention rather than visual perception were activated by unnoticed changes in fMRI studies of change blindness (see Table 1), and the results of Study I are in line with these findings, although it was not possible to determine the exact neural sources. It may be that, in other studies, the use of abstract simple stimuli or restriction of eye movements have occluded these effects (see Table 1). Further studies are needed to establish at which level the changes are first detected and which visual processing systems participate in the short latency registration of changes.

The further results of the present studies, those concerning vMMN modulation and face perception, support cortical sensory memory-related representations of implicitly detected changes, processing situated at considerably later stages of sensory processing compared to the results of Study I. This suggests the existence of more developed representations of changes. The question in some previous change blindness studies has been how detailed information exists in the visual system during the change blindness period. The vMMN is related to passive perception of the violation of regularities or expectations in the visual environment, and has been suggested to depend on the comparison processes of the high-capacity sensory memory traces of the change and no change scenes (Kimura et al., 2011). Such representations correspond to the perception of changes as changes over and above their physical features. However, this comparison process can occur passively, without having any effect on explicit awareness of those changes. Inducing change blindness requires an interruption of stimulation or a simultaneous transient distracting stimulus of at least 67–80 ms (Phillips & Singer, 1974a; Rensink et al., 1997). However, the span of iconic sensory memory is considerably longer, 150–500 ms (Sperling, 1960), which suggests that temporal integration across these gaps should be quite possible. In other words, automatic change detection does not seem to depend on the existence of iconic representations of the original and modified scenes and the process of comparing them. This is also compatible with other findings that detailed information about changes is preserved (Becker et al., 2000), also without much effect on change detection rates (Horowitz & Wolfe, 1998; Mitroff, Simons, & Levin, 2004; Varakin & Levin, 2006).

Despite the behavioural evidence of detailed and organized representations of prechange scenes, no previous studies have provided direct neural evidence for the existence of complex representations of changed objects during change blindness. The results of this research extend previous results by providing evidence of implicit representations of changing complex stimuli, at least for facial stimuli. It is known that the neural sources of the N170 response and representations of facial configurations are most probably supported by temporal areas of the fusiform face area and superior temporal sulcus (Sadeh,

Podlipsky, Zhdanov, & Yovel, 2010). These cortical areas are most probably part of the visual sensory memory system rather than of the spatial attention-related areas of the fronto-parietal attention network.

In studies II-IV the implicit representations were largely confined to the right hemisphere. This is compatible with the repeated observations that the right hemisphere is specialized in more holistic processing in face processing (Maurer, Grand, & Mondloch, 2002), processing related to implicit shifts of spatial attention (Gitelman et al., 1999) and also implicit processing of emotional stimuli (see, Gainotti, 2012 for a review), especially threatening ones (Sato & Aoki, 2006). The hemispheric differences in implicit change detection and the development of explicit change detection pose an important challenge for future neural change blindness studies.

In summary, implicit representations of changes are widespread at multiple levels in the visual processing stream. Contrary to the most radical views of implicit visual processing, many studies of change blindness suggest that implicit representations can be quite detailed and even have a complex structure. However, in comparison to conscious change detection, they are probably coarser and more short-lived. More studies are clearly needed to identify the levels, functions and mechanisms of implicit change detection.

4.2 The influence of the implicit change detection on the explicit one

The findings presented here are interesting with respect to the question of how implicit visual changes can become explicit. In light of the data of this research and other studies (Study II; Hollingworth et al., 2001; Hollingworth & Henderson, 2002; Varakin & Levin, 2006), the strength of the visual sensory memory trace seems not to have a compelling role in the development of explicit change detection. On the other hand, the enhancement of change detection in the case of facial configurations and their emotional expressions supports the view that the biological relevance of the change facilitates its reaching consciousness (Study III, Ro et al., 2001).

One way to reconcile the discrepancy between the independence of implicit change detection from, and its influence on, explicit change detection is to assign these properties to separate functional visual systems. The view emphasizing that visual sensory processes (ventral pathway) are relatively independent of spatial attention and action-related processes (dorsal pathway) could readily explain these findings (e.g., Goodale & Milner, 1992). Accordingly, change blindness can be explained mainly as a failure of the ventral pathway to notice and recognize the change: the volatile and superfluous visual sensory memory operates mainly with the resources of the ventral stream. The sensory memory may simply work as a platform or an active blackboard for the attentional system (Sperling, 1960), which would be

compatible with the view that the contents are available for further processing (Block, 2011). If the contents of the sensory memory do not accumulate and cannot be used as a guide in visual search (Hollingworth, 2001; Horowitz & Wolfe, 1998), then what guides implicit content to reach consciousness in explicit change detection is left open. More specifically, what kind of transsaccadic memory is sensitive to bottom-up effects in guiding visual search?

The attentional system, however, could benefit from shifts of implicit spatial attention for detecting changes. The implicit dorsal system may support memory accumulation for visual search, and may be able to register or even locate the change. The effect of spatial cues in alleviating or even abolishing change blindness can be readily explained by the operation of the dorsal system. A cue would necessitate implicit spatial attention to the location of the change, rendering serial top-down search unnecessary. Like attentional spatial cues, previous changes may guide attention to the locus of change (Busch, Dürschmid, & Herrmann, 2010; Busch, Fründ, & Herrmann, 2010; Niedeggen et al., 2001; Schankin & Wascher, 2007, 2008; Smith & Schenk, 2008). The behavioral findings of implicit change detection, directing the gaze to the location of the change, allowing guessing of its location or orientation, and hesitation in reporting the location of the change, thus affecting reaction times, are compatible with this possibility. The results of the fMRI studies of implicit change detection, reporting activity in the areas of the dorsal system in implicit change detection, (e.g., rIFG, SEF, see Table 1) are also in line with this view.

Social, and also emotional, content seems to have an alleviating effect on change blindness, although the physical differences are the same with socially or emotionally neutral stimuli. The present studies on face perception also suggest that the iconic memory content may include complex representations: for example, the modulation of the N170 component in Study III probably reflects cortical processing in the ventral stream. The more efficient detection of changes in facial configurations, however, may also be driven by subcortical mechanisms, as it is known that subcortical structures, such as the superior colliculus and pulvinar nuclei of the dorsal system, respond to facial stimuli, although at a fast and coarse level (de Gelder, Morris, & Dolan, 2005; Johnson, 2005; Morris, Öhman, & Dolan, 1999). In Study IV, the EPN modulation may in part reflect amygdalar effects on cortical processing (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004), and the link between ERP responses and behavioral results may be more direct than in the study with facial configurations. Nevertheless, implicit processing alone cannot guarantee explicit change detection. It can perhaps summon focal attention to the change location, and focal attention must remain long enough at the location of the change for explicit detection to occur. Our results are in line with this view. However, the greatest limitation of both our studies of implicit detection of changes in facial stimuli was that the relationship between the behavioural and neural levels cannot be addressed on the basis of their results. Though the ERP results provide potentially relevant information for explaining the behavioural

results, the enhanced detection rate cannot be linked causally as dependent on the observed implicit change detection.

Although the separate contributions of the dorsal and ventral visual pathways seem relevant for change detection, this is not directly supported by any of the existing studies. Studies on this issue are thus needed. For example, the contributions of dorsal and ventral streams could be teased apart using low and high spatial frequency or isoluminant and low-contrast images as stimuli, as these are known to separately activate the magno- and parvocellular visual systems related to the dorsal and ventral pathways, respectively. Also, studies with cross- or intermodal cues could provide evidence of the contribution of the ventral stream, since the dorsal system shares the spatial attention system with other modalities (Karns & Knight, 2009). Probably, the picture is more complicated, and it is known that ventral areas can guide visual search as well (Mazer & Gallant, 2003).

As described above, focal attention to the change location does not guarantee conscious detection of the change (Caplovitz et al., 2008; O'Regan et al., 2000). The contents have to be additionally encoded for visual working memory, and only these contents eventually reach consciousness (Kiefer et al., 2011). These authors also suggest that encoding and consolidation processes can work independently of attention, suggesting a double dissociation for attention and conscious visual awareness. Others have contested this, maintaining that attention is a necessary but not a sufficient condition for visual conscious awareness (Cohen, Cavanagh, Chun, & Nakayama, 2012; Smith & Schenk, 2008). Attention must, therefore, be appropriately deployed. Some have suggested that spatial, in particular, as opposed to object-based attention is needed (Koivisto, Kainulainen, & Revonsuo, 2009), in line with the current views on the development of explicit change detection in the change blindness literature (Busch, Dürschmid, & Herrmann, 2010; Busch, Fründ, & Herrmann, 2010; Niedeggen et al., 2001; Schankin & Wascher, 2007, 2008).

It could be argued that change blindness studies cannot address the question of how implicit contents ordinarily become explicit, since change blindness occurs only under specific circumstances, like with the occurrence of eye-movements or blinks. However, although there are clearly two mechanisms operating to enable explicit awareness of visual changes in ordinary and conscious change detection, it is also possible to hold that at some level these two eventually collapse into one. In every case, spatial focal attention may be needed for the changes to become explicitly detected, and the difference between the two modes of change detection would rather be in their ability to recruit focal attention. In change blindness, motion transients cannot compel and speed up spatial attention, as in the parallelly working change detection system. The remaining, attentional serial phase of the process may be the same, and the difference only in the speed of processing caused by the missing motion transient. This is supported by the finding that, in automatic change detection without intervening transients, change localization is at its ceiling whereas

identification takes considerably longer, and is restricted to one or two items in the scene (Hughes et al., 2012).

To summarize, our results and the results of other studies are limited in explaining how directly and to what extent implicit detection at the level of brain responses is related to those observed at the behavioural level. Only brain stimulation studies have shown a causal connection of some brain area to change detection (Beck et al., 2006; Tseng et al., 2010; Turatto et al., 2004). Similar studies are needed to establish a causal connection, for example, for the neural areas related to N170 or the EPN responses and the more efficient change detection performance correlating with them. Also, issues such as the role of conceptual knowledge (Hollingworth, 2012; Smith, Lamont, & Henderson, 2012) and search strategies should be elucidated for a proper understanding of the factors in the development of explicit change detection.

All in all, the present change blindness studies suggest an underdog, bottom-up role for implicit change detection in the competition against top-down influences on the contents of consciousness – but not entirely without importance. In the normal case, bottom-up and top-down influences work in concert with each other, but in the case of change and inattention blindnesses visual perception and change detection is driven by the top-down influences, and the discrepant bottom-up contents have to be able to override them to become conscious.

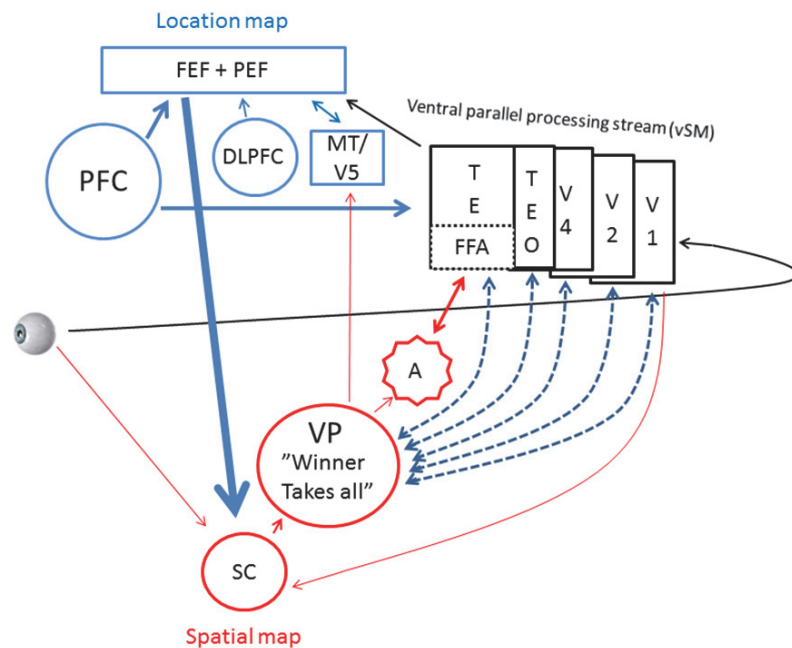
4.3 Interplay of implicit processing, attention, and explicit processing: towards a neuro-cognitive model of change blindness

The complicated view emerging from the literature and the results presented here challenges the existing theories of change blindness. As cognitive theories, leaning on functional concepts of information processing in visual perception, such as focal attention, change detection and short-term memory, these theories of change blindness cannot readily accommodate the results of the neural studies and their relation to the behavioural evidence for implicit change detection. In contrast to cognitive theories described in functional terms, theories of cognitive neuroscience are multi-level, with each level guiding and constraining empirical investigation and theory formation at the other levels (Bechtel, 2008; Craver, 2007; Revonsuo, 2006). Theory construction in change blindness studies has mostly failed to follow this pattern. Our studies, along with other neural studies of change blindness, call for a new model to explain their results, so that future studies are able to incorporate both the cognitive and neural aspects of change detection. For these reasons, a neurocognitive theory for change blindness is needed.

Clearly the existing neurophysiological data on implicit visual change detection and on the development of explicit change detection are too few and

scattered to enable the construction of a unified neurocognitive model by themselves. However, neurocognitive models of the basic processes related to visual change detection, such as attention, have been formulated on the basis of its cognitive models and neurophysiological findings. Since attention plays an essential role in change blindness, a neurocognitive model of attention capable of handling change detection could be useful in making sense of change blindness. A recent influential model has been proposed (Shipp, 2004), which concentrates on the integration of top-down and bottom-up processes in visual search and spatial attention, and contains resources for explaining these aspects, including in change blindness. Moreover, key areas of the brain stimulation studies of change blindness figure importantly in the model. Here, I present a suggestion for a modified version of this model that incorporates the relevant recent findings of change blindness studies, and also of emotion perception as addressed in Study IV (Morris et al., 1999; Troiani & Schultz, 2013). The proposed model is illustrated in Figure 4.

FIGURE 4 A neuro-cognitive model of attentional mechanisms relevant for change detection and change blindness.



Abbreviations: A = amygdala, DLPFC = dorsolateral prefrontal cortex, FEF + PEF = frontal and parietal eye fields, FFA = fusiform face area, MT = medial temporal cortex, PFC = prefrontal cortex, SC = superior colliculus, TE = temporal cortical areas, TEO = temporo-occipital cortical areas, VP = ventral pulvinar, vSM = visual sensory memory.

Black arrows and items represent the ventral visual stream participating in the conscious visual representation consisting of the high capacity iconic sensory memory. Colored arrows represent attentional modulations of the dorsal pathway in the ventral visual sensory memory system: red arrows indicate subcortical bottom-up and blue arrows fronto-parietal top-down influences. The weight of the line depicts the relative significance of the influence.

The model is essentially a premotor model of attention, linking visual attention closely to oculomotor functions and areas, which have a modulatory effect on visual areas, enhancing processing of one item at a time. Visual sensory memory is identified with the ventral pathway regions, whose contents compete parallelly for the spotlight of attention. More specifically, spatial attention is concerted by oculomotor areas SC, FEF-PEF, the latter in a top-down manner. The suggested site of competition for the spotlight of visual attention in this model is the ventral pulvinar (VP). It is heavily connected to all ventral pathway regions, and acts as a general salience map that integrates bottom-up and top-down influences in a “winner takes all” manner. Thus it selects one content of visual sensory memory at a time for further processing. The seriality of top-down search is implemented by this property of the spatial attention system. Usually, the winner is clear, but serial spatial attention as in visual search is started when none exists – as in the case of change blindness.

Bottom-up motion and change detection on this model occur via the superior colliculus, which has high receptivity to contrast in motion or large-scale changes in luminance related to sudden onsets. Under normal circumstances the motion detection system (SC-pulvinar-MT/V5) guides exogenous attention to the change location. If the motion transient is swamped by a sufficiently long mask duration, this system cannot guide attention to changes (Rensink et al., 1997; Tse, 2004). In this model, this system is the culprit responsible for change blindness. The same subcortical, colliculo-pulvinar pathway can respond to complex facial stimuli (Morris et al., 1999). They may enhance cortical processing, possibly via amygdala, and the results of the Studies III and IV may be due to the functioning of this system (see also Figure 4). Future studies are needed to confirm this hypothesis. Nevertheless, the electrophysiological activation related to unnoticed changes observed in the electrophysiological studies reflects cortical processing. In Study I, it may reflect processes of spatial attention related to the dorsal visual stream, while in Studies II-IV, the processing is most likely originating more from the ventral visual stream related to sensory memory.

Top-down influences are exerted by the fronto-parietal visual spatial attention network. The network comprises areas of the prefrontal cortex, especially its dorsolateral part (the DLPFC, of which the IFG is a part), which has been suggested to participate in integrating task-related top-down and stimulus-driven bottom-up signals in visual search (e.g., Asplund, Todd, Snyder, & Marois, 2010). Moreover, it includes the parietal eye-fields, which serve as a spatial representation for eye-movements and shifts of attention, and the frontal eye fields, which have more executive and memory-related functions. This system dictates the direction of top-down visual search, and

explicit change detection must also pass through this system. Recovery from change blindness is dependent on attention, and the frontal areas participate in maintaining the contents of attention across the interruptions. The question remains, how can the bottom-up influences blend in the activation of this system to achieve the desired effect? The answer is not quite clear, but the basic view is that attention has an amplificatory function: the site which has the strongest activation (most weight in the saliency map) gets selected. Contrary to icebergs, an implicit visual content needs most weight to rise above the surface.

In this model, too, the visual sensory memory serves as an active blackboard for attentional processes, housed by the ventral visual processing stream in this model. This is compatible with the observation that the sensory memory-dependent vMMN showed fading of representations of the change but that this had only a small effect on change detection. This also pertains to the theories of change blindness in that a lot of information could be represented about changed scenes and possible comparison of the pre- and postchange representations, but this need not necessarily affect change detection (Becker et al., 2000; Horowitz & Wolfe, 1998; Mitroff et al., 2004; Varakin & Levin, 2006). The effect of implicit representations on explicit change detection should be dealt with as an additional issue. Future studies of stored representations of changes across interruptions should take this possibility into account.

In light of the neurocognitive model, the view that recovery from change blindness requires attention and consolidation processes becomes intelligible at the neural level. Consolidation requires a sufficient number of attentional iterations by the VP as guided by the fronto parietal network and the SC, so that the changing content can be encoded into working memory. Before that, change processing remains implicit by nature. This notion of conscious change detection shares many features with existing models of consciousness (Baars, 1988; Baars, 1997). However, it is perhaps best compatible with the the “reverse hierarchy” models of conscious processing (Campana & Tallon-Baudry, 2013; Hochstein & Ahissar, 2002). Explicit change detection begins first with a coarse experience, “sensing”, of something changing in some region of the visual field. Sufficient attention to this location adds details to the first-pass coarse experience. Translated into the traditional concepts of awareness, phenomenal and access awareness (Block, 2005; Block, 2011), change blindness is clearly a failure of access awareness of changes. In my view, it is even possible that even if change-blind observers are phenomenally aware of the changed elements at some level without being able to access them, they nevertheless count as implicit on the definition used here (see section 1.1.1), which differs from the perhaps more common use of the term implicit to refer to a completely unaware type of processing. As long as explicit report of change is the criterion for the end of change blindness, it is difficult to determine whether the changes can be subjectively experienced or not at some unreportable level. In any event, the implicit change contents seem to constitute the potential contents of consciousness in the sensory memory store. The operations of the spatial attention network, however, may be largely outside of the sphere of

phenomenal experience (Tamietto et al., 2010), or perhaps help in building the three-dimensional structure of visual perception (Koivisto et al., 2009).

The practical significance of the neuro-cognitive model lies primarily in how well it can guide future neural studies of change blindness. Many key brain areas of the model, such as DLPFC, SC, and parietal cortical areas, have already been targets of studies of their functional role in change detection (see Table 3). Similarly as with existing brain stimulation studies of change blindness, other key areas of the model could serve as targets of investigation. For example, TMS stimulation of FEF or MT/V5 during change blindness could confirm their role in the development of explicit change detection. The model should also be in line with the results of ERP studies. Future ERP studies of implicit and explicit change detection with better source localization information than the previous ERP studies are needed to relate the electrophysiological data to the neurocognitive model.

While the existing theories cannot accommodate the findings of the neural studies, this model can. Furthermore, the explanatory power of the dual visual pathway view is conserved in this model, although the model emphasizes the interaction of both pathways in the development of explicit change detection. This model could thus be classified as a neurocognitive access failure view of change blindness.

4.4 Conclusions and future directions

Despite its preliminary nature, in my view the greatest value of a neurocognitive model lies in its potential for guiding future neural studies of change blindness and change detection. It offers a possibility to formulate specific hypotheses in testing its validity in different aspects of change blindness and its neural underpinnings. Future studies will hopefully offer expanded and rectified neurocognitive models of change blindness.

Perhaps where the model requires the most elaboration is in accommodating the biological relevance of the changes. The mechanisms related to the perception of faces and their perception have been relatively well studied at both the explicit and implicit levels. However, their role in generating shifts of attention to these stimuli, required for conscious detection, is not well known. Our results provide the first direct evidence for bottom-up effects in responses to facial and emotional stimuli within a top-down guided search paradigm. The effect of emotional content is a surprisingly neglected topic in change blindness studies. Further research is needed to study its effect on change detection performance and related neural processes, such as at which stage of processing the effect takes place, and hemispheric differences in the implicit processing of emotional changes. Improved knowledge of these issues could be potentially helpful also for a practical understanding of how to use emotional contents to render changes more easily - or less easily - detectable.

Of the workings of the visual system in general, change blindness is especially informative about the difficulty of implicit contents breaking through to consciousness. In my view, the most interesting question in blindness studies is whether the data we have can be applied in a significant way to study this issue. For example, can improved knowledge of the phenomenon of change blindness help in improving our ability to notice changes in our environment? Can bottom-up influences be spurred to reach the level of consciousness, thus counteracting the effect of inattentional or change blindness?

In the attentional capture and change blindness literature, there are suggestions that attentional set (Folk et al., 1992) and individual properties (Lechak & Leber, 2011) could help the implicit contents become conscious. Visual search is best with a relaxed, open mind set (Smilek, Enns, Eastwood, & Merikle, 2006). Also, a wider scope of attention and cultural tendencies to a more holistic processing can alleviate change blindness in the periphery of the visual field (Masuda & Nisbett, 2006; Zelinsky, 2001). Interestingly, so too does intelligence (Zhu et al., 2010), proofreading experience (Asano, Kanaya, & Yokosawa, 2008), attention to detail as in Asperger syndrome (Fletcher-Watson et al., 2012; Smith & Milne, 2009) and an appropriately formulated set of instructions emphasizing task centrality (Pearson & Schaefer, 2005). These studies suggest that the bottom-up effects could be enhanced by a certain attentional mindset or acquired individual abilities, and change detection performance improved accordingly. What is common to most of these findings is that top-down influences are minimized in relaxed, wide-scope holistic processing, thus maximizing the bottom-up effects on change detection. Targeted studies comparing different search strategies, with for example narrow and wide scope of attention, and the accompanying neural processes, would help us understand these aspects of change detection and their real-life applicability.

To conclude, the present research provide important novel pieces of evidence about the extent of implicit visual change detection. The empirical findings and the consequent theory developments can serve in the evaluation of the different theoretical views of change blindness, as well as a starting point for future neural theories of change blindness and visual change detection. The evidence yields a rather detailed account of the development and fragility of visual consciousness at the neural and cognitive levels. Potentially, this account can even serve as a theoretical base for the development of detectability, and ability of detection, of real-life visual changes.

YHTEENVETO (SUMMARY)

Visuaalisten muutosten esitietoinen havaitseminen

Tavanomaisissa olosuhteissa ihminen kykenee vaivatta havaitsemaan merkittävät muutokset ympäristössään. Kiitos havaintojärjestelmässämme kehittyneiden valmiuksien emme voi olla huomaamatta esimerkiksi yhtäkkiä kulman takaa ilmestyvää autoa. Tarkkaavuus kääntyy automaattisesti äkilliseen tapahtumaan, ja se nousee pian tietoisuuden keskiöön. Kognitiivisessa psykologiassa tätä kutsutaan tarkkaavuuden automaattiseksi suuntautumiseksi ja muutoksen automaattiseksi havaitsemiseksi. Luottamus näihin valmiuksiin on niin suuri, että ihmisillä on – tutkitustikin – arkikäsitys, että he kykenevät huomaamaan kaikki tällaiset tapahtumat ympäristössään.

Viime vuosikymmenten aikana kognitiivisten tieteiden tutkijat ovat havainneet, että tavanomainen muutoksen havaitseminen ei kuitenkaan ole niin erehtymätön kuin arkikäsitys antaa olettaa. Muutosten havaitseminen vaikeutuu merkittävästi, jos tarkkaavuuden taakkaa lisätään tarpeeksi suuntaamalla se esimerkiksi hyvin vaativaan tehtävään. Samoin huomaaminen vaikeutuu, jos se ajoittuu samanaikaiseksi silmänliikkeen, -räpäyksen tai voimakkaan valonväläyksen kanssa. Jälkimmäistä muutoksen havaitsemisen vaikeutta kutsutaan muutossokeudeksi (engl. *change blindness*). Muutossokeudessa suuret ja muuten ilmeiset muutokset jäävät havaitsematta pitkiksi ajoiksi. Jopa rakennuksen siirtyminen tai keskustelukumppanin vaihtuminen saattaa jäädä huomaamatta. Muutossokeus on ilmiönä niin voimakas, että havaitsijoiden on vaikea uskoa, millaisia muutoksia heiltä on voinut jäädä huomaamatta.

Muutossokeudessa muutoksesta voi tulla tietoiseksi vain suuntaamalla tarkkaavuus tahdonalaisesti muutokseen. On kuitenkin epäselvää, tuleeko huomaamisesta näin sattumanvaraista, vai voivatko esitietoisesti esitetyt muutokset vaikuttaa niiden havaitsemiseen. Jos muutokset havaitaan esitietoisesti, ne saataisivat edesauttaa niiden nousemista lopulta tietoisuuteen. Esitietoinen havainto saattaa vaikuttaa tarkkaavaisuuden suuntautumiseen antamalla muutoksille lisäpainoa näköaistinvaraisessa etsinnässä nopeuttaen siten tietoista havaintoa.

Tietoisuusteoreetikot ovat käyttäneet muutossokeusilmiötä apuna kehittellessään näkemyksiään tietoisuuden luonteesta. Radikaaleimman teorian mukaan emme kykene havaitsemaan muutoksia, koska yksinkertaisesti emme voi muodostaa niistä mielensisäisiä edustuksia ilman niihin suunnattua tarkkaavuutta. Yksinkertaisuuden periaatteen mukaisesti mieli representoi vain sen, mitä sen tarvitsee yksilön toiminnan kannalta. Tunne rikkaasta havaintosisällöstä on harhaa, ja todellisuudessa havainto olisi hyvin niukka tarkkaavuuden keskiötä lukuun ottamatta. Teorian mukaan muutosten huomaaminen olisi sattumanvaraista ja riippuisi tahdonalaisesta tarkkaavuuden suuntaamisesta muutoksiin.

Vaihtoehtoisten teorioiden mukaan muutossokeudessa ei ole kysymys edustusten muodostamisongelmasta vaan muistin, vertailukyvyyn tai tarkkaavuuden siirtymisen ongelmasta. Näiden ehdotusten mukaan esitietoisien muutosedustusten muodostuminen on mahdollista. Jotkin näistä teorioista sallivat

muutoksille suhteellisen mahdollisuuden vaikuttaa tietoisien muutoksen havaitsemisen kehittymiseen.

Kognitiivisten tieteiden kannalta muutossoikeus on teoreettisesti kiinnostava siinä suhteessa, että se paljastaa automaattisen muutosten havaitsemisjärjestelmän haavoittuvuuden. Sen lisäksi muutossoikeus on hyödyllinen menetelmällisesti: se tarjoaa mahdollisuuden tutkia esitietoista muutosten havaitsemista, kun muutoksia voidaan esittää pitkään ennen niiden nousemista tietoisuuteen. Samalla muutossoikeuden avulla voidaan tutkia, kuinka tietoinen ja tietoisuuden ulkopuolinen havaintojärjestelmä voivat vaikuttaa toisiinsa. Lähes kaikilla muilla implisiittisen havainnon tutkimusmenetelmillä ärsykkeet jäävät tietoisien havainnon ulkopuolelle.

Empiirisissä tutkimuksissa on havaittu viitteitä esitietoisesta muutosten havaitsemisesta. Emme niiden perusteella kuitenkaan tiedä, millaista esitietoinen muutosten havaitseminen on, kuinka laajaa se on ja mikä sen toiminnallinen rooli on. Monissa tutkimuksissa on esitetty todisteita esitietoisien muutosten havaitsemisen olemassaolon puolesta. Niissä on kuitenkin harvoin kyetty osoittamaan esitietoiselle havainnolle mahdollista toiminnallista roolia, poikkeuksena tutkimukset, joissa on havaittu muutosten tulevan paikannetuiksi esitietoisesti. Tämän tutkimuksen tavoitteena oli täydentää käsitystämme esitietoisien muutosten havaitsemisen laajuudesta ja niiden toiminnallisesta roolista.

Tässä tutkimuksessa pyrittiin selvittämään, millaisia edustuksia ihmismielessä voi muodostua esitietoisesti esitetyistä muutoksista, ja miten ne voivat vaikuttaa tietoiseen muutoksen havaitsemiseen. Tutkimuksissa mitattiin muutoksen havaitsemisen tasoa eri muutostilanteissa sekä muutossoikeuden aikaisia muutokseen liittyviä aivojen herätevasteita.

Esitietoisesta muutosten hyvin nopeasta rekisteröimisestä on saatu viitteitä aiemmissä tutkimuksissa mittaamalla aivojen herätevasteita muutossoikeuden aikana. Muutokseen liittyvien vasteiden kohdalla ei kuitenkaan pystytty sulkemaan pois mahdollisia eroja valmistautumisen tasossa väliin tulevana tekijänä muutossoikeus- ja muutoksen havaitsemistilanteiden välillä. Tutkimuksen tekijät varoittivat, että muutossoikeustilanteessa saattoi olla järjestelmällisesti enemmän huonomman valmistautumisen tilanteita kuin muutosten havaitsemistilanteissa, mikä saattoi heijastua muutokseen liittyvinä eroina aivojen herätevasteissa. Ensimmäisessä osatutkimuksessa tutkittiin, voidaanko valmistautumiserot estää sijoittamalla samaan ärsykejatkumoon. Ärsykkeet esitettiin lisäksi satunnaisin väliajoin, jolloin niiden ennakoiminen ei voinut heijastua eroina aivojen herätevasteissa. Aivojen herätevasteissa oli havaittavissa samantyyppisiä muutokseen liittyviä eroja kuin aiemmissä tutkimuksissa, eikä tämä tulos voinut johtua valmistautumiserosta eri esityssarjojen välillä. Tutkimus tuki sitä hypoteesia, että esitietoisesti esitetyt muutokset todella voivat tulla rekisteröidyiksi aivoissa näköhavainnon aikaisimmissa vaiheissa.

Toisessa osatutkimuksessa tutkittiin edelleen esitietoisien havainnon toiminnallista roolia muutossoikeudessa. Esitietoisien muutoksen rekisteröimisen mitattiin poikkeavuusnegatiivisuutta, sensoriseen muistin toimintaan perustuvaa, esitietoista muutosten havaitsemista heijastavaa aivojen herätevastekomponent-

tia. Se ilmenee aivojen sähköisessä aktivaatiossa, kun muutoksia esitetään harvoin ja satunnaisesti tarkkaavuuden ulkopuolella. Tulosten mukaan ärsykkeiden välistä aikaa pidennettäessä sensorinen muistijälki heikkenee niin, että poikkeavuusnegatiivisuus häviää, mutta tällä ei ollut juuri vaikutusta muutoksen havaitsemisen tehokkuuteen. Tutkimuksen perusteella esitetoinen muutosten havaitseminen – ainakaan sensoriseen muistiin perustuva – ei välttämättä tehosta tietoista muutosten havaitsemista. Tietoinen muutoksen havaitseminen ei tämän tuloksen perusteella riipu esitietoisesta muutosten havaitsemisesta.

Edellisen tutkimuksen perusteella esitetoinen muutoksen havaitseminen ei aina edesauta muutosten tulemistä tietoisiksi. Se ei kuitenkaan sulje pois mahdollisuutta, että esitetoinen muutosten havaitseminen ei joissain olosuhteissa voisi vaikuttaa niiden tulemiseen tietoisiksi. Aiempien tutkimusten perusteella tietoisien visuaalisen etsinnän tilanteessa kohteiden sosiaalinen tai biologinen relevanssi lisää niiden löytymisen todennäköisyyttä. Kolmannessa ja neljännessä osatutkimuksessa tutkittiin, voiko muutosten sosiaalinen tai biologinen relevanssi vetää tarkkaavaisuuden niihin samalla tavoin muutoksen havaitsemisen kuin visuaalisen etsinnän tilanteessa. Sosiaalisen ja emotionaalisen relevanssin havaitseminen vaatisi, että muutosten sisäisten edustusten olisi oltava kompleksisia, ei vain yksittäisistä piirteistä koostuvia. Tutkimukset kohdistuivat erityisesti kompleksisten esitietoisien muutosedustusten muodostumiseen esittämällä kasvoärsykejä ja merkityksettömiä yhdistelmiä samoista piirteistä esitietoisesti muutossokeustilanteessa ja mittaamalla aivojen herätevasteita, erityisesti N170- ja suhteellisen aikaista, pään takaosassa viriävää, emotionaalista relevanssia heijastavaa negatiivista EPN (*early posterior negativity*) -vastetta. Edellinen, N170-vaste, on sensitiivinen kasvoärsykeille ja jälkimmäinen, EPN-vaste, kasvonilmeiden emotionaaliselle relevanssille. Tulosten mukaan sosiaalisesti tai emotionaalisesti relevantti muutosten sisältö nopeuttaa sellaisten muutosten havaitsemista. Muutokset esitettiin niin, että niitä ei voitu tarkkailla enempää kuin ei-sosiaalisia tai vähemmän relevantteja muutoksia. Tällöin muutosten sisältö on luultavasti tullut esitietoisesti havaituksi, jotta se saattoi vetää tarkkaavuuden tehokkaammin puoleensa kuin sosiaalisesti tai emotionaalisesti neutraalien muutosten tapauksessa. Myös sekä N170- että EPN-vasteissa nähtiin eroja sosiaalisesti ja emotionaalisesti relevanttien muutosten yhteydessä jo ennen kuin ne havaittiin tietoisesti. Tulos viittaa kompleksisten implisiittisten muutosedustusten muodostumiseen ainakin kasvoärsykeiden tapauksessa.

Tutkimus laajentaa käsitystämme muutosten esitietoisien havaitsemisen laajuudesta. Muutos voidaan havaita usealla näköhavainnon tasolla ennen kuin se saavuttaa tietoisuuden. Tutkimustulokset tarkentavat käsityksiämme esitietoisien havainnon toiminnasta suhteessa tietoiseen havaitsemiseen. Muutoksen havaitseminen näyttäisi riippuvan siihen kohdistetusta tarkkaavaisuudesta, mutta muutoksen relevanssi voi vaikuttaa sen havaitsemista tehostavasti. Jatkossa tutkimusta voisi suunnata siihen, kuinka esitietoiselle muutoksen havaitsemiselle voisi antaa parempi mahdollisuus vaikuttaa tietoiseen vastinpariinsa, eli kuinka muutosten havaitsemista voisi entisestään tehostaa.

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ORIGINAL PAPERS

I

EVENT-RELATED POTENTIALS REVEAL RAPID REGISTRATION OF FEATURES OF INFREQUENT CHANGES DURING CHANGE BLINDNESS

by

Pessi Lyyra, Jan Wikgren, & Piia Astikainen, 2010

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RESEARCH

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Event-related potentials reveal rapid registration of features of infrequent changes during change blindness

Pessi Lyra*, Jan Wikgren, Piia Astikainen

Abstract

Background: Change blindness refers to a failure to detect changes between consecutively presented images separated by, for example, a brief blank screen. As an explanation of change blindness, it has been suggested that our representations of the environment are sparse outside focal attention and even that changed features may not be represented at all. In order to find electrophysiological evidence of neural representations of changed features during change blindness, we recorded event-related potentials (ERPs) in adults in an oddball variant of the change blindness flicker paradigm.

Methods: ERPs were recorded when subjects performed a change detection task in which the modified images were infrequently interspersed ($p = .2$) among the frequently ($p = .8$) presented unmodified images. Responses to modified and unmodified images were compared in the time window of 60-100 ms after stimulus onset.

Results: ERPs to infrequent modified images were found to differ in amplitude from those to frequent unmodified images at the midline electrodes (Fz, Pz, Cz and Oz) at the latency of 60-100 ms even when subjects were unaware of changes (change blindness).

Conclusions: The results suggest that the brain registers changes very rapidly, and that changed features in images are neurally represented even without participants' ability to report them.

Background

Experimental psychologists have recently demonstrated a noteworthy failure to detect changes in visual environment, named "change blindness" [1,2]. The best known method of experimentally inducing change blindness is the flicker paradigm [3], in which a briefly presented blank screen separates presentations of original and modified images.

The phenomenon of change blindness has led some researchers to theorize that we can only have detailed visual representations of our environment inside the focus of attention and in change blindness the unnoticed changed features would not be represented at all [1,4]. Call these no-representation accounts of change blindness. In other words, explicit change detection would only be possible when top-down focal attention is

directed to the locus of change [3]. Consequently, this account predicts that the changes are not registered even implicitly, as this would only be possible by having some representation of the changed features. However, some experimental evidence from gaze-tracking [5] and forced-choice tasks [6-8] has pointed towards the possibility that some implicit bottom-up processes may guide visual perception even during change blindness.

Change blindness has also attracted the interest of neuroscientists [7,9-20]. Investigating brain responses could be even more informative than behavioral measures about the causes of change blindness. Indeed, any brain response elicited by changed features during change blindness would count as counter-evidence to the no-representation account [1,4]. Some researchers have reported observing differential brain activity for changes during change blindness compared to no-change condition [7,9,10,12-16]. For example, evidence from event-related potentials (ERPs) of implicit change detection was provided in a study by Fernandez-Duque

* Correspondence: pessi.lyra@jyu.fi
Department of Psychology, PO Box 35, FI-40014 University of Jyväskylä, Jyväskylä, Finland

et al. [7], in which a continuous flicker paradigm was used. The authors compared responses at the latency of 240-300 ms in two separate stimulus blocks: one with no changes and the other in which unnoticed changes were present. However, responses to modified and unmodified images were not compared to each other, but instead unmodified pictures in these two conditions. For this reason it is possible that the result reflected implicit processing of the presence of changes, but not directly implicit responses to changed features in stimuli. In another ERP-study, Eimer & Mazza ([10], see also [13]) investigated brain responses to noticed and unnoticed changes using the S1-S2, or "one-shot", flicker paradigm in which the changes occur in S2. They also compared responses to S2 that contained unnoticed changes (change blindness) with responses to S2 that did not contain changes, when participants so correctly reported. The authors observed differences in responses at the early latencies of 30-80 and 90-130 ms after stimulus onset, possibly evoked by unnoticed changed features in the stimuli. However, in their setup, they could not exclude the possibility that effects of task preparation were responsible for this finding. They suspected that subjects' preparation to the task was systematically worse in change blindness trials than in trials in which participants correctly reported the absence of change.

In order to avoid the above mentioned problem, we employed a novel combination of experimental paradigms aimed to reveal implicit detection of changes during change blindness. An *oddball* version of the continuous flicker paradigm was applied, so that changes were infrequent and pseudo-randomly presented, unlike in the standard version of the S1-S2 flicker paradigm in which the stimulus types are presented pair wise with equal probabilities. The advantage of the oddball paradigm is that it allows comparison of the responses to different stimulus types (modified and unmodified images) which are presented in the same stimulus sequence and in which the occurrences of the changes cannot be predicted.

The oddball paradigm has previously been used in the studies of visual mismatch negativity (vMMN) [21]). However, we did not expect to see any vMMN for three main reasons. First of all, no trace of it was observed in a previous study investigating it in the change blindness condition [11]. Second, vMMN is usually elicited in a condition in which changes are not searched for, and thus not attended, but instead the subjects are concentrating on a primary task. Third, the stimulus material (natural scenes) itself differed from those of typical vMMN studies where the stimuli are usually simpler, for example changes are presented in a color of an object [22] or in an orientation of a bar [23].

The no-representation account of change blindness [4] predicts that the modified and unmodified images elicit ERPs of equal magnitude during change blindness. As mentioned, differential ERPs to changed features before subjects' conscious perception of the changes will be counter-evidence for no-representation theories of change blindness. Therefore, we hypothesized that despite the elimination of possible differences in task preparation, unnoticed changes in visual stimuli would evoke differences in brain responses, as observed, e.g., in the study by Eimer and Mazza [10].

Materials and methods

Participants

Fourteen volunteers, eight female and five male with age distribution of 19-33 years (mean age 22.9 years) participated in the study. All of them had normal or corrected-to-normal vision. The data of one participant, who did not follow the task instructions, were discarded. A written informed consent was obtained from the participants before the experimental treatment. The study conforms to The Code of Ethics of the World Medical Association (Declaration of Helsinki).

Procedure

During recordings, the participants were seated in a chair in a dimly lit room. They viewed the stimuli on a 17" monitor at a distance of approximately one meter. We chose to use images of size $8^\circ \times 11^\circ$, representing complex natural scenes (a sample pair of images with indicated change is given in Figure 1), as stimuli to allow as large changes as possible, as it has been shown that the size of targets affects both the amplitude and the latency of the responses to them [24]. Changes consisted in the appearance or disappearance of objects, or in a change of their position or color. All the images were shown to induce change blindness in a pilot study before the actual experiment. Since the changes in images were as large as possible, we used a variety of change types and locations in order to maximize the amount of change blindness trials, as it has been found that occurrences of previous changes can serve as cues for detection of subsequent changes [25]. We aimed to avoid the possible threat that the location or type of change would have any cueing effect by constructing different types of changes in different locations and randomized them across the blocks.

Images were presented for 500 ms, separated by 100-ms non-stimulated interval (stimulus onset asynchrony thus 600 ms). Such a short non-stimulated interval was used to prevent memory decay potentially affecting implicit processing of changed features. In oddball condition, a changed (deviant, $p = .2$) picture was infrequently interspersed between frequently presented

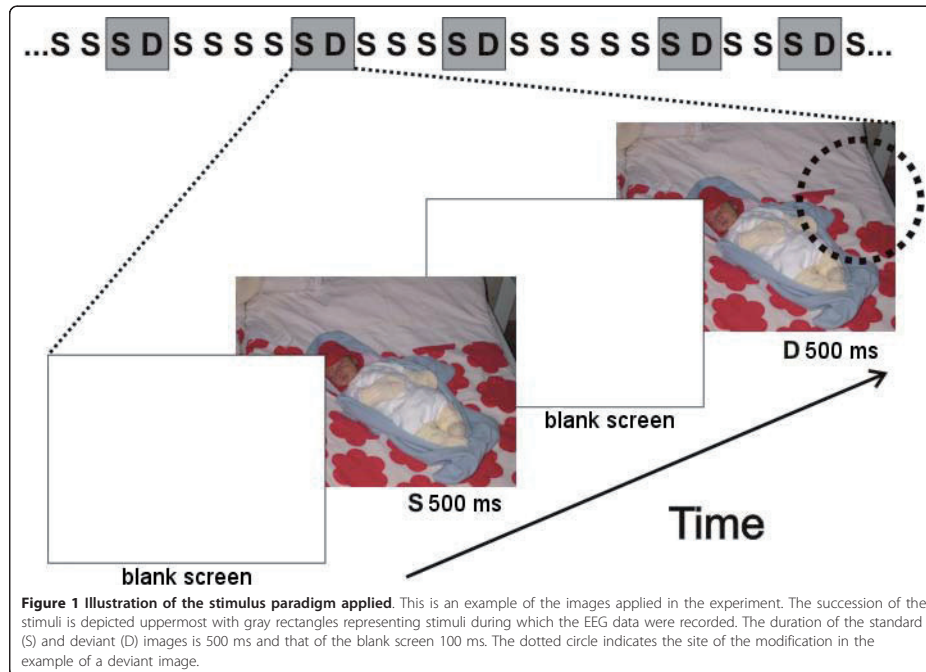


Figure 1 Illustration of the stimulus paradigm applied. This is an example of the images applied in the experiment. The succession of the stimuli is depicted uppermost with gray rectangles representing stimuli during which the EEG data were recorded. The duration of the standard (S) and deviant (D) images is 500 ms and that of the blank screen 100 ms. The dotted circle indicates the site of the modification in the example of a deviant image.

(standard, $p = .8$) pictures. Standards and deviants were presented pseudo-randomly with the restriction that there were up to seven but no less than three standards between consecutive deviants.

The subjects were familiarized with the task by administration of a rehearsal block similar to the ones used in the actual experiment, and data recorded from the rehearsal blocks were not used in the analyses. The actual experiment consisted of ten stimulus blocks, each block containing 250 stimuli (50 deviants). A break followed each stimulus block and the next block in the series was shown on the participant's request. To prevent effects of novelty for the first standard stimuli, a preparatory series of at least ten standard stimuli were presented before the appearance of the first deviant stimulus. The order of presentation of the ten blocks was randomized across the participants. An illustration of the stimulus condition is given in Figure 1.

The participants were instructed to search for an infrequent change in the pictures and to report identification of the change by pressing a button. They were instructed to press the button only when they identified the change for the first time, subsequent identifications

of changes did not require responses. After the initial identification, the participants were instructed to ignore the infrequently occurring identified change and search for more changes to make the attention mode of the change identification condition correspond to the change blindness condition (search changes versus focus on changes [7]).

EEG-recordings and data-analysis

Electroencephalography (EEG) was recorded on four channels using an elastic cap (Electrocap) with Ag/AgCl electrodes, from the international 10/20 system sites Fz, Cz, Pz and Oz. The linked left and right mastoids served as reference electrodes and one electrode located on the forehead as a ground electrode. The signals were amplified 5,000 times and band-pass-filtered with 0.1 to 30 Hz, and sampled continuously at 500 Hz.

The recorded EEG sweep consisted of a time interval from 100 ms before to 370 ms after stimulus onset for one deviant and the standard immediately preceding it. A 50-ms pre-stimulus period served as the baseline. Thus, in the analyses, there was an equal number of standards and deviants. The standard-deviant pair

immediately preceding pressing of the button was considered the moment when the subject consciously noticed the change. This stimulus pair was excluded from the analysis [7]. The preceding trials were considered the change blindness trials, and the trials starting from the button press were considered the change identification trials. Sweeps containing artifacts (maximum difference of values within the sweep exceeding 100 μ V in any electrode) were discarded, the average rejection rate being approximately 34%.

For the statistical analyses, a time window from 60 ms to 100 ms from stimulus onset was determined on the basis of the waveforms of grand-average ERPs (Figure 2) and the study of Eimer & Mazza [7]. Mean amplitude values for standard and deviant ERPs were extracted. The resulting mean values were analyzed by multivariate analyses of variance (MANOVA) for repeated measures with Electrode site (Fz, Cz, Pz and Oz), Stimulus type (standard, deviant) and Awareness (change blindness, change identification) as factors in each window. An alpha level of .05 was used in all the analyses.

In order to complement the deflection analysis with a temporal analysis we used global waveform analysis, an approach that preserves the temporal resolution of EEG (here, sampling frequency of 500 Hz) [18,26]. This approach does not qualify as a reliable identification procedure of ERP effects but it does qualify as a method of reliably revealing the temporal dynamics of the EEG by estimating the onsets and offsets of ERP effects, which are neglected by an inspection applying mean or peak values in an analysis window. We ran point-by-point paired t-tests between responses to standards and deviants in each electrode from the stimulus onset to the end of the measurement window (0-370 ms). To counteract the likelihood of exaggerated significant values associated with multiple t-tests an alpha level of .01 in at least 10 consecutive data points (20 ms) (e.g. [27]) was required to consider modulations in waveforms to be present.

Results

Behavioral data

In an image block, the average number of deviant pictures preceding explicit report of change detection (the number of presented changes during change blindness before subjects indicated change detection by a button press) was 14.27 (SEM = 1.29) out of 50. Since data concerning one pre-report presentation of a deviant picture was discounted from the analysis, the mean number of responses to deviants was 13.27 per image type, and thus 133 responses for the change blindness condition, and 357 responses for the change identification condition per subject in average.

Electrophysiological data

The grand average ERPs to standards and those to deviants are shown in Figure 2 for change blindness and change identification, together with the grand-average difference waves where responses to standards were subtracted from responses to deviants.

A 3-way MANOVA, Awareness (change blindness, change identification) * Stimulus type (standard, deviant) * Electrode site (Fz, Cz, Pz, Oz) at the time window of 60-100 ms from the stimulus onset revealed main effects of Electrode site, $F(3, 10) = 22.446, p < .001$, Stimulus type, $F(1, 12) = 8.887, p < .011$, and Awareness, $F(1, 12) = 22.446, p < .001$. The effect of Electrode site indicated that responses were more positive at the anterior than posterior electrode sites. Also the Stimulus type * Awareness was significant, $F(1, 12) = 6.638, p < .024$, suggesting that changes were processed differently during change blindness and change identification.

For change blindness trials (Figure 2), a further analysis with Stimulus type (standard, deviant) revealed a significant main effect of Stimulus type, $t(12) = 3.185, p = .008$, indicating that the presence of changes modulated brain responses despite the inability to report on the changes. The responses were more positive to deviants compared to standards at all the recording sites (mean differences in amplitudes 1.73 μ V, averaged across all electrode sites; see also Figure 2).

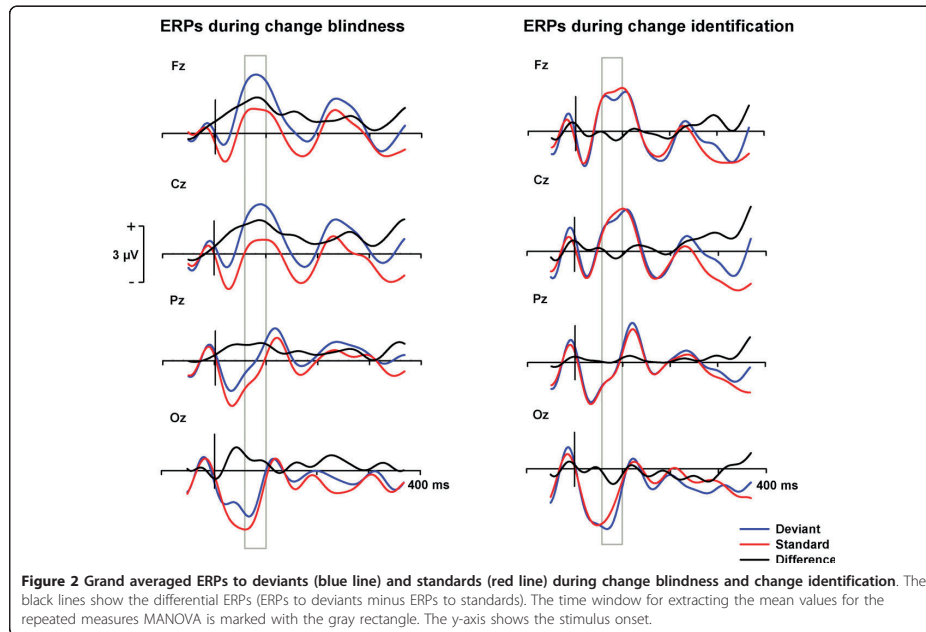
For the change identification trials (Figure 2), a paired t-test for the Stimulus type (standard, deviant), $t(12) = 1.399, p = .187$, did not reach significance.

On the basis of grand-average and difference ERPs (Figure 2), the observed effect during change blindness seems to linger over the anterior electrodes after the peak at the latency of 60-100 ms as compared to the most posterior electrode site of Oz. To examine temporal features of the differences between responses to standards and deviants in global waveforms, we ran two-tailed paired point-by-point t-tests for the data separately in each electrode. Such epochs in which responses differed for deviants and standards were found for three electrode sites, Fz (70-104 ms, all $p < .01$), Cz (76-104, all $p < .01$), and Pz (70-100 ms, all $p < .01$). At the Oz, the criterion of the alpha level under .01 was not quite reached, but the difference came close to significance at 66-86 ms (all $p < .02$).

No epoch reached significance in the point-by-point temporal analysis for the change identification trials.

Discussion

We studied electrophysiological correlates of change blindness in the oddball variant of the flicker paradigm during change blindness, i.e. stimulus presentation during which the subjects did not notice the change, and during which they could not anticipate when the



changes would occur. Intriguingly, and compatible with our hypothesis, we found that even during change blindness the occurrences of random changes modulated electrical brain responses at all electrode sites. There was a global positive difference at the latency of less than 100 ms in ERPs to infrequent images containing changes (deviants) compared to frequently presented images without changes (standards), indicating that the changed features are somehow represented in the brain even in the absence of the ability to anticipate or report on the occurrences of the changes. This difference in ERPs was confined to the change blindness situation.

Our results cannot be directly compared to the results of those experiments in which the S1-S2 and traditional continuous flicker of paradigms were applied. This is because search behavior in S1-S2 and traditional continuous flicker paradigms may differ from those in the oddball paradigm. In that sense, changes differ in saliency and infrequent changes may require different comparison mechanisms, e.g. searching for a violation in a rule rather than serial comparison of elements, or more sustained attention to specific locations in images. However, the search for implicit representations of changed features during change blindness is not affected, even if search behavior may differ from each

other in these different conditions. Any registration of changes still indicates that the changed features are represented at some level in the brain. Infrequent changes may also render such effects visible that would go unnoticed in successive presentation of original and modified pictures. Since visual search mechanisms differ in the manner described above, the oddball paradigm can reveal different aspects of brain processing, such as effects of neural dishabituation. Therefore, introducing the oddball paradigm may be an important methodological addition to the investigation of the change blindness phenomenon.

The early latency of the ERP effect (60-100 ms post-stimulus) suggests that the difference is unlikely to reflect any implicit processing of changes *per se* [28]. Instead, it may be due to preliminary processing of low-level features of images or effects of dishabituation in response to changed features after repetitive identical stimulation. Nevertheless, any such difference indicates that some neural representation exists for the features in which unnoticed changes occur.

The present results cannot be due to the effects of anticipation or task-preparation, which may be the case in a previous study with comparable results from the S1-S2 paradigm, namely, that by Eimer and Mazza ([10];

see also [13]). In their study, Eimer and Mazza also observed a wide-spread positive modulation in brain responses at the early latencies of 30-80 ms and 90-130 ms during change blindness in the S1-S2 paradigm with natural and complex stimuli (groups of faces) with large changes. The authors were unable to interpret this finding simply as a genuine stimulus-related modulation, but instead they proposed that it might be an instance of task-preparation related contingent negative variation, normally elicited by differences of expectations that would be present already before stimulus onset. They conceded that their change blindness trials might have included more trials from sequences with worse task preparation as compared to trials in which participants correctly reported the absence of change, as this could have resulted in the kind of differences in ERPs they observed. In the present study, however, such a bias in change blindness trials is not possible. Namely, because of the pseudo-random presentation of the stimulus types and the fact that data were analyzed only for the standards immediately preceding the deviants (because the occurrence of a standard after the deviant could be expected), both stimulus types were from the same sequence and preceded by numerous identical pictures. Thus, there could have been no systematic difference in subjects' state of preparation, as is possible in the S1-S2 paradigm.

The temporal analyses showed that the onsets and offsets of the differences between responses to (modified) deviant and those to (original) standard images were rather similar at the electrode sites of Fz, Cz, and Pz (significant differences in responses observed between 70 and 104 ms). Unlike these electrode sites, the difference did not quite reach statistical significance by the criterion that we used ($p < .01$) at the electrode site of Oz. Nonetheless, the offset of the effect seems, on the basis of the temporal analysis and the difference waves, more abrupt at Oz. This may indicate that the responses at this electrode site reflect different brain processes from the ones reflected in responses at the more anterior electrode sites.

In studies of conscious change detection using a S1-S2 or "one-shot" flicker paradigm, a difference in ERP amplitudes at latencies between of 60-150 ms from stimulus onset related to detected stimulus changes in comparison to stimuli containing no change has been observed [10,15,29-32]. However, the polarity of the difference in ERPs varies across studies. In most of the studies [15,29-32], images with detected changes elicited more positive ERPs than those without changes or with undetected changes. In the study of Eimer & Mazza [10], identified changes evoked a negative difference compared to the no-change situation. In the present study, the difference in ERPs to identified changes as

compared to no-change images did not reach significance in MANOVA or in the point-by-point temporal analysis, although there was some hint of differential activity at the Oz electrode in the grand average waveforms (Figure 2). The reason why the change related modulation did not reach significance in the present study may be in the differences of psychological states of the subjects. In other studies subjects focused on changes, while in the present study the participants were instructed to ignore the previously identified changes. The results, however, suggest that the modulation of ERPs by unnoticed changes observed in the change blindness trials reflects neural processes that are different from those related to explicit change identification.

One purpose of the study was to make the experimental conditions resemble those of behavioral studies, and therefore participants were allowed to search freely for the change. Moreover, since the main interest and analyses were on the latencies that precede even the most rapid eye-movements evoked by sensory stimulation [33], we decided not to constrain them. We endeavored to avoid any compromising effects of covert visual spatial attention or inhibition of eye-movements on responses to changes that might result from such restrictions. Constraining eye-movements has been suggested to result in obtaining data on active inhibition of eye-movements rather than responses to visual stimulation [34], and it has also been shown to affect change detection performance in the flicker paradigm [35].

Limitations

Our study is in line with the view that changed features are registered by the neural system during change blindness. However, with the present methods, it is not possible to determine whether the results are due to stimulus novelty, rareness or content of visual change. Also, as we used a conservative criterion of change detection - the changes had to be identified - it is possible that our results do not categorically reflect change blindness and change identification, but also partly some weaker form of change awareness, a phenomenal "sensing" of the changes as reported by Rensink [1]. Also, it is not possible to draw any conclusions of the neural sources of the ERP effects with few electrodes.

Conclusions

In sum, the present results show that the brain registers visual changes very rapidly, less than 100 ms after the change onset, even when the subjects are not aware of these changes. The results do not support the prevailing view that change detection depends merely on top-down focal attention [1,4]. The data concur with the results of behavioral and neurophysiological studies

[5-7,10,12-17] suggesting a role for bottom-up processes in change detection.

Abbreviations

EEG: Electroencephalogram; ERP: Event-related potentials; vMMN: Visual mismatch negativity; MANOVA: Multivariate analyses of variance.

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Authors' contributions

PL participated in the conception and design of the study, manufactured the stimuli, carried out electrophysiological measurements, ran the statistical analyses, and drafted the manuscript. JW participated in the conception and design of the study, carried out electrophysiological measurements, preprocessed the electrophysiological data, and helped to interpret the results and to draft the manuscript. PA participated in the conception and design of the study, helped to run the statistical analyses, to interpret the results and to draft the manuscript.

Competing interests

The authors declare that they have no competing interests.

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II

EXPLICIT BEHAVIORAL DETECTION OF VISUAL CHANGES DEVELOPS WITHOUT THEIR IMPLICIT NEUROPHYSIOLOGICAL DETECTABILITY

by

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Explicit behavioral detection of visual changes develops without their implicit neurophysiological detectability

Pessi Lyyra^{1*}, Jan Wikgren¹, Timo Ruusuvirta² and Piia Astikainen¹

¹ Department of Psychology, University of Jyväskylä, Jyväskylä, Finland

² Turku Institute for Advanced Studies, Department of Psychology, University of Turku, Turku, Finland

Edited by:

Hans-Jochen Heinze, University of Magdeburg, Germany

Reviewed by:

Juliana Yordanova, Institute of Neurobiology, Bulgaria
Ronald Rensink, University of British Columbia, Canada

*Correspondence:

Pessi Lyyra, Department of Psychology, University of Jyväskylä, PO Box 35, FI-40014, Jyväskylä, Finland.
e-mail: pessi.lyyra@jyu.fi

Change blindness is a failure of reporting major changes across consecutive images if separated, e.g., by a brief blank interval. Successful change detection across interrupts requires focal attention to the changes. However, findings of implicit detection of visual changes during change blindness have raised the question of whether the implicit mode is necessary for development of the explicit mode. To this end, we recorded the visual mismatch negativity (vMMN) of the event-related potentials (ERPs) of the brain, an index of implicit pre-attentive visual change detection, in adult humans performing an oddball-variant of change blindness flicker task. Images of 500 ms in duration were presented repeatedly in continuous sequences, alternating with a blank interval (either 100 ms or 500 ms in duration throughout a stimulus sequence). Occasionally ($P = 0.2$), a change (referring to color changes, omissions, or additions of objects or their parts in the image) was present. The participants attempted to explicitly (via voluntary button press) detect the occasional change. With both interval durations, it took 10–15 change presentations in average for the participants to eventually detect the changes explicitly in a sequence, the 500 ms interval only requiring a slightly longer exposure to the series than the 100 ms one. Nevertheless, prior to this point of explicit detectability, the implicit detection of the changes vMMN could only be observed with the 100 ms intervals. These findings of explicit change detection developing with and without implicit change detection may suggest that the two modes of change detection recruit independent neural mechanisms.

Keywords: change blindness, flicker paradigm, oddball paradigm, event-related potentials, visual mismatch negativity

INTRODUCTION

The human visual system is equipped with an automatic mechanism for detecting sudden changes in the environment. Abrupt stimulus appearance or motion captures attention in a bottom-up way, even if these are not targets of visual search (Yantis and Jonides, 1984). However, this mechanism is prone to error if the load of attention is increased (inattention blindness, see Mack and Rock, 1998) or if the change occurs simultaneously with some interruptive events. Massive changes may go easily unnoticed by this way, a phenomenon usually known as “change blindness” (for reviews, see Simons and Levin, 1997; Rensink, 2002). Change blindness can be observed as a failure to detect a considerable and otherwise easily detectable change when a flash of light, blink, saccade, or a large transient stimulus immediately precedes the change. The flicker paradigm, where a brief blank screen (or inter-stimulus interval, ISI) separates the two images across which a change is introduced, is a method that has firmly established the phenomenon of change blindness. It is also the most frequently used paradigm to induce the effect experimentally (Rensink et al., 1997).

Change blindness, as observed through failures in tasks to voluntarily (explicitly) report on the occurrences of the changes, is held to entirely reflect errors in top-down guided

focal attention (Rensink et al., 1997; O’Regan and Noë, 2001). However, there is also accumulating behavioral (Hayhoe et al., 1998; Fernandez-Duque and Thornton, 2000; Hollingworth et al., 2001; Fernandez-Duque et al., 2003; Koivisto and Revonsuo, 2003; Laloyaux et al., 2006) and brain imaging (Beck et al., 2001; Huettel et al., 2001; Niedeggen et al., 2001; Fernandez-Duque et al., 2003; Pessoa and Ungerleider, 2004; Eimer and Mazza, 2005; Schankin and Wascher, 2007, 2008; Kimura et al., 2008; Khittl et al., 2009; Lyyra et al., 2010) evidence of implicit change detection by the visual system during change blindness. It has been suggested that changes are initially detected implicitly to guide focal attention to the locus of the changes and, thereby, to eventually allow the explicit detection and identification of changes supported by focal attention (cf. Chun and Nakayama, 2000; Niedeggen et al., 2001). Similarly, there is both behavioral (Watanabe, 2003) and electrophysiological evidence that changes are implicitly localized before their identification already during change blindness (Schankin and Wascher, 2007, 2008) or “sensing” the presence of change without identification (Busch et al., 2010a,b) suggesting that change localization and identification follow each other sequentially in the same visual processing stream. This view regards implicit change detection as a pre-requisite for explicit change detection. However, the

dissociation between neural mechanisms for the (explicit) identification and (implicit) localization of a visual object (Goodale and Milner, 1992) also leaves open a possibility that explicit and implicit modes of visual change detection may recruit distinct and mutually independent neural mechanisms. This possibility is also indicated by distinct ERP-markers found for explicit and implicit change detection (Fernandez-Duque et al., 2003; Kimura et al., 2008). Furthermore, while explicit change detection is associated with attentional visual short-term memory with a limited capacity (e.g., Rensink, 2000), it is possible that the neural traces of implicit change detection is held to be solely supported by visual sensory memory with limited time span and reportability of its contents (Sperling, 1960). The observation of distinct markers cannot, however, yield direct evidence in support of independent functioning between explicit behavioral change detection and implicit change detection. To substantiate this possibility, it should be shown that explicit change detection could occur with and without the presence of implicit change detection.

To this end, we investigated whether explicit detection of visual changes, as indexed by voluntary behavioral responses to them, can only develop when implicit detection of these changes, as reflected by the visual mismatch negativity (vMMN) of event-related potentials (ERPs) of the brain (for a review, see Pazo-Alvarez et al., 2003; Czigler, 2007; Kimura et al., 2011), also takes place. vMMN is a neurophysiological index of pre-attentive detection of visual changes on the basis of visual sensory memory (e.g., Astikainen et al., 2008). Its pre-attentive nature is reflected by the fact that, unlike with explicit change detection, voluntary attention need not be directed toward the changes to detect them. Its implicit nature is, in turn, reflected by no need to be declaratively aware of the changes. vMMN is elicited at the posterior electrode sites at around 150–300 ms following change (e.g., Czigler, 2007). Although explicit detection of visual changes is relatively insensitive to the duration of the blank interval separating the changed and unchanged images (Rensink et al., 2000), vMMN, in contrast, is known to diminish when ISI is prolonged (Astikainen et al., 2008), reflecting most probably the time span of visual sensory memory (Sperling, 1960). A behavioral index of explicit detection of visual changes and vMMN as an index of their implicit detection is, therefore, a perfect combination to investigate whether explicit detection could develop without implicit one. Previously, in change blindness studies using short intervals or change-occluding stimuli between images (30–100 ms, Schankin and Wascher, 2007, 2008) change-related electrophysiological responses have been observed, but not in similar studies using longer intervals (500 ms: Eimer and Mazza, 2005; 900 ms: Henderson and Orbach, 2006). We thus tested the implicit detection of the changes as indexed by vMMN to an image with change as interspersed with a repeated image with no change. To vary the elicibility of vMMN, two durations of blank intervals (ISIs) between the images delivering the change were used: a short interval (100 ms ISI) expected to lead to vMMN, and a long interval (500 ms) unlikely to produce vMMN. ERPs were recorded in trials prior to the first explicitly detectable image with change. We hypothesized that if the explicit detection of the changes is conditional upon their implicit detection, the explicit detection of the changes should fail if vMMN fails to be generated by

images with change (with longer ISIs). If, on the other hand, the explicit detection of the changes can bypass visual sensory memory and directly recruit attentional memory (Rensink et al., 1997), the explicit detection should emerge even when vMMN remains unobservable in preceding trials.

MATERIALS AND METHODS

PARTICIPANTS

Twenty-two volunteers, 14 female and eight male with age distribution of 19–33 years (mean age 23.2 years, s.e. 4.03) participated in the study. All of them had normal or corrected-to-normal vision. Before the experimental treatment, the participants were informed about the nature and purpose of the study, and a written consent was obtained from them approved by the ethical committee of University of Jyväskylä. The study conforms to The Code of Ethics of the World Medical Association (Declaration of Helsinki).

STIMULI AND PROCEDURE

Participants viewed the stimuli while they were seated in a chair in a darkened room. The stimuli appeared on a 17" monitor at a distance of approximately one meter from the participant.

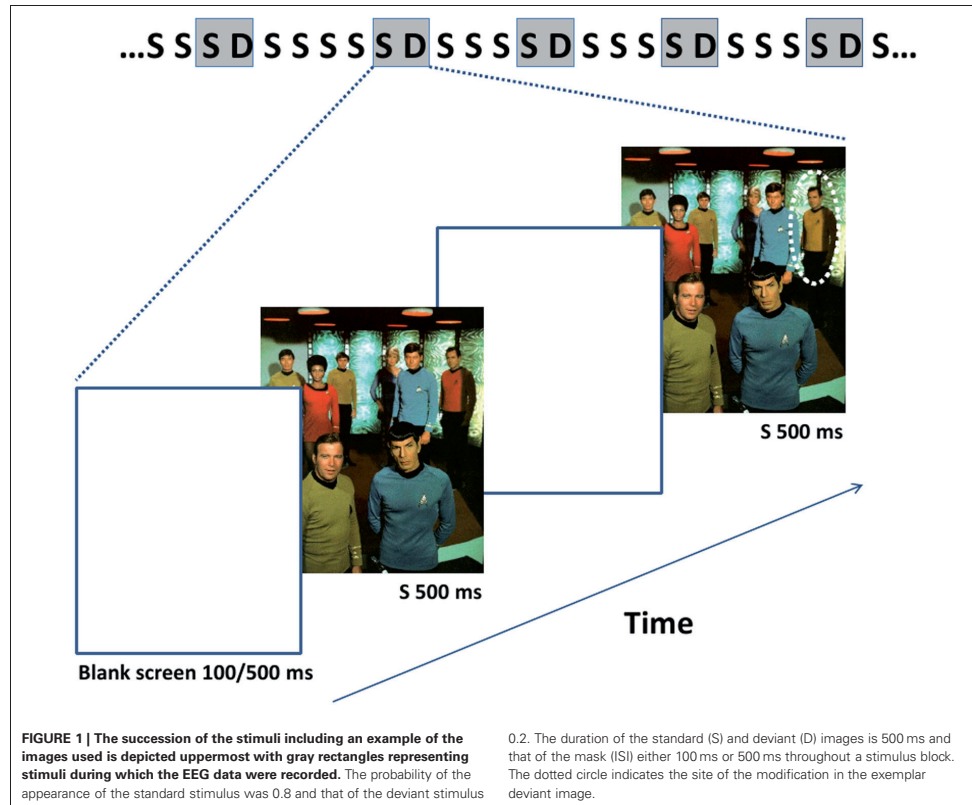
We used the same images of complex natural scenes as stimuli as in (Lyrra et al., 2010) (see **Figure 1**). There were a total of 10 original images and their modified versions with different kinds of changes, whose presentation order was randomized across participants. Changes across the images referred to appearances or disappearances of objects, or changes in their position or color. The direction of the changes (disappearance vs. appearances of objects) was counterbalanced across participants. Each of the images was 500 ms in duration and blank screen, i.e., ISI, of 100 ms in duration in one condition, and 500 ms in another condition separated consecutive image pairs. Ten stimulus blocks with different 50 image pairs were presented. In five of the blocks, a 100 ms ISI was used, and 500 ms ISI in the other five blocks. The order of the blocks was counterbalanced across the participants.

An image with change was infrequently and pseudo-randomly interspersed ($p = 0.2$) with its frequently presented pair without change ($p = 0.8$) (oddball condition). There were up to seven but no less than three image presentations with no change separating image presentations with change.

The participants were instructed to search for a change in the images in each stimulus sequence, and to report of noticing the change for the first time by pressing a button. They were also instructed to silently count the number of the remaining observable change occurrences in the sequence. Change detection performance was measured for each subject as the average number of presentation cycles of the changed images in one stimulus sequence required for the explicit behavioral report of change detection (button press). Occasional button presses to misses and false alarms (less than 3%) were used to distinguish them from change blindness, and successful detection was corrected on the basis of the counting task.

EEG-RECORDINGS AND DATA-ANALYSIS

Electroencephalography (EEG) was recorded with Brain Vision Recorder software (Brain Products GmbH, Munich, Germany)



from 29 channels of the international 10/20 system (FP1, FP2, Fz, F3, F4, F7, F8, FC1, FC2, FC5, FC6, Cz, C3, C4, CP1, CP2, CP5, CP6, T7, T8, Pz, P3, P4, P7, P8, Oz, O1, and O2) using an elastic cap (Electrocap) with Ag/AgCl electrodes. Average reference was used in the recordings and the extraction of ERPs. An electrode on the forehead was used as a ground electrode. The original EEG signals were sampled continuously at 1000 Hz, amplified and band-pass-filtered online with 0.1 to 100 Hz. The data were further processed with Brain Vision Analyzer 2.0 (Brain Products GmbH, Munich, Germany). The independent component analysis (ICA) function of the Brain Vision Analyzer 2.0 software was used to identify and correct for blinks and eye movements in the EEG. Channels with excessive muscular artifacts were removed. Data with voltage gradient over $80 \mu\text{V}/200 \text{ ms}$ and maximum and minimum voltages exceeding $\pm 80 \mu\text{V}$ at any channel were marked as containing artifacts. The signals were off-line band-pass filtered from 0.1 to 30 Hz. Sweeps containing artifacts were discarded for all channels, the average rejection rate

being 12.4% (0 to 65%, s.e. 20.89). Only subjects with more than 15 sweeps in the averaging after the artifact rejection were included in the ERP-averages (mean number of sweeps 57.7 for the 100 ms ISI condition and 74.1 for the 500 ms ISI condition). The rejection was done for each condition and all subjects, and this procedure led to 18 subjects in each ISI condition (100 and 500 ms) that were, however, not the same for both conditions.

As we were interested in implicit change processing, only data during change blindness, from the time period before the button press in the stimulus sequence were used for the ERP analysis. We excluded one presentation of change immediately preceding the button press not to confound implicit change processing with initial explicit change detection. For the ERP analyses, sweeps of the electrophysiological responses to the changed images and to the unchanged images immediately preceding them were picked in a time window of 100 ms before and 300 ms after stimulus onset. These responses were averaged

across each subject. This way the sweeps were from responses to image pairs close to each other in the stimulus sequence, and a similar amount of responses to changed and original images included in the averages. A 100 ms pre-stimulus period served as a baseline, against which the ERPs were corrected in both conditions.

A prominent differential ERP for the unnoticed changes of negative polarity is observable in the grand averaged waveforms (see Figures 2 and 3) in the posterior and postero-temporal electrode sites (P7, P8, Oz, O1, O2), especially in the condition of 100 ms ISI. These differential ERPs resembled in their latency, scalp topography, and stimulus and attentive conditions the visual analog of the mismatch negativity (MMN) of ERPs (Pazo-Alvarez et al., 2003; Czigler, 2007). For assessing response amplitudes, a time window of 200–260 ms (for vMMN, see e.g., Astikainen et al., 2008; Pazo-Alvarez et al., 2003; Schankin and Wascher, 2007, 2008; Kimura et al., 2008) was selected for which mean values from each electrode were extracted. The resultant values were submitted to a repeated measures multivariate analysis of variance (MANOVA). Electrode site (P7, P8, Oz, O1, O2) and Stimulus type (No change, Change) as within-subject factors in each ISI condition (100 ms and 500 ms). This is due to two things. First, a response to the presentation of the blank screen is visible in the pre-stimulus period of the ERPs of the 100 ms ISI condition suppressing their amplitudes (see Figure 3), which makes the conditions differ slightly in functional terms with respect to each other. Second, the subjects are only partly same in both conditions, so they cannot be incorporated in the same statistical model. Only results involving Change as a factor are reported here.

Explicit change detection performance was measured by the average number of presentations of images containing a change in a stimulus sequence required for explicit report of initial change detection (button press). The performance in the distinct ISI-conditions was compared by paired *t*-tests.

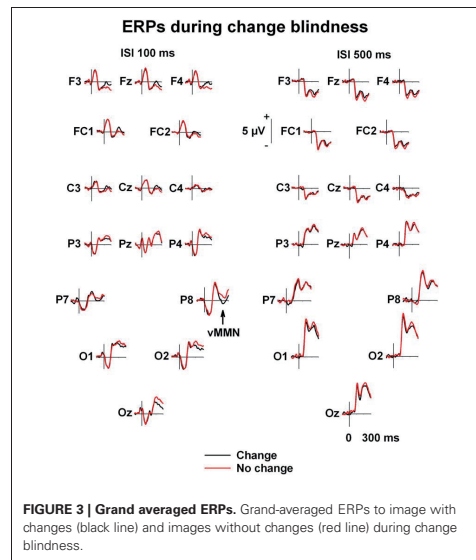


FIGURE 3 | Grand averaged ERPs. Grand-averaged ERPs to image with changes (black line) and images without changes (red line) during change blindness.

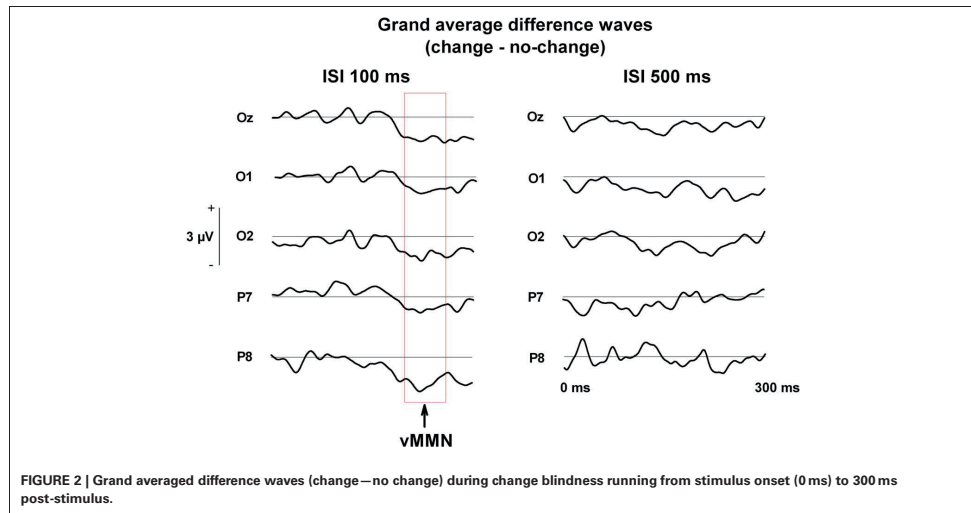


FIGURE 2 | Grand average difference waves (change – no change) during change blindness running from stimulus onset (0 ms) to 300 ms post-stimulus.

RESULTS

BEHAVIORAL DATA

It took for the participants an average of 10.30 (s.e. 6.49) presentations of changed images in a stimulus sequence until they were able to detect the changes with the 100 ms ISIs while it took an average of 13.94 (s.e. 8.03) such presentations with 500 ms ISIs. This difference between these numbers was significant, $t(21) = 2.15, p < 0.05$, indicating a slightly earlier detection of the changes with the shorter ISIs.

ELECTROPHYSIOLOGICAL DATA

In the condition of 100 ms ISI, the MANOVA with Electrode site and Change as factors for the mean voltages in the time window of 200–260 ms revealed the main effect of Change, $[F(1, 17) = 8.06, p < 0.02]$, indicating that changes were implicitly detected with the shorter ISI. The Electrode site \times Change interaction was not significant, $[F(4, 14) = 1.45, p = 0.27]$, indicating no specific role for any of the electrode sites in the detection (Figures 2 and 3).

In the stimulus condition of 500 ms ISI, the main effect of Change did not quite reach significance, $[F(1, 17) = 3.09, p = 0.097]$, nor did the interaction effect, $[F(4, 14) = 0.85, p = 0.52]$.

DISCUSSION

We assessed explicit detection, as reflected by voluntary behavioral responses, and implicit detection, as reflected by ERPs of the brain, of a rare pair of images with change as interspersed with a repeated pair of images with no change. There was a blank interval of either 100 ms or 500 ms between the paired images across which the changes were produced. Both intervals allowed the explicit detection of the images with changes. The detection developed slightly faster across the trials with the 100 ms (after presentation of 11 changed images) than with the 500 ms ISI (after presentation of 14 changed images). Prior their explicit detectability, i.e., during change blindness, images with changes were detected implicitly, as reflected by the posterior electrical brain responses 200–260 ms after the change onset (vMMN) but only with the 100 ms ISI.

With the shorter ISI of 100 ms, we found vMMN to unnoticed images with change. Similarly, traces of implicit change detection, as reflected by differential electrophysiological responses at 200–300 ms post-stimulus, have been observed by Schankin and Wascher in a couple of studies using a short ISI (30 ms) or transient change-occluding stimuli (50 ms in Schankin and Wascher, 2007; 100 ms in Schankin and Wascher, 2008; cf. Fernandez-Duque et al., 2003; Kimura et al., 2008). More specifically, Schankin and Wascher observed a contralateral modulation of the N2pc-component at postero-temporal electrode sites 220–260 ms (Schankin and Wascher, 2007), and 245–295 ms after stimulus onset (Schankin and Wascher, 2008) elicited by changes presented in the right or left visual hemifield, reflecting the location of the unnoticed change in the display.

Despite the longer ISI of 500 ms, in comparison to 100 ms ISI, only slightly delayed the explicit detectability of images with changes, we failed to observe a robust vMMN to these images when 500 ms ISI was applied. This finding was expected since it is known that vMMN is dependent on active sensory memory trace of the standards (for the memory comparison hypothesis of

MMN, see Näätänen, 1992). Indeed, vMMN to even perceptually simpler changes (in orientation of a bar) in repeated visual stimuli has been found to disappear along with the lengthening of blank ISIs from 400 ms to 1100 ms (Astikainen et al., 2008). Previous studies with longer ISIs between the images delivering the change (900 ms in Henderson and Orbach, 2006; 500 ms in Eimer and Mazza, 2005) have failed to observe vMMN or other deflection in the N2-latency in response to unnoticed images with change. Indeed, Schankin and Wascher (2007) associated these negative findings with the extinction of the memory trace of the first image of a pair and, thereby, with the crash down of the whole process of comparison between the second and the first image of a pair. This account could well also explain our negative finding with the longer, 500 ms ISI and the positive one with the 100 ms ISI.

Our finding of the explicit detection of implicitly undetectable images with change questions the view that implicit change detection is needed for the development of the ability to detect changes explicitly. Furthermore, given the previous findings of implicit without explicit change detection (Fernandez-Duque et al., 2003; Eimer and Mazza, 2005; Schankin and Wascher, 2007, 2008; Kimura et al., 2008; Khittl et al., 2009; Lyyra et al., 2010), our finding of an opposite dissociation may even suggest that the implicit and explicit modes of change detection may recruit functionally independent neural mechanisms.

vMMN to images with change with the 100 ms intervals between the images of a pair may also have been modulated by other temporally overlapping ERP components linked to specific aspects of change, such as its target status or mere occurring probability (vMMN and N2pb, see Luck, Hillyard, 1994; Henderson and Orbach, 2006), its spatial location (N2pc, see Eimer and Mazza, 2005; Schankin and Wascher, 2007, 2008), or visual awareness of changes (visual awareness negativity, VAN, Koivisto and Revonsuo, 2003; Busch et al., 2010a,b). The N2pb has been associated with explicitly detected changes (Luck, Hillyard, 1994). Like N2pb, VAN has been linked to explicit change detection (Koivisto and Revonsuo, 2003) and also to “sensing” of presence of changes before their detection (Busch et al., 2010a,b). In the present study, a possibility of explicit detection of images with change was minimized. The threshold for the participants’ responses to these images was set as low as possible. No identification of the changes was required and we excluded the last explicitly undetectable change in stimulus sequence from analyses and ERP-extraction, and it is for these change presentations that sensing or localization has been found to occur (Niedeggen et al., 2001; Mitroff et al., 2002). Accordingly, the N2pc component related to spatial attention has been observed in change blindness experiments specifically in the S1–S2 paradigm during change blindness (Schankin and Wascher, 2007, 2008) and “sensing” of the changes (Busch et al., 2010a,b). For these reasons, we consider that the differential ERP-response we observed for unnoticed changes was most likely vMMN in particular. Therefore, our study also leaves open the possibility that a shift of spatial attention to the changes is necessary, even if not sufficient, for explicit identification (see Watanabe, 2003; Schankin and Wascher, 2007, 2008; Busch et al., 2010a,b), and that vMMN reflects another type of implicit change detection that is not

even necessary for explicit change detection. However, if it is unlikely that the vMMN we observed reflects localization of the changes or sensing of changes, it is not clear what kind of processing the vMMN we observed reflects in our study. Implicit change detection may only consist of registration of the features of the changing objects (Lyrra et al., 2010), although there is also interesting behavioral evidence suggesting that information about the identity of the changing objects or their features could be implicitly processed (Angelone et al., 2003). vMMN itself is a component that is elicited by single features but also for complexes of features (e.g., Müller et al., 2010). Moreover, it is even possible that vMMN does not reflect a unitary process throughout the period of change blindness but rather progressing (implicit) change detection (cf. Rensink, 2002). A study showing, e.g., distinct brain responses to implicit detection of random groups of single features versus organized combinations of the same features could shed more light on the issue of how far the changes are processed implicitly.

Some theorists have challenged the existence of implicit change detection (Mitroff et al., 2002). Their criticism lies in the reliability of behavioral measures of change awareness. Unconfidence of the subjects about the content of their perceptual experience and in conservative response criteria of explicit awareness may allow residual explicit awareness to affect indirect behavioral measures (see, however, Fernandez-Duque and Thornton, 2003; Laloyaux et al., 2006). In the present study, we used a fairly liberal response criterion, that is, button press at the first explicitly detectable occurrence of change not requiring identification. Nevertheless, even if we excluded the change occurrence immediately preceding explicit change detection from ERP-extraction, the subjects might have been marginally aware of or "sensed" the change even at some point before the button press. Therefore, the implicit nature of the detection stands in our study in the failure of the declarative consciousness to access the changes to allow the changes to be reported behaviorally. It is thereby possible that implicit changes may have made a difference in the phenomenal subjective experience of the subjects, even though they have not been able to access this information to report on it. Nevertheless, we think that our interpretation of the independence of the pre-attentive vMMN from explicit behavioral detection requiring focal attention holds.

Manipulating the duration of the blank interval led to a couple of incompatibilities with regard to the ERPs between the two ISI conditions. The amplitudes in the ISI100 condition are decreased and their polarity even partly reversed due to the ERP-response to the blank interval (cf. Schankin and Wascher, 2007, 2008) as compared to the ISI500 condition in which the response to the blank screen has dissipated. We see this incompatibility as no threat to the present results, since the two ISI conditions were not compared to each other, only ERPs to changed and unchanged images within each ISI condition. For each ISI condition, the stimulus conditions are identical, and the differences can thus only be due to the unnoticed changes in the stimuli. Also because of surprisingly good change detection performance together with artifact rejection, the sweep numbers for ERP extraction were relatively low for some participants in either ISI condition. However, most sweep numbers were close to the average (57.7 for the 100 ms ISI condition and 74.1 for the 500 ms ISI condition), and we used

methods such as ICA in ocular correction to enhance the signal to noise ratio. Moreover, the trial numbers were lower for the ISI100 condition than the ISI500 condition. Low numbers of trials rather occludes potential effects, but still the effect of change in ERPs reached significance in the ISI100 condition, and the negative result in ISI500 condition was not due to its poorer signal to noise ratio. To further investigate the reliability of our results in this respect, we reanalyzed the results using only the data on the 12 participants with more than 30 trials in ERP-averages in both conditions. The results were similar to the original ones; the ERPs differed significantly in response to unnoticed changes in the ISI100 condition ($p < 0.05$), but not in the ISI500 condition ($p = 0.09$).

In the ERPs of the anterior electrode sites, there is a positive change-related amplitude difference visible at the same latency as the vMMN (see Figure 3). Positive differential ERPs have been reported accompanying vMMN in a number of studies (see Czigler, 2007 for a review). However, a similar ANOVA for the frontal electrode sites (F3, F4, Fz, FC1, FC2, Cz) as for the posterior electrode sites did not reveal any significant change-related amplitude differences.

The development of explicit change as a function of repeated occurrences of change without the guidance of implicit change detection would be in line with the view that a major factor in overcoming change blindness is top-down visual search strategy (Sampanes et al., 2008). In future studies, selectively affecting this strategy (attention to single objects as opposed to sets of objects) could provide a means to further explore on the aspects that dissociate explicit from implicit change detection, the latter of which rather utilizes elementary visual attributes. Nevertheless, we cannot exclude the possibility that some aspects of implicitly processed information about changes could affect their explicit detection. For example, it has been shown that socially relevant changes are detected faster than neutral ones (David et al., 2006) and that information about the emotional content of visual stimuli could be processed implicitly (Pasley et al., 2004). ERPs related to emotional processing could be used to investigate implicit processing of emotional contents of the changes, and their relation to change detection performance in the change blindness condition.

In sum, our results suggest that, despite implicit detection of visual changes remains unobservable, the changes still can build up an ability to detect the changes explicitly. Namely, despite the implicit detection of the visual changes fails due to long stimulation intervals beyond the temporal span of a memory system involved, the visual information, on which such detection is based, may still be successfully stored for these periods and used to prepare the visual system for the explicit detection of changes. Together with previous findings of implicit despite the absence of explicit change detection, our finding of the opposite dissociation suggests that implicit and explicit modes of change detection may recruit functionally distinct memory-based mechanisms of the brain.

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III

IMPLICIT BINDING OF FACIAL FEATURES DURING CHANGE BLINDNESS

by

Pessi Lyyra, Hanna Mäkelä, Jari K. Hietanen, & Piia Astikainen, 2014

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Implicit Binding of Facial Features During Change Blindness

Pessi Lyyra^{1,2*}, Hanna Mäkelä¹, Jari K. Hietanen², Piia Astikainen¹

1 Department of Psychology, University of Jyväskylä, Jyväskylä, Finland, **2** Human Information Processing Laboratory, School of Social Sciences and Humanities, University of Tampere, Tampere, Finland

Abstract

Change blindness refers to the inability to detect visual changes if introduced together with an eye-movement, blink, flash of light, or with distracting stimuli. Evidence of implicit detection of changed visual features during change blindness has been reported in a number of studies using both behavioral and neurophysiological measurements. However, it is not known whether implicit detection occurs only at the level of single features or whether complex organizations of features can be implicitly detected as well. We tested this in adult humans using intact and scrambled versions of schematic faces as stimuli in a change blindness paradigm while recording event-related potentials (ERPs). An enlargement of the face-sensitive N170 ERP component was observed at the right temporal electrode site to changes from scrambled to intact faces, even if the participants were not consciously able to report such changes (change blindness). Similarly, the disintegration of an intact face to scrambled features resulted in attenuated N170 responses during change blindness. Other ERP deflections were modulated by changes, but unlike the N170 component, they were indifferent to the direction of the change. The bidirectional modulation of the N170 component during change blindness suggests that implicit change detection can also occur at the level of complex features in the case of facial stimuli.

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* E-mail: pessi.lyyra@jyu.fi

Introduction

Cognitive psychologists have discovered an astounding inability to detect considerable and obvious changes in visual scenes presented after a global transient event, for example an eye-blink or a “flicker” – a brief blank screen with a blink-like effect. Once detected, the change becomes impossible to ignore. To recover from this “change blindness” [1–3] – to consciously recognize the change and report on it – seems to require focal attention [4]. However, it remains controversial whether unnoticed changes are, nevertheless, registered implicitly, and if so, what kinds of representations exist outside conscious visual perception, and whether they can contribute to overcoming change blindness.

A number of studies have reported evidence of implicit representations of changes during change blindness as revealed by indirect measurement techniques in the absence of overt reportability of the change. These studies have employed behavioral [5–9], brain-imaging [10–12], and electrophysiological methods in investigation [9,13–17], and have presented evidence that at least single feature changes are implicitly registered. For example, electrophysiological studies have revealed short-latency brain responses to explicitly undetected changes in complex natural scenes, with objects or their features appearing, disappearing, or changing color or location [14]. There is also evidence of implicit localization of changes as indicated both by the N2pc-component of event-related potentials (ERPs) occurring contralaterally to the changes [16,17] and by eye-tracking studies showing

the viewer’s gaze to linger in the location of the implicit changes [5]. If, as these experiments suggest, implicit representations of the changed features exist, an interesting follow-up question would be to investigate whether the implicit detection of changes occurs only at the level of single features or if it is possible to implicitly perceive changes in objects that are composed of complexes of single features.

In previous studies, the implicit registration and localization of changes involved changes in single features. It has been suggested that the detection of these types of changes does not require focal attention. According to an influential view of human perception, referred to as the feature integration theory, the distinct visual features of which coherent objects consist in human perception are correctly bound together only within the sphere of focal attention [18–22]. Evidence for this has been provided in visual search experiments showing inefficient, serial search for feature conjunctions and efficient, parallel search for single features [18]. Thus, if successful change detection requires focal attention and, on the other hand, if complexes of the stimulus elements lose their structural composition [23] and become randomly conjoined [19,20] when presented outside of focal attention the complex organization of the elements in a changing stimulus cannot *prima facie* facilitate change detection in change blindness.

In contrast to feature integration in object perception in the visual domain, which operates by decomposing objects first into elementary parts and their edge and contour features [24], face perception has been described to operate in a holistic manner

already at the first stages of visual processing [25]. Indeed, recent cognitive neuroscience research has strongly indicated that faces are perceived holistically and that basic facial features are already bound together by the brain's subcortical face-processing route, which is involved in coarse and fast face detection [26]. Also, according to the feature integration theory, during the initial feedforward pass, visual processing of single features activates a number of potential, internally consistent feature conjunctions, the forming of which can be constrained by expectation, semantic knowledge [21], and cortical specialization [27]. As humans are specialized in perceiving faces, it is possible that changes in a facial configuration could be represented without awareness of those changes and they could also facilitate the detection of these changes. Moreover, it has been suggested that a lack of awareness, as in change blindness, does not necessarily imply lack of attention [28], and some attentional operations may support initial feature binding. For example, attention distributed over multiple objects has been shown to enable more detailed processing compared to processing of an object outside of attention, but not as much as with focused attention [21].

It has also been shown that cortical brain areas related to face perception are activated in response to facial stimuli, even without any conscious awareness of them (fusiform face area, superior temporal sulcus) [29,30]. The fusiform face area is said to play a role in the encoding of invariant facial features, important for facial identity recognition, whereas the superior temporal sulcus is involved in processing more dynamic information such as facial expressions [31]. N170 is a component of ERPs that has been thought to reflect the representation of "the concept of a face" (structural encoding of holistic face configuration) [26]. It has been shown that realistic and schematic pictures of faces generally elicit similar N170 responses [32,33]. The N170 response may also be sensitive to facial emotional expressions [34–36], although some earlier studies do not show this effect [37,38]. In a study using an inter-ocular suppression paradigm, intact faces presented to participants below the threshold of awareness elicited an enlarged N170 response compared to scrambled faces in postero-temporal areas [30]. In another study comparing subconsciously presented emotional expressions to neutral ones, the former elicited an enhanced EPN-like response, a response sensitive to emotionally and motivationally salient stimuli, approximately 220 ms after stimulus onset [39]. These results among others on non-conscious face-perception [26,40–42] indicate that facial features are bound together and that these feature complexes can be detected by the brain, even without awareness of them.

In studies measuring change detection performance, it has been shown that socially relevant changes, including changes involving faces, are often detected more easily than socially neutral ones (gradual changes in facial expressions vs. gradual color changes [43]; people vs. objects [44]; heads vs. objects: [45]). These authors have explained the more efficient change detection in socially relevant stimuli as a result of the interplay between salience and attentional effects. Compared to neutral stimuli, socially relevant stimuli draw attention for longer periods of time. Thus the earlier detection of changes in faces than in other objects may be due to the stronger allocation of attention to faces. However, even if attention plays an important role here, it is still possible that the eventual change detection depends on the perception of simple features or luminance changes in facial stimuli rather than combinations of single features. Whether complex facial configurations could be perceived implicitly and whether this could have a bottom-up effect on explicit change detection were questions left open by these studies. We reasoned that, by using controlled facial stimuli and measuring face-related ERP components, especially

the N170 response, we could approach the issue of whether visual feature complexes are implicitly represented in the case of facial stimuli during the change blindness.

Using schematic faces and scattered groups of physically identical features (scrambled faces) as stimuli, we investigated the implicit detection of changes in facial and non-facial stimuli in the change blindness paradigm while recording ERPs. Four stimuli, two faces and two scrambled faces were presented at a time. Occasionally, one of the faces changed to a scrambled face or vice versa (between-category change). Alternatively, a face or scrambled face changed to another exemplar of the same category (within-category change). For faces, the within-category change of facial feature arrangement led to a change in facial expression. At the behavioral level, our main hypothesis concerned the between-category changes: we expected that changes involving the presence or absence of facial configural information in a stimulus (between-category changes) would be detected faster than changes in within-category changes. If, as expected by the social bias of attention hypothesis, more attention is allocated to intact faces than to scrambled ones, the deformation of faces should be detected faster than the formation of a face from scrambled features. For within-category changes, we expected that changes in intact faces would be more easily detected than those in scrambled faces. At the electrophysiological level, we expected to observe a modulation of the face-sensitive N170 response during change blindness, indicating implicit change detection of facial configuration. We hypothesized that an enlargement of the N170 response would be observed for the changes from scrambled features to faces, and an attenuation of the N170 response for changes in the other direction. Since previous studies have evidenced N170 response sensitivity to facial expressions [34–36], it was possible that the N170 response would also show an amplitude modulation for within-category changes involving faces. Because the experimental paradigm involved the presentation of repeated, unchanged visual displays interspersed by changed ones, we also expected to observe a visual mismatch negativity (vMMN) response to the changed stimuli. It has been shown that the vMMN response is elicited by regularity violations, also when participants are unaware of changes in stimuli [46–48].

In sum, we sought out evidence of implicit change detection in complex facial configurations during change blindness, evidence that was provided by revealing modulation of the face-sensitive N170 ERP response to configural stimulus changes of facial stimuli without explicit behavioral change detection.

Methods

Participants

Twenty-one healthy volunteers (fourteen females, age range 19–39 years, mean age 25.8 years) took part in the study. One participant was left-handed, the rest were right handed, and all had normal or corrected-to-normal vision. Because of timing problems with the stimulus presentation, the electroencephalogram (EEG) data on four participants were discarded. Data on seventeen participants were analyzed (eleven females, age range 19–39 years, mean age 25.7 years, all right-handed).

Ethics Statement

According to Finnish regulations (Act on Medical Research and Decree on Medical Research 1999, amended 2010), specific ethics approval was not necessary for this study. Written informed consent was obtained from the participants before the experimental treatment. The study conforms to The Code of Ethics of the World Medical Association (Declaration of Helsinki).

Stimuli and Procedure

The participants viewed the stimuli on a 17" monitor (Eizo Flexscan CRT display, refresh rate 85 Hz) at a distance of 60 cm.

Two types of images were used: a set of three schematic faces (neutral face, happy face, and fearful face), and a set of three scattered constellations of the same facial features (scrambled faces, see Fig. 1). Randomly changing constellations of scrambled face elements were not used, since it has been shown that non-similarity of the stimuli affects the N170 response [33,49] and, therefore, had the potential to act as a confounding factor. The scrambled and schematic faces covered roughly a similar spatial area. Four stimuli, two faces and two scrambled faces were presented at a time at four locations around a fixation cross (see Fig. 1).

Stimuli were continuously presented as flickering stimulus sequences of one to five change trials. In one trial, an original, repeatedly presented stimulus was visible for 250 ms, followed by a 500-ms non-stimulated interval (flicker), after which either the original or a changed version of it was presented for 250 ms. The first change occurred after presentation of at least three successive non-changing stimuli. Between the change trials, there were between three and seven presentations of non-changing stimuli. Thus, we used an oddball version of the flicker paradigm in which changes occurred infrequently with a probability of 20% [14,15].

Compared to the more commonly used alternating flicker paradigm, the infrequent presentation of the changes increases their novelty and change value, which is required for the elicitation of related ERP components such as vMMN.

The changes consisted of an occasional change in one of the faces/scrambled faces. There were four different types of changes (Fig. 1). In the so-called between-category changes, an intact face changed to a scrambled face (FaceScra) and a scrambled face changed to an intact face (SeraFace). The two other types of changes were within-category changes. In a case of a face changing to another face, a change in the arrangement of local features led to a change in facial expression. In a case of scrambled faces, one scrambled face changed to another scrambled face (see Fig. 1). No two similar intact or scrambled faces were presented simultaneously. One type of change was presented at one location throughout a stimulus sequence, and the change types and locations were randomized within the experiment. A stimulus sequence consisted of twenty-seven stimulus presentations lasting 21 seconds at most. The duration of the whole experiment ranged from 42 to 60 minutes, consisting of between 143 and 205 (mean 201.0) stimulus sequences. During pilot testing with a different subject group, we tested the behavioral change detection of the different change types. We found that between-category changes were clearly more easily detected than within-category changes.

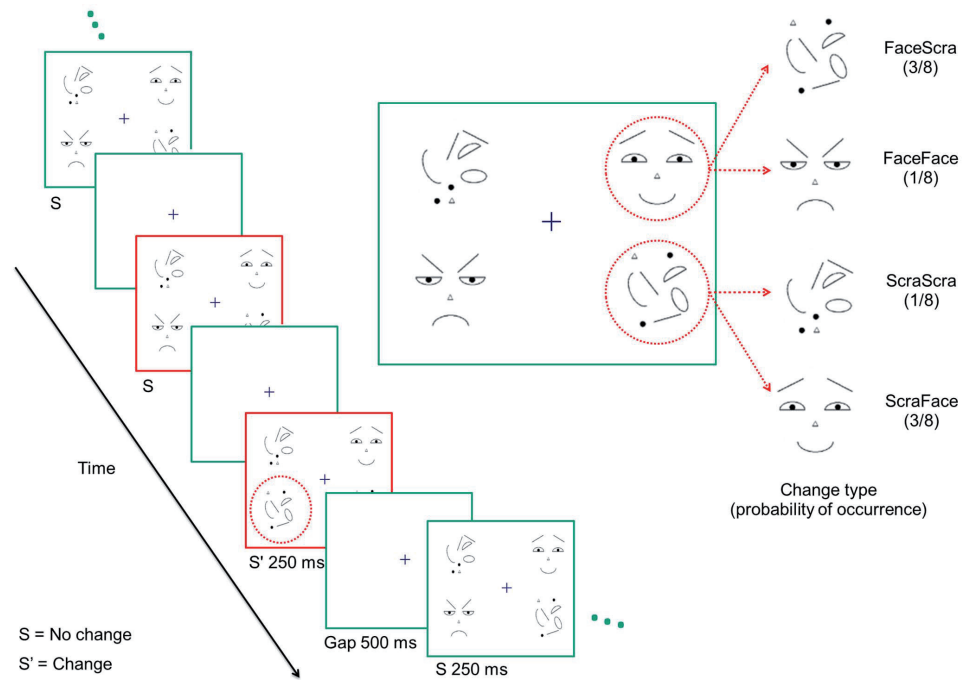


Figure 1. An excerpt from a stimulus sequence. The No change and Change conditions consist of an image pair separated by the blank interval within the same stimulus trial, indicated by the red frames (previous no change image+change image). ERPs were extracted from responses to these images and the preceding blank interval. doi:10.1371/journal.pone.0087682.g001

Therefore, to obtain roughly an equal amount of data for each change type from the change blindness periods, we increased the number of stimulus sequences containing between-category changes; first to $P = .333$, and, after six participants, to $P = .375$ for both between-category change types. For within-category changes, we used $P = .166$ and $P = .125$ for faces and scrambled faces, respectively.

The participants were instructed to search for an infrequent change in the images and to report the change by pressing one of two adjacent buttons, depending on which side of the display they perceived the change happening. In some change detection studies, participants are required to report the change once they identify it. However, in these cases it is possible that people are somehow aware of the changes before they decide to report them, and therefore it is not clear whether the results reflect change blindness or awareness of the changes. Therefore, we used a strict criterion of change detection and instructed the participants to press the button once they could “sense” the location of the change, though no conscious recognition of the change was required [50,51]. When the participant reported localizing the change by pressing the correct button, the stimulus sequence came to halt [52] and the participant initiated the next stimulus sequence with another button press. The change trials before the explicit report, except for the last one immediately preceding the report, made up the change blindness condition.

The experiment was divided into two blocks, each comprising one half of the experiment. In one block, the participants fixated a cross in the middle of the scene and tried to detect changes in the stimuli around the cross without changing fixation [10,53,54]. In the other block, participants were allowed to search freely for the change, but, to provide a contrast for the fixation condition, were instructed to look at only one stimulus at a time in the matrix. As both search strategies are frequently used in change blindness studies, and as the data analysis showed that the search strategy did not have a significant interaction effect with any of the manipulated factors, we averaged the data of the two search conditions in order to increase the power of the experiment.

EEG-recordings and Data-analysis

EEG was recorded with Ag-AgCl electrodes from twenty-one channels (FP1, FPz, FP2, F3, Fz, F4, F7, F8, C3, Cz, C4, P3, Pz, P4, T3, T4, T5, T6, O1, O2, Oz) according to the international 10–20 system. Each channel was referred to the average of the other electrodes (common reference), amplified 10,000 times, online band-pass filtered (0.1–100 Hz, 24 dB per octave), and digitized at a 1000-Hz sampling rate. Horizontal and vertical eye movement potential was recorded bipolarly using electrodes placed laterally 1 cm from the outer canthus of left eye and 1 cm above the right eye. The impedances of all electrodes were kept below 3 k Ω . The data were further processed using Brain Vision Analyzer 2.0 (Brain Products GmbH, Munich, Germany). Channels with excessive muscular activity were omitted from the analyses. The data were offline band-pass filtered (0.1–30 Hz, 24 dB per octave) and corrected for ocular movements with the algorithm implemented in the Vision Analyzer software [55]. As we were interested in implicit change detection, we analyzed only the data concerning change blindness, that is, from the period before explicit change detection. The button press marked explicit detection, and the responses to changes immediately preceding change detection were discarded from the analyses. Epochs from 150 prestimulus to 300 ms poststimulus for each stimulus condition were selected for ERP extraction. ERPs were averaged and corrected against a 150-ms pre-stimulus baseline. Data were segmented separately for the stimuli containing changes (S' in

Fig. 1) and the stimuli immediately preceding the changed pictures (S in Fig. 1). Thus, in the analyses, there were an equal number of responses to change and no-change images. Sweeps containing artifacts (maximum voltage 200 μ V, minimum voltage -200μ V, maximum allowed voltage step 50 μ V/ms, and maximum difference of values within the sweep exceeding 100 μ V in any electrode) were discarded. The mean number of artifact-free trials in the analysis was 46.7 for ScraFace, 77.8 for ScraScra, 48.6 for FaceFace, and 51.8 for FaceScra. The number for ScraScra trials was therefore significantly greater than for others ($p < .01$).

Based on previous research and a visual inspection of the waveforms of grand-average ERPs, mean amplitude values were calculated for each participant with regard to three components: the P1 (90–110 ms post-stimulus), the N170 (150–170 ms post-stimulus), and vMMN (250–300 ms post-stimulus). To analyze the effects of changes in different change types, we calculated mean difference amplitudes (Change – No change) for all three components. Since the P1 and vMMN responses were distributed across the occipito-temporal channels, differential change processing between change type conditions was analyzed with an analysis of variance (ANOVA) for repeated measures. For this, we used the mean difference amplitudes from channels T5, T6, O1, and O2 as a dependent variable with Hemisphere (Left, Right), Channel (Temporal, Occipital), and Change type (Schematic to Schematic, Schematic to Scrambled, Scrambled to Scrambled, Scrambled to Schematic) as factors. The N170 amplitude analyses were based on ERPs recorded from electrodes T5 and T6, as these recording sites are typically the most sensitive to facial stimuli [32]. For N170, we performed an ANOVA analysis on the mean difference amplitudes using the factors of Hemisphere and Change type. To test whether change had an effect on ERP responses in the different change types, the difference amplitudes of all the components were also analyzed with one-sample t-tests against zero. The behavioral data were measured as the mean number of change occurrences required for explicit change detection in each Change type condition, and subjected to an ANOVA for repeated measures with the factor of Change. Bonferroni corrections were used when appropriate. An alpha level of .05 was used in all the analyses.

Results

Behavioral Results

Change detection performance was measured as the mean number of change occurrences required for the change to be explicitly detected within each change type condition. The results are presented in Table 1. An ANOVA showed that the detection of changes differed between change types, $F(3, 48) = 204.4$, $p < .001$. Detection was more efficient for both between-category changes compared to both within-category changes, all p s $< .01$ (Bonferroni corrected). For between-category changes, there was no difference in detection when a face changed to a scrambled face or when the opposite change occurred. However, for within-category changes, changes involving faces (i.e. the expression change) were detected more efficiently than those involving scrambled faces, $t(16) = 5.4$, $p < .01$.

ERP Results

P1 component. A Channel * Hemisphere * Change type ANOVA conducted for P1 difference amplitudes (Change – No change) revealed no significant main effects or interactions between any of the factors. A further analysis (data averaged across all conditions) with a one-sample t-test against zero showed

Table 1. Mean number of change presentations required for explicit change detection.

	ScraFace	FaceScra	ScraScra	FaceFace
N	1.80	1.84	3.65	2.67
S.E.	.45	.29	.93	.33

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that the P1 response was not modulated by the change occurrence ($p > .60$).

N170 component. For the N170 difference amplitudes, a Hemisphere * Change type ANOVA revealed a main effect of Change type, $F(3, 48) = 3.1, p < .05$, and an interaction of Hemisphere * Change type, $F(3, 48) = 2.5, p < .075$. Because of this interaction, we analyzed the N170 difference amplitudes separately for electrode sites T5 and T6. The mean amplitudes of the N170 component at electrode sites T5 and T6 in all change type conditions are given in Table 2.

A one-way ANOVA conducted for the data from electrode site T5 showed no significant main effect of Change type. For electrode T6, an ANOVA revealed a significant main effect of Change type, $F(3, 48) = 3.7, p < .02$. Pairwise comparisons revealed significant differences between FaceScra and ScraFace, and also between FaceScra and ScraScra conditions, $t(16) = 2.6, p < .05$ for both. Finally, we checked, using one-sample t-tests against zero,

whether there was a significant modulation of the N170 response at T6 electrode by a change in different change type conditions. These analyses revealed significant differences in N170 responses to changed vs. unchanged stimuli in both between-category change conditions: an enhancement of the N170 amplitude by scrambled-to-face changes (ScraFace), $t(16) = 2.2, p < .05$, and an attenuation of it by face-to-scrambled changes (FaceScra), $t(16) = -2.1, p < .05$. Neither within-category changes resulted in a significant N170 amplitude modulation. The N170 responses to unchanged and changed stimuli in both between-category change conditions are illustrated in Figures 2 and 3. The mean amplitudes of the N170 component at electrode sites T5 and T6 in all change type conditions are given in Table 2.

vMMN component. A Hemisphere * Channel * Change type ANOVA on the vMMN responses revealed no main effect or interaction involving Change type. The main effect of Hemisphere was significant, $F(1, 16) = 4.7, p < .05$, indicating that the overall response modulation by different change types was greater in the right than left hemisphere. Further one-sample t-tests revealed that the vMMN response was modulated by the change occurrence in the right hemisphere, $t(16) = -2.5, p < .05$, but not in the left hemisphere, $t(16) = 1.4, p = .11$. The mean amplitudes of the vMMN responses averaged over all the electrode sites and change type conditions are given in Table 3.

Discussion

We investigated the implicit detection of changes in visual stimuli containing feature complexes by presenting schematic faces and scrambled faces as stimuli in a change blindness paradigm. In addition to measuring behavioral change detection performance, we also measured event-related potentials in the change blindness period. The stimuli were presented in a matrix of two intact and two scrambled faces, with one changing in one of four possible change directions (intact to scrambled, intact to another face, scrambled to intact, or scrambled to another scrambled). The results showed that behavioral change detection was clearly more efficient for between-category changes, i.e., a scrambled face changing to a coherent face or vice versa, as compared to within-category changes, i.e., an intact face or a scrambled face changing to another face/scrambled face, respectively. More importantly for the present study, we found that even during change blindness, changes in configurations of simple features (formation or deformation of a coherent facial image) significantly influenced the amplitude of the face-sensitive N170 response. A change from a scattered positioning of the local features (scrambled face) to a face-like configuration resulted in increased N170 amplitudes, whereas disintegration of an intact face into a scrambled one led to decreased N170 amplitudes. This result shows that the visual system implicitly, in the absence of overt reportability, processes information about the facial configuration of the changed stimuli that consist of the same elementary components. The present results show that during change blindness, the brain is capable of integrating single features into feature complexes at relatively early processing stages in the case of facial configurations. These findings are compatible with the suggestion that the N170 response reflects structural encoding of the holistic face configuration [26]. Interestingly, an earlier P1 response (90–110 ms post-stimulus) was not at all modulated by the changes in stimulus configurations.

At 250–300 ms after stimulus presentation, a sustained change-related enhanced negativity developed at the posterior electrode sites. Since the changes were presented infrequently, in a pseudo-random manner (i.e. oddball condition), this negativity is most

Table 2. The mean amplitudes of the N170 component in the change blindness condition.

T5				
	Between-category changes		Within-category changes	
	ScraFace	FaceScra	ScraScra	FaceFace
μV	-2.92	-2.44	-2.39	-2.65
S.E.	1.32	1.35	1.18	1.03
	No change	No change	No change	No change
μV	-2.84	-2.84	-2.30	-2.30
S.E.	1.13	1.43	1.18	1.41
	Difference	Difference	Difference	Difference
μV	-.08	.40	-.09	-.34
S.E.	.96	1.25	.62	1.23
T6				
	Between-category changes		Within-category changes	
	ScraFace	FaceScra	ScraScra	FaceFace
μV	-4.34	-2.47	-3.39	-3.38
S.E.	2.20	2.27	1.71	2.00
	No change	No change	No change	No change
μV	-3.84	-3.25	-3.05	-3.42
S.E.	2.73	2.51	1.59	2.11
	Difference	Difference	Difference	Difference
μV	-.60	.78	-.34	-.04
S.E.	1.14	1.50	1.17	1.08

doi:10.1371/journal.pone.0087682.t002

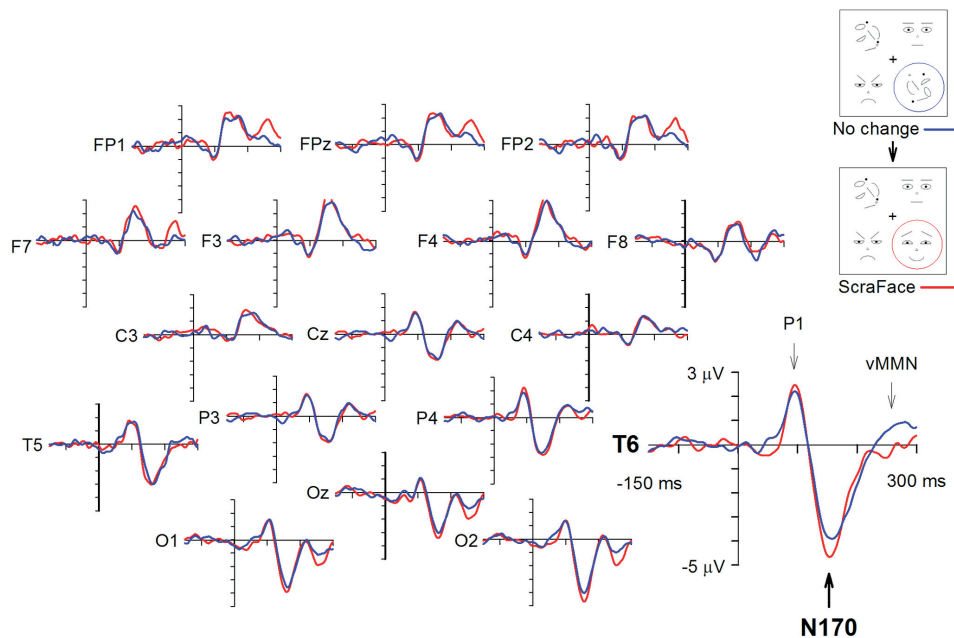


Figure 2. Grand average ERPs during change blindness in the FaceScra condition. The No change image was preceded by an identical image, and the Change image by the No change image. The timelines start from the onset of the Change or No change image after the blank interval. doi:10.1371/journal.pone.0087682.g002

likely visual mismatch negativity. In the same latency range, the change-related N2pc [16,17] and attentional negativity [56] have been observed, the first also during change blindness. Further studies are needed to determine whether this negativity reflects “genuine” vMMN elicited by regularity violation [47] or the effects of spatial attention (N2pc). It is notable that this differential negative deflection, like the N170 modulation, was more pronounced in the right hemisphere, which specializes in the processing of visual configural information [57]. Furthermore, vMMN studies using facial emotional expressions as deviant stimuli have reported similar right hemispheric dominance in the vMMN response [47,48].

Previous findings of change detection performance have shown that changes involving faces or other socially relevant stimuli are more easily detected than changes in socially neutral objects [43–45,58]. Our results replicated and built on these results. In previous studies, the superior performance associated with social stimuli has been explained by attentional bias to these stimuli. This can also explain our observation that faces changing to scrambled faces or faces changing their expression were more efficiently detected than non-faces changing to other non-faces. However, our results also revealed the efficient detection of changes from scrambled faces to faces. If the bias to social stimuli results from attention allocation to social stimuli during the presentation of pre-change stimuli, the deformation of faces should have been detected more efficiently than the formation of a face from a scrambled one. However, in our data, the forming of a face from a scrambled face was detected as efficiently as the deforming of a face.

Moreover, the forming of a face was detected more efficiently than a change in face expression. Thus, our data cannot be explained merely by the social bias of attention hypothesis. A plausible explanation is that the visual system is capable of implicitly detecting changes in facial structure and that these changes, then, draw focal attention to the change location before explicit detection of the change. At the neural level, the subcortical network that responds to faces and modulates subsequent cortical activity may support the implicit holistic representations and shifts of attention [26]. Thus, the N170 modulation can be seen as a marker of an ability to discern the presence and absence of facial configuration in visual stimuli, which may in turn be a prerequisite for the attentional shift required for the change detection of facial stimuli. It may be that non-facial stimuli are not processed implicitly to the same extent.

Despite these observed findings, our results do not necessarily contest the view that focal attention is required for the changes to be detected consciously, in the sense that a voluntary behavioral report can be given on the change [4]. Even if attention could be captured in a bottom-up manner before the explicit change detection [16,17,52,59], the eventual explicit change detection could nonetheless require focal attention. Change blindness studies have revealed a bias of spatial attention toward the change location, as indicated by modulations of spatial attention related ERPs (N2pc) by the change location in change blindness [16,17], confined perhaps to the change presentation immediately preceding the one leading to eventual reported detection [16,17,59–61].

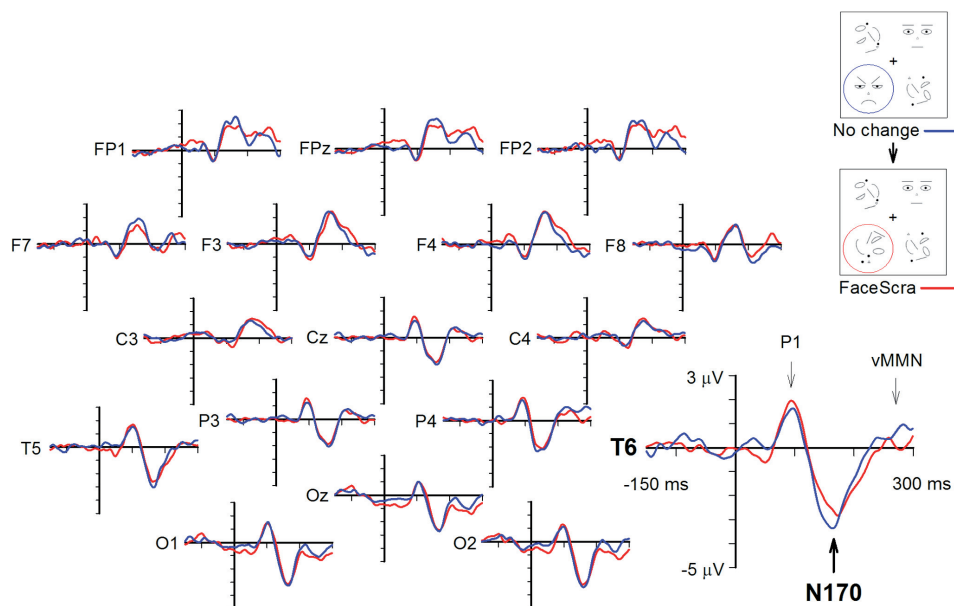


Figure 3. Grand average ERPs during change blindness in the ScraFace condition. The No change image was preceded by an identical image, and the Change image by the No change image. The timelines start from the onset of the Change or No change image after the blank interval. doi:10.1371/journal.pone.0087682.g003

As attention is held to be dissociable from awareness [28], it is possible to explain our results concerning implicit feature binding partly in terms of the interplay between attention and awareness effects. As it has been suggested, an automatic shift of implicit spatial attention precedes focused attention and explicit change detection in change blindness. This could allow the implicit binding of facial features outside the sphere of focal awareness. According to the feature integration theory, multiple possible combinations of visual stimulus features and elements are spontaneously formed in the first feedforward pass of visual processing [21,62,63]. The role of focused attention, as in visual serial search, is to select the correct conjunctions and provide more detailed spatial information about its objects [21]. However, already before the attentional constraints of reentrant processing,

ontogenic factors as well as cortical specialization can constrain feature combinations, as presumably in the case of face perception [20,21]. In addition, the participants may have deployed a broader window of attention before the initial localization of the change, and narrowed it down after the change localization. With attention distributed over multiple items in the scene, this could have enhanced the processing of the items, although to a less extent for each of them as compared to when being a sole target of focused attention.

Because of the privileged status and dedicated brain mechanisms of face perception, the evidence of feature integration observed in this study can only support implicit configural processing of facial features. It is not possible to draw any further conclusions about instantaneous implicit configural processing in general. Moreover, in our study, the same three configurations were used as nonfacial stimuli throughout the experiment, and it is possible that the participants may have learned these specific constellations of elements in the progression of the experimental task. It would require change detection studies using randomly changing combinations of features as changes to address implicit visual processing of feature combinations in general.

Change blindness is primarily a failure of the conscious access required for reporting the presence of change. If, as suggested by some theorists [64], access to the contents of focal attention is limited within the ample contents of visual awareness, it could be that the participants were aware of the changing stimuli at some unreportable level. As mentioned above, explicit change detection may be preceded by a feeling of change, and participants can even wait for one presentation cycle before reporting the change, to be

Table 3. The mean amplitudes (μV) of the vMMN response in the change blindness condition.

	Left hemisphere	Right hemisphere
Change	-.39	-.27
S.E.	.90	1.06
No change	-.24	.09
S.E.	.81	1.09
Difference	-.15	-.37
S.E.	.57	.43

doi:10.1371/journal.pone.0087682.t003

sure that they have detected it. The change blindness period may thus be contaminated by initial explicit change detection, especially if the change detection task is easy, as in the between-category change conditions. However, in the present study, we used a sensitive criterion for change blindness, requiring only localization of the change rather than conscious recognition of it. We also excluded the trials immediately preceding the report from the ERP data concerning the change blindness condition. Therefore, we think that our ERP results reflect implicit change detection, defined as registration in the brain of the presence of change in the display, notwithstanding the failure to explicitly report it.

It has been found in a number of studies that N170 responses to facial stimuli are reduced when preceded by the same facial stimuli, or even by different stimuli of the same category, especially compared to N170 responses to the same facial stimulus preceded by a non-facial stimulus [65–68]. A similar adaptation effect is evident in change blindness studies using facial and non-facial stimuli, namely if the changed facial stimuli are preceded by relatively similar facial stimuli. Thus, it is possible that the adaptation effect differs across change conditions and contributes to the differential processing of changes between the within- and between-category conditions. The lack of N170 modulation in the FaceFace situation could therefore be partly due to this adaptation-related amplitude reduction. A study by Ganis and Schendan [67] made a direct comparison to determine whether this kind of an effect is due to adaptation by previously presented faces or to an increase of amplitude caused by a non-face adaptor stimulus. It was found that only adaptor faces, not adaptor objects, affected the N170 amplitudes to the adapted faces relative to a baseline. Hence in our study, the adaptation effect may have concerned only the FaceFace condition, and not necessarily others, for example the ScraFace condition. Nevertheless, in these adaptation studies, the adaptor stimulus has been presented before the target in a conscious condition. In our study, the changed facial stimuli are implicitly presented and preceded by more than one presentation of the stimuli. The role of the preceding stimuli's adaptation effect on the changed facial stimuli is an interesting question for future change blindness studies using facial stimuli. The probabilities of occurrence and lengths of stimulus sequences differed between the within- and between-category conditions, and this may have had some minor adaptation- or task-related effects on behavioral and ERP-results. However, the probabilities and lengths were similar within the between- and within-category change conditions, respectively. Neither the adaptation or presentation frequency issues concern the bidirectional N170 modulation observed in the between-category change conditions.

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Our results not only corroborate previous theories of change blindness by showing that single visual features are represented and compared in the memory during change blindness [9,13–15], but also by demonstrating that the visual representation is relatively organized in the case of facial stimuli even outside focal attention and awareness. If changes are implicitly represented, then it is an open question whether change blindness is due to a failure of memory, a failure of a comparison process between pre- and post-change representations, or the inability to access information about the changes and to report them explicitly [3]. The present results concerning the N170 component do not cast light on whether the representations of the original and modified displays were compared or not, since the amplitude of the N170 response seemed to only reflect the appearance or disappearance of a facial configuration in the display, not the processing of change in them. Instead, the vMMN response seemed to be sensitive to the changes in a more general way: a similar deflection was elicited by all types of changes, highlighting the processing of change rather than changed features in the visual display. The vMMN-modulation is thus difficult to explain without postulating some kind of a comparison process for pre- and post-change representations.

In sum, we found that behaviorally undetected changes in facial configurations during the change blindness nevertheless affected the face-sensitive N170 ERP response. The N170 modulation was elicited by both the formation and deformation of a face during change blindness, which suggests that implicit representations of complex facial stimuli can exist during change blindness. On the basis of the present study, it cannot be established whether this holds for other types of complex stimuli. Nevertheless, our results may help us to understand what kind of information is retained across interruptions of stimulation and why changes involving facial stimuli seem to be more easily detectable than non-facial ones.

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Author Contributions

Conceived and designed the experiments: PL HM PA JH. Performed the experiments: PL HM. Analyzed the data: PL HM. Contributed reagents/materials/analysis tools: PL JH. Wrote the paper: PL HM PA JH.

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IV

ANGER SUPERIORITY EFFECT FOR CHANGE DETECTION AND CHANGE BLINDNESS

by

Pessi Lyyra, Jari K. Hietanen, & Piia Astikainen, March 2014

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Anger superiority effect for change detection and change blindness

Pessi Lyyra^{1,2}, Jari K. Hietanen¹ & Piia Astikainen²

¹ Human Information Processing Laboratory, School of Social Sciences and Humanities, FIN-33014 University of Tampere, Tampere, Finland

² Department of Psychology, PO Box 35, FIN-40014 University of Jyväskylä, Jyväskylä, Finland

Corresponding author:
Pessi Lyyra
E-mail: pessi.lyyra@uta.fi

Abstract

In visual search, an angry face in a crowd “pops out” unlike a happy or a neutral face. This “anger superiority effect” conflicts with views of visual perception holding that complex stimulus contents cannot be detected without focused top-down attention. Implicit visual processing of threatening changes was studied by recording event-related potentials (ERPs) using facial stimuli using the change blindness paradigm, in which conscious change detection is eliminated by presenting a blank screen before the changes. Already before their conscious detection, angry faces modulated relatively early emotion sensitive ERPs when appearing among happy and neutral faces, but happy faces only among neutral, not angry faces. Conscious change detection was more efficient for angry than happy faces regardless of background. These findings indicate that the brain can implicitly extract complex emotional information from facial stimuli, and the biological relevance of threatening contents can speed up their break up into visual consciousness.

Keywords: change detection; change blindness; nonconscious perception; anger superiority effect; face perception ; EPN ; N170

1 INTRODUCTION

Emotionally significant, especially threatening, stimuli occupy perhaps the most privileged place in the processing stream of visual information in humans. Behaviorally, they capture and hold attention automatically (Anderson, 2005), amplify perceptual processes (Fox et al., 2000; Öhman, Flykt, & Esteves, 2001), facilitate learning (Öhman & Soares, 1998) and initiate physiological fight or flight responses (LeDoux, 1996). At the level of the brain, the processing of threatening stimuli is faster and more distributed than the processing of neutral stimuli, thanks to the dedicated neural systems evolved to process threatening stimuli, even outside of attention and awareness (Öhman, 2009; LeDoux, 1996). It has been proposed that, in the human brain, at least two systems for perceiving naturally threatening stimuli have been evolved: one related to detection of predators of primates, such as snakes, and another related to detection of dominance-submissiveness for which visual analysis of faces expressing threat is especially relevant (Öhman, 1986).

In a number of studies, faces expressing anger have been shown to pop out more easily when presented simultaneously among neutral or happy faces than the other way around (Hansen & Hansen, 1988). This phenomenon has been dubbed the “anger superiority effect”, and it has been proposed as one example of the workings of the dominance-submissiveness system in the visual system (Öhman, 2009). Some controversy has been raised about the reliability of the phenomenon (Becker et al., 2011), but it has been convincingly shown, at least with faces of males (Becker et al., 2007), schematic faces (Öhman, Lundqvist, & Esteves, 2001), and facial expressions of prototypical emotions (Pinkham et al., 2010) as stimuli. Hansen and Hansen (1988) already noted that the phenomenon is hard to explain without some kind of implicit preattentive processing of the angry faces. They suggested a parallel, high capacity search mechanism for the detection of angry faces which enables only facial expressions expressing threat to capture attention and pop out.

Face perception and perception of emotional expressions have been shown to occur outside of attention, as shown by distractor effects on the pri-

mary task at the behavioral level (e.g., Eastwood, Smilek, & Merikle, 2003). Also cortical and subcortical, especially the colliculo-pulvino-amygdalar pathway, is activated in response to implicitly presented facial expressions in cortically blind (Morris et al. 2001), and in intact observers by using visual masking (Morris, Öhman & Dolan, 1999). Relatively early face-specific electrophysiological responses, such as the P1 response (e.g., Eimer & Holmes, 2002), N170 response (Blau et al. 2007; Leppänen et al., 2007; Wronka & Walentowska, 2011), responses sensitive to emotional saliency, like the 'early posterior negativity' (EPN) (Schupp et al., 2004; Jiang et al. 2009), and the visual mismatch negativity (vMMN) response related to the perception of regularities in the emotional content of stimuli (Astikainen & Hietanen 2009; Stefanics et al. 2012) have been observed to be preattentively modulated by facial emotional expressions.

One effective method to study implicit perception is the change blindness paradigm. In change blindness, viewers have difficulties in spotting differences between two consecutive images owing to interruption of the stimulation or presentation of global distracting stimuli simultaneously with the change (Simons & Rensink 2005, Rensink 2002). The difference can go unnoticed for considerable periods of time, even if the changes would otherwise be detected immediately. Because of this, the period of change blindness offers an opportunity to investigate the implicit processing of sensory stimuli by behavioral and neural measures.

The change blindness phenomenon has spurred the view that outside focal attention, visual representation is sparse, and that focal attention is needed for representation of the changed features, and especially so for combinations of those features (O'Regan & Noe 2001, Treisman 1998). According to a more moderate view, "proto-objects", preliminary coarse representations of objects of the visual scene can be formed outside the sphere of focal attention (Rensink 2002). Both these views hold that information carried by complexes of features nevertheless cannot exert a bottom-up effect on change detection, which relies solely on top-down attentional search.

Implicitly presented changes have been shown in a number of studies to affect electrophysiological and behavioral measures already during change blindness (Fernandez-Duque et al., 2003; Kimura, Katayama, & Ohira; 2008; Eimer & Mazza, 2005, Khittl, Bauer & Walla, 2009; Beck et al., 2001; Huettel, Guzeldere, & McCarthy 2001; Pessoa & Ungerleider, 2004; Schankin & Wascher 2007, 2008; Lyyra, Wikgren, & Astikainen, 2010; Lyyra et al., 2012). To date, only one study has investigated implicit processing of emotionally significant changes by electrophysiological measures in the change blindness paradigm (Lyyra et al., 2014). However, this study focused only on face perception in the change blindness paradigm in general by comparing change blindness-related ERPs to faces and scrambled faces, and the effect of emotional content was not controlled for. Therefore, it is an open question whether in addition to general facial configural information, specific information about the emotional content of the facial configuration could be extracted, and whether the anger superiority effect could carry over to change detection.

We searched for implicit change detection of distinct emotional expressions in the change blindness flicker paradigm. As angry faces in a crowd of happy faces are detected faster in a search task than a happy face in an angry crowd (Hansen & Hansen, 1988), we used a crowd of happy or angry faces as the unchanged images while one of these faces changed to an angry or a happy face, respectively. We hypothesized that the appearance of an angry face would be detected faster than that of a happy one. An anger superiority effect for change detection at the behavioral level could show that emotion-specific facial representations are among the proto-objects that are formed outside focal attention – and that these can have a bottom-up effect on change detection performance. As described above, in electrophysiological studies of the perception of facial expressions, the effects of emotional expressions are typically investigated as modulations of the relatively early responses, such as the P1, N170 and EPN event-related potential (ERP) responses. We hypothesized that these electrophysiological responses would be modulated differently for the appearance of angry vs. happy faces. Enlarged P1, N170 and EPN responses to the appearance of angry faces together with an elevated level of change detection performance would show that such complex information as that present in distinct emotional expressions, especially threat, can be implicitly extracted during change blindness. Such a result would be informative about the function of nonconscious visual perception, especially its influence on its conscious counterpart, which has been a neglected topic in studies of nonconscious visual perception (Eastwood & Smilek, 2005).

2 EXPERIMENT 1

2.1 Material and Methods

2.1.1 Participants

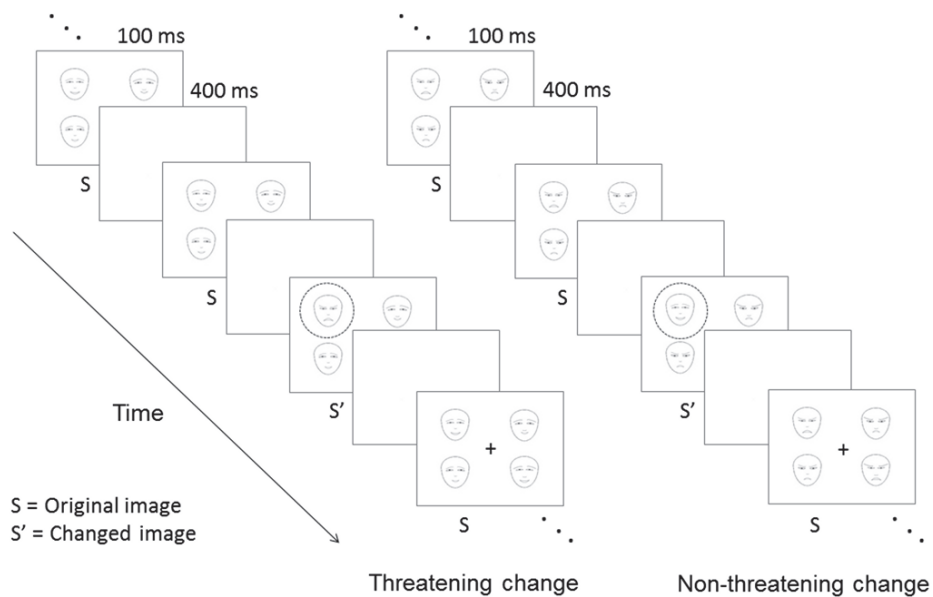
16 healthy volunteers (nine females and seven males, mean age 24.0 years) with normal or corrected-to-normal vision participated in the study. A written informed consent was obtained from the participants before the experimental treatment, and they were rewarded with movie tickets. The study conforms to the Code of Ethics of the World Medical Association (Declaration of Helsinki). Data from four participants were discarded because of excessive blinking (more than one-third of trials rejected), leaving data on twelve participants for inclusion in the statistical analyses (six females, six males, age range 20–29 years, mean age 23.7 years, S.D. = 2.8 years).

2.1.2 Stimuli and procedure

Four schematic faces all with either a happy or an angry expression were shown at a time around a fixation cross for 100 ms, separated by an interval of 400 ms. The faces differed slightly with respect to the size of and distance between elementary parts of the face (eyes, eyebrows, mouth), and these elementary parts were the same for stimuli of positive and negative valences, only inverted to create the facial expression of opposite valence (see Fig. 1). Pictures of these four faces were presented in a series of 3–27 presentations. Occasionally (20% of the presentations), a change of expression in one location of one of the faces occurred: in one condition, one of the happy faces turned into an angry one (Threatening change), and in the other condition one angry face showed a change in expression from anger to happiness (Non-threatening change, see Fig. 1). The series of stimuli for each change condition were randomly presented with equal probabilities. Changes were presented equiprobably in each of the four locations. Participants were instructed to search for ‘a face with a change of expression, and report the change location (left or right) by pressing the one of two buttons corresponding to the side of the change on screen. Either five oc-

currences of the change or a successful report of the change location ended the series (Niedeggen, Wichmann & Stoerig, 2001), and the participant initiated the following series by another button press. The experiment lasted 30 minutes, with from 94 to 228 (mean 162.6, S.D. 35.48) series presented, depending on the change detection rate.

FIGURE 1 Fig. 1. An illustration of the stimulus displays and sequences with changed expressions indicated by dotted circles in the threatening and non-threatening change conditions in Experiment 1.



2.1.3 EEG recordings and data analysis

An electroencephalogram (EEG) was recorded with Ag-AgCl electrodes from 21 channels (FP1, FPz, FP2, F3, Fz, F4, F7, F8, C3, Cz, C4, P3, Pz, P4, T3, T4, T5, T6, O1, O2, Oz) according to the international 10-20 system against average reference. The EEG signal was amplified 10 000 times, online band-pass filtered (0.1–100 Hz, 24 dB per octave) and digitized at a sampling rate of 1000 Hz. Impedances were kept below 2 k Ω . The signal was then offline band-pass filtered (0.1–30 Hz, 24 dB per octave). For the ERPs, a window from 100 ms before stimulus onset to 400 ms post-stimulus was selected. ERPs were averaged and corrected against a 100-ms pre-stimulus baseline. Sweeps containing artifacts (maximum voltage 70 μ V, minimum voltage -70 μ V, and maximum difference of 100 μ V within the sweep in any electrode) were discarded, with an average rejection rate of approximately 10%.

Change detection performance was measured as the mean number of change occurrences before the change was detected. These data were separately measured for each change-type condition.

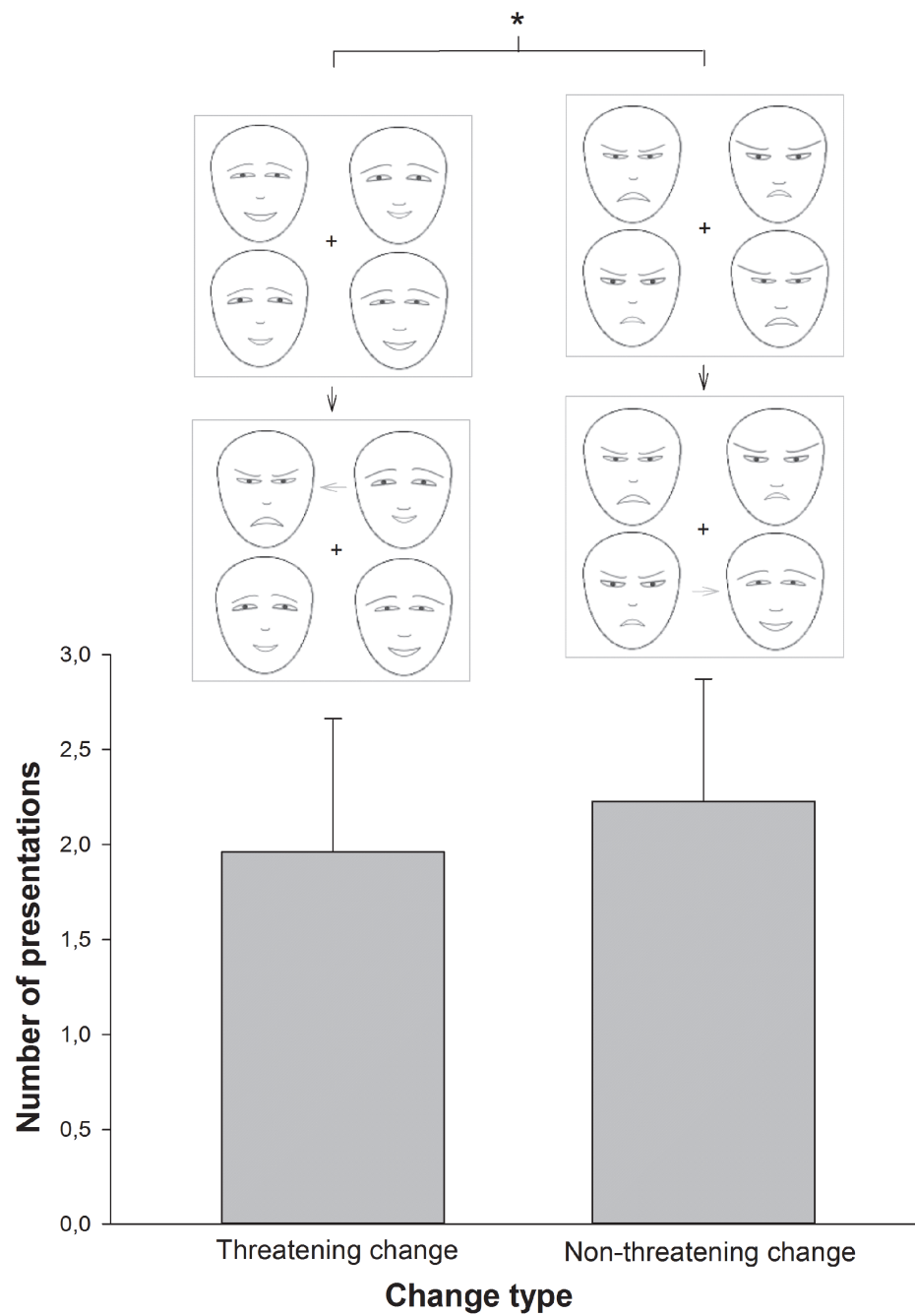
For the statistical ERP analyses, three time windows of face-specific ERPs were determined on the basis of the waveforms of grand-average ERPs (Figures 2 and 3): P1 (90–110 ms post-stimulus), N170 (150–170 ms post-stimulus) and EPN (250–350 ms). Mean amplitude values for ERPs to changed and original images in each emotion condition were extracted. For the original stimuli only those preceding the changes in the stimulus sequence were selected for the analyses. Thus, in the analyses, there were equal numbers of changed and unchanged stimuli. For the P1 and EPN time windows, the resulting values were analyzed with multivariate analysis of variance (MANOVA) for repeated measures with Hemisphere (Left, Right), Channel (Temporal [T5,T6], Occipital [O1,O2]), Emotion (Threatening change, Non-threatening change) and Change (Change, No change) as factors. N170 responses were extracted from electrode sites T5 and T6, and a MANOVA was conducted with factors of Hemisphere (T5, T6), Emotion and Change. An alpha level of .05 was used in all the analyses. T-tests were two-tailed. Partial eta squared (η_p^2) presents effect size estimates for MANOVA and Cohen's *d* for paired t-tests.

2.2 Results

2.2.1 Behavioral results

On average, participants detected threatening changes (angry face among happy faces) after 1.97 presentations (S.D. = .70) while non-threatening changes (happy face among angry faces) were detected after 2.28 change occurrences (S.D. = .63). The detection of threatening changes was significantly more efficient than the detection of non-threatening changes (see Fig. 2), as confirmed by two-tailed paired t-test, $t(11) = -2.68$, $p = .02$, $d = .47$.

FIGURE 2 The mean number of change presentations required for explicit report of change detection in Experiment 1.



2.2.2 Electrophysiological results

P1. For the P1 amplitudes, the main effect of Channel, $F(1, 11) = 5.59, p < .05, \eta_p^2 = .34$, and the interactions of Hemisphere * Channel, $F(1, 11) = 8.92, p < .02, \eta_p^2 = .45$, and Hemisphere * Channel * Emotion, $F(1, 11) = 8.15, p < .02, \eta_p^2 = .43$, reached significance, indicating that the P1 amplitudes were more positive at temporal compared to occipital sites in general, and even more so in the right hemisphere. This was confirmed by further MANOVAs for each Hemisphere, in which only the main effect of channel reached significance for the right hemisphere, $F(1, 11) = 10.70, p < .01, \eta_p^2 = .33$, but not for the left hemisphere. The interaction of Channel * Emotion did not reach significance for either hemisphere. No main or interaction effect involving the factor of Change reached significance for the P1 amplitude. However, the interaction of Emotion * Change was marginally significant, $F(1, 11) = 2.64, p = .082, \eta_p^2 = .25$, suggesting that the brain may respond to implicitly presented threatening changes already at this early latency.

N170. There were no significant main effects or two-way interactions for the N170 amplitudes. However, a three-way interaction between Hemisphere * Emotion * Change was significant, $F(1, 11) = 5.45, p < .05, \eta_p^2 = .33$, suggesting that the difference in the N170 amplitude for threatening vs. non-threatening changes was pronounced in the right hemisphere. This was further analyzed by paired channel-by-channel t-tests, which revealed that threatening changes evoked marginally more negative N170 amplitudes compared to the preceding unchanged stimulus, $t(11) = -2.02, p = .068, d = .19$, at the T6 electrode site, but not at T5. For non-threatening changes, the effects were not significant at either recording site (all $t_s < 1$).

EPN. A MANOVA conducted for the EPN amplitudes revealed no significant main effects for any of the factors. However, a significant interaction between Emotion and Change was observed, $F(1, 11) = 10.11, p < .01, \eta_p^2 = .48$, indicating that, at the EPN response latency, changes were processed differently depending on their emotional content. A further MANOVA with factors of Hemisphere * Channel * Change conducted for each Emotion condition (Threatening change, Non-threatening change) revealed that threatening changes elicited more negative amplitudes than the preceding scenes with only happy faces, as shown by the main effect of Change, $F(1, 11) = 13.35, p < .01, \eta_p^2 = .55$. No significant difference in amplitude was observed in responses to changed and original stimuli for non-threatening changes.

FIGURES 3 Brain responses during the change blindness period for the non-threatening change condition (happy face appearing in angry crowd) in Experiment 1. Top: Waveforms of grand average ERPs. The black line depicts responses to an angry crowd immediately preceding the change and the red line depicts responses to the changed crowd with one happy face. The position of the vertical axis indicates the onset of the stimulus display. Bottom: Scalp topographies of the mean differential voltage amplitudes between changed and original stimuli.

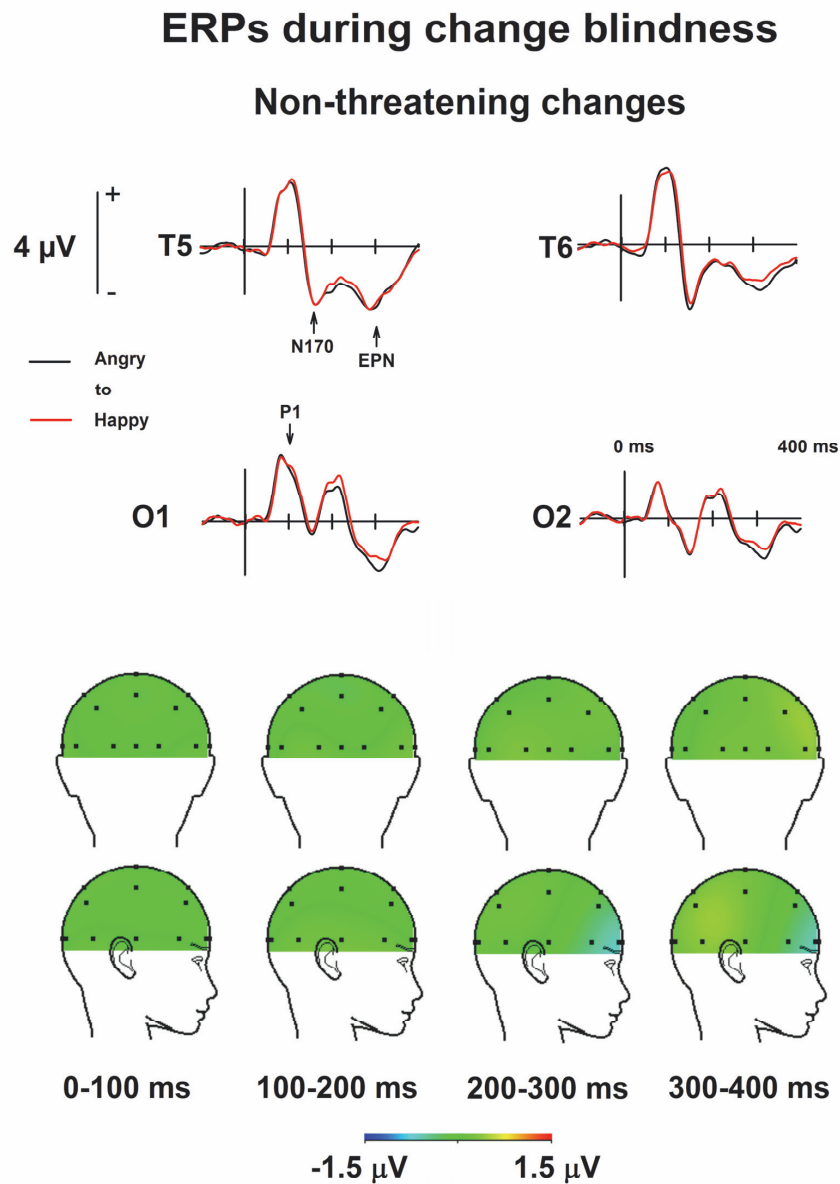
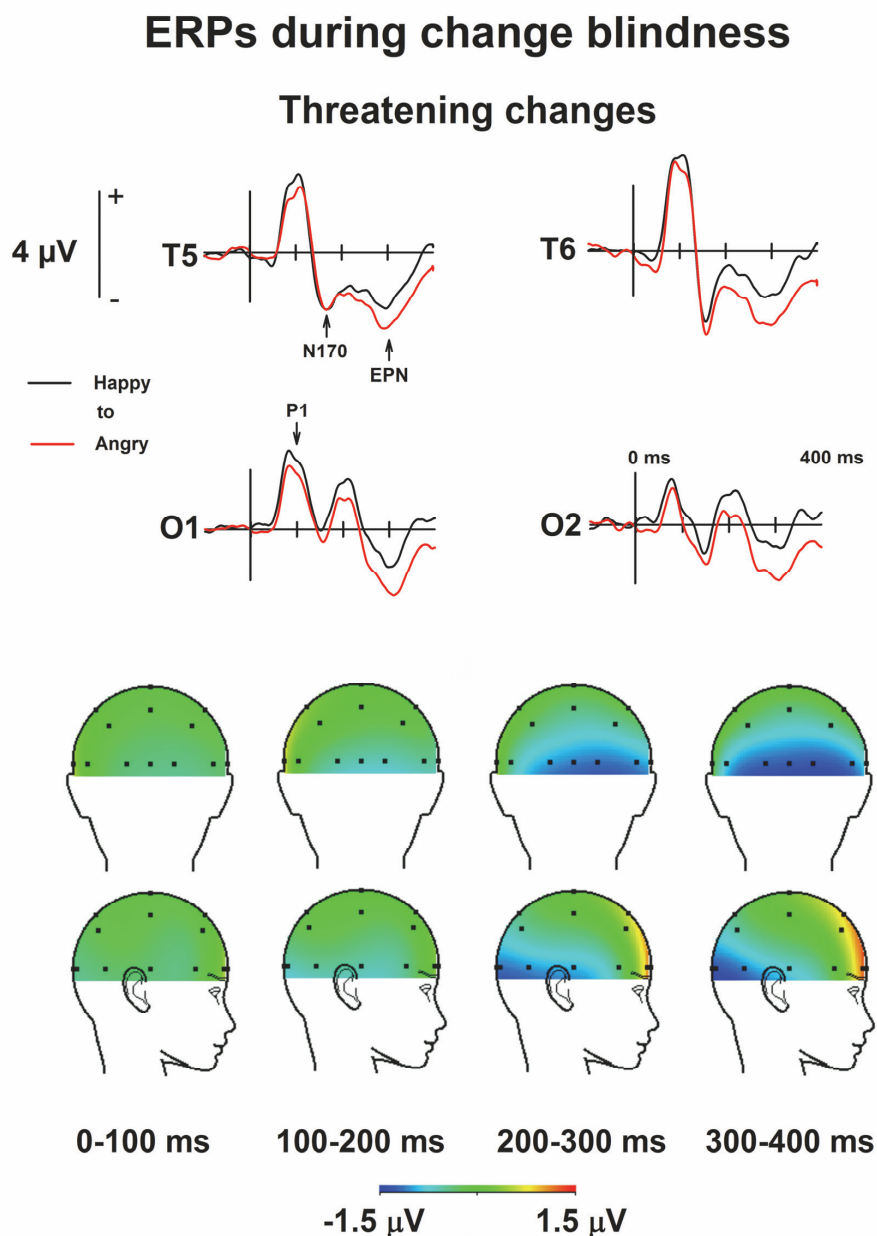


FIGURE 4 Brain responses during the change blindness period for the non-threatening change condition (angry face appearing in happy crowd) in Experiment 1. Top: Waveforms of grand average ERPs. The black line depicts responses to a happy crowd immediately preceding the change and the red line depicts responses to the changed crowd with one angry face. The position of the vertical axis indicates the onset of the stimulus display. Bottom: Scalp topographies of the mean differential voltage amplitudes between changed and original stimuli.



2.3 Discussion

We investigated explicit and implicit detection of changes in facial expressions of schematic faces in the change blindness paradigm. At the behavioral level, we found that changes involving an angry face appearing among happy ones (threatening change) were more efficiently detected than changes involving a happy face appearing among angry ones (non-threatening change), thus showing an anger superiority effect for change detection. For implicit change detection measured by ERPs in the change blindness period, we found that the N170 and EPN responses at the posterior-temporal sites were modulated according to the emotional content, threatening or non-threatening, in the stimuli: threatening changes elicited differential responses at the N170 and EPN latencies, especially in the right hemisphere, while the non-threatening changes did not elicit differential activities. The modulation of the N170 and EPN responses suggests that information about the emotional content of distinct facial expressions has already been extracted before explicit awareness of that content.

However, as it has been shown that the background may affect visual search so that an angry crowd may compromise the efficiency of the search (Frischen, Eastwood, & Smilek, 2008), the better detection rates for threatening changes may actually be due to the greater distracting effect of the threatening than non-threatening context on search of the non-threatening changes. Furthermore, the V-shaped form of the eyebrows is suspected to potentially attract attention so that the threatening expressions themselves are not necessarily configurally perceived, and the perception of threatening faces may be based on perception of single features (Aronoff, Barclay, & Stevenson, 1988).

3 EXPERIMENT 2

To investigate whether the anger superiority effect would hold in the change blindness paradigm irrespective of the effect of context, another experiment was run, devised to eliminate the effect of context by making the initial display identical for both change conditions. We hypothesized that the anger superiority effect would be observed similarly as in Experiment 1, this time independently of any potential effect of the context on change detection.

To eliminate the possibility that the perception of the threatening facial expressions is based on single features such as processing of the V-shaped eye-brows, we presented the stimulus faces both in upright and inverted orientations. In inverted orientation, happy faces contained the V-shaped eye-brows and inverted U-shaped mouth. Thus, if the anger superiority effect is based on configural processing of threatening faces, upright angry faces should be detected more efficiently than inverted happy faces. Regarding the detection of upright vs. inverted angry faces, we expected that the changes in inverted faces would possibly be detected less efficiently than those in upright faces. Although it has been shown that, for schematic faces, stimulus inversion does not completely disrupt the configural processing (Lundqvist, Esteves, & Öhman, 1999, 2004), stimulus inversion is, nevertheless, known to impair face processing (Freire, Lee, & Symons, 2000).

At the electrophysiological level, emotional facial stimuli elicit larger N170 and EPN amplitudes compared to neutral ones (Blau et al., 2007; Leppänen et al., 2007; Wronka & Walentowska, 2011; Jiang et al., 2009; Schupp et al., 2004), so we expected to see increased N170 and EPN amplitudes elicited by emotional stimuli compared to the neutral ones. However, it is not quite clear whether the emotional-neutral differential response is different for negative vs. positive facial expressions. The only study we are aware of, that specifically compared EPN amplitudes elicited by happy faces and angry faces compared to neutral ones, showed that both happy and angry faces elicited larger EPN amplitudes compared to the neutral faces, but there was no difference between the emotional faces in a task with consciously perceived stimuli (Calvo &

Beltrán, 2013). Here, we studied the possible differential N170 and EPN responses to angry and happy faces compared to neutral faces in the change blindness paradigm.

3.1 Materials and Methods

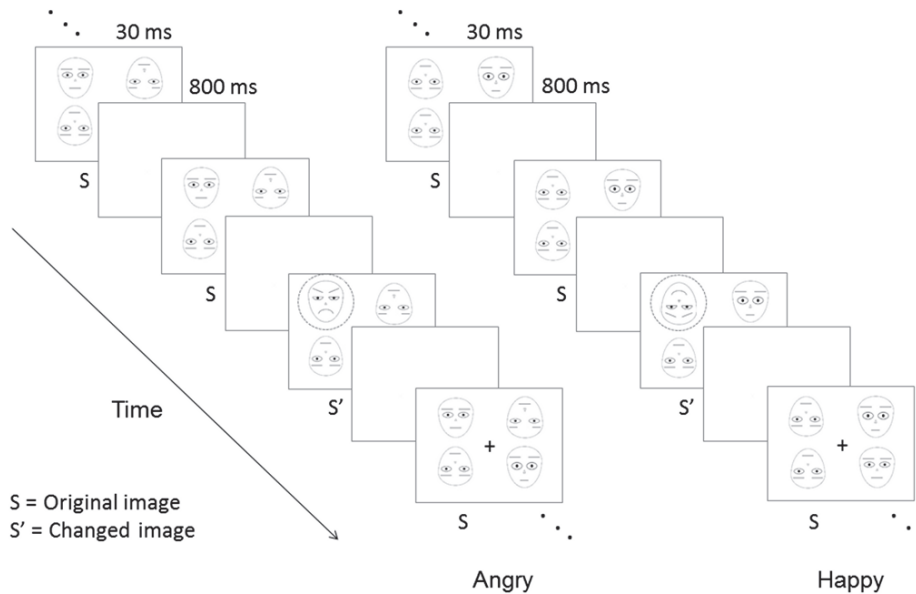
3.1.1 Participants

12 healthy volunteers (9 females), with age range of 18.1–51.9 years (mean age 27.45 years, S.D. = 9.11) participated in Experiment 2, a sample totally independent from that of Experiment 1. Two participants were left-handed, and the rest right handed, all having normal or corrected-to-normal vision. A written informed consent was obtained from the participants before the experimental treatment, and they were rewarded with movie tickets. The study conforms to the Code of Ethics of the World Medical Association (Declaration of Helsinki).

3.1.2 Stimuli and procedure

The experimental setup was as in Experiment 1 with the following discrepant methodological details. The stimuli were schematic faces, similar to the ones used for example in (Öhman, Lundqvist & Esteves 2001), and also for these images the elementary parts making up the eye-brows, eyes and mouths were inverted to create the expression of opposite valence as in Experiment 1 (see Fig. 5). There were two different change conditions: angry and happy condition. In the initial display for the both change conditions, four schematic neutral faces were presented. In the stimulus displays, two faces were upright and two were inverted, and the locations of these were randomly assigned. An infrequent expression change (happy or angry) occurred randomly for one neutral face in a similar stimulus sequence as in Experiment 1. The changes occurred for upright or inverted faces randomly with equal probabilities. The orientation of the changing face stayed always the same. All faces were shown at a time around a fixation cross for 30 ms, separated by an interval of 800 ms with the same presentation probabilities as in Experiment 1. The experiment lasted 45 minutes, with from 275 to 465 (mean 375) stimulus sequences presented, depending on the change detection rates.

FIGURE 5 An illustration of the stimulus displays and sequences with changed expressions indicated by dotted circles in the threatening and non-threatening change conditions in Experiment 2.

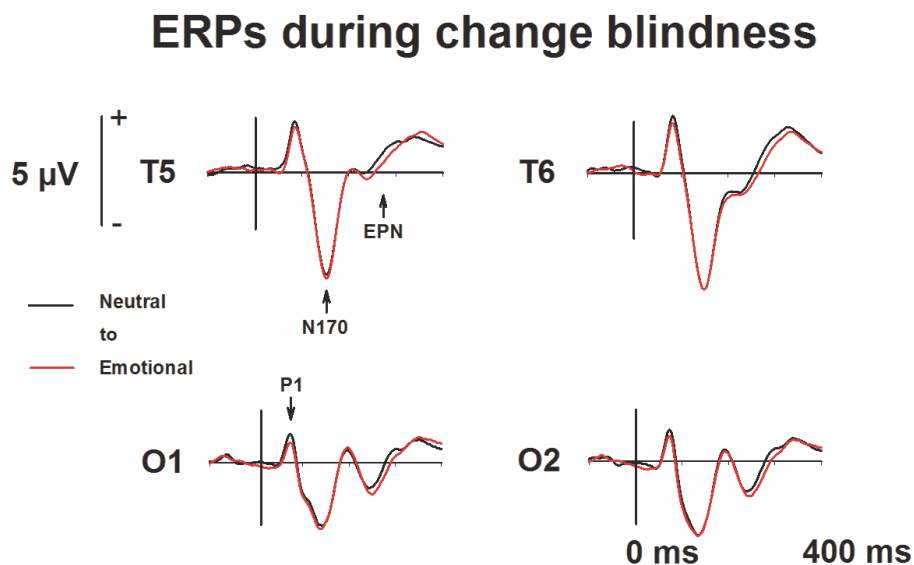


3.1.3 EEG-recordings and data-analysis

The recording and analysis of the EEG data were as in Experiment 1 except for that the ERPs were possible to be averaged and corrected against a longer (200-ms) pre-stimulus baseline, allowed by the longer gap between the images. The average rejection rate of the ERP segments was approximately 21%.

For the statistical analyses, three time-windows were determined for the same ERPs as in Experiment 1 using the same electrode sites. The time windows were also as in Experiment 1, except a time window of 250 ms to 300 ms, instead of 250 ms to 350 ms as in Experiment 1, was identified for the EPN, based on the grand average ERP waveforms (see Fig. 6). The resulting values were analyzed with analyses of variance (MANOVA) for repeated measures for each hemisphere with Orientation (Upright, Inverted) Emotion (Happy, Angry), Channel (temporal, occipital) and Change (Change, No change) as factors.

FIGURE 6 Waveforms of grand average ERPs during the change blindness period in Experiment 2. The black line depicts responses to a neutral crowd immediately preceding the change and the red line depicts responses to the change (one face with an emotional expression, happy or angry, appearing in neutral crowd). The position of the vertical axis indicates the onset of the stimulus display.



As in Experiment 1, change detection performance was measured as the mean number of change occurrences required for the change detection. This was analyzed within each Emotion * Orientation condition.

3.2 Results

3.2.1 Behavioral results

The detection rates in each change condition are given in Table 1. Despite orientation, change from neutral to angry was detected with less repetitions on average (2.71, S.D. = .49) than a change from neutral to happy expression (2.96, S.D. = .34), as indicated by the MANOVA main effect of Emotion, $F(1, 11) = 17.94$, $p < .01$, $\eta_p^2 = .62$. There were no difference between change detection efficacy for the inverted faces (2.90, S.D. = .42) and upright faces (2.76, S.D. = .46), $F(1, 11) = 2.65$, $p = 0.132$, $\eta_p^2 = .19$. Also the interaction of Emotion * Orientation, $F(1, 11) < .00$, $p = 0.97$, $\eta_p^2 < .00$ was non-significant.

TABLE 1

Mean number of change presentations required for explicit change detection				
	Angry	Inverted angry	Happy	Inverted happy
N	2.64	2.78	2.90	3.03
S.D.	.52	.54	.42	.33

3.2.2 Electrophysiological results

P1. The MANOVA revealed a significant main effect of change, indicating that implicitly presented changed images elicited reduced P1 amplitudes compared to previous unchanged images in the time window of 90–110 ms, $F(1, 11) = 15.01$, $p < .01$, $\eta_p^2 = .58$. The interactions of Hemisphere * Emotion, $F(1, 11) = 5.40$, $p < .05$, $\eta_p^2 = .33$, and Hemisphere * Emotion * Change, $F(1, 11) = 18.56$, $p < .01$, $\eta_p^2 = .63$, also reached significance. Further MANOVAs for each hemisphere revealed an Emotion * Change interaction for the P1 amplitudes at electrode sites only in the left hemisphere, $F(1, 11) = 5.39$, $p < .05$, $\eta_p^2 = .33$. Yet further MANOVAs for each emotion condition in the left hemisphere revealed that changes from neutral to happy faces elicited smaller P1 amplitudes compared to previous no change images, $F(1, 11) = 16.43$, $p < .01$, $\eta_p^2 = .60$, but not so for angry faces as changes ($F < .1$). No main or interaction effects for the orientation of the faces were found.

N170. There were no significant main or interaction effects for the N170 amplitudes. However, the Hemisphere * Change interaction was marginally significant, $F(1, 11) = 3.78$, $p < .08$, $\eta_p^2 = .26$, indicating that changes elicited marginally larger N170 responses in the left hemisphere than in the right hemisphere.

EPN. A MANOVA conducted for the mean amplitudes of the occipitotemporal electrode sites revealed the main effects of Channel, $F(1, 11) = 9.03$, $p < .02$, $\eta_p^2 = .45$, and Change, $F(1, 11) = 11.03$, $p < 0.01$, $\eta_p^2 = .50$, indicating that changed stimulus displays including emotional expressions evoked EPN-like negative differential responses compared to unchanged displays with neutral expressions. Also, the Hemisphere * Orientation * Change interaction was significant, $F(1, 11) = 9.03$, $p < .02$, $\eta_p^2 = .45$. Paired comparisons of the amplitudes in the right hemisphere, but not in the left hemisphere, revealed that, for upright faces, the changed faces elicited larger negativities than the unchanged ones, $t(11) = -4.35$, $p < .01$, $d = .56$, but there was no difference in responses to inverted faces ($t < 1$). No main or interaction effect including the factor of Emotion reached significance.

3.3 Discussion

We found that the threatening changes were again detected more efficiently than the non-threatening changes in the facial expressions. As the context for the changes was identical for the threatening and the non-threatening changes, the anger superiority effect observed in Experiment 2 similarly as in Experiment

1 supports the view that the threat-related content of the changes itself, not the context, can speed up change detection in the change blindness condition.

Stimulus inversion did not significantly affect the change detection rates, even though the alpha-level of less than .20 suggests that the possibility of compromising effect of inversion on change detection cannot be completely ruled out on the basis of the present results. More importantly, there was no difference for the anger superiority effect for upright and inverted threatening faces. This suggests that configural perception of the schematic threatening faces is not completely disrupted by the stimulus inversion. This result is also compatible with earlier findings showing configural processing for inverted schematic faces (Lundqvist, Esteves, & Öhman, 1999, 2004).

The emotional expression changes in the facial stimuli elicited larger EPN amplitudes compared to all neutral prechange views. However, there was no difference in the EPN amplitudes as a function of the emotional content of the change. The lack of the anger superiority effect at the neural level responses in Experiment 2 is probably due to the fact that when contrasted to neutral faces, emotional facial expressions of both negative and positive valences tend to elicit enhanced negativities (Calvo & Beltrán, 2013). Experiments 1 and 2 together seem to show that, for the measured ERP responses, the background seems to have an important role in determining the emotional relevance of the facial expression change: The threatening background in Experiment 1 could have occupied attentional resources and thus contributed to attenuated neural responses to non-threatening changes.

Changes to the upright faces elicited more negative amplitudes than changes to inverted ones in the right hemisphere. This may reflect the specialization of the right hemisphere in holistic, configural processing of visual information, especially of upright faces (Cattaneo et al., 2013).

4 GENERAL DISCUSSION

We examined implicit detection of emotionally significant changes in the change blindness paradigm by measuring change detection performance and ERPs evoked by unnoticed changes in two experiments with happy and angry faces as changes. The changes occurred in one face either in a crowd of expressive faces, where a happy face changed to an angry face or the direction of the change was the opposite (Experiment 1), or in a neutral crowd where one face changed to angry or happy face (Experiment 2). Threatening changes were detected more efficiently in both experiments, irrespective of the expression of the non-threatening background faces. Face perception related ERPs also indicated that the changes were implicitly detected, and the N170 and the EPN responses showed that the angry and happy emotional contents of the stimuli evoked differential responses, but only when they were contrasted to each other, not when contrasted to a neutral crowd.

In the visual search paradigm, the target face (deviant facial expression) is presented simultaneously with the other (distracting) stimuli. In this case, information about threat is present already from the beginning of stimulation. In the change blindness paradigm, instead, the changed stimulus is presented after the original images and an unstimulated period. Thus, the search conditions differ significantly between these two paradigms. In change blindness, information about the previous stimulus has to be retained across the relatively long unstimulated period, and information about the whole view accumulates throughout the stimulus sequence, after which the change is introduced (e.g., Hollingworth, 2012). This kind of visual search requires resources of sensory memory for the pre- and post-change views to be compared with each other. In the visual search paradigm, it is suggested that a parallel mechanism is responsible for the pop out effect for angry faces (Hansen & Hansen, 1988). In change blindness, this pop-out effect is eliminated by the interval inserted between the original and modified scenes. Therefore, compared to non-threatening changes, the enhanced detection of threatening changes is not necessarily due to their special relevance as changes but to their tendency to capture and hold attention

just like in the visual search paradigm. Consequently, our observation of a “neural anger superiority effect” in the change blindness condition can rather provide insight regarding how long information about emotionally significant stimuli is implicitly retained such that it can continue to affect change detection performance. Most likely, a parallel mechanism enabling comparison of the original and modified facial stimuli enables the implicit detection of angry faces, as indexed by the EPN modulation in Experiment 1. Although angry faces do not immediately capture the attention, as in the visual search paradigm, the information about the presence of angry faces can possibly guide attention to their location in the scene, and speed up their emergence into consciousness over multiple presentations.

It is also notable that in a continuous change blindness flicker paradigm, the change amount in the first change (original to changed) is the same as in the second change (changed to original) after the first appearance of the changed image. Therefore, it is not always necessarily clear which direction of the change is responsible for possible differences in change detection rates. However, we used the continuous oddball paradigm in the current experiments. In the oddball paradigm, the repeated stimulus becomes the “standard” stimulus while the changing stimulus is a “deviant” stimulus, creating an asymmetric contrast between these stimuli and enhancing significantly the change value of the changed image. Therefore, the superior detection of the threatening changes most likely reflect the first direction, not the second direction of the changes. Moreover, for the ERP results, there is no such question since the ERP responses were analyzed only for the changed images and the original ones immediately preceding them.

The EPN was measured by subtracting the response to the repeatedly presented unchanged stimulus from the response to the occasionally presented changing one. Therefore, an electrophysiological response related to stimulus rarity (i.e. visual mismatch negativity, vMMN) may overlap with the EPN response. It is, indeed, possible that the negativity we observed was partly a vMMN, which is usually posteriorly recorded between 100 and 400 ms after stimulus onset (Stefanics et al., 2012; Astikainen & Hietanen, 2009; Kimura, Schroger, & Czigler, 2011; Kimura et al., 2012). However, since the EPN response was observed in response to an angry face appearing among happy ones, but not vice versa, the responses seemed to be modulated not by rareness but as a function of the emotional content of the change. Thus, the negative differential deflection observed for threatening changes seemed to reflect implicit registration of a change in a threatening direction. This interpretation is strengthened by considering that the presentations of non-threatening changes (3 angry faces + 1 happy face), in fact, included more angry faces than the presentations of threatening ones (3 happy faces + 1 angry face). It should also be noted that physically the change was of equal size, involving the same physical elements in both conditions. Therefore, it is highly unlikely that the negative difference can be attributed to differences in the extent of physical changes in the stimuli, but reflects changes in the processing of information encoded in the complex

configuration of the stimuli. The vMMN is also sensitive to regularity violations related to emotional expressions in faces over and above the physical features of the facial stimuli (Stefanics et al., 2012; Kimura et al., 2012). A distinct, domain-specific generator for the emotional vMMN response, including temporo-occipital areas and the amygdalae have been suggested (Stefanics et al., 2012), similar to that previously suggested for the EPN response (Schupp et al., 2003). As it seems not entirely clear to what extent the emotional vMMN and EPN responses reflect different processes related to the visual processing of emotional expressions, further studies on their function are needed to resolve this issue.

Our observation of the implicit detection of emotional stimuli during change blindness is also informative for the theories of change blindness. Influential theories of change blindness and visual perception have maintained that top-down attention is needed to form coherent object representations and to maintain their coherence for change detection across interruptions, at least in the case of complex stimuli. In the absence of attention, visual perception would disintegrate into short-lived primitive features in sensory memory (Treisman, 1998; Rensink, 2002). Our results support the view that this is not necessarily the case for face-like stimuli, and complex representations of facial features can be formed outside of attention. Thus, extraction of information about the emotional content of facial stimuli is possible even outside of attention, and this information can have an effect on explicit change detection performance.

It is often maintained that top-down focal attention is needed to eventually observe changes across disruptions in stimulation (Rensink, O'Regan, & Clark, 1997). While this is largely compatible also with the results of our experiment, it does not, however, mean that there can be no bottom-up effect exerted by the implicitly presented stimuli. Possibly, unnoticed changes attract spatial attention to the change location, and this may enable focal attention eventually to detect the change (Niedeggen, Wichmann, & Stoerig, 2001). Our experiment suggests that emotionally significant stimuli can exert a detectable bottom-up effect on change detection performance (Eastwood & Smilek, 2005). Although proto-objects are volatile and subject to backward masking, it may be that proto-objects of threatening faces can capture attention over multiple presentations in a way that outlives the visual persistence of the proto-object. The enhancement of detection for threatening changes was relatively small (11% in Experiment 1, 9% in Experiment 2), suggesting that change detection is still largely dependent on other, presumably top-down factors. The bottom-up effect we observed may be confined to implicit detection of evolutionarily significant stimuli such as snakes, spiders and faces, the visual processing of which may be supported by dedicated, fast brain systems (LeDoux, 1996; Öhman, 1986). Future studies are needed to show whether other kinds of emotional stimuli can similarly affect change detection and indirect neural measures.

The anger superiority effect seems to hold for the change blindness paradigm similarly to found previously for the visual search paradigm. This evidence may help us in understanding the interaction of conscious and nonconscious perception in general: the enhanced conscious detection of threatening

changes compared to non-threatening ones suggests that the biological relevance of the threat content can influence how fast implicit contents can reach consciousness, even when the ordinary pop-out mechanism is eliminated. Modulation of the N170 and EPN responses by unnoticed emotional expressions suggests that complex representations of emotional facial stimuli can be formed during change blindness, a finding potentially informative regarding the neural mechanisms related to the emergence of the anger superiority effect.

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