Brain mechanisms of unconscious cognitive control

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Publication date
2009

1. Introduction

Common sense suggests that our choices are primarily influenced by consciously perceived information, which can be used to cautiously weight available alternatives and to select the appropriate action. However, a closer inspection of our day-to-day behavior suggests otherwise. To illustrate, imagine yourself driving home after a long day of work. Today, you have been extremely busy and, although you are not finished yet, you decided to head home anyway. While driving home, instead of focusing on the road ahead, you are reflecting about what happened that day at work and the work you have to catch-up on during the weekend. Suddenly, you arrive at your destination.

How can it be that you drove all the way home without having any memory of the events along the way? Crucially, your eyes must have been open all the time and you must have processed large amounts of information, and taken a large number of actions, to get home safely. However, very little of this information has reached your conscious awareness. Notwithstanding, you have produced rather complex and intelligent behavior, including shifting gears, monitoring other cars, adjusting your speed and steering, listening to the radio, and so forth. You did it all seemingly unconsciously, on automatic pilot; just as a plane can fly on automatic pilot (without being conscious).

This example illustrates that (at least part of) our everyday behavior unfolds entirely automatically and unconsciously, without requiring any conscious or voluntary control. In fact, this might not be as strange as it sounds since there seem to be many creatures capable of performing rather complex behaviors, probably without having a single conscious experience (e.g. bees, ants). All this suggests that there is a distinction between absorbing and acting on visual information, versus consciously seeing. However, accepting this idea has consequences. It immediately brings to mind the question whether all cognitive and neural operations can be initiated unconsciously or whether this might only be the case for highly trained and over-learned behaviors (e.g. driving a car). Maybe other cognitive operations, even more intelligent and complex ones, require consciousness? Or might these also unfold completely unconsciously?

In this thesis, I will explore the human ability to control behavior unconsciously and the extent and depth to which unconscious information is processed in the human brain; hotly debated issues in the field of Cognitive Neuroscience. Before outlining how, I will first give a brief overview of what is already known about this topic.

On the unconscious influences of our behavior

In the last decades, experimenters have revealed many intriguing observations of the influence of unconscious information on behavior, for example by studying brain-lesioned patients. When people suffer from a lesion in primary visual cortex, they lose their ability to detect visual stimuli presented in the hemifield contralaterally to their lesion. Notwithstanding the lack of conscious experience, some of these patients are still able to categorize or respond to stimuli presented in the blind part of their visual field when asked for a forced–choice response, a phenomenon termed "blindsight". Blindsight patients have for example been shown to be able to follow the path of a moving stimulus, verbally classify color stimuli, accurately point to objects, recognize facial expressions and even circumvent collision to various obstacles and barriers in their "blind" hemifield (de Gelder & Rouw, 2001; de Gelder et al., 2008; Lamme, 2001; Stoerig & Cowey, 1997; Weiskrantz, 1996). It is important to note that the patients themselves often claim to have no conscious awareness at all of any of these features, which reveals that a substantial amount of perceptual processing can occur in absence of consciousness, yet influence behavior.

The operation of unconscious perception/cognition has not only been studied in patients, but even more so in healthy participants. In order to do this, experimenters have designed many experimental protocols in which the perception of a stimulus is carefully manipulated. In a laboratory setting, masking is the most common and productive method of choice (Breitmeyer, 1984). In typical backward masking experiments (see Figure 1.1a), participants have to quickly respond to a target (e.g. a large arrow contour) that is rapidly preceded (< 100 ms) by another stimulus (e.g. a small arrow), the so-called prime. Because the prime is presented very briefly (e.g. 14 ms) and fits within the contour of the target (the "mask"), its visibility is strongly reduced (e.g. Kunde, 2003; Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003). Under specific conditions the prime can even be impossible to see. Importantly, the same briefly presented stimulus is perfectly visible when presented in isolation. Thus, stimuli that enter the visual system later in time can have large effects on the awareness of earlier presented stimuli. Interestingly, even when masked stimuli are not perceived consciously, they can still influence perceptual and behavioral processes, as evidenced by faster response times and fewer errors when the prime and the target are pointing into the same direction (congruent trials) than when they are pointing into different directions (incongruent trials). Apparently, the direction of an arrow can activate a corresponding response tendency in the absence of conscious awareness of the arrow itself. With this in mind, if we go back to the driving-example, it suddenly becomes clear that we might indeed be able to navigate home by processing information unconsciously on many occasions (e.g. to “decide” to go left or right at a crossroads).

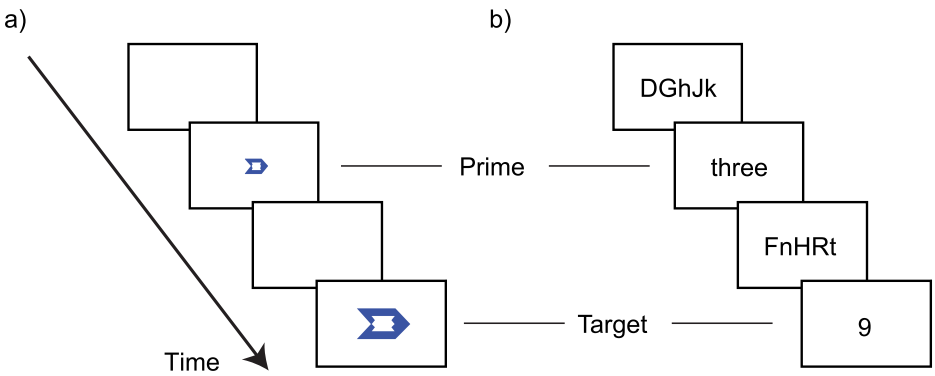

Figure 1.1 The masking paradigm

a) A typical sequence of events in a backward masking experiment. Participants have to quickly respond to a target (the large arrow) that is rapidly preceded (< 100 ms) by another stimulus (the small arrow), the so-called prime. The prime can either be congruent (pointing into the same direction) or incongruent to the target (pointing into the other direction). The prime is not visible when it is presented very briefly (e.g. 14 ms), because the target also functions as the metacontrast mask. b) A typical sequence of events in a pattern masking experiment. Subjects have to classify the target as a number larger or smaller than 5. The prime can be congruent (prime and target both falling on the same side of 5), and incongruent (prime and target are not falling on the same side of 5). The prime is not visible when it is presented very briefly (e.g. 33 ms).

More complex unconscious information processing

Recently, evidence for more complex unconscious information processing has been obtained, for example by using slightly more abstract stimuli, such as words or numbers. For instance, in the task depicted in Figure 1.1b, participants have to respond to target-numbers (the number 9) larger than five with their right hand, and to target-numbers smaller than five with their left hand. Before each target a prime-number is presented (the word “three”). Because the prime-number is presented briefly and sandwiched between random letter strings it cannot be perceived consciously; a phenomenon called pattern masking (Enns & Di Lollo, 2000). Again, participants are faster and produce fewer errors to congruent than to incongruent trials, which indicates that, also at a slightly more abstract level, unconscious information is able to influence our behavior (Dehaene et al., 1998).

The last couple of years, a plethora of even more astounding effects of unconscious stimuli on behavior, perception and cognition are revealed. To name a few, unconscious information has been shown to influence motivation (Pessiglione et al., 2007), the value of rewards (Pessiglione et al., 2008), emotional face/word processing (Naccache et al., 2005; Whalen et al., 1998), object recognition (Stoerig &

Cowey, 1997), semantic processing (Dehaene et al., 2001) and online action execution (Binsted, Brownell, Vorontsova, Heath, & Saucier, 2007). Furthermore, people are able to classify masked letters as consonants or vowels (Kiesel, Kunde, & Hoffmann, 2007b), masked words as representing small or large objects (Kiesel, Kunde, Pohl, & Hoffmann, 2006) or even analyze chess configurations unconsciously (Kiesel, Kunde, Pohl, Berner, & Hoffmann, 2009). These recent and thought-provoking results have furthers stressed the possible contribution of unconscious processes in shaping our everyday, but rather complex behavior. Given the extensive number of studies indicating that unconscious stimuli can affect high levels of cognitive processing one might wonder whether there are any limits to the scope and depth of unconscious information processing.

Are there any limits to unconscious cognition?

Although the evidence for unconscious influences on actions and decision-making is rapidly accumulating, much controversy surrounds the actual complexity and depth of unconscious information processing. Overall, the general assumption is that unconscious information can influence several highly automatic, "low-level" cognitive processes (e.g. reading, motor preparation), but that there are some more complex, "high-level" cognitive processes that are (intuitively) so strongly associated with conscious awareness that it seems impossible that these could also be triggered unconsciously. In this respect, perhaps the most hotly debated case is the existence of unconscious cognitive control (Dehaene et al., 2003; Eimer & Schlaghecken, 2003; Jack & Shallice, 2001; Kiesel, Kunde, & Hoffmann, 2007a; Lau & Passingham, 2007; Mayr, 2004; Umilta, 1988; van Gaal, Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008). Cognitive control is an umbrella term that refers to all cognitive processes that regulate and monitor ongoing actions to optimize goal-directed behavior, especially in novel, changing and non-routine situations (Miller, 2000; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). To illustrate, cognitive control seems necessary to plan series of events, to flexibly change plans and actions, to detect and learn from errors, to overcome/monitor response conflict, to select relevant sensory information and to inhibit inappropriate actions.

Empirically, the relationship between consciousness and cognitive control is nicely illustrated by an experiment of Merikle, Joordens and Stolz (1995). In their experiment, prime-words were presented either very briefly (e.g. 43 ms) or slightly longer (214 ms) and were preceded and followed by letter strings, which functioned as masks. Immediately after the second mask, a three-letter word-stem was presented. Participants were instructed to complete the word-stem with any word that came to mind, *except* the prime-word that was just presented. Interestingly, participants were perfectly able to exclude prime-words that were presented for a long duration, whereas they still used prime-words that were presented briefly on many occasions. This suggests that visual information activates several cognitive processes automatically and unconsciously, which can only be inhibited when information is perceived consciously. Nicely summarized by Dehaene (2008), it seems that "the ability to inhibit an automatic stream of processes and to deploy a novel strategy depends crucially on the conscious availability of information."

Another suggested limit of unconscious information processing is its apparent short-lived nature (Dehaene & Naccache, 2001). Masked priming studies showed that the effects of unconscious stimuli on behavior (and brain activity) are of a fleeting form since behavioral priming effects are generally absent when the interval between the masked prime and the target is longer than ~500 ms (Dupoux, de Gardelle, & Kouider, 2008; Greenwald, Draine, & Abrams, 1996; Mattler, 2005). These results imply that bridging information across time cannot occur if subjects are not aware of the stimulus (Dehaene & Naccache, 2001). On the other hand, conscious information can be held active for a long time, stored in working memory and used strategically to control behavior.

This phenomenon was nicely illustrated by Kunde (2003) using the task depicted in figure 1.1a. He showed that the conscious experience of response conflict on the previous trial influences control mechanisms on the current trial. More specifically, the correspondence effect (mean RT congruent trials – mean RT incongruent trials) on the current trial was smaller when trials were preceded by an incongruent trial compared to a congruent trial. These results are generally interpreted by assuming that, following the detection of conflict, PFC-mediated control processes increase future performance by increasing top-down control over sensory processes (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Egner & Hirsch, 2005; Kerns et al., 2004). However, the occurrence of specific stimulus/response repetitions might also explain some of the variance in conflict tasks (Hommel, Proctor, & Vu, 2004; Mayr, Awh, & Laurey, 2003; Nieuwenhuis et al., 2006). Crucially, in Kunde's experiment, regulatory control was absent when conflict-inducing stimuli were experienced unconsciously. Along similar lines, some authors have observed that "unconscious errors" do not trigger post-error control adaptations (post-error slowing in the trial following the error) whereas "conscious errors" do (e.g. Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001). In combination, this suggests that conscious information can be used strategically to plan, guide and control future behaviors, whereas unconscious information cannot. These (and other) results have led several authors to conclude (implicitly or more explicitly) that, although many aspects of our behavior can be triggered unconsciously, some cognitive control operations are in the exclusive domain of consciousness (Dehaene & Naccache, 2001; Eimer & Schlaghecken, 2003; Hommel, 2007; Libet, 1999; Pisella et al., 2000; Shiffrin & Schneider, 1977).

Brain mechanisms underlying conscious and unconscious information processing

The question which cognitive processes can operate outside of conscious awareness and which cannot, naturally relates to the way conscious and unconscious stimuli are processed in the human brain. In 2001, Dehaene and colleagues showed that unconscious (masked) words are still processed in extra-striate visual cortex and a region in the posterior fusiform gyrus corresponding to the visual word form area. These results provided evidence for the processing of unconscious stimuli in relatively high-level cortical brain areas (see also Dehaene et al., 1998). Crucially, in this study, they also observed that the neural activations evoked by unconscious words were radically reduced compared to the neural activations induced by conscious words. Whereas conscious words evoked large-scale frontoparietal activations, unconscious words did not, and activated only local and specialized neural processors (see also Dehaene et al., 2003). Interestingly, the strength of unconscious activations was observed to decay with increasing depth, highlighting the fleeting nature of unconscious information; this time in the brain.

Recently, researchers from many different labs have obtained similar results by using various paradigms (e.g. attentional blink, dichoptic fusion, attentional blindness) and neuroscientific methods (e.g. fMRI, electroencephalographic recordings (EEG), positron emission tomography (PET)) (Gross et al., 2004; Kouider, Dehaene, Jobert, & Le Bihan, 2007; Melloni et al., 2007; Moutoussis & Zeki, 2002; Rees, Kreiman, & Koch, 2002; Sergent, Baillet, & Dehaene, 2005; Tononi, Srinivasan, Russell, & Edelman, 1998). Based on these findings (amongst others), it has been argued that the prefrontal cortex (PFC) might play a “special role” in generating conscious experience and that unconscious stimuli cannot activate prefrontal cortices (e.g. Crick & Koch, 2003; Dehaene et al., 2003; Dehaene & Naccache, 2001; Rees et al., 2002). If unconscious information cannot active the PFC and it also “disappears” rapidly, it seems reasonable to assume that cognitive control functions (which rely on the PFC), cannot operate unconsciously.

In this thesis I put this long-held assumption to a direct test. In doing so, I mainly focused on a special case of cognitive control, namely inhibitory control. This is a rather extreme PFC-mediated form of cognitive control (Aron, 2007; Simmonds, Pekar, & Mostofsky, 2008) that allows people to cancel a planned or already initiated action, which becomes necessary when routine actions have to be overcome for optimal performance. The question is now: can humans change or inhibit a dominant response tendency based on unconscious information when necessary, or do we have to be conscious of the critical (control-initiating) stimulus for doing so? More specifically, if we go back to the example given in the beginning of the introduction: if we are driving in the "unconscious mode" and a pedestrian unexpectedly crosses the street, are we then able to avoid an accident (e.g. by breaking fiercely)?

How to study the possibility of unconscious inhibitory control?

Inhibition paradigms come in many flavors. The most famous of which are stop-signal task, the Go/No-Go task and a class of task known as conflict tasks (e.g. the Stroop, the Simon or the flanker task). A key feature of these tasks is that a planned or already triggered response must be inhibited or overcome in the course of action. I set out to modify these existing paradigms in such a way that we could study the possibility of unconsciously triggered cognitive control. To this end, I masked stop-signals in a stop-signal task (chapter 2 and 3), No-Go signals in a Go/No-Go task (chapter 4 and 5, 8) and flanker-like distractor stimuli in a masked priming task (chapter 6 and 7). Although this seems a rather straightforward approach, this method differs substantially from the way unconscious information processing has been studied thus far, as it combines two factors that, to our knowledge, have been rarely combined before.

First, in the majority of my experiments (chapter, 2-5, 8) the unconscious stimulus of interest is highly task-relevant and attended. For example in the stop-signal task, participants perform speeded right- or left-hand responses to go-signals, but are instructed to refrain from responding when the go-signal is occasionally followed by a stop-signal (Logan, 1994). I mixed conscious (weakly masked) and unconscious (strongly masked) stop trials with regular go trials to examine the possibility of unconsciously triggered inhibitory control. Importantly, in this task, the stop-signal is the key stimulus and is actively attended and processed. This is important, since it has been shown that attended and task-relevant stimuli are processed faster and more deeply in the human brain than unattended and task-irrelevant information (Lamme & Roelfsema, 2000). This becomes even more evident since, recently, it has been shown that attention can be oriented towards unconscious stimuli and enhances the influence of unconscious information on subsequent behavior (Naccache, Blandin, & Dehaene, 2002; Sumner, Tsai, Yu, &

Nachev, 2006). In contrast, in typical masked priming paradigms, the unconscious stimulus is usually irrelevant and generally participants are even instructed to ignore all stimuli preceding the target.

Second, and perhaps more importantly, the unconscious stimulus of interest is strongly associated with high-level cognitive control functions that strongly rely on prefrontal cortices. In other words, the task-set of the participant requires a deep level of information processing of the unconscious stimulus, which is the case to a lesser extent in previous masking studies. The combination of both factors allowed us to tap more directly into the possible depth and scope of unconscious information processing in the human brain than previous masked priming studies (or studies using related paradigms).

By continuously exploring the range of cognitive processes that do not require consciousness, the long-term goal of these experiments is to contribute eventually to answering one of the hardest questions in science: what is the function of consciousness (if any)? Furthermore, by exploring what types of neural activity can be triggered by unconscious stimuli and what types of activity cannot, I hope that these experiments might contribute to our understanding of what specific brain mechanisms are linked to conscious awareness.

Outline of this thesis

The research described in this thesis can be divided roughly in two parts. In the first part of this thesis, I mainly (however not exclusively) focused on cognitive control operations that I call *online cognitive control* processes. This is done to highlight that behavioral adaptations based on unconscious control signals are implemented *directly* (in the current trial). These processes are sometimes also referred to as *reactive control processes* (Braver, Gray, & Burgess, 2007). In the second part of this thesis, I mainly focused on *regulatory cognitive control* processes (sometimes also referred to as *proactive control*). The implementation of such preparatory control processes are reflected in behavioral adaptations *after* the experience of (unconscious) conflict/errors (in the next trial).

In the next chapter (chapter 2), by masking stop-signals in a stop-signal task, I aimed to test the possibility of unconsciously triggered inhibitory control. We report that unconscious information is able to initiate high-level inhibitory control processes, thereby breaking the proposed intimate relationship between consciousness and cognitive control.

In follow-up experiments (chapter 3-5) I set out to further explore the underlying neural mechanisms of the phenomenon. The main goal of these chapters was to examine whether unconscious control stimuli are able to active prefrontal control networks, commonly activated during consciously triggered cognitive control. In chapter 3 and 4, the main focus was on the temporal and relatively broad spatial dynamics of unconscious response inhibition using EEG, whereas the main goal of chapter 5 was to test the depth of processing of unconscious stimuli using methods that allow more spatial precision in the neuro-anatomical inferences (fMRI).

Chapter 6 deals with the structural basis of interference control on consciously and unconsciously presented conflict-inducing stimuli. To this end, a voxel-based morphometry study was performed to examine whether individual differences in pre-SMA structure (associated with conscious conflict resolution) can predict individual variability in the ability to inhibit (un)conscious irrelevant distrators and subsequently select the appropriate action.

In chapter 7 and 8, I shifted my focus away from *online* control adjustments towards understanding the impact of unconscious stimuli on the *regulatory* changes in cognitive control. As mentioned before, it is generally observed that unconscious information processing is fleeting, which suggests that (relatively) long-term influences should be absent if subjects are not aware of a stimulus. To test this assumption, the data presented in chapter 3 and 6 was re-analyzed. This time, we focused our analyses on those trials that followed trials containing unconscious conflict-inducing stimuli (chapter 7) or an unconscious No-Go stimulus that was responded to ("unconscious errors") (chapter 8). This allowed us to examine the potential lifetime and long-term influence of unconscious information on subsequent behavior and brain activity.

In the final chapter (chapter 9), I will summarize and interpret the obtained results and outline possible future directions for the study of unconscious cognition.

Publications and co-authors

All chapters that are included in this thesis are accepted or submitted for publication in international peer reviewed journals and are included in slightly adapted form to increase the consistency of the thesis. Here, I would like to express my gratitude towards several colleagues with whom I collaborated extensively during my PhD project and who have made important contributions to the experiments/papers. On the next page is a list of references to acknowledge them.

Chapter 2

van Gaal, S., Ridderinkhof, K. R., van den Wildenberg, W. P. M., & Lamme, V. A. F. (2009). Dissociating consciousness from inhibitory control: Evidence for unconsciously triggered response inhibition in the stop-signal task. *Journal of Experimental Psychology: Human Perception and Performance, 35*, 1129-1139.

Chapter 3

van Gaal, S., Ridderinkhof, K. R., Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. F. (2008). Frontal cortex mediates unconsciously triggered inhibitory control. *Journal of Neuroscience*, *28*, 8053-8062.

Chapter 4

van Gaal, S., Lamme, V. A. F., Fahrenfort, J. J., & Ridderinkhof, K. R. Dissociable brain mechanisms underlying the conscious and unconscious control of behavior *(revised and resubmitted, Journal of Cognitive Neuroscience)*.

Chapter 5

van Gaal, S., Ridderinkhof, K. R., Scholte, H. S., & Lamme, V. A. F. Unconscious activation of the prefrontal No-Go network *(revised and resubmitted, Journal of Neuroscience).*

Chapter 6

van Gaal, S., Scholte, H. S., Lamme, V. A. F., Fahrenfort, J. J., & Ridderinkhof, K. R. Pre-SMA grey-matter density predicts individual differences in action selection in the face of conscious and unconscious response conflict *(revised and resubmitted, Journal of Cognitive Neuroscience)*.

Chapter 7

van Gaal, S., Lamme, V. A. F., & Ridderinkhof, K. R. Unconsciously triggered conflict adaptation *(submitted)*.

Chapter 8

Cohen, M. X*, van Gaal, S.*, Ridderinkhof, K. R., & Lamme, V. A. F. Unconscious errors enhance prefrontal-occipital oscillatory synchrony *(revised and resubmitted, Frontiers in Human Neuroscience)*. * Equal contribution

Other publications:

van Gaal, S., & Fahrenfort, J. J. (2008). The relationship between visual awareness, attention, and report. *Journal of Neuroscience*, *28*, 5401-5402

Jolij, J., Scholte, H. S., Van Gaal, S., & Lamme, V. A. F. The brain decides late: long latency visual evoked potentials reflect perceptual decisions. *Journal of Cognitive Neuroscience (accepted pending minor revisions).*

Fahrenfort, J. J., Heinen, K., van Gaal, S., Scholte, H. S., & Lamme, V. A. F. Object classification in the absence of visual awareness and figure ground segregation: an fMRI study *(submitted)*.

Fahrenfort, J. J., Scholte, H. S., van Gaal, S., & Lamme, V. A. F. Tunnel vision in early visual cortex: Suppression of cortical activity in the periphery of figure-ground segregation *(submitted)*.

Wokke, M., van Gaal, S., Ridderinkhof, K. R., & Lamme, V. A. F. On the flexibility of unconsciously triggered inhibitory control *(in preparation)*.