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CAMILE MARIA COSTA CORRÊA

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Camile Maria Costa Corrêa

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### THE ROLE OF AWARENESS, NEUROMODULATION AND METACOGNITION IN HUMAN DECISION MAKING

ACADEMISCH PROEFSCHRIFT ter verkrijging van de graad van doctor aan de Universiteit van Amsterdam op gezag van de Rector Magnificus prof. dr. ir. K.I.J. Maex ten overstaan van een door het College voor Promoties ingestelde commissie, in het openbaar te verdedigen in de Agnietenkapel op woensdag 28 november 2018, te 10:00 uur

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Faculteit der Maatschappij- en Gedragswetenschappen

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"Es denkt in mir" - F. Nietzsche."We are a way for the cosmos to know itself" – C. Sagan.

### 1. Introduction

How do humans make (good) decisions? Although we might attribute our decisions to conscious control, research has shown that large parts of our decision making machinery operates outside of conscious awareness (D'Ostilio & Garraux, 2012; Lau & Passingham, 2007; van Gaal & Lamme, 2012; Van Opstal et al., 2011). This thesis has two main goals: 1) to further unravel the role of conscious awareness in human decision making and cognition, and 2) to further understand why we sometimes become aware of information in our environment and why sometimes not. Before explicitly addressing these issues let me first consider what is broadly known about how (visual) information is processed in the human brain and the neural mechanisms involved in both conscious and unconscious information processing.

### Unconscious information processing is powerful

A large body of literature has shown that in the initial processing stages the brain responds to visual information as in a reflex: fast, automatically and unconsciously (Lamme & Roelfsema, 2000). Information is first processed in low-level regions (e.g. V1, A1) and is then sent to higher-level regions in the cortical hierarchy (e.g. information flows unidirectionally from primary to associative cortices). This initial reflex-like process is referred to as the fast feedforward sweep (FFS) of information processing and it is responsible for the detection and categorization of objects (Fahrenfort, Scholte, & Lamme, 2008; Kafaligonul, Breitmeyer, & Öğmen, 2015; VanRullen, 2007). It has been observed that the FFS is entirely unconscious and can activate a broad set of cortical areas, including areas in the ventral and dorsal visual pathways (Dehaene et al., 2001; Fang & He, 2005; Naccache & Dehaene, 2001). Besides visual information processing, several recent studies have shown that even high-level cognitive processes may unfold fully unconsciously through the FFS, as depicted schematically in Figure 1.1. Some examples are the unconscious extraction of quantities (e.g. numbers) (Naccache, 2001; Van Opstal, de Lange, & Dehaene, 2011), semantic relations (Devlin et al., 2004; Luck, Vogel, & Shapiro, 1996; Yeh, He, & Cavanagh, 2012), the emotional valence of words and pictures (Gaillard et al., 2006; Naccache et al., 2005), the value of rewarding stimuli (Pessiglione et al., 2007, 2008; Schmidt et al., 2010) and even schematic chess configurations (Kiesel et al., 2009). Interestingly, unconscious stimuli have also been shown to modulate activity in prefrontal regions, typically recruited in "cognitive control tasks" in which participants have to flexibly organize their thoughts and actions to optimize goal-directed behavior (Jiang et al., 2013; Ridderinkhof et al., 2004). For example, response inhibitory processes (Hughes, Velmans, & De Fockert, 2009; van Gaal et al., 2008; van Gaal et al., 2010; van Gaal et al., 2011) and task-switching (Lau & Passingham, 2007; Reuss et al., 2011) have been observed to be influenced by unconscious stimuli.

In sum, many perceptual, emotional and higher-order cognitive functions can be influenced by unconscious stimuli. This observation raises questions about the extent to which conscious awareness may actually be relevant or beneficial for certain perceptual or cognitive processes (Dehaene & Naccache, 2001). For example, are there any specific cognitive functions that require conscious stimulus processing to unfold, and if so, why? To address this issue scientists have carefully compared behavioral and neural measures in situations in which individuals were aware of certain information versus situations in which they were not, also referred to as the "minimal contrast approach" (Dehaene & Changeux, 2011). This revealed several neural mechanisms that were uniquely observed when subjects could consciously access information.



*Figure 1.1.* Illustration of several brain areas and some of their corresponding (perceptual/emotional/cognitive) functions that are influenced by unconscious information.

### Conscious information processing

Recurrent processing (RP) is the stream of processing by which primary (e.g. visual) areas are reactivated by higher-order (e.g. visual) brain areas. Thus, after information has been sent forward to higher-level areas, information is subsequently fed back to lower-level brain regions (see **Fig. 1.2**). Over the years, several authors have argued that this feedback process is crucial for

stimulus awareness (Boehler et al., 2008; Dehaene et al., 2006; Lamme, 2006; Lamme, Super, & Spekreijse, 1998; Pascual-Leone & Walsh, 2001). Hence, several influential theories of consciousness focus on the distinction between FFS and RP processing, for example, the global neuronal workspace theory (Dehaene & Changeux, 2011; Fisch et al., 2009; Gaillard et al., 2009), the information integration theory (Tononi, 2004; Tononi, 2008) and local recurrency models (Block, 2005; Lamme, 2003, 2006; Pascual-Leone & Walsh, 2001). Accordingly, one may argue that whether a certain type of cognitive process requires conscious awareness may depend on the necessity of RP for that cognitive process to unfold.



**Figure 1.2. Illustration of the feedforward and feedback processing pathways in the human brain.** Feedforward processing refers to information flow (green dotted arrows) from lower-level to higher-level (visual) areas, while feedback processing (blue solid arrows) refers to subsequent reactivation of lower-level brain areas (e.g. V1) by higher-level brain areas (e.g. IT: inferotemporal cortex).

# Consciousness might be required for durable information maintenance and performance monitoring

Which cognitive processes may depend on recurrent processing to unfold? Due to the involvement of RP, conscious access of information is associated with a massive cortico-cortical exchange of information, which may allow for the widespread and flexible routing of information between different brain regions (Dehaene et al., 2006; Dehaene & Naccache, 2001). This may allow for the durable maintenance of information and may trigger an increase in the flexibility of information processing. Therefore, it has been argued that consciousness may be associated with high-level cognitive functions that require long distance recurrent connectivity and the use of information over an extended period of time. Examples of these functions are working memory (but see Dutta et al., 2014; Pan et al., 2013; Soto, Mäntylä, & Silvanto, 2011), which is probably dependent on the integrity of the dorsolateral prefrontal cortex

(Damasio, Everitt, & Bishop, 1996; Dehaene et al., 2014; Kane & Engle, 2002; Mazoyer et al., 2001), which may be crucial to hold information online for longer periods of time (Curtis & D'Esposito, 2003; Fuster, 2008). Another potential example is the ability to perform multi-step calculations (2+2-3) (Sackur & Dehaene, 2009), which has been suggested to require conscious control in order to exchange information in a slow and serial manner (Dehaene & Cohen, 2007; Dehaene & Sigman, 2012; van Gaal et al., 2014). Others have suggested that certain types of learning may also require conscious experience of the to be learned information (not to be confused with implicit learning, which relates to situations in which participants can learn important features of or relations between consciously perceived stimuli without being aware of what has been learned, e.g. Cleeremans, Destrebecqz, & Boyer, 1998; Reber, 2013).

In the scientific search for cognitive and perceptual operations that might necessarily need consciousness to unfold, cognitive control has for a long time been one of the other favorite candidates. Cognitive control is an umbrella term for many cognitive functions that allow an organism to flexibly adapt to (unexpected) changes in the environment (Ridderinkhof et al., 2004) and it includes cognitive functions such as response inhibition, conflict resolution, performance monitoring and task-switching (van Gaal, de Lange, & Cohen, 2012). Performance monitoring is essential for the accurate updating of decision parameters in order to avoid errors in the (near) future (Fuster, 2016; Ridderinkhof et al., 2014; Ullsperger, Danielmeier, & Jocham, 2014; Ullsperger et al., 2014). Overall, when deviations from the expected outcome of a decision are detected these have to be communicated to brain structures that can implement counteractive mechanisms, thereby correcting and optimizing ongoing or future actions (Ullsperger et al., 2014). Generally it is thought that the medial frontal cortex is mainly involved in the evaluation of outcomes and the detection of performance errors and conflicting response tendencies, whereas it is the lateral and orbitofrontal prefrontal cortex that are involved in the subsequent implementation of appropriate adjustments (Ridderinkhof et al., 2004). Because cognitive control therefore is thought to require flexible routing mechanism of information from e.g. medial to lateral prefrontal regions (Jiang et al., 2018), these processes might need consciousness (and recurrent processing), as they can probably not unfold on feedforward activity only.

In the first two experimental chapters of this thesis we aim to tackle the question to what extent performance monitoring mechanisms, and especially the evaluation of decision outcomes and the potential to learn from these, are related to conscious awareness.

### Sources of variability in (conscious) perception

The second part of the thesis focuses more on why a stimulus that is difficult to perceive sometimes becomes aware and sometimes not. For example, imagine that one performs a difficult perceptual decision making task in which you have to decide on the orientation of a noisy Gabor stimulus. In order to process the identity of the stimulus and to decide between the two response options (left vs. right), people aim to take into account all the available sensory evidence: the observer has to absorb all the sensory evidence for both the "left" and "right" decision (Deco et al, 2013; Shadlen & Kiani, 2013). If performance on such a task is calculated across trials a d-prime (d') can be calculated (based on the number of hits an false alarms) in the Signal Detection Theoretical (STD) framework. D' equals zero when there is no sensory evidence available to distinguish between the two stimulus classes, forcing the observer to guess (Green & Swets, 1966). In case the two stimuli are distinguishable, for example by increasing the contrast of the Gabor stimulus, d' will become higher, and above zero (d'>0). In this case, d' is a measure of discriminatory performance between the two stimuli (left vs right-oriented Gabors) but d' can also be calculated in a (yes-no) detection task (stimulus present vs absent) and then reflects stimulus detectability.

Importantly, the observer's performance is not a perfect representation of the true stimulus evidence but it is corrupted by both external noise and internal noise in the system, which eventually leads to decision variation across multiple trials. Interestingly, even when a stimulus is repeatedly presented in the same way (e.g. with the same contrast), participants often make different decisions about them (Glimcher, 2005; Wyart & Koechlin, 2016). To better understand the reasons behind this variability in decision making and stimulus reportability, we aim to increase our understanding of the sources of this intrinsic variability in our perception. One prime candidate that may partly explain these perceptual fluctuations are ongoing and intrinsic variations in the brain's arousal state, due to the release of neuromodulatory neurotransmitters, such as noradrenaline, dopamine and acetylcholine (Aston-Jones & Cohen, 2005). These neuromodulators are diffusely released in the cortex during perceptual decision-making and, based on recent studies, seem to reflect remarkably specific cognitive and behavioral processes associated with our decisions (de Gee et al., 2017; de Gee, Knapen, & Donner, 2014; Kloosterman et al., 2015; Murphy et al., 2014; Nieuwenhuis, Aston-Jones, & Cohen, 2005). Neuromodulation is therefore a potential contributor to choice and perceptual variability in perceptual decision-making tasks. This topic is specifically addressed in Chapter 3 of this thesis.

### Perceptual awareness versus metacognitive evaluation

Perceptual awareness reflects the subjective perceptual experience of a person (the "content" of the experience), whereas metacognition, on the other hand, relates to the knowledge about that subjective experience (or more generally about task performance): the "knowing" about our perception or performance (Lau & Rosenthal, 2011). Therefore, metacognition is also referred to as "second-order" or "type 2" performance. Metacognitive accuracy can vary across individuals and across trials. For instance, when there is a large degree of overlap between one's first-order decision accuracy (e.g. discrimination d' on the orientation of a Gabor) and confidence about the correctness of those decisions, so when someone is highly confident about the decision when being correct and not confident when being incorrect, metacognitive accuracy is high (Fleming & Lau, 2014). Recent developments have made it possible to calculate meta-d' in the SDT framework (Fleming & Lau, 2014). Meta-d' directly reflects a person's metacognitive accuracy, or in other words, the accuracy of one's insight in "first-order" or "type 1" task performance. This recently introduced measure allows us to study the association between metacognition (second order performance) and cognition in similar ways as has been done previously when studying the association between perceptual awareness (first-order performance) and cognition (see e.g. van Gaal et al., 2012).

In the final chapters of this thesis we therefore further explore the relationship between internal variations in the brain's arousal state and metacognitive accuracy (Chapter 4) and the role of metacognition in the monitoring and updating of our decisions (Chapter 5-6).

### Main research questions

To summarize, in this thesis we are interested in unraveling what is the role of awareness, neuromodulation and metacognition in human decision making. For that, the work presented in this thesis is built around three main questions:

- How does the level of awareness of decision outcomes modulate the way people learn, decide and monitor their own behavior? (Chapters 2-3).
- How do stimulus-evoked fluctuations of brain's arousal state affect perceptual awareness and metacognitive evaluation of decision accuracy? (Chapter 4).
- What is the role of metacognition in monitoring and updating our decisions? (Chapters 5-6).

### Methodological approaches

To address the above outlined research questions, in the studies reported in this thesis, we manipulated perceptual awareness in two ways, either by using the masking technique or by presenting stimuli at the threshold of perception. Masking is a common method to manipulate stimulus awareness (Fig. 1.3A). In a typical backward masking experiment participants have to quickly respond to a target, for example a large arrow pointing to a specific direction. This target is then rapidly preceded (<100 ms) by another stimulus, e.g., a smaller arrow, called a prime, pointing in a specific direction as well. In the meta-contrast masking paradigm illustrated in **Figure 1.3A**, the prime is presented very briefly (e.g. 14 ms) and fits within the contour of the target (i.e., the 'mask'), which strongly reduces its visibility (e.g. Kunde, 2003; Vorberg et al., 2003). Without the masking procedure, primes are perfectly visible when presented in isolation. Interestingly, even when masked stimuli are not perceived consciously they can still influence behavioral responses. For example, faster response times and fewer errors are typically observed when the prime and the target are pointing into the same direction (congruent trials) than when they are pointing into different directions (incongruent trials). Thus, the direction of an arrow can activate a corresponding response tendency in the absence of conscious awareness of the arrow itself. Crucially, (meta-contrast) masking is a paradigm in which we externally manipulate consciousness by increasing or decreasing the masking strength.

Another way of manipulating consciousness is by presenting stimuli at the threshold of perception. For instance, in a perceptual discrimination task (Fig. **1.3B**) people are required to make a judgement about the orientation of a Gabor patch embedded in noise. The level of difficulty can be individually staircased (by varying the amount of noise in the stimulus) in such a way that every participant is correct in, for instance, 70% of the occasions. This paradigm is interesting, because even when the stimulus is presented the same way on each trial (e.g. with the same contrast or the same noise level), participants may sometimes perceive the stimulus and respond correctly, and sometimes may not perceive the stimulus and respond incorrectly (Charles et al., 2013; Wyart & Tallon-Baudry, 2008). This variation in perception is thought to rely on intrinsic fluctuations in neuromodulation of the brain, i.e. the brain's arousal state (Aston-Jones & Cohen, 2005). Crucially, in contrast to the masking paradigm, threshold stimulation paradigms do not manipulate consciousness externally, but because the stimulus strength/contrast remains constant across trials, conscious awareness is likely determined by internal fluctuations in neural activity (Dehaene & Changeux, 2005).



**Figure 1.3. Examples of task designs in which consciousness was manipulated throughout this thesis. (A)** Masked priming experiment. Primes can be congruent or incongruent with the direction of the target and participants respond to the direction of the target while attempting to ignore the prime. The figure depicts a congruent trial. (B) Perceptual discrimination experiment. Participants report the direction of a Gabor patch (clockwise or counterclockwise), after which veridical feedback is presented, which is either masked or unmasked. The figure depicts unmasked feedback due to the absence of backward masks. (C) Binary choice experiment. Two response options are shown until the participant choses one of them. The probability of left/right responses can be manipulated by manipulating the reward probability of each response option (e.g. 70/30 %). Feedback visibility can be manipulated by varying the presentation duration of the word (correct/error) and the backward mask. The figure depicts masked feedback, due to the short duration of backward masks.

### Overview of this thesis

In **chapter two** we tested the possibility to learn from reinforcements (reward vs no reward) at different levels of stimulus visibility and we examined the underlying neural mechanisms related to learning from these decision outcomes (external feedback), while measuring electroencephalographic recordings (EEG). Participants performed a binary choice task (**Fig. 1.3C**), a

modified version of a probabilistic reversal learning task (Cohen, Elger, & Ranganath, 2007), in which we manipulated the visibility of rewards using a standard masking technique (Ogmen, Breitmeyer, & Melvin, 2003). Response-reward contingencies reversed several times over the course of the experiment and participants were instructed to select the response option that was most often rewarded. Furthermore, we used computational modeling to evaluate the existence of learning from outcomes at different levels of visibility, and to characterize the computational signature of such learning. We combined EEG measurements with a computational modeling approach to investigate, at the time of reward processing and on a trial-by-trial basis, the neural correlates of the different processes influencing participants' future choices and how those were affected by reward visibility.

In chapter two we were able to track participants' expectations of being rewarded on each single trial due to reinforcement learning modelling, but unfortunately we could not evaluate subjects' confidence in being rewarded with the same level of scrutiny. Therefore, in **chapter tree** we followed up on this initial study and tested the extent to which subjective awareness is necessary to process feedback and how our confidence in previous decisions modulates the impact of this feedback. Specifically, we asked how the metacognitive evaluation of decision accuracy affects subsequent feedback processing using two dependent measures thought to reflect phasic, feedback-related, arousal: pupil size and the P3, an event-related potential (ERP) component from the EEG (Jepma et al., 2016; Nieuwenhuis, Aston-Jones, & Cohen, 2005). An additional manipulation of feedback awareness by means of masking allowed us to track how feedback modulated pupil size and the P3 depending on the level of feedback awareness and confidence in the previous decision.

In **chapter four**, we focused on the relationship between stimulus triggered arousal (as measured by stimulus evoked pupil size fluctuations) and perceptual performance and metacognitive evaluation during a Gabor discrimination task (see **Fig. 1.3B**). Because stimulus parameters were kept constant, differences in performance and metacognition could be attributed to internal changes in the brain arousal state (Aston-Jones & Cohen, 2005; Eldar, Cohen, & Niv, 2013). We investigated how pupil dilation relates to both participants' task performance (type 1 measures, e.g. d' and criterion) and introspection of their performance (type 2 measures, e.g. meta-d' and meta-criterion) in a signal detection theory (SDT) framework (Fleming & Lau, 2014; Maniscalco & Lau, 2012).

In **chapter five** we addressed the question whether metacognition is necessary for a specific case of performance monitoring, namely conflict adaptation (Desender, Van Lierde, & Van den Bussche, 2013; van Gaal, Lamme, & Ridderinkhof, 2010). Conflict adaptation refers to the phenomenon that the effect of a prime on the speed of response to a target (e.g. **Fig. 1.3A**) is smaller when the trial is preceded by an incongruent prime-target pair compared to a congruent prime-target pair. We report two behavioral experiments in which we explored the role of objective conflict (whether prime and target where the same or different) and subjective conflict experience (whether participants indicated they have experienced conflict on the previous trial, irrespective of the objective conflict) on conflict adaptation.

In **chapter six** we explored whether people can use their metacognition to detect subtle unconscious biases in their decisions when they supposedly decide 'freely' (Kiesel et al., 2006; Schlaghecken & Eimer, 2004). We explore this issue using a probabilistic reinforcement learning task in which participants were free to choose between two response options, of which one was unconsciously primed (being the prime congruent or incongruent to the most rewarded response option). This experimental setup allowed us to test whether "internal conflict" leads to impairments in choosing the best of two alternative actions and if so, whether this leads to corresponding changes in metacognitive evaluations of task performance (Fleming & Dolan, 2014). The latter would reflect that internal conflict between unconscious drives and learned optimal responses can potentially explain changes in decision-making performance (Desender et al., 2014).

### Publications and co-authors

Some of the chapters included in this thesis are submitted for publication in journals in slightly adapted form. Here I would like to express my gratitude to several colleagues who have made important contributions to the experiments and papers, in various stages of the process. In the following, there is a list of references in order to acknowledge them:

### <u>Chapter 2</u>

Correa, C.M.C., Noorman, S., Jiang, J., Palminteri, S., Cohen, M.X, Lebreton M. and van Gaal, S. (in press, *Journal of Neuroscience*). How the level of reward awareness changes the computational and electrophysiological signatures of reinforcement learning.

Author contributions: CMCC and SVG conceived the experiment. CMCC, SN and JJ performed the experiments. CMCC, SN and SVG performed EEG analyses. ML and SP performed modeling analyses. CMCC, SP, ML and SVG wrote the manuscript. MXC and ML provided expertise and feedback. SVG supervised the project.

### <u>Chapter 3</u>

Correa, C.M.C., de Gee, J.W., Weaver, M., Donner, T.H. and van Gaal, S. (in preparation) Decision confidence mediates outcome-evoked pupil dilation and P3 waveforms during sensory decision making.

Author contributions: CMCC, JWG and SVG conceived the experiment. CMCC performed the experiments. CMCC, MW and SVG performed EEG analyses. JWG performed pupil analyses. CMCC, MW, JWG and SVG wrote the manuscript. THD provided expertise and feedback. SVG supervised the project.

### <u>Chapter 4</u>

Correa, C.M.C.\*, de Gee, J.W.\*, Weaver, M., Donner, T.H. and van Gaal, S. (in preparation) Pupil dilation oppositely predicts perceptual sensitivity and metacognitive insight during human perceptual decision-making. (\*shared first authors).

Author contributions: CMCC, JWG and SVG conceived the experiment. CMCC performed the experiments. CMCC and JWG performed behavioral analyses. JWG performed pupil analyses. CMCC, JWG and SVG wrote the manuscript. THD and MW provided expertise and feedback. SVG supervised the project.

### <u>Chapter 5</u>

Correa, C.M.C., Jiang, J. and van Gaal, S. (in preparation) Breaking the flow: No evidence for a role of subjective conflict experience on conflict adaptation.

Author contributions: CMCC, JJ and SVG conceived the experiment. CMCC performed the experiments. CMCC and SVG performed behavioral analysis. CMCC, JJ and SVG wrote the manuscript. SVG supervised the project.

This dataset has been included in this paper: Jiang, J.\*, Correa, C.M.C.\* Geerts, J. and van Gaal, S. (2018). The relationship between conflict awareness and

behavioral and oscillatory signatures of immediate and delayed cognitive control. *Neuroimage*, 177, 11-19 [\*shared first authors]

### <u>Chapter 6</u>

Correa, C.M.C., Carpenter, J., Fleming, S. and van Gaal, S. (in preparation) Subliminal cues impact performance but not metacognition for free choices.

Author contributions: CMCC, JC, SF and SVG conceived the experiment. CMCC performed the experiments. CMCC and JC performed the behavioral analysis. CMCC and SVG wrote the manuscript. SF provided expertise and feedback. SVG supervised the project.

# 2. How the level of reward awareness changes the computational and electrophysiological signatures of reinforcement learning

**Correa**, C.M.C.<sup>1</sup>, **Noorman**, S.<sup>1</sup>, **Jiang**, J.<sup>3</sup> **Palminteri**, S.<sup>4,5,6</sup>, **Cohen**, M.X<sup>7</sup>, **Lebreton** M.<sup>\*,^,8</sup> **van Gaal**, S<sup>\*,^,1,2,9</sup>

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### Abstract

The extent to which subjective awareness influences reward processing, and thereby affects future decisions is currently largely unknown. In the present report, we investigated this question in a reinforcement-learning framework, masking, combining perceptual computational modeling and electroencephalographic recordings. Our results indicate that degrading the visibility of the reward decreased -without completely obliterating- the ability of participants to learn from outcomes, but concurrently increased their tendency to repeat previous choices. We dissociated electrophysiological signatures evoked by the reward-based learning processes from those elicited by the reward-independent repetition of previous choices and showed that these neural activities were significantly modulated by reward visibility. Overall, this report sheds new light on the neural computations underlying rewardbased learning and decision-making and highlights that awareness is beneficial for the trial-by-trial adjustment of decision-making strategies.

### Introduction

How we make decisions on a day-to-day basis depends strongly on the outcomes that have been associated in the past with the presently available courses of action. Actions that have been often linked with rewards (such as food or money) are more likely to be repeated than actions that have not been rewarded (or punished even) (Berridge & Robinson, 2003; Dayan & Balleine, 2002; Rangel, Camerer, & Montague, 2008). Generally, the notion of reward is strongly associated with subjective evaluation, related to conscious processes such as "pleasure", "liking" and "wanting" (Berridge & Robinson, 2003). However, how human decision making changes depending on reward awareness is unclear. Assessing how the level of awareness of information changes or may bias value-based learning and decision-making may prove critical to understanding apparent irrationality observed in human behavior (Evans, 2008; Evans & Stanovich, 2013; Kahneman, 2003; Newell & Shanks, 2014; Weber & Johnson, 2009).

Rewards are crucial to two fundamental steps in the decision-making process. First, in decision situations, expected rewards act as incentives, which determine choices and increase the amount of motor or cognitive effort one is willing to expend to reach a goal (Berridge, 2004; Schmidt et al., 2012). Second, after a decision has been enacted and the action effectuated, the obtained reward -or absence of reward- drives important learning processes: successful actions are reinforced, while unsuccessful ones are discouraged (Sutton & Barto, 1998). Despite rewards being strongly associated with subjective feelings, notably to emotions and to the notion of expected pleasure (Berridge & Robinson, 2003), recent studies have reported that reward cues that are masked from awareness can still directly influence task performance (Aarts et al., 2008; Bijleveld, Custers, & Aarts, 2012; Capa et al., 2013; Pessiglione et al., 2007). These results suggest that the incentive properties of reward information may be processed outside the scope of awareness in the human brain to facilitate human performance (but see Bijleveld et al., 2014 for results challenging this view).

On the other hand, little is known about the propensity of reward to *reinforce* successful actions and how reward awareness modulates these mechanisms. To address this question, thirty-two participants performed a modified version of a probabilistic reversal learning task (similar to Cohen, Elger, & Ranganath, 2007) in which we manipulated the visibility of reward using a standard masking technique (Ogmen et al., 2003). Participants were instructed to choose one of two response options, which led probabilistically either to a significant reward (50 cent coin) or a negligible one (1 cent coin), from now on referred to

as the "reward" and "no-reward" conditions for simplicity. Response-reward contingencies reversed several times over the course of the experiment and participants were instructed to select the response option that was most often rewarded (**Fig. 2.1A**). Masked and unmasked feedback were mixed within blocks to explore the relative weighting of both types of feedback in a context in which easy and difficult to perceive feedback were available. We used a computational modeling approach to evaluate the existence of learning from rewards at different levels of visibility, and to characterize the computational signature of such learning. We combined EEG measurements with this computational modeling approach to investigate, at the time of reward processing and on a trial-by-trial basis, the neural correlate of the different processes influencing participants' future choices and how those were affected by reward visibility.

### Materials and methods

### Participants

Thirty-two students from the University of Amsterdam (8 men; aged 22.25±3.1) participated in the experiment for course credits or financial compensation. All participants gave their written informed consent prior to participation, had normal or corrected-to-normal vision and were naive to the purpose of the experiments. All procedures were executed in compliance with relevant laws and institutional guidelines and were approved by the local ethical committee of the University of Amsterdam.

### Task

Stimuli were presented using Presentation software (Neurobehavioral Systems, Inc) against a black background at the center of a 20-inch VGA monitor (frequency 60 Hz), which was viewed by the participants from a distance of approximately 80 cm. Participants should fixate at the center of the screen and choose between a left or a right box distant 15 cm from each other by pressing a correspondent left or right chair button (parallel button). The chosen square was illuminated in blue for 600 ms, indicating the participants' response followed by a reward (50 cent coin) or a punishment (1 cent coin) that could be shown on a visible (100 ms) or masked (17 ms) way. Stimuli were used similarly to those by (Zedelius, Veling, & Aarts, 2012). A variable time, 1500 to 2500 ms inter-trial-interval separated each trial. If participants did not select a target after 1500 ms, a "too late!" message was displayed.

Sides were rewarded in a 70/30% fashion. This probability condition was reversed several times along the 1200 trials so that, in order to decide advantageously, participants had to keep track of eventual "rule changes". We

refer to the choices made on the 30% probability side as "incorrect" choices, and those made according to the 70% rewarded side as "correct" ones. Probabilities were fixed across trials within blocks, which lasted 75–125 trials. The block length had a minimum value, but it was dependent on how fast participants could learn the rule at stake. In order to assure that everyone could learn the probabilities, for at least 10 trials in a row they should have been able to choose the "correct side" option for more than 60% of the last 25 trials, otherwise additional trials could be added until this condition was completed. Self-paced rest breaks were given every 70 trials, presenting participants the percentage of correct sides they have chosen according to the rule at stake. This break never coincided with changing probabilities conditions and participants were told about that.

In 10% of the trials a forced choice discrimination question asked "Which coin did you just see?" while displaying a 1 cent or a 50 cent coin. This question was randomly asked for the same amount of times for visible and masked coins. Participants were instructed that the probability of the correct response being a 1 cent or 50 cent coin was 50%. Participants were explained that they would get paid according to their performance at the end of the experiment. Finally, all participants received a bonus of €5 on top of what they had already received. Participants were instructed to choose one of the two targets on each trial, to pay attention to the reward, and to try to win as much money as possible.

### Models Building Blocks

We designed 18 different models, all adapted from a Q-learning model. Our Q-learning included 3 basic modules: learning, choice and perseveration.

**Learning.** The basic idea is that participants learn by trial and error to compute a value Q for each option (choosing the left or the right cue). At each trial t, after a choice is made and the outcome of the choice  $R_t$  is revealed, the Qvalue of the chosen option ( $Q_{C,t+1}$ ) is updated by integrating a so-called prediction-error  $\delta_t$ , which compares what was expected ( $Q_{C,t}$ ) to the actual outcome:

$$\begin{split} \delta_t &= R_t - Q_{C,t}.\\ \text{This update is typically scaled by a learning rate } \alpha, \text{ such that:}\\ Q_{C,t+1} &= Q_{C,t} + \alpha \times \delta_t. \end{split}$$

**Choice.** To account for the fact that people try to maximize their expected outcome, but can make errors or explore locally sub-optimal options, the choice  $(C_t)$  is typically implemented as a softmax function:

$$P(C_t = a) = \left(1 + \exp\left(\beta \times \left(Q_t(a) - Q_t(b)\right)\right)\right)^{-1},$$

where  $\beta$  is the slope of the logistic choice function –the inverse temperature parameter- which we refer to as the value weight.

**Perseveration.** In order to capture the tendency of participants to stick to their previous choices independently of the received reward, we also included a perseveration bias  $\pi_t$  in the choice function. This function becomes:

$$P(C_t = a) = \left(1 + exp\left(\beta \times \left(Q_t(a) - Q_t(b)\right) + \pi \times P_t\right)\right)^{-1},$$
  
where

 $P_{t+1} = \begin{cases} 1 i f C_t = a \\ -1 i f C_t = b \end{cases}$ 

and  $\pi$  governs the weight of the past choice on the present decision –referred to as the perseveration weight.

When both learning and perseveration are present, the relative importance of  $\beta$  and  $\pi$  allows the model capture participants tendency to trade-off between sampling from learned value ( $\beta$ ) vs simply repeating previous choices ( $\pi$ ).

### Model Space

Given that our task incorporates two types of reward - masked vs. unmasked several scenarios are possible for learning and perseveration, which can be accounted for by different models. We first assumed that all models share a common basic block, that is, people learn from unmasked reward. Additionally, people can learn from masked reward, either at the same pace or at a different pace than after unmasked reward. Likewise, the value weight parameter can be identical or different after unmasked vs masked reward. As for the perseveration, it can be absent after both masked and unmasked reward, present and of identical strength, or present with different strengths. Those 3 learning, 2 choice-temperature and 3 perseveration scenarios were therefore combined, generating 18 possible models in our model space (Fig. 2.2A/B).

### Parameter optimization

We optimized the models free-parameters ( $\alpha$ 's and  $\beta$ 's) by minimizing the negative log likelihood (LLmax) of the participant observed choices under the model using Matlab's fmincon function, initialized at multiple starting points of the parameter space.

### Model Comparison

Negative log-likelihoods (LLmax) were used to compute the Bayesian information criterion (BIC), for each model, at the individual level ( $BIC = 2 \times (LLmax) + df \times log(n_{trial})$ ), and used to approximate the model evidence (e = -BIC/2). Individual model evidences were then fed to the mbb-vb-toolbox (https://code.google.com/p/mbb-vb-toolbox/) to run a Bayesian Model Comparison (Daunizeau, Adam, & Rigoux, 2014). This Bayesian procedure estimates, among other criteria, the exceedance probability (denoted XP) for each model within a set of models, given the data gathered from all participants. Exceedance probability quantifies the belief that the model is more likely than all the other models of the set. An exceedance probability greater than 95% for one model within a set is therefore typically considered as significant evidence in favor of this model being the most likely.

### Model identifiability and parameter recovery

Using random permutations of individual parameters estimated from fitting the complete model (i.e. model 18) to the choices of our 32 participants, we simulated the behavior of cohorts of 32 synthetic subjects with the 18 different models in our model set. Then, we ran our Bayesian model-comparison (BMC) analysis on those 18 different simulations, and checked that all models are identifiable, i.e. can be correctly estimated as the most probable model in the set of 18 models by the BMC approach when they were actually used to generate the data. This first analysis intends to verify that nothing in the design of the model set, the parameter estimation or the model comparison approach, unduly advantages model 18 (e.g. that it is the most complex model), leading to mistakenly over-estimate the probability that model 18 explains our participants' choices in lieu of other models. Next, because our models are nested, we assessed the parameter recovery in the full-model case (model 18): we computed the Pearson correlation between the parameters used to generate the data, and the parameters estimated by the maximum-likelihood fitting procedure. Additionally, we estimated the correlation between estimated parameters.

### Parameters and model recovery

Simulations demonstrated excellent model and parameter recovery properties of our model space (Palminteri, Wyart, & Koechlin, 2017).

### EEG measurements

EEG data was recorded and sampled at 512 Hz using a BioSemi ActiveTwo system. Sixty four scalp electrodes were measured, as well as 4 electrodes for horizontal and vertical eye-movements (each referenced to their counterpart)

and 2 reference electrodes on the ear lobes. After acquisition, standard preprocessing steps were performed in EEGLAB toolbox in Matlab. Data were bandpass filtered from 0.5 to 40 Hz off-line for ERP analyses. Epochs ranging from 1.8 s before to 2 s after reward presentation were extracted. Linear baseline correction was applied to these epochs using a -200 to 0 ms window. The resulting trials were visually inspected and those containing artifacts were removed manually. Moreover, electrodes that consistently contained artifacts were interpolated. Finally, using independent component analysis, artifacts caused by blinks and other events not related to brain activity were removed from the EEG data.

### ERP analyses

We focused on ERP components related to reward outcome processing with different latencies and topographical distributions. To zoom in on these specific components a central region of interest (ROI) was defined comprising of 15 midline electrodes (Fz, F1, F2, FC1, FCz, FC2, Cz, C1, C2, CPz, CP1, CP2, Pz, P1, P2), where both the relevant components can be observed (fronto-central FRN and ventro-parietal P3) (Chase et al., 2011; Cohen et al., 2007; Cohen, Wilmes, & van de Vijver, 2011; Ullsperger et al., 2014). Selecting a predefined ROI limits the number of comparisons that need to be performed, but we note that the results were robust and were not dependent on the specific sets of electrodes used as a ROI (Fig. 2.4). We investigated the effect of reward outcome separately for masked and unmasked trials. To correct for multiple comparisons due to the number of time-points tested, p values were FDRcorrected at an alpha-level of 0.05. All statistical analyses were performed in Matlab (Mathworks). Based on this ERP analysis three time-windows of interest were selected for follow-up analyses in which we related model parameters to single trial EEG responses.

### Single trial regression analyses

Multiple regressions of ERP amplitude on three model parameters were conducted. For each subject, each electrode, and each time point, the three parameters (PE, |PE|, switch/repeat on the next trial) were entered as predictor variables, and the ERP amplitudes as observations in the regression model. We checked that the correlations between the time-series of the 3 predictors were low (absolute value of pearson's R averaged over subjects <.2), resulting in low multi-collinearity indices (variance inflation factors: VIF<sub>PE</sub>=  $1.0596\pm0.0099$ ; VIF<sub>|PE|</sub>=  $1.0524\pm0.0147$ ; VIF<sub>switch/repeat</sub>=  $1.0712\pm0.0145$ ). Beta-coefficients assigned to each predictor column, which reflect the regression weights between each of the three parameters and ERP amplitude, were estimated at the individual level, separately for each electrode and time point.

The significance of the predictors was assessed at the population-level using random-effects (t-tests) on the regression coefficients averaged across the predefined time windows (100-300 ms, 300-500 ms, 500-800 ms) and the predefined ROI.

### Code availability

The codes used to analyze data from the current study are available from the authors on reasonable request.

### Data availability

The datasets generated during and/or analyzed during the current study are available from the authors on reasonable request.

### Results

### Model-free behavior

Participants were able to perform the task well and they accurately tracked probability reversals (mean correct response = 71.3±1.51%). In order to assess the reward discriminability in the masked (M) and unmasked conditions (UM), we computed participants' d-prime, an unbiased measure of stimulus visibility, from the forced-choice discrimination trials that were presented throughout the task (10% of all trials, hence 120 trials in total). Although the overall discriminability was low in the masked condition, both masked and unmasked conditions exhibited above-chance accuracy in this discrimination test (UM: 96±1.15% correct, d'=3.97±0.14; t<sub>31</sub>=28.38, p<0.001; M: 55.7±1.13% correct, d'=0.35±0.07; t<sub>31</sub>=4.91, p<0.001). Given that chance-level performance on such a forced-choice discrimination task is a typical criterion used to show that participants are unable to perceive a stimulus consciously (Overgaard & Sandberg, 2012; Sandberg et al., 2010), this result implies that we cannot consider that the masked reward was nonconscious in all participants and for all trials.

Having established that participants performed the task correctly, we turned to a typical behavioral analysis of learning. Following previous studies (Chase et al., 2011; den Ouden et al., 2013), we computed participants switch rates after positive and negative outcomes, in both unmasked and masked conditions. Critically, participants switched their response more often after no-reward than after reward, and did so in both the unmasked and in the masked condition (unmasked: difference  $36.06\pm0.59\%$ ,  $t_{31}$ =10.76, p<0.001; masked: difference  $4.90\pm0.15\%$ ,  $t_{31}$ =5.65, p<0.001). The fact that participants tended to switch their choices significantly more after no-reward (1 cent) versus reward (50 cent) is generally interpreted as evidence for learning. It would therefore be tempting to conclude that our participants significantly learned from both unmasked and masked reward. However, this interpretation of switch patterns may not be devoid of statistical confounds, especially in designs where conditions (in this case masked and unmasked) are intermixed. Indeed, this pattern of results could easily be produced by participants learning the value of options from unmasked rewards and deriving all choices from those values - i.e. in the total absence of learning from masked reward. This is why we turned to model-based behavioral analyses that are devoid of this statistical confound, aiming at showing that learning from masked reward outcomes is still present when these issues are taken into account.



**Figure 2.1. Experimental setup and behavior. (A)** Two response options (white boxes on the left/right of fixation) were shown on the screen until a response was given. A correct response was rewarded with a 70% probability (50 cent coin) and not rewarded with a 30% probability (1 cent coin). Reward visibility was manipulated by masking. Unmasked (long coin presentation, short backward mask presentation) and masked (short coin presentation, long backward mask presentation) reward trials were mixed within blocks and randomly chosen across trials (each with a 50% probability). Which response option was most rewarded changed every 75-125 trials. **(B)** The percentage of switches after specific trials. M: masked; UM: unmasked; +: reward; -: no-reward; error bars represent ±s.e.m.

### Computational modeling

A simple delta-rule was used to capture how individuals updated the value of the chosen options after receiving reward. Following classical associative learning algorithms, the extent to which previous reward is integrated in the future option value was controlled by a *learning rate*  $\alpha$ . Choices were derived from a logistic (soft-max) choice function, on the difference between option values. The slope of this choice function – typically referred to as choice

temperature - was defined as *the value weight*  $\beta$ . Although very popular and accounting for a wide range of behavior, this learning mechanism might not account for the full choice pattern of participants in our task: indeed, within blocks, our participants might identify the best option and therefore start disregarding the feedback, putting more weights on their priors. To account for this behavior, we added a perseveration module to our computational model. Perseveration – defined as the tendency to repeat a choice regardless of the previous outcome - was integrated as an additional "bias" in the choice function, which regulated the probability of choosing the same option as that in the previous trial (den Ouden et al., 2013; Rutledge et al., 2009; Seymour et al., 2012; Voon et al., 2015). The extent to which perseveration contributed to the final choice was determined by a *perseveration weight*  $\pi$  (see Fig. 2.2A, Materials and Methods). We then systematically explored how masked versus unmasked reward impacted those different modules, by creating sets of models allowing - or not allowing - parameters to differ between those two conditions (see Materials and Methods and Fig. 2.2B). We thereby built 18 different models, which were subsequently fit to the behavior, using a maximum likelihood procedure. A model recovery (Fig. 2.2C) and a parameter recovery (Fig. 2.2D) analysis confirmed that our modelling approach is suitable to address our questions of interests (Palminteri et al., 2017) (see also Materials and Methods). Regarding our participants' data, a Bayesian model comparison approach identified model 18 as the best among our designs to explain the behavior (exceedance probability>80%, see Fig. 2.2C). The best fitting model differentiates *learning rate*, *value weight*, and *perseveration* weight parameters after unmasked and masked reward. Importantly, because our model space included models explicitly omitting learning from masked reward (Fig. 2.2B), this model comparison result demonstrates the existence of learning from masked reward, even when perseveration effects are taken into account.



**Figure 2.2. Modeling approach. (A)** The computational architecture used to build the model space. **(B)** Model space. Eighteen models were built by systematically combining the different options available for the different computational modules. **(C)** Model identifiability analysis. Data from 32 synthetic participants were simulated with each of our 18 models. Bayesian model selection was used to identify the most probable model generating the data, using model exceedance probability. Results show that, in each case, the good model was identified, with exceedance probability≥80%. **(D)** Parameter recovery analysis. Data from 32 synthetic participants were simulated with the full model (model 18). The 6 estimated parameters per participants were then correlated with the true parameters used for simulating the data, using Pearson correlation across participants (diagonal). Results show very good identifiability (all diagonal R<sup>2</sup>>.75). The correlation between estimated parameters is shown off-diagonal. Results show very little correlation between parameters (all off-diagonal R<sup>2</sup><.17). **(E)** Model comparison. Results of a Bayesian model comparison analysis on our participants' data. Bar height indicates the exceedance probability of each model. M: masked; UM: unmasked; 6: value weight;  $\alpha$ : learning rate;  $\pi$ : perseveration weight.

Participant-level data reveals that the best fitting model gives a very good account of participant's learning and switch behavior (average likelihood per trial=78.70±2.11%; **Fig. 2.3A** for three representative participants (s10, s20, s30)). We then turned to the analysis of the best fitting model parameters (**Fig. 2.3B**). Learning rates appeared to be higher after unmasked than masked reward ( $\alpha_{UM}$ =0.67±0.03;  $\alpha_{M}$ =0.19±0.02, t<sub>31</sub>=17.01, p<.001), and so did value weights ( $\beta_{UM}$ =1.94±0.18;  $\beta_{M}$ =0.93±0.12, t<sub>31</sub>=7.24, p<0.001). However, the opposite was found for the weight put on previous choices ( $\pi_{UM}$ =0.67±0.15;  $\pi_{M}$ =1.67±0.21, t<sub>31</sub>=-4.72, p<0.001) (**Fig. 2.3B**).

These results lead to several crucial insights concerning reward learning. First, they demonstrate the existence of robust learning from masked rewards. Second, they clearly illustrate changes, due to reward visibility, in the trade-off between the tendency to base choices on the learned options' values, and the tendency to repeat previous choices regardless of previous outcome. This thus suggests that the reliance on the longer term priors, based on the accumulation of recent choices, is increased when the outcome on the current trial is masked and therefore unreliable.



**Figure 2.3.** (A) Time course of the learning task by three representative participants (participant numbers 10, 20 and 30). The x-axis represents blocks of trials during the experiment and the y-axis represents the local fraction of left-hand responses selected by the participant. Thick black and gray lines represent the reward probability in the different blocks (75-125 trials). Gray-dotted lines represent the local fraction of left-hand responses. Green thick line represents the local probability of left-hand responses predicted by the computational model. Both behavioral choices and model predictions averaged over 12 trials bins, and aligned on block transitions). (B) Model parameters for masked and unmasked conditions. Left: value weight. Middle: learning rate. Right: perseveration weight. M: masked reward, UM: unmasked reward. Error bars represent  $\pm$  s.e.m.

### ERPs and model-based EEG results

Having established, thanks to the manipulation of reward visibility, a clear computational dissociation between the contributions of learning versus choice perseveration to the behavior of our participants, we next aimed at dissociating the neural signatures of those components by leveraging electrophysiological recordings. In order to first identify the electrophysiological time-windows of interest, we performed an ERP analysis of reward-related activity, contrasting reward versus no-reward outcomes, at our central region of interest, which was based on previous studies (Cavanagh et al., 2010; Cohen et al., 2011; Ullsperger et al., 2014) (see Materials and Methods).

Our analysis of event-related potentials revealed three significant events in the neural signal evoked by fully conscious (unmasked) outcomes: an early Feedback-Related Negativity (FRN) at fronto-central electrodes ("early" event), which was followed by a second, more centrally distributed negative component ("middle" event), and a final parietal P3 component ("late" event) (**Fig. 2.4A**, FDR corrected across time, p<0.05). Crucially, while masked outcomes also elicited an early fronto-central FRN, neither the second negative ERP component nor the P3 component could be observed in the masked condition (FDR corrected across time, p<0.05, **Fig. 2.4B**).



Figure 2.4. Model free ERP results. ERPs for no-reward (red lines) and reward (green lines) for unmasked (A) and masked conditions (B). Time=0 ms is reward presentation. The lower dotted

black lines indicate significant time-windows, FDR corrected across the entire ERP time-window (p<0.05). Topographical distribution maps of the reward valence effect (no-reward minus reward, - vs +) were taken from the three broad time-windows (100-300 ms, 300-500 ms and 500-800 ms; scaling maps unmasked reward from left to right: [-2:2], [-5:5], [-2:2]; scaling maps masked reward: [-2:2]). Error bars represent ± s.e.m.

In order to relate the contributions of the different computational modules identified in our best fitting model (model 18, Fig. 2.2) to electrophysiological signatures of outcome-guided decision-making, we then turned to a modelbased analysis of the EEG signal. In each participant, at each electrode and at each time point, we estimated a multiple regression with the trial-wise timeseries of electrophysiological activity as the dependent variable, and trial-wise time-series of latent variables as independent variables (see Experimental **Procedures**). Three such independent variables, derived from our best fitting model, were included in this multiple regression: the signed prediction error, the unsigned prediction-error (typically interpreted as a measure of surprise (Cavanagh & Frank, 2014; Pearce & Hall, 1980)), and a variable indexing whether participants switched or repeated their choice from the previous to the next trial, which is directly related to the perseveration process (switch/stay behavior). Previous research has shown the existence of temporally overlapping but spatially separate contributions of the signed prediction error, reflecting the valence of the prediction error (positive or negative) and the unsigned prediction error (the absolute degree of expectation violation also referred to as surprise) to reward learning (Fouragnan et al., 2017).

In our model-based analyses, we focus on the three contiguous time-windows in which the model-free effects were most pronounced (early: 100-300 ms, middle: 300-500 ms and late: 500-800 ms). The signed PE regression results showed two clear peaks strongly overlapping in time with the early two ERP components that were revealed in the model-free ERP analysis (**Fig. 2.5A**). For both masking conditions, the signed prediction error was encoded in the early FRN (unmasked:  $t_{31}$ =6.8, p<0.001; masked  $t_{31}$ =4.2, p<0.001, difference:  $t_{31}$ =3.0, p=0.005, early time-window). Similar results were obtained for the mid-latency negativity (unmasked:  $t_{31}$ =11.2, p<0.001; masked:  $t_{31}$ =3.0, p=0.005; difference:  $t_{31}$ =8.1, p<0.001, middle time-window). In contrast, the later P3 component appeared only reached significance in the masked outcome conditions, although both conditions did not differ significantly (unmasked:  $t_{31}$ =0.85, p=0.40; masked:  $t_{31}$ =4.1, p<0.001, late time-window, **Fig. 2.5A**).


**Figure 2.5. Model-based EEG analysis of the signed PE. (A)** The time courses of regression weights of the signed PE regressed on the reward-locked EEG signal derived from a central ROI. Effects are plotted separately for unmasked (green) and masked (black) reward outcomes. Shaded areas indicate the s.e.m. Topographical maps show the regression weights during the relevant time windows. Both unmasked and masked reward showed early and mid-latency EEG-PE covariations which are shown in b. Note that the polarities of these components are reversed compared to the ERP results, which in accordance with our expectations, because these ERP modulations are all associated with negative PE values, leading to a reversal of the polarities (maps: 100-300 ms and 300-500 ms; scaling: early masked = [-0.5:0.5], mid-latency masked

0.5:0.5], early unmasked = [-1:1], middle unmasked = [-3:3]). Bar plots of the signed PE effect for the three time-windows of interest. **(B)** The time courses of regression weights of the unsigned PE, or the level of surprise, regressed on reward-locked EEG signal derived from a central ROI. Both unmasked and masked rewards showed late EEG-surprise covariations (maps: 300-800 ms; scaling: masked=[-0.5:0.5], unmasked=[-2:2]). Bar plots of the surprise effect. **(C)** The time courses of regression weights of switch/stay behavior regressed on the reward-locked EEG signal derived from a central ROI. Both unmasked and masked reward showed late EEG-switch/stay behavior covariations (maps: 300-800 ms; scaling: masked=[-3:3], unmasked=[-3:3]). Bar plots of the switch/stay behavior effect. Error bars represent  $\pm$  s.e.m. M: masked reward, UM: unmasked reward.

Analyses of the unsigned prediction error signals (i.e. the level of surprise) revealed a rather different pattern of results. For both masked and unmasked reward, and in line with previous findings (Fischer & Ullsperger, 2013; Fouragnan et al., 2017; Mars et al., 2008), this variable was represented in the later P3-like component (time-window 300-500 ms: unmasked:  $t_{31}$ =5.5, p<0.001; masked:  $t_{31}$ =1.8, p=0.08; time-window 500-800 ms: unmasked:  $t_{31}$ =8.4, p<0.001; masked:  $t_{31}$ =2.2, p=0.03, see **Fig. 2.5B**, note that headmaps are shown for the middle and late windows combined: 300-800 ms). In both time-windows the effects were stronger for unmasked than masked rewards (all ps<0.001). No significant effects were observed in the early time-window (all ps>0.3).

Finally, we observed a strong relation between switch/stay behavior on the next trial, closely related to the perseveration parameter in the modeling approach, and a broad central positivity (Fig. 2.5C). This effect was already present from the early time-window onwards and was always present irrespective of reward visibility (time-window 100-300 ms: unmasked  $t_{31}$ =2.9, p=0.006; masked  $t_{31}$ =2.9, p=0.006; difference  $t_{31}$ =-0.8, p=0.4; time-window 300-500 ms: unmasked  $t_{31}$ =5.1, p<0.001; masked  $t_{31}$ =5.6, p<0.001; difference t<sub>31</sub>=0.5, p=0.6; time-window 500-800 ms: unmasked t<sub>31</sub>=7.1, p<0.001; masked  $t_{31}$ =3.8, p<0.001; difference  $t_{31}$ =2.2, p=0.034; Fig. 2.5C, note that headmaps are shown for the middle and late windows combined: 300-800 ms). Interestingly, these effects were very similar for masked and unmasked rewards until ~500 ms after stimulus presentation and significant visibility-related differences only started to emerge in the late time-window. Thus, a larger parietal positive component was associated with an increased likelihood of switching the response option on the next trial. This last analysis not only replicates previous findings about the electrophysiological signature of model-free switching behavior after fully conscious reward (Chase et al., 2011; Fischer & Ullsperger, 2013), but also extends them to the case where reward visibility is very low.

#### Discussion

In the present report, we combined a reinforcement learning task, a masking procedure, computational modeling and EEG recordings to investigate the impact of reward visibility on different cognitive processes involved in probabilistic reward-guided learning. In behavioral analyses, we observed that participants switched their responses after unmasked and masked unfavorable outcomes (no-reward) more often than after favorable outcomes (reward), which is typically interpreted as evidence for learning in both conditions. However, we demonstrated that this approach can largely overestimate or even erroneously validate the existence of learning from masked rewards, in tasks where trials are inter-mixed. To overcome this potential confound, we combined computational modeling with a model-comparison approach. First, we designed a set of 18 models, built on mixtures of unmasked and masked modules, accounting for reward-based learning and choice perseveration. Reward-based learning was simply operationalized as prediction-error based learning, in line with popular model-free reinforcement-learning algorithms (Berridge, 2004; Dayan & Balleine, 2002; den Ouden et al., 2013; Sutton & Barto, 1998). We then systematically compared the ability of these models to explain our behavior with a rigorous Bayesian model-comparison approach (Daunizeau et al., 2014). In our model set, which comprised models with and without learning modules from masked feedback, a model including both the masked and unmasked learning modules was identified as the best model. This approach operationalized a clear testing of learning from masked outcomes and provided clear evidence toward the existence of such learning. Our best fitting model also included modules for perseveration after masked and unmasked reward.

An analysis of the best fitting model parameters revealed that learning rates were significantly positive for both visibility modules, although smaller for the masked feedback module. This confirms that participants indeed used both unmasked and masked (although to a lesser extend) reward outcome to inform further decisions. Our results show that the perseveration parameter was also significantly positive for both the visibility modules, although perseveration was smaller for the fully conscious module. This indicates that participants were biased toward repeating previous choices, independently of the outcome of their decisions, an actually frequent observation in human and non-human reinforcement learning tasks (den Ouden et al., 2013; Lau & Glimcher, 2005; Rutledge et al., 2009; Schönberg et al., 2007; Seymour et al., 2012). Although often given a low-level interpretation and a connotation of sub-optimality (Voon et al., 2015), perseveration can also constitute the implementation of higher-level –behavior: in our task, it is likely that, within a block, participants

identified the "good" option based on the integration of information over a long sequence of trials, and therefore decided to ignore irrelevant negative reward basing their choices only on their prior. After masked reward, participants persevered more than after fully conscious reward, revealing that participants stuck to their decision strategy, based on the integration of information over a longer sequence of trials, when full conscious awareness of the outcome was (often) lacking.

Regarding electrophysiological signatures of reinforcement-learning, we observed three neural events evolving over time that were modulated by unmasked outcomes (reward vs no-reward): an early fronto-central FRN, a midlatency central negativity, and a late centro-parietal P3 component. Crucially, only the fronto-central FRN, which peaked ~200 ms after outcome presentation, was also modulated by masked outcomes. Many studies have reported that this signal, closely related to the response-locked error related negativity (ERN) and originating from the medial frontal cortex (MFC) (Debener et al., 2005), distinguishes positive from negative outcomes (Pfabigan et al. 2011; Cavanagh et al. 2010; Hajcak et al. 2006; Chase et al. 2011; Cohen et al. 2007; Holroyd et al., 2003; Fouragnan et al. 2017) in reinforcement-learning tasks (Holroyd & Coles, 2002). This response may reflect a "fast alarm" signal (or alertness response (Fouragnan et al., 2017)) that indicates the value of the incoming evidence, which is then accumulated in later stages of the decision making process (Chase et al., 2011; Fouragnan et al., 2017; Ullsperger et al., 2014). Oppositely, the late parietal P3 ERP component was only observed after fully conscious reward. This signal, building on accumulating incoming evidence (Chase et al., 2011; Ullsperger et al., 2014), has been reported to predict behavioral adaptation and the associated update of new stimulus-response associations in memory (Chase et al., 2011; Ullsperger et al., 2014). Our ERP results fit nicely in current theoretical models of conscious and unconscious processes (Dehaene et al., 2014; Lamme, 2006; van Gaal & Lamme, 2012). Within these frameworks, the FRN may reflect a fast feedforward and nonconscious high-level response, whereas the P3 may reflect more conscious, and longer lasting neural responses, potentially dependent on recurrent interactions.

Although those first EEG analyses outlined important dissociations between learning from reward at different levels of awareness, it is rather difficult to connect these neural signals to precise cognitive processes, using cross trial averaging and traditional contrast-based ERP methods (Cohen & Cavanagh, 2011; Debener et al., 2005; Pernet, Sajda, & Rousselet, 2011; Pfabigan et al., 2011). We therefore ran additional regression analyses in combination with computational modeling to investigate whether single-trial measures of reinforcement learning were influenced by the visibility of probabilistic rewards (Cavanagh et al., 2011; Cohen & Cavanagh, 2011; Pernet et al., 2011). We focused our investigations on the EEG-correlates of three main computational variables: the prediction-error (signed PE), the level of surprise (unsigned PE) and switch/stay behavior on the next trial. This analysis revealed a striking similarity of neural PE correlates after both unmasked and masked reward outcomes. Both the early and the mid-latency negative ERP components were associated with PE computation (see also Fouragnan et al. 2017), whereas the parietal P3 was not. These findings support previous results showing that the FRN reflects signed PE signals (Holroyd & Coles, 2002; Overbeek, Nieuwenhuis, & Ridderinkhof, 2005), likely emerging from dopaminergic projections to the MFC (Park et al., 2012; Schultz, 2007; Walsh & Anderson, 2012), although especially the early response has also been linked to noradrenergic and serotonergic modulations (discussed in Fouragnan et al. 2015). Interestingly, whereas the two early neural events coded for a signed PE signal, the later P3 component was particularly modulated by the unsigned PE, reflecting the level of surprise. Although this corroborates similar results obtained with different techniques and methods (Fouragnan et al., 2017; Mars et al., 2008), we crucially show here that the level of surprise is also encoded in parietal EEG fluctuations elicited by masked reward outcomes. Finally, the EEGswitch/repeat correlations that we report here are in line with previous studies showing that trial-by-trial switch behavior can be observed at parietal channels as a late positive P3 component (Chase et al., 2011; Fischer & Ullsperger, 2013). In a previous study in which the authors combined computational modeling and RL it has been shown that this neural event did not differ when participants received actual reward about their choice or merely fictive reward. Here we show that this effect likely represents decision strategies that are formed over longer timescales. Overall, these results show that several cognitive processes important for reward-based learning, namely PE (valence) computation, surprise and switch/stay implementation are processed in the human brain and these cognitive processes are temporally and spatially dissociated in time (see also Fouragnan et al. 2017).

# 3. Decision confidence mediates outcome-evoked pupil dilation and P3 waveforms during sensory decision making

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#### Abstract

The extent to which subjective awareness is necessary to process performance outcome and how decision confidence modulates the impact of this outcome is largely unknown. To test this issue, human participants (N=32) performed a challenging perceptual decision task in which they had to judge the direction of a noisy Gabor stimulus (clockwise vs counterclockwise) while performance was staircased at 70% correct. On each trial, participants had to indicate the confidence in their decision, after which veridical outcome was presented (error vs correct). Outcome visibility was manipulated using the masking technique, leading to easily perceived (unmasked) and poorly perceived (masked) outcome. Electroencephalography (EEG) and pupil size measures revealed that unmasked outcome triggered a prediction error response in both pupil size measures as well as the P3 ERP component. However, interestingly, after masked outcome this was not the case. Instead, the pupil dilated more for error outcome than for correct outcome, while the P3 separated sure versus unsure trials. These results suggest that confidence modulations on outcomeevoked processing depend on outcome awareness, which may reflect the necessity of awareness for integrating performance outcomes with confidence estimates to update and optimize future decisions.

## Introduction

Our decisions are often accompanied by a sense of confidence in their accuracy. We have metacognitive awareness of how good our decisions are, even when there is no explicit outcome provided (de Gee et al., 2017; de Gee, Knapen, & Donner, 2014; Urai, Braun, & Donner, 2017). Clearly, there is considerable variation in people's ability to construct metacognitive estimates of task performance, especially evident in the lack of accurate metacognitive evaluations in several psychiatric conditions, such as obsessive compulsive

disorder and anxiety (Grupe & Nitschke, 2013; Hermans et al., 2008; Stern et al., 2013). However, there is also considerable variation in metacognitive performance within individuals when multiple decisions are compared, for example due to attentional differences (Rahnev et al., 2011).

The intrinsic variability in decisions and its associated confidence is often attributed to spontaneous fluctuations of neural activity in the brain regions computing decisions (Beck et al., 2012; Faisal et al., 2008; Fox et al., 2006; Glimcher, 2005; Lin et al., 2015; Shadlen & Newsome, 1998; Shadlen et al., 1996). A major source of these internal fluctuations are variations in the cortical arousal state that are mediated by catecholaminergic (norepinephrine and dopamine) neurotransmitter systems, broadly projecting to large parts of the cerebral cortex (Aston-Jones & Cohen, 2005; Harris & Thiele, 2011; Lee & Dan, 2012; McGinley et al., 2015; McGinley, David, & McCormick, 2015; Murphy et al., 2014; Polack et al., 2013; Safaai et al., 2015; Steriade, 2000). These phasic (fast) modulations in the release of neuromodulation may be captured in the size of the P3 ERP component, as measured with electroencephalographic (EEG) recordings over centro-parietal electrode sites (Brown et al., 2015; Jepma et al., 2016; McCormick, 1989; Nieuwenhuis, Aston-Jones, & Cohen, 2005; Pineda, Foote, & Neville, 1989; Polich, 2007). Interestingly, non-luminance mediated change in the diameter of the eve's pupil has also been shown to reflect a peripheral marker of neuromodulatory activity and cortical arousal state (Beatty, 1982; de Gee et al., 2014; Eldar, Cohen, & Niv, 2013; Gilzenrat et al., 2010; Joshi et al., 2016; Lempert, Chen, & Fleming, 2015; McGinley et al., 2015; Nassar et al., 2012; Varazzani et al., 2015). Recent animal studies have revealed a tight coupling between pupil diameter and neural responses in the locus coeruleus and inferior and superior colliculus (Joshi et al., 2016; Varazzani et al., 2015; Wang et al., 2012), which is supported by recent human fMRI studies (de Gee et al., 2017; Murphy et al., 2014). Further, dopaminergic neurons respond to novel and unexpected stimuli and DA is critical for cognitive flexibility (Cools & Robbins, 2004; Wise, 2004). Moreover, the P3 has also been used as an electrophysiological correlate of outcome-evoked phasic catecholamine release in the cortex (Nieuwenhuis et al., 2005; Polich, 2007; Rangel-Gomez et al., 2013). Yet, how the metacognitive assessment of the accuracy of our decisions affects subsequent outcomeevoked information processing, as reflected in the P3 and pupil diameter, remains unknown.

To test this, we used pupillometry and EEG to systematically quantify the interplay between decision confidence and outcome processing. Human participants (N=32) performed a challenging perceptual decision-making task in

which they had to judge the direction of a noisy Gabor stimulus while their performance was staircased at 70% correct. On each trial, participants had to indicate the direction of the Gabor stimulus and their confidence in this decision in a single response. Thereafter, the outcome of the decision was signaled using the Dutch words for "error" and "correct" ("goed" and "fout" respectively, see **Fig 3.1A**). On half of the trials, the outcome word was masked from awareness to reveal to what extent awareness of the outcome of a decision is crucial for interactions between decision confidence and outcome evaluation. We focused our analysis on the P3 ERP component, an electrophysiological index of phasic catecholamine release in the cortex, and pupil diameter, a peripheral marker of catecholamine release.

## **Materials and Methods**

#### Participants

Thirty-two students from the University of Amsterdam (23 women; aged 18-24) participated in the study for course credits or financial compensation. All participants gave their written informed consent prior to participation, had normal or corrected-to-normal vision and were naive to the purpose of the experiments. All procedures were executed in compliance with relevant laws and institutional guidelines and were approved by the local ethical committee of the University of Amsterdam.

## Tasks

Participants participated in three experimental sessions, separated by less than one week from each other. We will first explain the main task, performed in session two and three, and thereafter the tasks performed in the first session.

## Main task: orientation discrimination task (sessions 2 and 3)

Stimuli were presented on a screen with a spatial resolution of  $1280 \times 720$  pixels, run at a vertical refresh rate of 100 Hz. Each trial consisted of seven consecutive intervals (**Fig. 3.1A**): (i) the baseline interval (0.6 s); (ii) the stimulus interval (500 ms; interrogation protocol), the start of which was signaled by a tone (200 ms duration); (iii) the response period (terminated by the participant's response); (iv) a delay (uniformly distributed between 1.5 and 2 s); (v) the outcome interval (0.5 s), the start of which was signaled by the occurrence of a tone (200 ms duration); (vi) a delay (uniformly distributed between 1.5 and 2 s); the outcome identity response period (terminated by the participant's response); (vii) an inter-trial interval (ITI; uniformly distributed between 1 and 1.5 s).

During Gabor presentation the luminance across all pixels was kept constant. A sinusoidal grating (1.47 cycles per degree) was presented for the entire stimulus interval. The grating was either tilted 45° (clockwise, CW) or 135° (counter-clockwise, CCW). Grating orientation was randomly selected on each trial, under the constraint that it would occur on 50% of the trials within each block of 60 trials. The grating was presented in a Gaussian annulus of 11.4 cm, with a 10.85 degrees visual angle (1.47 cycles per degree). Outcome was signaled by the Dutch word "goed" (correct outcome) or the word "fout" (incorrect outcome), from now on referred to as "correct" and "error" outcome. The words were presented for three frames just below fixation. Outcome was either masked, by presenting both forward as well as backward masks (masks1-masks2-outcome-masks3-masks4) or unmasked, by presenting only forward masks (masks1-masks2-outcome). Each mask consisted of 6 randomly scrambled letters (without the letters making up the words "goed" or "fout"). Masks' types were presented two frames each. Outcome type (masked vs. unmasked) was randomly selected on each trial, under the constraint that it would occur on 50% of the trials within each block of 60 trials (Fig. 3.1A).

Participants were instructed to report the orientation of the Gabor, and simultaneously their decision confidence in this decision, by pressing one of four response buttons with their left or right index or middle finger: left middle finger: CCW, sure; left index finger: CCW, unsure; right middle finger: CW, sure. Participants were also instructed to report the identity and visibility of the outcome by pressing one of four response buttons with their left or right index or middle finger: left middle finger – "error", seen; left index finger – "error", unseen; right middle finger – "correct", unseen; right middle finger – "correct", seen. We defined unmasked outcome trials as trials on which the outcome was unmasked and participants reported it as "seen". We defined masked outcome trials as trials on which the outcome trials as trials on which outcome was masked and participants reported it as "unseen".

Throughout the main experiment, the contrast of the Gabor was fixed at the individual threshold level that yielded about 70% correct choices. Each participant's threshold contrast was determined before the main experiment, using an adaptive staircase procedure, and was adapted during the experiment after each block. Participants performed between 12 and 17 blocks (distributed over two measurement sessions), yielding a total of 720–1020 trials per participant.

#### Tasks performed in the first session

#### Passive viewing task

In this control task, participants fixated their gaze at the center of the screen and passively viewed the words "goed" (correct) and "fout" (error), randomly presented for 100 times. Words were presented for three frames (100 Hz refresh rate) and were not masked.

#### Forced-choice visibility task

In this control task, the words "goed" (correct) or "fout" (error) were presented in the same way as in the main experiment (see above), that is, in a masked or unmasked manner (same timings and presence or absence of masks as described above). Participants were instructed to report the identity of the presented words, by pressing one of two response buttons with their left or right index finger: left – "error"; right – "correct" (the stimulus-response mapping was counter-balanced across trials, and was indicated on the screen after each trial). Participants performed two blocks, yielding a total of 200 trials per participant. In total we tested 49 participants in the first behavioral and eye-tracking session. Six subjects did not enter the main experiment due to various reasons (e.g. drop-out, extensive blinking). Of the remaining 43 subjects, the 32 subjects with the lowest discrimination performance score were invited for the second and third session. Discrimination performance for the 32 included subjects varied between 49% and 73% correct. Included subjects were on average 98.87% (SEM=0.02) correct in the unmasked condition and 61.9% (SEM=0.02) correct in the masked condition. The average percentage of correct responses for masked words exceeded chance-level performance ( $t_{31}$ =11.26, p<0.001).

## Priming task

In this control task, participants were instructed to respond as fast and accurately as possible to eight Dutch words, five of positive (laugh, happiness, peace, love, fun) and 5 (death, murder, angry, hate, war) of negative in valence, by pressing one of two response buttons with their left or right index finger: left – negative; right – positive. Unknown to our participants, these words were preceded by the masked words "goed" and "fout", respectively "correct" and "incorrect", three frames each before the positive or negative word targets (12 frames each) in 100 Hz refresh rate. This yielded congruent and incongruent trials. Participants performed six blocks, yielding a total of 480 trials per participant.

## Procedures

Participants were seated in a silent and dark room (dimmed light), with their head positioned on a chin rest, 60 cm in front of the computer screen. The main task was performed while measuring Pupil and EEG responses.

## Eye data acquisition and preprocessing

The diameter of the left eye's pupil was tracked at 1000 Hz with an average spatial resolution of 15–30 min arc, using an EyeLink 1000 system (SR Research, Osgoode, Ontario, Canada). Periods of blinks and saccades were detected using the manufacturer's standard algorithms with default settings. The subsequent data analyses were performed using custom-made Python software. The following steps were applied to each pupil recording: (i) linear interpolation of values measured just before and after each identified blink (interpolation time window, from 150 ms before until 150 ms after blink), (ii) temporal filtering (third-order Butterworth, low-pass: 10 Hz), (iii) removal of pupil responses to blinks and to saccades, by first estimating these responses by means of deconvolution, and then removing them from the pupil time series by means of multiple linear regression (Knapen et al., 2016), and (iv) conversion to units of modulation (percent signal change) around the mean of the pupil time series from each block.

# Quantification of outcome-evoked pupillary responses

We computed outcome-evoked pupillary response amplitude measures for each trial as the mean of the pupil diameter modulation values in the window 0.4 s to 1.9 s from outcome, minus the mean baseline pupil value during the 0.5 s before the outcome. This time window was determined by testing the grand mean (across all trials) outcome-evoked pupillary response against 0 (see **Fig. 3.2A**).

# EEG data acquisition and analysis

EEG data was recorded and sampled at 512 Hz using a BioSemi Active Two system. Sixty-four scalp electrodes were distributed across the scalp according to the 10–20 International system and applied using an elastic electrode cap (Electro-cap International Inc.) Additional electrodes were two electrodes to control for eye-movements (left eye, aligned with the pupil, vertically positioned, each referenced to their counterpart), two reference electrodes at the ear lobes to be used as reference and two electrodes for heartbeat (positioned at the left of the sternum and in the right last intercostal space).

## Preprocessing

Standard pre-processing steps were performed in EEGLAB toolbox in Matlab. Data were bandpass filtered from 0.1 to 40 Hz off-line for ERP analyses. Epochs ranging from -1 to 2 seconds around outcome presentation were extracted. Linear baseline correction was applied to these epochs using a -200 to 0 ms window. The resulting trials were visually inspected and those containing artifacts were removed manually. Moreover, electrodes that consistently contained artifacts were interpolated, entirely or per bad epoch. Finally, using independent component analysis, artifacts caused by blinks and other events not related to brain activity were manually removed from the EEG data.

# Quantification of outcome-related ERP components

We focused on ERP components related to outcome processing with different latencies and topographical distributions. To zoom in on these specific components, a central region of interest (ROI) was defined (including the averaged signal of electrodes F1, Fz, F2, FCz, FC1, FC2, Cz, C1, C2, CPz, CP1, CP2, Pz, P1, P2).

## Task performance

To assess how participants used the available response options we plotted the frequency of choosing each of the 4 response buttons (**Fig. 3.1B**). Also, to check participants metacognition about their own performance we used a d-prime measure of their accuracy when discriminating between sure and unsure responses (**Fig. 3.1C**). To assess whether masked words produced an effect in behavior in our priming control task, isolated from the task context, we analyzed differences in reaction times and accuracy between congruent and incongruent conditions (**Fig. 3.1D**). We further investigated the effect of outcome awareness (unmasked/masked); correctness (correct/incorrect) and confidence on being correct (sure/unsure) on both the pupil percentage of signal change and event-related potentials (ERPs) following the presentation of the outcome. Repeated-measures ANOVAs were performed considering 8 trial types, namely 2 (awareness) \* 2 (correctness) \* 2 (confidence) in post-outcome time windows. Statistical analyses were performed in Matlab (Mathworks).

## Results

# Behavior: Gabor discrimination and confidence

The adaptive staircase procedure performed before the main experiment was successful, as evidenced by an accuracy level for Gabor orientation of 70.9% (SEM=0.44) in the main experiment, averaged across the two experimental sessions. Further, participants chose each of the four response options approximately equally often, enabling similar trial numbers in each cell for our

follow-up analyses (CCW-sure: 0.248; CCW-unsure: 0.240; CW-unsure: 0.252; CW-sure: 0.260, see **Fig. 3.1B**). Participants were significantly better for Gabor decisions classified as sure compared to unsure, indicating that, at the group level, participants were able to accurately introspect their performance on the Gabor orientation task (**Fig. 3.1C**; Gabor d' sure=1.71, SEM=0.069; Gabor d' unsure=0.61, SEM=0.039;  $t_{1,31}$ =12.34, p<0.001). As one would expect, participants responded faster when they were correct compared to when they were incorrect (1.28 seconds, SEM=0.039 vs. 1.41 seconds, SEM=0.041;  $t_{1,31}$ =8.49, p<0.001) and they were faster when they indicated to be sure compared to unsure about their Gabor orientation response (1.19 seconds, SEM=0.038 vs. 1.46 seconds, SEM=0.044;  $t_{1,31}$ =12.89, p<0.001).

#### *Behavior: outcome visibility*

In the main task, outcome sensitivity (d') was high for unmasked trials (d'=7.97, SEM=0.29) and low on masked trials on which participants reported not to have seen the outcome (d'=0.62, SEM=0.07). Although masked and subjectively indicated as unseen (see **Fig. 3.1A**), participants still had above chance performance for masked trials ( $t_{1,31}$ =9.2, p<0.001). We are aware of issues regarding post-hoc trial selection, for example when sorting trials based on single trial unseen vs seen scores, as discussed in Shanks (2017), therefore we refer to masked and unmasked trials throughout this manuscript and do not claim unconsciousness of the stimulus material in any condition.

## Behavior: masked priming

Before we explore the impact of masked and unmasked outcomes on pupil size and P3 amplitudes we wanted to make sure that masked stimuli were able to induce typical behavioral priming effects. Therefore subjects have also performed a priming task with the same stimuli as used in the main task, now used as primes (see **Methods**). Although strongly masked, positive and negative words did impact behavior as indicated by this priming task (**Fig 3.1D**). Reaction times were slower to incongruent trials (e.g. the word "correct" paired with a negative target word), compared to congruent trials (e.g. "correct" paired with a positive target word) (incongruent: 0.484 seconds, SEM=0.010, congruent: 0.477 seconds, SEM=0.010; t<sub>1,31</sub>=4.529, p<0.001). Overall accuracy was high, but still accuracy was worse on incongruent trials than on congruent trials (incongruent: 95.0, SEM=0.8; congruent: 96.3, SEM=0.4; t<sub>1,31</sub>=2.083, p=0.046).



**Figure 3.1. Task description and behavioral results. (A)** Sequence of events during a single trial. Participants had to report the direction and level of confidence in the decision about a Gabor patch by pressing one of four buttons (CCW sure; CCW unsure, CW unsure, CW sure). After the decision interval veridical outcome was presented, which could be either masked or not masked. Outcome was followed by a forced-choice visibility question asking for both the outcome identity (correct/error) and its visibility (seen/unseen). Participants indicated their response by pressing one of four buttons (error seen; error unseen, correct unseen, correct seen). **(B)** Fraction of trials per Gabor response option among the four possible response categories. **(C)** Signal detection theoretic d', separately for sure and unsure trials. Data points, individual subjects. Stats, paired samples t-test. **(D)** Reaction time (left panel) and accuracy (right panel) in the priming task. Error bars, SEM.; stats, permutation test. CCW = counter-clock-wise, CW = clock-wise.

#### Outcome-related pupil modulations

Next we focused on outcome-evoked pupil modulations. Across all trials, pupil diameter was strongly modulated during the outcome interval and differed significantly from baseline between 400 and 1900 ms (**Fig. 3.2A**). From now on we refer to this as the outcome-modulated interval. We extracted the pupil response during this entire interval (400-1900 ms time-window) to test how pupil dilation was modulated by decision correctness, decision confidence and outcome visibility.

First, we observed a 3-way interaction between decision confidence, correctness and visibility ( $F_{1,31}$ =9.28, p=0.0047). To further unpack this interaction we performed two 2-way ANOVAs on masked and unmasked outcome separately. After unmasked outcomes, the pupil dilated more after a negative outcome (indicating that the response was incorrect) compared to a positive outcome (main effect of correctness:  $F_{1,31}$ =45.75, p<0.001). Crucially, this correctness effect was modulated by participants confidence in their previous Gabor decision ( $F_{1,31}$ =23.38, p<0.001), in such a way that the difference between error and correct outcome processing was larger for sure responses than unsure responses (**Fig. 3.2B**). In contrast, in the masked condition, negative outcomes yielded larger pupil dilation than positive outcomes ( $F_{1,31}$ =4.96, p=0.033), but this effect was not modulated by decision confidence (**Fig. 3.2C**).

We wondered whether the outcome-related pupil dilation may have been driven by low-level stimulus characteristics, such as luminance, or potentially by the intrinsic valence of the words used as outcome (e.g. being of positive/negative valence). To test this we performed a control task, performed before the main task, in which we displayed the two words fully visible and the words were only passively viewed (see **Methods** for details). Control analyses demonstrate that our pupil dilation effects cannot be explained by an intrinsic pupil response to positive/negative valence of the words or their luminance (or other low-level characteristics), because during passive viewing participants pupil responses showed the exact opposite pattern of correctness as observed during the main task (compare the results of **Fig. 3.2D** to **Fig 3.2E**).



**Figure 3.2.** Pupil dilation results. (A) Group average outcome-elicited pupil response time course. Grey box: time window for computing scalar response amplitudes. Black bar: time course significantly different from 0 (p<0.05, paired-samples t-tests). (B) Pupil dilation after unmasked outcome sorted by correctness and confidence. (C) Pupil dilation after masked outcome sorted by correctness and confidence. (D) Group average pupil response during the passive viewing task with unmasked "correct" and "incorrect" words presented. Shadows indicate the SEM. Black bar: time courses for significant differences. (E) Group average outcome-elicited pupil response time

course after correct and incorrect unmasked outcome. Black bar, time courses significantly different. All panels: Shading or error bars, SEM. Labels: = reflects a main effect between the two separate lines in the plot. \ reflects a main effect of the factor plotted on the x-axis. X reflects and interaction effect between the factors plotted.

## Outcome-related P3 ERP modulations

We focused on ERP components related to outcome processing to determine whether outcome-related brain responses were impacted by correctness, decision confidence and the level of outcome awareness (**Fig. 3.3**). We focused our hypothesis-driven analyses on the P3 ERP component, which has been strongly linked to pupil-linked neuromodulation (Correa et al., 2017a; Jepma et al., 2016; Nieuwenhuis, 2011) and outcome processing (Nieuwenhuis et al., 2005). A 3-way repeated measures ANOVA on the amplitude of the P3 component revealed that there was a triple interaction between the factors correctness, confidence and awareness ( $F_{1,31}$ =4.73, p=0.037, based on a central ROI, 500-800 ms, see **Methods**). Further, in general P3 amplitude was larger for unmasked outcomes than masked outcomes (main effect of awareness:  $F_{1,31}$ =62.84, p<0.001) and awareness interacted with correctness ( $F_{1,31}$ =42.05, p<0.001) and confidence ( $F_{1,31}$ =6.66, p=0.015).

To further understand the relationship between the factors we performed two 2-way ANOVAs with the factors correctness and confidence, separately for masked and unmasked outcome, similarly as for our pupil dilation results. In the unmasked condition the P3 component was larger for negative compared to positive outcomes ( $F_{1,31}$ =67.07, p<0.001, **Fig. 3.3A/B**) and this effect interacted with decision confidence ( $F_{1,31}$ =7.8, p=0.01, **Fig. 3.3A/B**), mimicking our pupil dilation results (the difference between error and correct outcome was larger for sure responses than unsure responses). On the other hand, when outcomes were masked, the pattern of results was very different. The amplitude of the P3 was larger for unsure compared to sure decisions (main effect of confidence:  $F_{1,31}$ =0.25, p=0.01, **Fig. 3.3C/D**) but the correctness effect was absent ( $F_{1,31}$ =7.8, p=0.98).



**Figure 3.3. P3 ERP results. (A)** Time courses of the ERP time-locked to the unmasked outcome presentation, based on centrally located electrodes (see inset). The ERP curves show the response (mV) according to accuracy and confidence in the previous decision. **(B)** ERP amplitude from 500-800 ms from unmasked outcome onset according to accuracy and confidence in the decision. Error bars, SEM. **(C)** Time courses of ERP, time-locked to the masked outcome presentation, based on centrally located electrodes (see inset). The ERP curves show the response (mV) according to accuracy and confidence in the decision. **(D)** ERP amplitude from 500-800 ms from masked outcome onset according to accuracy and confidence in the decision. Error bars, SEM. Labels: = reflects a main effect between the two separate lines in the plot. \ reflects a main effect of the factor plotted on the x-axis. X reflects and interaction effect between the factors plotted.

#### Discussion

We investigated how decision correctness, decision confidence and outcome awareness affects outcome processing during a simple perceptual decisionmaking task. We focused our analyses on two measures, pupil diameter and the P3 ERP component, both arising after outcome presentation and both considered proxies of the brain's central arousal state, which is modulated by the catecholaminergic neurotransmitter system (NE and DA) (Jepma et al., 2016; Nieuwenhuis, 2011; Nieuwenhuis et al., 2005). In the following, we will first summarize and interpret the results obtained for fully visible outcomes, after which we will discuss the results related to masked outcomes.

In our task, visible (unmasked) error feedback generated a larger P3 ERP amplitude and stronger pupil dilation compared with correct outcomes, which might indicate a surprise for receiving "error" as feedback in a staircased 70% correct task (Braem et al., 2015). Further, we observed a clear prediction error pattern for both measures for fully visible outcomes (**Fig. 3.2** and **Fig. 3.3**): the correctness effect (error vs correct outcome) was modulated by participant's confidence in the previous decision. We observed the largest P3/pupil responses on confident decisions ("sure" trials) that nonetheless led to error feedback, therefore likely signaling surprise about receiving an incorrect outcome (and the need of behavioral adaptation). Similarly, on unsure trials on which subjects nonetheless received positive feedback, larger ERP/pupil amplitude signaled surprise about the correctness of the previous decision, as

compared with sure trials on which subjects turned out to be correct in the end (on these trials there was no surprise about the outcome that was received). Therefore, these findings mimic a typical temporal reward prediction error response, reflecting the difference in value between a received reward and a predicted reward (Schultz, 1998). The observation that both pupil dilation and the P3 component signal a prediction error signal is in line with observations that DA activity is linked to prediction errors (Bayer & Glimcher, 2005; Lak, Stauffer, & Schultz, 2014; Schultz, Dayan, & Montague, 1997; Schultz, 1998). They are also in line with the locus coeruleus LC-P3 theory (Levy et al., 2010), which suggests that the P3 may reflect the response of the LC-NE system to the outcome of internal decision processes and the consequent effects of NE potentiation (tuning) required for behavioral adaptation. Likewise, pupil dilation has been associated with tracking uncertainty (de Gee et al., 2014; Lempert et al., 2015; Urai et al., 2017), predicting both confidence and metacognitive accuracy for auditory decisions (Lempert, Chen, & Fleming, 2015). In our study, higher than predicted rewards (generating positive PE) would elicit brief catecholamine activations (DA, NE), while lower-thanpredicted rewards (generating negative PE) would induce decreases in activity. Our interpretation for our findings in unmasked condition is that accurately predicted rewards do not change the overall arousal because it configures a condition in which no behavioral updating is necessary. However, the increment of arousal, as measured with both the P3 amplitude and pupil dilation, may be required for behavioral updating.

In contrast to the results obtained based on fully visible outcomes, the results for masked outcomes were rather different. Data revealed that the pupil tracked only the difference between correct and incorrect decisions (larger pupil for error feedback), whereas the P3 tracked participants' decision confidence (outcome processing on unsure trials generated larger P3 amplitudes than on sure trials). While not claiming unawareness of the masked outcomes, it is striking that the incorporation of decision confidence and outcome value seemed to require full awareness, because none of the masked effects mimicked the response observed for fully visible feedback. Speculatively, the contradictory results obtained for pupil diameter (tracking correctness) and P3 amplitude (tracking confidence) may be explained by a potential two-component structure of phasic dopamine responses proposed recently, namely an initial fast stimulus detection process followed by a response valuation mechanism, accounting for subjective reward value (Schultz, 2016). Although speculatively, it may be that pupil size fluctuations reflect the first component of this response and the P3, the latter. We suggest this hypothesis because the initial component of the phasic dopamine reward

PE is a brief response that occurs in response to a variety of unpredicted events (Schultz, 2016). In our study, pupil dilation separated correct (frequent) from incorrect (rare) trials, these ones associated with a larger pupil amplitude. Through stimulus-driven salience, the early dopamine activation component might serve to transiently enhance the ability of rewards to induce learning and action. Higher salience would induce faster learning (Pearce & Hall, 1980). The initial dopamine response component might boost and sharpen subsequent reward value processing and ultimately increase action accuracy. Also, signals from the anterior cingulate cortex (ACC) to locus coeruleus (LC), indicating an adverse outcome during decision tasks (Botvinick, 2001), are possibly complemented by signals from the orbitofrontal cortex (OFC) to LC, indicating absence of an expected reward, leading to augment the LC phasic mode. This, in turn, would improve performance on subsequent trials by enhancing the LC phasic response to subsequent stimuli and thereby augmenting the gain of units responsible for task execution. In our study, even in the presence of masked outcome, such correctness effect could be detectable by pupil dilation.

Overall from our study we observed that cortical and pupil signals were sensitive enough to reflect differences in reward valence and in people's ongoing expectations even when outcomes were not reportable. However, it was only during full outcome awareness that both the P3 ERP and the pupil dilation measures mirrored a prediction error signal, reflecting an integration of outcome correctness modulated by the confidence in the decision. This offers further support for the utility of P3 and pupil dilation as proxies for neuromodulations accounting for outcome processing.

# 4. Pupil dilation oppositely predicts perceptual sensitivity and metacognitive insight during human perceptual decision-making

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#### Abstract

People often make different decisions, and experience varying degrees of decision confidence, when faced with the same external evidence from moment-to-moment. Such variability of performance and metacognitive insight may be attributed to fluctuating noise levels in the brain's decision-making circuits. Non-luminance related variations in pupil size are considered a proxy for these sources of noise and are driven by neuromodulatory fluctuations in arousal state. Here we investigate how pupil-linked arousal predicts sensory performance and the reliability decision-making of metacognitive introspection. Thirty-two participants performed a challenging perceptual decision-making task that allowed us to compute signal detection theoretic (SDT) measures of perceptual sensitivity and metacognitive insight. We observed that pupil responses scale linearly with decision accuracy (SDT d'): large pupil dilation was associated with better discrimination performance. In sharp contrast, larger pupils were predictive of worse metacognitive insight (SDT meta-d' efficiency). These results show that bottom-up stimulus encoding and top-down metacognitive evaluation are differentially affected by fluctuations in the brain's arousal system.

## Introduction

When people are repeatedly presented with the same sensory input they often make different decisions (Glimcher, 2005; Gold & Shadlen, 2007; Shadlen et al., 1996; Sugrue, Corrado, & Newsome, 2005; Wyart & Koechlin, 2016). Here we address how such variability in decision-making occurs when confronted with the same objective evidence. In the absence of external stimulation the state of

neural networks fluctuates on slow and rapid time-scales. These moment-tomoment fluctuations are associated with varying levels of alertness, arousal and attention, which may contribute to variability in decision-making (Glimcher, 2005; Shadlen et al., 1996). These state fluctuations (also called cortical state) are controlled by neuromodulatory systems of the brainstem, which have widespread projections to the cortex, and strongly shape stimulus driven neuronal responses (Aston-Jones & Cohen, 2005). For example, it has been shown that fluctuations in network state activity influences the latency, magnitude and variability of the sensory evoked neural signal (Lima, Singer, & Neuenschwander, 2011; McGinley et al., 2015; Zagha et al., 2013). This interaction between internal fluctuations in cortical state and sensory evoked neural responses may explain variations in task performance and behavior, that were previously marginalized as noise (de Gee et al., 2014; Kahneman & Beatty, 1966; Nassar et al., 2012; Urai et al., 2017).

Recent studies have shown non-luminance driven fluctuations in pupil size may reflect a proxy for neuromodulatory activity and the level of the cortical arousal state (Aston-Jones & Cohen, 2005; de Gee et al., 2014; Gilzenrat et al., 2010; Harris & Thiele, 2011; Lee & Dan, 2012; Schwalm & Jubal, 2017). Both network state fluctuations and variations in pupil size are driven by the release of noradrenaline (NA) and acetylcholine (ACh) (Aston-Jones & Cohen, 2005; Goard & Dan, 2009; Reimer et al., 2016). Although the pupil may act as a physiological index of the arousal system, ranging from aroused (wide pupils) to unaroused (constricted pupils) levels (McGinley et al., 2015; Reimer et al., 2014), it is challenging to identify which specific elements of decision processes are associated with phasic (fast) moment-to-moment changes in arousal. Here we investigate how phasic stimulus-related arousal changes, as measured by pupil size, associate with the accuracy of perceptual decisions and the ability to evaluate the reliability of such decisions, referred to as metacognitive insight.

Participants performed a challenging perceptual decision-making task in which they discriminated the orientation of a low-contrast Gabor stimulus while simultaneously indicating their confidence in this decision (**Figure 4.1A**). Discrimination performance was individually titrated using an adaptive staircase procedure to ensure that differences in behavior could only be attributed to internal noise fluctuations in the brain's decision-making circuits. This set-up allowed us to link stimulus-elicited pupil responses to participants' perceptual sensitivity (type-1 measures: e.g. d' and criterion) and metacognitive insight (type-2 measures, e.g. meta-d' and meta-criterion) in a signal detection theoretic (SDT) framework (Fleming & Lau, 2014; Green & Swets, 1966; Maniscalco & Lau, 2012).

## Materials and methods

#### Participants

Thirty-two students from the University of Amsterdam (23 women; aged 18-24) participated in the study for course credits or financial compensation. All participants gave their written informed consent prior to participation, had normal or corrected-to-normal vision and were naive to the purpose of the experiment. All procedures were executed in compliance with relevant laws and institutional guidelines and were approved by the local ethical committee of the University of Amsterdam.

## Behavioral task

Participants participated in three experimental sessions, each separated by less than one week. Participant inclusion criteria are explained in detail elsewhere (Correa et al., 2017a). Here we focus on the main perceptual task that is relevant for addressing the questions in this paper. In the orientation discrimination task, participants had to decide on the direction of a Gabor stimulus and had to indicate their confidence in this decision. Each trial consisted of eight consecutive intervals (**Figure 4.1A**): (i) the baseline interval (0.6 s); (ii) the stimulus interval (500 ms; interrogation protocol), the start of which was signaled by a tone (200 ms duration); (iii) the response period (terminated by the participant's response); (iv) a delay (uniformly distributed between 1.5 and 2 s); (vi) the feedback interval (0.5 s), the start of which was signaled by the participant's response); (vii) an inter-trial interval (ITI; uniformly distributed between 1 and 1.5 s).

The luminance across all pixels was kept constant. A sinusoidal grating (5 cycles per degree) was presented for the entire stimulus interval. The grating was either tilted 45° (clockwise, CW) or 135° (counter-clockwise, CCW). Grating orientation was randomly selected on each trial, under the constraint that it would occur on 50% of the trials within each block of 60 trials. The grating was presented in a Gaussian annulus, with an average distance (± SD) to fixation of 1.47 degrees. Participants were instructed to report the orientation of the grating, and simultaneously their decision confidence, by pressing one of four response buttons with their left or right index or middle finger: left middle finger: CCW, sure; left index finger: CCW, unsure; right middle finger: CW, sure. Participants were encouraged to use the confidence buttons equally often. Further, participants received veridical feedback about their decision, which was signaled by the Dutch word "goed"

(correct feedback) or the Dutch word "fout" (incorrect feedback). The words were presented for 30 ms. Feedback was either masked or unmasked (50/50). Further, participants were instructed to report the identity and visibility of the feedback by pressing one of four response buttons with their left or right index or middle finger: left middle finger – "error", seen; left index finger – "error", unseen; right index finger – "correct", unseen; right middle finger – "correct", seen. In the present study we will focus on the Gabor response only. Feedback-related data is presented in Correa et al., (2017a).

Throughout the main experiment, contrast of the grating was fixed at the individual threshold level that yielded about 70% correct choices. Each participant's threshold contrast was determined before the main experiment, using a staircase procedure that could be adapted at the end of each block of the main experiment, to yield 70% correct choices. Participants performed between 12 and 17 blocks (distributed over two measurement sessions), yielding a total of 720–1020 trials per participant. Stimuli were presented on a screen with a spatial resolution of 1280×720 pixels, run at a vertical refresh rate of 100 Hz.

## Eye data acquisition

Participants were seated in a silent and dimmed light room, with their head positioned on a chin rest, 60 cm in front of the computer screen. The diameter of the left eye's pupil was tracked at 1000 Hz with an average spatial resolution of 15–30 min arc, using an EyeLink 1000 system (SR Research, Osgoode, Ontario, Canada). We also acquired EEG data, but these were not analyzed for the present study.

# Analysis of task-evoked pupil responses

Periods of blinks and saccades were detected using the manufacturer's standard algorithms with default settings. Subsequent data analyses were performed using custom-made Python software. The following steps were applied to each pupil recording: (i) linear interpolation of values measured just before and after each identified blink (interpolation time window, from 150 ms before until 150 ms after blink), (ii) temporal filtering (third-order Butterworth, low-pass: 10 Hz), (iii) removal of pupil responses to blinks and to saccades, by first estimating these responses by means of deconvolution, and then removing them from the pupil time series by means of multiple linear regression (Knapen et al., 2016), and (iv) conversion to units of modulation (percent signal change) around the mean of the pupil time series from each block.

# Quantification of stimulus-evoked pupillary responses (SPR)

We computed stimulus-evoked pupillary response (SPR) amplitude measures for each trial as the mean of the pupil diameter modulation values in the window -0.5 s to 3.0 s from stimulus onset, minus the mean baseline pupil value during the 0.5 s before the stimulus. SPR was negatively correlated to pretrial baseline pupil size. To isolate the task-evoked component, we removed effects of pretrial baseline pupil size from SPR (via linear regression). In all analyses, we used eight equally populated bins of single-trial SPR amplitudes, sorted by amplitude. As a control analysis, trial-to-trial variations in RT had been removed (via linear regression) from the pupil response (see **figure 4.4**).

## Analysis and modeling of choice behavior

Reaction time (RT) was defined as the time from stimulus offset until the button press. In a model-free analysis, we computed the proportion of "CW"-choices separately for the eight SPR bins. We then modeled the effects of phasic arousal (as indexed by SPR) on choice behavior using two approaches.

## SDT modeling of perceptual sensitivity

We computed the SDT-metrics d' and criterion (Green & Swets, 1966) separately for the eight bins of SPR. We estimated d' as the difference between z-scores of hit- and false-alarm rates. We estimated criterion by averaging the z-scores of hit- and false-alarm rates and multiplying the result by -1.

## SDT modeling of metacognitive efficiency

We computed the SDT-metrics meta-d' efficiency and meta-criterion separately for the eight bins of pupil size. Type-2 meta-d' efficiency (here often referred to as metacognitive insight) is a relative measure of metacognitive sensitivity and reflects the extent to which confidence estimates accurately reflect the correctness of the decision (meta-d'/d') (Fleming, 2017; Fleming & Lau, 2014; Maniscalco & Lau, 2012). If meta-d' is equal to d' then a subject is metacognitive "ideal", translating all the available information from the type-1 task into performance in the type-2 task (Fleming & Daw, 2017). Metacriterion, on the other hand, measures the overall level of confidence expressed, independent of whether the trial is correct or incorrect (Fleming & Lau, 2014).

## Linking SDT measures to pupil measures

Next, we used sequential polynomial regression analysis (Draper & Smith, 1998) to quantify the dependence of all behavioral measures on SPR. This procedure allowed us to systematically test whether SPR predominantly exhibited no (zero-order polynomial), a monotonic (first-order polynomial), or a

non-monotonic (second-order polynomial) effect on behavior. The behavioral metric y was modeled as a linear combination of polynomial basis functions of eight SPR bins:

$$\mathbf{y} \sim \beta_0 + \beta_1 T P R^1 + \beta_2 T P R^2 \tag{1}$$

with  $\beta$  as polynomial coefficients. The corresponding regressors were orthogonalized, and each model was sequentially tested in a serial hierarchical analysis, based on F-statistics. This analysis was performed at the group level, and it tested whether adding the next higher order model yielded a significantly better description of the response than the respective lower order model. We tested models from the zero-order (constant, no effect of SPR) up to the second-order (quadratic, non-monotonic). If the first-order model was significantly better than the zero-order model at the group level, we fitted a linear model and tested the corresponding linear correlation coefficients across the group. If the second-order model was significantly better than the first-order model between SPR and behavior for each subject and tested the second-order coefficients across the group.

Having established robust first-order (monotonic) relationships between SPR and behavior, we then characterized the timing of these effects by means of a sliding window (linear) correlation analysis over the interval from 1 s before the Gabor to 3 s after response (window length: 250 ms, step size: 25 ms). We computed separate, baseline-corrected SPR values (see section *Quantification of stimulus-evoked pupillary responses*) for each position of the window. Per time window, we then sorted trials by the SPR-values into eight bins, and correlated these values with behavioral metrics for the corresponding bins. This yielded time courses of the correlation between SPR and behavior.

## Statistical comparisons

We used nonparametric paired permutation tests to test for significant relationships between behavioral estimates and stimulus-evoked pupil responses. Statistical tests were performed at the group level, using the individual participants' mean parameters as observations. For each comparison, we randomly permuted the labels of the observations (e.g., the regressor label of the beta estimates), and recalculated the difference between the two group means (10,000 permutations). The p-value was the fraction of permutations that exceeded the observed difference between the means. Trials were pooled into eight bins of stimulus-evoked pupil responses (pupil size) amplitudes.

#### Results

The individual staircase procedure was successful, as indicated by an average Gabor orientation accuracy of 70.9% (SEM=0.44). Participants distributed their responses equally across the four possible response categories (**Figure 4.1B**). **Figure 4.1C** shows that participants were able to introspect their perceptual performance well since d' was considerably higher for sure than unsure responses.



**Figure 4.1. Task, response distribution and sensitivity dependent on decision confidence. (A)** Sequence of events during a single trial. Participants reported the direction and level of confidence in the decision about a Gabor patch by pressing one of four buttons (CCW sure; CCW unsure, CW unsure, CW sure). After the decision interval veridical feedback was presented (see Methods for details). (B) The proportion of trials per Gabor response option. CCW=counter-clockwise, CW=clock-wise. (C) Signal detection theoretic d', separately for sure and unsure trials. Data points, individual subjects. All panels: group average (N=32); error bars, s.e.m.; stats, permutation test.

In order to quantify the association between trial-to-trial fluctuations in stimulus-evoked pupil-linked arousal and participants' perceptual accuracy we binned pupil size per subject in eight bins (SPR bins) and regressed it to predefined type-1 and type-2 measures of performance (within-subject analysis). **Figure 4.2A** shows the average time course of the pupil from stimulus (Gabor) onset, plotted as the percentage signal change from baseline (see **Methods** for details). Across all trials, pupil diameter was strongly modulated during the stimulus presentation interval. For our main analyses, we extracted the pupil response during the post-stimulus interval to regress it to behavioral measures (time-window used: 0.5-3 seconds, highlighted in a transparent box in **Fig. 4.2A**, see **Methods** for details). We will show in **Fig. 4.3** that our results do not depend on the time-window that is selected for these analyses.



**Figure 4.2.** The relation between phasic stimulus-evoked pupil responses and type-1 and type-2 performance. (A) Task-evoked pupil response time course locked to stimulus onset. Figures (B) until (G) depict the relationship between pupil size and various behavioral measures (8 pupil bins; linear fits were plotted wherever the first-order fit was superior to the constant fit (see Materials and Methods). (B) Reaction time, (C) d', (D) criterion, (E) confidence, (F) meta-d', (G) meta-criterion. All panels: group average (N=32); shading or error bars, shaded areas, s.e.m.; stats, Wilcoxon signed-rank test.

#### Stimulus-evoked pupil responses are associated with type-1 performance

**Figure 4.2B** shows that RT, reflecting a global measure of task demands and participants' effort, is longer when the pupil is larger (r=0.172, p=0.047). More importantly, large SPRs were consistently accompanied by an improvement in participants' d' (**Fig. 4.2C**). The relationship between pupil and d' was positive and linear: larger pupils were associated with better perceptual discrimination (r=0.212, p=0.002). Although we observed a relationship between pupil size and d', such a relationship was absent between pupil dilation and criterion (r=0.12, p=0.122, **Fig. 4.2D**).

#### Stimulus-evoked pupil responses are associated with type-2 performance

Next, we investigated the relationship between pupil size and participant's metacognitive efficiency of their performance. First, as expected based on the generally observed positive relationship between d' and confidence (when performance is higher, confidence is higher, see also **Fig. 4.1C**), pupil dilation also showed a positive and linear relation with participants' overall confidence expressed in their decision (**Fig. 4.2E**). Confidence was higher when pupil size

was larger (r=0.342, p<0.01). However, although pupil size increases linearly and positively with d' and confidence, the opposite pattern was observed for meta-d' efficiency: the reliability of metacognitive evaluation. Meta-d' efficiency (meta-d'/d') reflects the ability to introspect the reliability of perceptual performance, corrected for individual differences in direct task performance (d') (Fleming, 2017; Fleming & Lau, 2014; Maniscalco & Lau, 2012). **Fig. 4.2F** shows that larger stimulus-evoked pupil responses are associated with a lower meta-d' efficiency (r=-0.147, p=0.035). Finally, **Fig. 4.2G** shows that meta-criterion, the overall tendency to report being sure versus unsure (being conservative or liberal in the expression of confidence) is not related to pupil size (r=0.039, p=0.646).

To rule out that none of these results were biased by differences in RT between pupil bins we ran all of the above analyses while regressing out RT. In **Figure 4.3** we show that these results were very similar while regressing out RT.



*Figure 4.3.* The relationship between phasic decision-related pupil responses and type-1 and type-2 performance measures while regressing out reaction times (see *Materials and Methods* for details).

Finally, to better understand the temporal profile of the association between pupil size and type-1 (d' and criterion) and type-2 (confidence, meta-d' and meta-criterion) measures of performance, we plotted the correlation

coefficient between pupil size and the relevant performance measures, either time-locked to the Gabor (top panels) or time-locked to the response (bottom panels) for comparison (**Fig. 4.4**). The Gabor-locked analysis shows that pupil dilation correlates positively with d' and confidence, but interestingly, it shows that this relationship is already observed before the response (**Fig. 4.4A and 4.4B**). Notice that criterion shows a positive correlation with pupil size, but only after the response has been given (**Fig. 4.4C**). On the other hand, participants' meta-d' correlated negatively with pupil size both before and after Gabor presentation (**Fig. 4.4B**).



**Figure 4.4. Time course of the correlation between pupil size and type-1 and type-2 measures of performance, both Gabor-locked (top, A, B) and response-locked (bottom, C, D).** (A and C) Sliding window linear correlation between pupil response, d' and criterion. (**B and D**) Sliding window linear correlation between pupil size, confidence, meta-d' and criterion. Pupil size is included as a reference in all figures. All panels: group average (N=32), dotted vertical line, median RT; horizontal colored lines, significant time windows (compared to zero; p<0.05 uncorrected); shading, s.e.m.; stats, permutation test.

#### Discussion

In the present study we showed, for the first time, that pupil dilation predicts participants' perceptual sensitivity and metacognitive insight in opposite ways. Under high stimulus-evoked pupil dilation (i.e., higher arousal), participants

were better at discriminating the orientation of low-contrast Gabor patches (as reflected in a higher d'), but at the same time had more difficulty judging the accuracy of this decision, as reflected by a lower meta-d' efficiency.

These findings are in line with an influential theory of catecholamine function, which proposes that norepinephrine and dopamine activity are related to gain regulation in sensory brain regions, tuning neural network dynamics to optimize information processing, possibly enabling stimuli to be better encoded under high stimulus-elicited phasic arousal (Aston-Jones & Cohen. 2005). Arguably, glutamate and norepinephrine release mutually enhance and amplify activation of prioritized representations, increasing perceptual and memory selectivity under arousal (Mather et al., 2016). Although most of the studies have been performed in animals, recently, Warren and collaborators (2016) reported that the effect of baseline catecholamine levels, either indexed by pupil diameter or actively manipulated by pharmacological interventions (norepinephrine transporter blocker atomoxetine), affects the precision of object representations in the human ventral temporal cortex. It has also recently been shown that elevated arousal levels, measured by pupil size, enhance contrast perception (Kim, Lokey, & Ling, 2017). Note that an increase in pupil diameter does not increase perceptual sensitivity per se (Bullock et al., 2017; Campbell & Green, 1965).

Pupil dilation has been linked to behavioral measures at different stages during the decision process. For example, when pupil dilation is inspected after a decision has been made, stronger pupil dilation has been associated with lower confidence in the previous decision, especially for participants with good metacognitive insight (Lempert et al., 2015). The authors argued that increased pupil dilation may have served as a proxy of uncertainty, predicting both confidence and metacognitive accuracy in their study. Several other studies have also addressed the association between pupil dilation and feedback anticipation and feedback processing. For example, Urai and collaborators (2017) investigated post-response pupil size modulations before performance feedback and observed that larger pupil responses were accompanied by lower choice accuracy in the previous decision, in line with the Lempert et al., study. Generally, differences in the timing of the pupil measures may account for this different pattern of results. In the present study, pupil analyses were timelocked to stimulus presentation and response execution, and responsefeedback intervals were relatively short (~2 seconds). Therefore, pupil size was not related to signaling confidence in the preceding response, but was related to processes evolving during decision formation. Also, the finding of impoverished metacognitive insight under high arousal levels reported here is

in line with a recent study in which noradrenergic blockade by propranolol increased metacognitive performance, but had no significant impact on d' (although the results also hinted towards better discrimination performance, Hauser et al., 2017).

How can we explain the differential association of phasic arousal, indexed by pupil size fluctuations, with direct perceptual sensitivity and metacognitive insight? A possible mechanism may be that phasic neuromodulation suppresses 'top-down' signals more than 'bottom-up' signals (Friston, 2010; Gil, Connors, & Amitai, 1997; Hsieh, Cruikshank, & Metherate, 2000; Kimura, 1999; Kobayashi et al., 2000). During perceptual decisions, bottom-up signals encode the available sensory evidence, while top-down signals might encode prior beliefs about the upcoming stimulus (Friston, 2010; Pouget et al., 2013). This interpretation is in line with recent studies by De Gee and collaborators (2014, 2017), who investigated how phasic task-related arousal modulations associate with decision bias in a yes-no detection task. They observed that pupil size was larger before "yes" than before "no" choices, especially for conservative participants indicating "yes" (signal present) against their overall decision bias. Pupil size correlated with activity in the locus coeruleus (LC) and other brainstem nuclei in its vicinity, and these brainstem signals in turn predicted the observed changes in choice bias (de Gee et al., 2017). The authors interpret these findings by suggesting that through a relative suppression of 'top-down' signals, phasic arousal might reduce the weight of the prior (reflecting subjects' intrinsic bias) relative to the sensory evidence (the likelihood). If the prior reflects a conservative bias, reducing its weight would reduce this bias. In our task, however, participants were asked to judge CW or CCW orientations, instead of presence and absence of a signal. Note that in our study pupil dilation varied with the perceptual sensitivity d' but was not predicted of participants' choice bias.

Metacognition can be thought of as a higher-order process that evolves during decision formation and depends on the integration of perceptual information with other sources of information, such as interoceptive states and general arousal (Allen et al., 2016; Hauser et al., 2017). Thus, it may be that through a suppression of "top-down" signal flow, phasic arousal might reduce the weight of top-down metacognitive signals compared to bottom-up stimulus-related signals, in line with the neural gain hypothesis (Aston-Jones & Cohen, 2005; Eldar, Cohen, & Niv, 2013).

Finally, we would like to note that it is unlikely that spontaneous changes in pupil size provided higher contrast sensitivity, driving discrimination

performance and potentially confidence. It has been shown previously that elevated arousal level induced by reward increases contrast perception, but mainly for stimuli presented at relatively high contrast (Kim et al., 2017) (note that we used low contrast stimuli here). Further, the pupil-d' correlations that we have observed here occurred *after* the presentation of the Gabor stimulus (see **Figure 4.4**), and not before (data not shown here). Having said that, future studies should focus on the influence of arousal on low level visual stimulus characteristics to increase our understanding of how arousal may specifically modulate different (low-level) aspects of perception (see (Azevedo, Badoud, & Tsakiris, 2017; Lojowska et al, 2015) for examples).

In conclusion, we found that pupil size during stimulus encoding predicts perceptual sensitivity (d') and metacognitive insight (meta-d' efficiency) in opposing directions: larger pupils were associated with enhanced d', but a reduced meta-d' efficiency. Therefore, phasic arousal indexed by pupil dilation accounts for a significant portion of the variability of perceptual performance and metacognitive evaluation during repeated perceptual decisions on the same external input.
# 5. Breaking the flow: No evidence for a role of subjective conflict experience on conflict adaptation

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#### Abstract

Cognitive control over conflict is an important skill for successful decisionmaking. Research in this field employs typical "conflict tasks" in which taskirrelevant information either helps (congruent trials) or hinders (incongruent trials) task performance. The conflict effect is the impact of incongruent information, generating slower reaction times and more errors after incongruent trials as compared to congruent ones. On the other hand, conflict adaptation is the reduction of the impact of conflict information in the subsequent trial when conflict is detected on the current trial. It has been shown previously that conflict detection and subsequent cognitive control operations may operate unconsciously, for example when conflict-inducing stimuli are masked from awareness. However, it has been proposed recently that, although people may be unaware of the conflict-inducing stimulus itself, such "unconsciously triggered control operations" may be driven by metacognitive awareness of conflict, which may arise from the feeling of task difficulty or response slowing on incongruent compared to congruent trials. Here we present data from two experiments in which we explored the role of objective conflict and subjective conflict experience in conflict adaptation after masked primes. Participants were required to always respond to the target direction (an arrow), but also had to indicate their subjective experience of conflict induced by the masked prime (a smaller arrow), either every four trials (experiment 1) or on every trial (experiment 2). Behaviorally, current trial conflict effects were always present. Subjective conflict was associated with current trial conflict detection, meaning that participants were able to introspect about the presence of conflict in the current trial. However, conflict adaptation was only present when there was no conflict question in between the trials ("uninterrupted trials"). Crucially, objective conflict adaptation was absent in trials following a subjective question, which indicates that when assessing the capacity of participants to feel the conflict after masked primes,

metacognitive questions might disrupt unconscious conflict adaptation. Also, we found no modulation or direct effects of subjective conflict on conflict adaptation. In summary, in this study we did not find evidence for a role of subjective conflict experience in trial-by-trial cognitive control operations after masked conflict primes.

#### Introduction

There has been considerable debate about the potential for unconscious information to affect cognitive and neural processes. Overall, there seems to be consensus that some cognitive processes can be influenced and (partly) unfold unconsciously, including motor preparation (Boy et al., 2010; Eimer & Schlaghecken, 1998; Sumner et al., 2007), task switching (Lau & Passingham, 2007; Reuss et al., 2011), response inhibition (van Gaal et al., 2008; van Gaal et al., 2010) and conflict detection (D'Ostilio & Garraux, 2012b; Xiang, Wang, & Zhang, 2013). Other, possibly more complex cognitive processes (e.g. flexible adjustments of behavior, working memory, serial step algorithms), however, might require awareness of the relevant stimulus material to be fully operational (Ansorge et al., 2011; Dehaene et al., 2003; Kunde, 2003). It has been hypothesized that consciousness might become beneficial when information has to be held online for longer periods of time to guide future decision making (Dehaene & Naccache, 2001; Horga & Maia, 2012; van Gaal, Lamme, & Ridderinkhof, 2010). For example, debates in the field focus on the possibility of unconscious working memory (Soto & Silvanto, 2014) and the cognitive adaptation after the presence of unconscious conflict (Desender & Van den Bussche, 2012; Jiang, Zhang, & van Gaal, 2015; van Gaal, Ridderinkhof, et al., 2010). This paper focuses on the latter debate.

Conflict adaptation has been observed in several "conflict tasks" such as the Stroop (Egner & Hirsch, 2005; Kerns et al., 2004; Larson, Kaufman, & Perlstein, 2009), the Simon (Kerns, 2006; Stürmer et al., 2002; Wühr & Ansorge, 2005) or the Flanker task (Gratton, Coles, & Donchin, 1992; Ullsperger, Bylsma, & Botvinick, 2005; Verbruggen et al., 2006). These tasks can be performed to study conflict monitoring/detection mechanisms on the current trial as well as sustained conflict-induced control adaptations on the next trial, also referred to as the "Gratton" effect (Gratton et al., 1992) or the conflict adaptation effect. To explore the role of conflict awareness in conflict adaptation several masked priming studies have been designed in which participants are required to perform a speeded two-choice response to a target arrow that can be preceded by masked prime arrow. These studies have revealed that, although the prime arrows cannot be perceived, they are still processed, as evidenced by faster response times (RTs) and fewer errors when the prime and target are congruent than when they are incongruent, referred to as the conflict effect (D'Ostilio & Garraux, 2012; Desender, Van Lierde, & Van den Bussche, 2013; Jiang, Zhang, & van Gaal, 2015; Kunde, 2003; van Gaal, Lamme, & Ridderinkhof, 2010; Xiang et al., 2013). Crucially, the presence of conscious response conflict during trial n–1 (previous trial) influences cognitive control mechanisms on trial n (current trial) in such a way that the correspondent conflict effect on trial n is smaller when trials are preceded by an incongruent trial compared to a congruent trial, referred to as conflict adaptation. Interestingly, in some studies, behavioral adaptation after unconscious conflict has been observed (Atas et al., 2015; Desender et al., 2013; Jiang et al., 2015; Reuss et al., 2014), whereas in other studies it was not (Ansorge et al., 2011; Kunde, 2003). How come this discrepancy?

There might be several reasons for these inconsistent findings, including an insufficient intensity of the conflict in masked priming studies (Hommel, 2015) due to heavy masking and therefore a strong decrease in stimulus strength. Other accounts have focused on the temporal aspects of the tasks that are used. Van Gaal and colleagues (2010) have argued that unconscious conflict adaptation might be undetectable when the time between trials is relatively long, or task performance is interrupted, because of the fleeting nature of unconscious cognitive process (Greenwald, Draine, & Abrams, 1996). Another limit of unconscious processes may be related to the (absence of) flexible routing of information from one brain region to another. It has also been shown recently that the routing of information from the "conflict detector", the anterior cingulate cortex (ACC), to the "control implementer", the dorsolateral prefrontal cortex (DLPFC), is absent after unconscious conflict, but clearly present after conscious conflict (Jiang et al., 2015).

However, even if we assume that conflict adaptation can be triggered, in some circumstances, by unconscious conflicting primes, it does not necessarily mean that the cognitive adaptation mechanism itself do not require awareness of the conflict. In fact, it has been argued that some of the observed conflict adaptation effects might be driven by metacognitive awareness of the conflict (Desender et al., 2016; Desender, Van Opstal, & Van den Bussche, 2014; Questienne, Opstal, & Dijck, 2016). So, although the prime stimulus itself might be fully masked and hence imperceptible to the subject, people might become aware of its influences on (the fluency of) behavior or task performance, for example by the recognition of a slowing of the response or a feeling of trial difficulty. Subsequently, this conscious subjective experience, triggered by the unconscious stimulus of the conflict, might trigger cognitive adaptation mechanisms. In a recent study Desender and colleagues (2014) have asked

whether participants thought there was conflict on each trial in a masked priming task and have shown that conflict adaptation was only present in trials with a correct conflict experience (meaning that there was conflict on the trial and that participants "felt the conflict", or that there was no conflict and the participants did not feel it). This study revealed that the combination of objective conflict and subjective experience of this conflict triggered behavioral adaptation.

Here, we follow up on this work to explore the role of objective conflict (whether prime and target where the same or different) and subjective conflict experience (whether participants indicated they have experienced conflict on the previous trial, irrespective of the objective conflict) on the current trial processing of conflict and on conflict adaptation. In other words, we are interested in isolating behavioral indices of both current trial control (congruency effects) as well as trial-by-trial control (conflict adaptation effects). If conflict experience indeed drives (unconsciously triggered) conflict adaptation one would expect to find conflict adaptation only in trials in which conflict was experienced on the previous trial, but not when conflict was not experienced on the previous trial.

To study this we designed a task in which conflict was difficult to detect because prime arrows were masked. Crucially, we also introduced questions after some of the trials in which participants had to indicate to what extent they experienced conflict on the just preceding trial. In experiment 1, we always presented three trials that were uninterrupted, so not followed by this conflict question, and could therefore be used to accurately tap into conflict detection and adaptation mechanisms. However, on each fourth trial in a row a conflict question was presented. The design from experiment 1 allows us to isolate trials that are not interrupted by a conflict question from the ones that are interrupted by a conflict question. In experiment 2 we used the same stimuli and task design but in this task participants were asked about the subjective feeling of conflict after each trial. This design led to a more continuous assessment of conflict experience and had the advantage that we could collect more trials per "subjective conflict condition", as compared with experiment 1.

This design allowed us to test two main questions. First, to what extend can participants introspect their conflict experience and what are the behavioral precursors of that (e.g. do participants experience conflict more often when they are slow on that trial?). Second, we were able to test to what extent the subjective experience of conflict on the previous trial modulates conflict adaptation on the next trial. Doing so, we can isolate two measures of conflict adaptation. Objective conflict adaptation is the expected reduction in the conflict effect (the difference in the error rate/reaction time between a current incongruent minus congruent trial) when the previous trial was objectively incongruent (prime and target were in opposite directions). On the other hand, subjective conflict adaptation is the expected reduction in the conflict effect when the previous trial was subjectively experienced as conflict, regardless its actual (objective) congruency.

#### Methods

## Participants

For experiment 1, 33 participants (21 females) and for experiment 2, 32 participants (24 females), graduate students of the University of Amsterdam, participated for course credit or financial compensation. All experimental procedures were in line with the relevant laws and regulations and have been approved by the ethical committee of the department of Psychology of the University of Amsterdam. Participants provided written informed consent before experimentation.

## Apparatus and stimuli

For both experiments, stimulus presentation was controlled by Presentation software (Neurobehavioral Systems, Inc.). Stimuli were presented against a grey background at the center of a 20-inch VGA monitor (frequency 60 Hz), which was viewed by the participants from a distance of approximately 80 cm. Similar to our previous studies (Jiang et al., 2013; van Gaal et al., 2010), an arrow version of the meta-contrast masked priming task was used, in which two small black arrows were used as primes, and two larger arrows served as targets (**Figure 5.1A**). The primes fitted exactly within the inner contour of the target.

# Experimental design and procedures

## Experiment 1

On each trial, a fixation appeared for 500 ms, then a prime arrow was presented for 17 ms, followed by a blank interval of 33 ms and a target stimulus (presented for 100 ms). Trials were categorized as being congruent or incongruent based on the correspondence of the direction of both the prime and the target. All primes were strongly masked and therefore visibility of the primes was reduced. Crucially, after every fourth trial, the subjective conflict experience on the previous trial was assessed by presenting participants with the following forced-choice question: "Do you think there was a conflict between the two arrows on this trial?". Participants could answer this by

pressing the left or right buttons on their chair. In contrast to the target responses, there was not time pressure for participants to answer the conflict question. In this trial, there was a variable ISI between the target and conflict question (900, 1000, 1100 and 1200 ms).

In order to establish that the participants had a sense of what was meant by 'conflict', participants first performed two short practice blocks, the first of which contained only weakly masked primes. Then, they performed the actual experiment comprising two different kinds of tasks and eleven blocks in total. The ratio of congruent and incongruent trials was 1:1 during every block. Eight blocks of 160 trials each were devoted to the main task, which contained the subjective conflict discrimination trials as described above. The responses on the conflict question were used to compute d' (Wickens, 2002) as an index of how well participants were able to discriminate the conflict that was induced by the masked primes, henceforth called conflict-d' (Desender et al., 2014).

During two other blocks of 160 trials each, participants completed a prime discrimination task. The timing and event sequence was the same as during the main task with the exception that participants were instructed not to respond to the target, and instead focus on the prime during that trial in every fourth trial. Then, 750 ms after the target presentation, a question regarding the direction of the prime was presented. Participants could answer by pressing either the left or right button to indicate prime direction, without any speed pressure. The responses to the prime question were also used to compute d' (Wickens, 2002), henceforth called perceptual d'.

We also collected EEG and EMG data while human participants performed the task. In the present paper we report only the behavioral data derived from it. Neural data was not collected for experiment 2.

#### Experiment 2

Experiment 2 was very similar to experiment 1, except that in this experiment a subjective conflict question was presented after each trial. Thirty two participants performed eight blocks of 80 trials each. Feedback of the percentage of correctly detected targets was shown after each block.

#### Exclusion criteria for participants

Depending on the specific analysis that was performed, some participants' had too low numbers of trials in one or more of the relevant conditions. This is mainly due to the subjective experience questions, for example some participants are rather conservative in indicating there was conflict. Therefore, similar as Desender et al. (2014), for each specific analysis only participants with 10 or more trials per cell were retained in the specific analyses.

### Behavioral data analysis

Analysis were performed in MATLAB (R2012b, the MathWorks, Inc.). Incorrect trials, trials following errors and correct trials with RT <100 or >1000ms were excluded from all RT analyses. Trials were split into four categories: objectively incongruent and conflict experienced (hit); objectively incongruent but no conflict experienced (miss); objectively congruent but conflict experienced (false alarm); and objectively congruent and no conflict experienced (correct rejection). We classified the hit and false alarm categories as "conflict experienced", and the other two categories as "conflict not experienced". Subsequently, repeated measures ANOVAs were performed on the mean reaction times (RTs) and error rates (ERs). To analyze general congruency effects as well as conflict adaptation effects for uninterrupted trials the factors were Previous trials congruency (congruent/incongruent) and Current trial congruency (congruent/incongruent). To analyze the role of subjective conflict experience in the current trial conflict effect (for trials following a subjective question) the factors were Conflict experience (yes/no conflict), and Current trial congruent (congruent/incongruent). Finally, for the analysis of conflict experience on conflict adaptation the factors were Conflict Experience in previous trial (ves/no conflict), Previous trial congruency (congruent/incongruent) and Current trial congruency (congruent/incongruent) as within-subject variables. A one sample t-test on d' (Desender et al., 2014; Jiang et al., 2013; van Gaal et al., 2010) was used to compute the conflict d' (conflict experience) and perceptual d' (prime visibility). For the prime visibility analysis a two-tailed significance level of 0.05 was used for all statistical tests.

#### Results

#### Discrimination results

To assess the ability of participants to "feel the conflict" we computed d' for conflict detection (Wickens, 2002), henceforth called conflict-d' (Desender et al., 2014). For this analysis, trials with an incorrect target response were omitted. Incongruent trials were treated as signal, and congruent trials as noise. The extreme proportions (hits and false alarms) of 0 and 1 were adjusted to 0.01 and 0.99 (similar to Desender et al., 2014). This analysis revealed that conflict-d' was significantly larger than zero for experiment 1 (d'=0.81, t32=6.27, p<0.001), and for experiment 2 (d'= 0.45, t15=4, p<0.001) indicating that participants were able to discriminate the presence of conflict with above chance accuracy. Perceptual d', exclusively done at the end of experiment 1, and in a separate experimental block in which trials did not require a target

response (see **Methods**), also differed significantly from chance level (M=0.62, t32=5.71, p<0.001, corresponding to 61.17%). This perceptual d' was close to the d' of 0.55 observed in Desender et al. (2014). Note that in this study we did not aim for a d' of 0 because the main goal of this study was to explore potential modulatory influences of conflict experience (present vs absent) on conflict processing and conflict adaptation. Crucially, conflict-d' was higher than perceptual d' (t32=2.23, p=0.016; see **Figure 5.1B**), indicating that participants were better at conflict detection when they could use both visual information as well as motoric information, compared to when they could only use visual information.

#### Conflict effects in behavior

#### Experiment 1

We first tested the presence of conflict processing on trials that were not preceded by a subjective conflict question (uninterrupted trials). A two-way repeated measures ANOVA on reaction times (RTs) and error rates (ERs) with the factors Previous trial congruency and Current trial congruency revealed that there was a clear current trial conflict effect, as reflected in slower reaction times and more errors to incongruent than congruent trials (RT: F1,32=565.19, p<0.001; ER: F1,32=62.61, p<0.001). Further, the conflict effect was smaller when the prior trial was incongruent compared to when it was congruent, an index of conflict adaptation (**Figure 5.2A**, RT: F1,32=9.53, p=0.004; **Figure 5.2B**, ER: F1,32=18.04, p<0.001).



Figure 5.1. Task and Conflict effects (A) Schematic representation of the experimental task and the stimuli. Primes could be congruent or incongruent with the direction of the target (50/50

congruent/incongruent trials). After every fourth trial a conflict question was presented to evaluate the subjective experience of conflict on the just preceding trial. **(B)** Definitions of the relevant behavioral measures. Objective conflict adaptation is defined as the size of the conflict effect on trial N (current trial), when the previous trial (N-1) was objectively incongruent (prime and target were in opposite directions) or objectively congruent (prime and target were in the same directions). Subjective conflict adaptation is defined as the size of the conflict effect on trial N (current trial) when the previous trial (N-1) was subjectively experienced as having conflict or not (irrespective of the actual prime-target correspondence in the previous trial). Current trial effect relates to the performance in the current trial (N) dependent on whether conflict was subjectively experienced or not on that trial.

Next, we tested the role of subjective conflict experience in the current trial conflict effect. For that, we selected only the trials that were followed by a subjective question (one in every four trials). Besides a typical slowing for incongruent trials (RT: F1,32=117.28, p<0.001), participants were also slower when they reported to have experienced conflict compared to when they reported not to have experienced it (Figure 5.2C, RT: F1,32=21.64, p<0.001). However, for reaction times, we found no interaction between subjective and objective conflict (F1,32=0.02, p=0.9). For the error rates, as expected, participants made more errors on incongruent compared to congruent trials (Figure 5.2D, ER: F1,32=26.76, p<0.001) and when reporting to have experienced conflict rather than no-conflict (F1,32=22.28, p<0.001). Interestingly, for error rates, there was an interaction between objective and subjective conflict, since participants made most errors on incongruent trials that were also experienced as conflicting ones (interaction between Conflict experience and Congruency F1,32=6.16, p=0.02).

By investigating the influence of subjective conflict experience on objective conflict adaptation, a 3-way ANOVA showed no interactions (Conflict experience in previous trial x Previous trial congruency x Current trial congruency, RT:  $F_{1,18}$ , p=0.001, p=0.97; ER:  $F_{1,18}$ =0.82, p=0.37). Also, we did not find conflict adaptation based on objective conflict for reaction time or error rates (Current trial congruency x Previous trial congruency RT:  $F_{1,18}$ =0.66, p=0.43; ER:  $F_{1,18}$ =0.51, p=0.49). This interaction was also absent when considering conflict adaptation based on subjective conflict (Current trial congruency x Previous trial conflict (Current trial congruency x Previous trial conflict experience **Figure 5.2E**, RT:  $F_{1,18}$ =0.02, p=0.89; **Figure 5.2F**, ER:  $F_{1,18}$ =0.98, p=0.33) However, there was a main effect of the Previous trial conflict experience on error rate ( $F_{1,18}$ =5.93, p=0.02) meaning that participants made more errors on the current trial when the previous trial was experienced as conflict (**Figure 5.2F**).

Overall, these results indicate the absence of the objective conflict adaptation effect (**Figure 5.1B**). It might be that the subjective question interfered the flow of the trials in such a way that it could have abolished the typical objective conflict adaptation effect and therefore also the other possible interactions related to it. We elaborate on this issue further in the Discussion section of this chapter.



**Figure 5.2.** Behavioral results from Experiment 1. (A) Conflict effects in trial N for reaction times (mean reaction time on incongruent trials – mean reaction time on congruent trials (B) and error rates (mean percentage of errors on incongruent trials – mean percentage of errors on congruent trials), as a function of prime-target correspondence in trial N - 1 (congruent vs. incongruent). (C) Mean reaction times for congruent and incongruent trials before the conflict question as a function of conflict experience (conflict experienced vs. conflict not experienced). (D) The mean error rates for congruent and incongruent trials before the conflict question as a function of conflict effects on reaction times of the trials that followed the conflict question as a function of conflict experience on the preceding trial. (F) Conflict adaptation effects

on error rates of the trials that followed the conflict question as a function of conflict experience. In all panels, error bars reflect SEM.

# Experiment 2

We investigated the presence of objective conflict processing from experiment 2. in which all trials were preceded and followed by a subjective question. Participants were slower and had a trend to commit more errors for incongruent as compared to congruent trials (RT:  $F_{1.30}$ =220.12, p<0.001; ER:  $F_{1,30}$ =3.43, p=0.074). They were also slower and made more errors when subjectively reporting conflict as compared with no-conflict (Figure 5.3A, RT:  $F_{1,30}$ =17.89, p<0.001; Figure 5.3B, ER:  $F_{1,30}$ =10.96, p=0.002). Here, the interaction between objective and subjective conflict was present for both reaction times and error rates. Interestingly, for reaction times, this effect means that the difference between incongruent minus congruent, i.e., the conflict effect on the current trial, was bigger when participants experienced no-conflict (RT:  $F_{1,30}$ =4.5, p=0.04). On the other hand, for the error rates, we found an interaction between objective and subjective conflict that was on the opposite direction from the one we observed in experiment 1. For experiment 2, participants made more errors for incongruent relative to congruent trials, but only in trials experienced as no conflict (interaction between Conflict experience and Congruency F<sub>1,30</sub>=10.1, p=0.0003, Figure 5.3B).

By investigating the influence of subjective conflict experience on objective conflict adaptation a 3-way ANOVA showed no interactions (Conflict experience in previous trial x Previous trial congruency x Current trial congruency, RT:  $F_{1,15}$ =0.76, p=0.4; ER:  $F_{1,15}$ =1.18, p=0.29). When we tested the conflict adaptation effect based on objective conflict we found no effect (Current trial congruency x Previous trial congruency RT:  $F_{1,15}$ =0.28, p=0.6; ER:  $F_{1,15}$ =2.72, p=0.12), in accordance with the results from experiment 1. By testing the conflict adaptation effect based on subjective conflict, there was conflict adaptation for reaction times, but not for error rates (Figure 5.3C, RT:  $F_{1,15}$ =4.7, p=0.047; Figure 5.3D, ER:  $F_{1,15}$ =0.13, p=0.72). This could have suggested the presence of subjective conflict adaptation, however this effect is in the opposite direction as one would expect. The conflict effect is reduced for incongruent trials, but only if it was reported as *no conflict* (Figure 5.3D). This reversed pattern suggests that conflict adaptation could not be generated exclusively on subjectively perceived conflict.



**Figure 5.3.** Behavioral results from Experiment 2. (A) The mean reaction times for congruent and incongruent trials before the conflict question as a function of conflict experience (conflict experienced vs. conflict not experienced). (B) The mean error rates for congruent and incongruent trials before the conflict question as a function of conflict experience. (C) Conflict adaptation effects on reaction times of the trials that followed the conflict question as a function of conflict experience on the preceding trial. (D) Conflict adaptation effects on error rates of the trials that followed the conflict question as a function of conflict experience. In all panels, error bars reflect SEM.

#### Aggregate analysis

Below we report the results of the aggregated data of experiment 1 and 2, which contains the data (subjective trials) from both datasets combined, in order to increase power.

Overall, participants were slower and committed more errors for incongruent as compared to congruent trials (RT:  $F_{1,63}$ =304.55, p<0.001; ER:  $F_{1,63}$ =23.98, p<0.001) and they were slower and made more errors when subjectively reporting conflict as compared with no-conflict (**Figure 5.4A**, RT:  $F_{1,63}$ =40.04, p<0.001; **Figure 5.4B**, ER:  $F_{1,63}$ =32.24, p<0.001). Here, the interaction between objective and subjective conflict was not present for neither reaction times nor error rates (RT:  $F_{1,63}$ =2.73, p=0.10; ER:  $F_{1,63}$ =0.84, p=0.36). Note that previously, in experiments 1 and 2, there was an interaction for error rates that was cancelled out in this aggregate analysis, because the direction of this effect was opposite for experiments 1 and 2. Next, we investigated the influence of subjective conflict experience on objective conflict adaptation and a 3-way ANOVA showed no interactions (Conflict experience in previous trial x Previous trial congruency x Current trial congruency, RT:  $F_{1,34}$ =0.1, p=0.75; ER:  $F_{1,34}$ =0.003, p=0.96). Also in this analysis we did not find conflict adaptation based on objective conflict (Current trial congruency x Previous trial congruency RT:  $F_{1,34}$ =0.96, p=0.33; ER:  $F_{1,34}$ =0.07, p=0.79). Moreover, when testing the conflict adaptation effect based on subjective conflict (interaction Previous trial conflict experience and Current trial conflict), there was no conflict adaptation for error rates, but a trend for interference in reaction time (**Figure 5.4C**, RT:  $F_{1,34}$ =3.44, p=0.072; **Figure 5.4D**, ER:  $F_{1,34}$ =0.24, p=0.63). If anything, this trend reflects that the conflict effect was larger when the previous trial was experienced as conflict compared to no conflict.

Overall the aggregate analysis means that also with a bigger sample we did not obtain evidence for a role of conflict experience in conflict adaptation, nor did we observe it based on objective conflict. In the discussion section we elaborate further on these absence of effects.



**Figure 5.4. Behavioral results from the aggregate analysis. (A)** The mean reaction times for congruent and incongruent trials before the conflict question as a function of conflict experience (conflict experienced vs. conflict not experienced). **(B)** The mean error rates for congruent and incongruent trials before the conflict question as a function of conflict experience. **(C)** Conflict adaptation effects on reaction times of the trials that followed the conflict question as a function of conflict experience on the preceding trial. **(D)** Conflict adaptation effects on error rates of the

trials that followed the conflict question as a function of conflict experience. In all panels, error bars reflect SEM.

### Discussion

In conflict tasks, participants are typically slower and make more errors to incongruent trials (e.g. prime and target arrow are pointing in different directions) as compared to congruent trials (e.g. prime and target arrow are pointing in the same direction). However, this conflict effect tends to reduce if the previous trial also contained an incongruent prime-target pair, which is called the conflict adaptation effect. In two experiments we have explored the role of subjective conflict experience, the metacognitive judgment of the presence or absence of conflict, on behavioral performance during a conflict task. In a conflict priming paradigm in which the visibility of the conflict-inducing prime stimulus was manipulated by masking, participants were required to always respond to the target direction, but also had to indicate their subjective experience of conflict, either once every four trials (experiment 1) or on every trial (experiment 2).

Our experimental setup allowed us to differentiate between *objective* and *subjective* conflict adaptation. Objective conflict adaptation is defined here as a reduced conflict effect after an incongruent trial, compared to a congruent trial, based on the actual (in)congruency of primes and targets on the previous trial. On the other hand, an influence of subjective conflict experience on conflict adaptation could be observed in two different ways: first, by a modulation of the objective conflict adaptation effect by the subjective experience of conflict in the previous trial; and second, by a direct influence of subjective conflict effect of the current trial, regardless of the actual presence of conflict in the previous trial (these different measures are illustrated in **Figure 5.1B**).

First of all, we tested to what extent subjects are able to introspect whether conflict has occurred, over and above their visual experience of the presented prime-target pairs. Interestingly, based on metacognitive introspection, participants were able to dissociate conflict (incongruent) from no conflict trials (congruent), although primes were difficult to perceive and were heavily masked. In experiment 1, participants had a higher *conflict d'*, the discrimination of the presence/absence of conflict after actively responding to the direction of the target, than *perceptual d'*, which was derived from a separate task in which participants only had to perceive the direction of the primes. This suggests that when conflict is induced after actively performing the task, participants are able to introspect this internal conflict and this

information boosts their performance as compared to their performance on a visual discrimination task only.

Further, in both experiments, we observed current trial conflict effects: participants were slower and committed more errors when primes and targets were in opposite directions. This conflict effect is thought to reflect competition between response options (Eriksen & Eriksen, 1974). Participants also tend to categorize these trials in accordance with their experience of conflict. They were slower and made more errors on trials that they labeled as having conflict compared to trials that they labeled as having no conflict. This is in line with influential theoretical models of conflict monitoring (Botvinick et al., 2001; Weissman & Carp, 2013), indicating that participants are indeed able to introspect their "internal conflict". Also, Marti and colleagues have observed that participants are capable of assessing their reaction times, and that their introspections were highly correlated with objective time measures (Marti et al., 2010). Likewise, in our experiment, it is possible that participants are able to introspect about the conflict, not necessarily because of its objective presence, but as a consequence of accessing their 'internal conflict', as reflected by slower response times.

Because participants are able to introspect their conflict, independent of actually seeing a mismatch between primes and targets, this subjective experience may even drive conflict adaptation after masked (in)congruent primes (see Figure 5.1B). First we tested whether there was objective conflict adaptation after masked primes by only selecting the uninterrupted trials of experiment 1. Indeed, for the uninterrupted trials we found objective conflict adaptation, replicating previous studies that have shown that conflicting information at low levels of stimulus awareness can still trigger conflict adaptation mechanisms (Atas et al., 2015; Bodner & Dypvik, 2005; Desender et al., 2013, 2014a; Jiang, Zhang, & van Gaal, 2015; Reuss et al., 2014; van Gaal et al, 2010). Moreover, if the experienced conflict is responsible for conflict adaptation effects for the masked primes (Desender et al., 2014), this effect should be modulated by the subjective experience of conflict on trial N-1. However, we did not observe this modulation, but we also did not find objective conflict adaptation on trials that were interrupted by subjective conflict questions. Therefore, we also looked at whether subjective conflict directly modulated conflict adaptation on trial N (see Figure 5.1B), but again we did not see that effect.

Although the role of experience in adaptation effects has been largely overlooked in prior research, (Kunde, Reuss, & Kiesel, 2012) the role of

metacognition in unconscious conflict adaptation is still controversial. A recent study (Desender, Van Opstal, & Van den Bussche, 2014), showed that the experience of conflict, and not response conflict per se, was the crucial factor for adaptation effects. The authors reported that conflict adaptation was present only after trials on which participants experienced response conflict and conflict was also objectively present (which the authors labeled as "correct experience"). Here, however, we did not find that subjective experience influenced conflict adaptation in any way. If anything, a subjective conflict adaptation effect went in an opposite direction as expected, since the conflict effect was larger (and not smaller) when the previous trial was experienced as conflict compared to no conflict (**Figs 5.3C** and **5.4C**).

However, we do not argue that conflict experience does not play a role in conflict adaptation. The weak conflict effect triggered by primes (masked from awareness) may have accounted for the absence of this effect. Studies show that conflict adaptation may be subject to a relatively rapid decay (Duthoo et al., 2014; Egner, Ely, & Grinband, 2010; Haynes, Driver, & Rees, 2005). Moreover, conflict adaptation is stronger when conflict is triggered more strongly (van Gaal et al., 2010), suggesting that if a prime is masked, its unconscious neural trace may decay rapidly and can be easily interfered when the trials are interrupted.

Indeed, Duthoo and colleagues (2014) showed that the conflict adaptation effect decreases with increasing inter-trial-intervals. We suggest that this may be especially the case in our study, in which the conflict-inducing stimulus is masked and located in trials followed by a time consuming subjective question. Therefore, because conflict effects are rather subtle when the conflicting information is presented at lower levels of visibility (Greenwald, Draine, & Abrams, 1996; van Gaal et al., 2010), the temporal decay of conflict information plus the interference with a conflict question may be a crucial reason why we did not observe conflict adaptation effects on trials that followed a conflict question, nor any possible modulations from subjective experiences.

In conclusion, the present study examined the role of subjective experience of conflict on direct conflict processing and trial-by-trial conflict adaptation mechanisms. Our findings show that although conflict is observable after masked primes, the conflict adaptation (depended on the previous trial congruency) is present only for uninterrupted trials. So, when assessing the capacity of participants to feel the conflict, metacognitive questions might disrupt unconscious conflict adaptation. Second, we did not find evidence that conflict adaptation was influenced by the subjective experience of the conflict,

and therefore cannot conclude that subjective conflict experience plays a role in conflict adaptation with masked primes.

#### 6. Subliminal cues impact performance but not metacognition for free choices

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#### Abstract

Can we detect subtle unconscious biases in our decisions? Clearly, subliminal information has been shown to affect our behavior, however, to what extent people are able to detect these biases metacognitively is not well known. Here we explore this question using a probabilistic reinforcement learning task in which participants were free to choose between two response options. In each block however, one response was rewarded more often that the other (e.g. 80 20) and participants were instructed to optimize the amount of reward they received in every block. Subjects made responses either to a "cued target arrow", the direction of which participants were instructed which button to press, or a bidirectional "free target", to which participants could choose the response that they believed yielded most likely a reward. Targets were always preceded by prime arrows that could be congruent or incongruent with the most rewarded response option in a block. After each free trial, participants rated their confidence in receiving a reward. We show that prime congruency affects immediate decisions. When participants were free to decide, they chose more often congruently with the direction of the prime. However, prime and response congruency did not influence participants' confidence in receiving a reward. In sum, participants' decisions were directly affected by unconscious information, whereas on the other hand, metacognitive processes related to the confidence in their decisions were not, suggesting that participants were unaware that their decisions were biased. We discuss the dissociation between performance and metacognitive assessment in this task in relation to other recent findings observed in different contexts.

#### Introduction

How accurate are we in detecting subtle unconscious biases in our supposedly conscious choices? A wealth of recent studies has shown that unconscious information can bias our decisions, from very simple decisions to more complex

processes (Lau & Passingham, 2007; Reuss et al., 2011; van Gaal et al., 2010; Wang, Xiang, & Li, 2013, but see Newell & Shanks, 2014 for a critical review). In the lab, we and others have studied the influence of unconscious information on cognition and behavior using masked priming tasks (Desender et al., 2014; Jiang et al., 2015; Wenke, Fleming, & Haggard, 2010). To illustrate, in a typical task, participants respond to a target arrow that follows a briefly presented prime stimulus, which is a smaller version of the target. This prime is presented so briefly that it is masked from consciousness. Participants are instructed to ignore the primes and respond only to the targets. In these tasks, depending on the prime-target relationship, trials can be either congruent (both stimuli mapped to the same response, e.g. prime left, target left) or incongruent (each mapped to a different response, e.g. prime left, target right). Participants' performance (error rates, reaction times) is facilitated on congruent trials as compared to incongruent trials, which is called the congruency effect (D'Ostilio & Garraux, 2012; Desender, Van Lierde, & Van den Bussche, 2013; Jiang, Zhang, & van Gaal, 2015; Kunde, 2003; van Gaal, Lamme, & Ridderinkhof, 2010; Xiang et al., 2013).

Beyond this congruency effect, other interesting phenomena has also been reported, for example Schlaghecken & Eimer (2004) showed that unconscious primes are capable of biasing "free decisions". Although masked primes could not be consciously discriminated, they systematically affected free choices between response alternatives. This demonstrates that deliberate responses are not immune to unconsciously triggered biases, suggesting that free choices are not that "free" at all (Kiesel et al., 2006; Schlaghecken & Eimer, 2004).

Although the idea is intriguing that both instructed as well as free choices are biased by unconscious information (Kiesel et al., 2006; Schlaghecken & Eimer, 2004) it is largely unknown whether people are truly unaware that their decisions are biased by unconscious information, or whether people have some form of metacognitive awareness of these biases. For instance, imagine that a person is not aware of the existence of the conflicting stimuli themselves, but that he/she is aware of the effect that they indirectly generate. It has for example been argued that people may experience a sense of reduced fluency of responding or that people may experience a form of internal conflict (Desender et al., 2014) that is triggered by unconscious stimuli.

This issue relates to the relationship between unconsciously driven decisions and a process called metacognition. Metacognition is the ability to recognize one's own successful cognitive processing (Fleming & Lau, 2014). Often, people are relative good in tracking their performance and they report higher confidence for correct decisions than incorrect decisions. Further, people can be aware of their mistakes even without explicit feedback, reporting levels of confidence in their decisions that correlate with objective performance (Charles et al., 2013; Fleming et al., 2010). Metacognition also helps people to avoid making mistakes or spending time and resources on decisions that are based on unreliable evidence (Yeung & Summerfield, 2012). However, dissociations between performance and metacognitive measures have also been found (Fleming & Dolan, 2014). For example, in the famous case of blindsight, patients have a very low confidence in their subjective experience but can still show relatively high objective task performance (Cowey, 2010; Cowey & Stoerig, 1995, but see also Lau & Passingham, 2006).

The relationship between unconsciously driven responses and metacognition has recently been addressed in the context of conflict adaptation. In masked priming tasks it has been shown that the presence of conscious response conflict on trial n-1 (previous trial) influences cognitive control mechanisms on trial *n* (current trial) in such a way that the congruency effect on trial *n* is smaller when trials are preceded by an incongruent trial compared to a congruent trial, referred to as *conflict adaptation*. Interestingly, in some studies, behavioral adaptation after unconscious conflict has been observed (Desender & Van den Bussche, 2012; Desender et al., 2013; van Gaal, Lamme, & Ridderinkhof, 2010). However, does this really mean that people can indeed adapt their behavior over time unconsciously? Some people have argued it may not (Desender & Van den Bussche, 2012; Desender et al., 2014). Although the stimulus itself may be processed unconsciously, this does not mean that people are also fully unaware of the *consequence* that these unconscious stimuli have on behavior or cognition (for example RT slowing or the experience of internal conflict on trial *n*).

If metacognitive processes could drive adjustments in behavior, it could be considered a crucial factor for the changes that are observed over trials in performance, even when primes are masked. An exemplary study showed recently that conflict adaptation was only present in situations in which a correct conflict experience was felt, when participants reported the feeling of incongruency between prime and target, indicating that an intuition of correctly feeling the presence of a conflict might be necessary for triggering behavioral adaptation (Desender et al., 2014). Although intriguing, however, we have recently attempted to replicate these results and we failed to do so (Correa et al., (2017c)). In a very similar experiment and by assessing participants metacognition on a trial by trial basis, objective conflict adaptation was absent in trials following a subjective question, indicating that metacognitive questions might disrupt unconscious conflict adaptation. In sum, considering that unconscious information can bias our decisions to some extent, it remains unclear whether these stimuli also affect the metacognition of decision-makers and whether metacognition is necessary for the performance changes in tasks using unconscious information.

Here we follow up on that work and test whether and how differences in the ease of action selection (or internal conflict) affects the sense of confidence about our decisions. More specifically, this study aims to investigate how subliminal cues influence behavioral performance during reward learning and how such cues influence our (metacognitive) confidence about these decisions. To test this, we designed a novel task in which participants performed a reward learning task in which the probability that a left/right hand response was most often rewarded was manipulated. Participants could initiate their response by the presentation of a target. The target could either be a unidirectional arrow, which we call the forced cued trial, or a bidirectional arrow, which we call the free cued trial. These targets were always preceded by a briefly presented (subliminal) prime, which could point either to the left or to the right. In the forced cued condition targets pointed to a single direction and therefore the prime-target pair could be incongruent or congruent. On these trials participants had to respond as fast as possible to the cued direction of the target arrow. In the free cued condition participants were free to choose the response that they believed would most likely provide a reward (e.g. 80% left response is rewarded and 20% right hand response is rewarded). So, one response would yield reward more often than the other, which creates internal conflict between the unconsciously primed response direction and the learned reward contingency. For instance, on a congruent trial a prime points to the same direction as the most rewarded direction. After these free choice trials participants gave their metacognitive evaluation of how confident they were about receiving a reward on the current trial.

This experimental setup allowed us to test whether internal conflict leads to impairments in choosing the best of two alternative actions and if so, whether this will lead to corresponding changes in metacognition. If so, we expect to observe a higher frequency of choices for the most rewarded side when the prime points in the same direction as compared to when the prime points into the opposite direction. The question is then whether participants will also experience higher confidence in receiving reward after congruent choices (no internal conflict) compared to incongruent choices (with internal conflict). If so, this would reflect that internal conflict between unconscious drives and learned optimal responses has a potential causal role in explaining changes in decisionmaking performance (Desender et al., 2014).

### Methods

## Participants

Thirty five participants, graduate students of the University of Amsterdam, participated for course credits or financial compensation. All experimental procedures were in line with the relevant laws and regulations and have been approved by the ethical committee of the department of Psychology of the University of Amsterdam. Participants provided written informed consent before experimentation. From the initial sample, one participant was excluded due to the absence of data in a specific trial condition, which generated empty data cells in the analysis phase. Overall, 34 participants had their data further analyzed (26 females, 8 males; mean age = 21.09 +-2.47 SD).

## Procedures

Participants were seated in a silent room with dimmed light. The experiment was programmed with Cogent 2000 (www.vislab.ucl.ac.uk/cogent.php) in MATLAB (Mathworks). Stimuli were presented against a grey background at the center of 60 Hz monitor which was viewed by the participants from a distance of approximately 80 cm. Overall, the study consisted of two parts: the reward learning task and the prime recognition task.

## Reward Learning Task

In the reward learning task participants were asked to follow (cued trials) or deliberately decide (free trials) while paying attention to the reward probabilities from both key options (left or right), as questions regarding probabilities of reward would be asked. They were instructed that the key associated probabilities were set randomly at the start of each block. The task consisted of 6 blocks, each with 70 trials: 50 free trials and 20 cued trials. During cued trials, a primed cue (one direction arrow) was briefly presented for 16.7 ms, followed by a blank (33 ms) and by an one direction arrow (250 ms). Participants were instructed to ignore the prime and to press the key (left D key or right K key), according to the target direction within 500 ms. They would not win anything from these trials but, if they were too slow, they would lose a virtual "1 euro". The purpose of these cued choice trials was to keep participants actively processing both primes and targets.

During free trials, a primed cue (one direction arrow) was also briefly presented for 16.7 ms, but now following a blank (33 ms), followed by the target bidirectional arrow (250 ms). In this condition, participants were free to press

either the left or the right key to learn which one had a higher chance of winning. The six blocks contained three probability pairs for obtaining a reward (0.8/0.2, 0.5/0.2, 0.2/0.5, left/right, respectively, in random order). To illustrate, 0.2/0.5 means that a left hand response is rewarded in 20% of the occasions and a right hand response in 50%. Note that the probability values therefore are independent and do not need to add up to 100%. Within each probability set, response hand (left/right) was not counterbalanced across participants. This means that the left option was rewarded more frequently as compared to the right option. After the subject's key press (1500 ms), they were asked about their confidence in receiving a reward on that trial. They were asked to respond by pressing one of four keys (S, D, K, L), their estimations respectively meaning, from left to right, the least confident to the most confident. After this judgment, participants were informed whether they had won "1 euro" or "nothing" for that trial (Figure 6.1). At the end of each block, participants were asked to first estimate the reward probability from the left key on a scale from 0 to 100, then to rate their confidence in the previous estimation on a scale from 0 (the lowest confident) to 100 (the highest confident). The same questions applied for the right response key. Finally, participants were questioned about their overall satisfaction with their decisions in the block, also using the scale from 0 to 100. For each question participants could move an arrow (using the arrow keys on the keyboard) along a scale to a position corresponding to their answer.

#### Prime recognition task

After completing the reward learning task, participants were informed of the presence of primes and then asked to complete a forced-choice prime recognition task to determine whether they were conscious of the primes during the experiment. During the task, participants had to identify the direction of the *prime arrow* using the same (left/right) key presses used during the previous experiment. To ensure the validity of the prime recognition task, the task was matched with the reward learning task such that the prime arrows were followed by target arrows. Also, to prevent any unconscious action bias from influencing the conscious judgment of the prime arrow, participants had to wait 600 ms after the prime was presented to make their response (Vorberg et al., 2003). Participants were informed they could make their choice by a tone that was played for 150 ms.

The prime recognition task consisted of two blocks of 72 trials each with the same ratio of cued and free target arrows as the reward learning task as to maintain consistency. A measure of prime discriminability (d') was then calculated for participants (Green & Swets, 1966).

#### A Cued Choice Condition



**Figure 6.1. Reward learning task and trial conditions. (A)** Cued choice trial. Briefly flashed primes precede an unidirectional target to which participants should respond. When responding later than 500 ms, participants received a "too late" message followed by a "lose 1 euro" message. (B) Free choice trial. Briefly flashed primes precede a bidirectional target to which participants were free to choose the key direction that they judged would give a reward. Primes could be congruent or incongruent with the more rewarding key press. The reward probability on free choice trials was manipulated across blocks. On some blocks the left was rewarded more often and on some blocks the right (see Methods for details). (C) Prime visibility trial. Primes and targets are displayed the same way as in the reward learning task. Participants should try to identify the prime direction by pressing the left/right buttons while ignoring the target direction.

#### Results

#### Prime Discriminability

A measure of d' was calculated from the prime recognition data for each participant to determine whether prime arrows were indeed masked from consciousness. The mean d' for the entire sample was larger than zero (d'= 0.4 $\pm$ SD: 0.47,  $t_{33}$ = 5.15, p<0.001). Given that chance-level performance on such a forced-choice discrimination task is a typical criterion used to show that participants are unable to perceive a stimulus consciously (Morten Overgaard & Sandberg, 2014; Sandberg et al., 2010) this result implies that we cannot consider that the masked prime was nonconscious in our entire participant sample. Therefore, for further behavioral analyses, we also report results in median-splits samples, where we separated seventeen good discriminators (GD) from seventeen bad discriminators (BD) (GD: mean d'=0.76;  $T_{16}$ =7.47, p<0.001; BD: mean d'=0.06;  $T_{16}$ =2.37, p=0.03). We will show throughout this paper that the reported results in performance and metacognition do not scale with prime visibility. However, we would like to note that we are aware of issues regarding post-hoc trial selection, for example when sorting trials based on d', as discussed in Shanks (2017). Therefore we report these median split results without drawing strong conclusions about the existence of unconscious information processing in the present study.

#### Free choice decisions

In order to measure the impact of primes on free choices we performed a three-way ANOVA on participants' free choices (n=34) with the factors prime direction, response direction and reward probability. Figure 6.2A shows the probability of choosing each key according to the prime-choice pair, plotted for each reward probability. Note that the values add up to 1 within a probability condition and therefore reflect the occurrence of each of the four response options in a specific block of trials. Participants chose more frequently the options congruent with the prime direction ( $F_{1,33}$ =22.5, p<0.001). Also, participants' choices were influenced by the probability of the reward, as indicated by the fact that participants chose the most rewarded response option more frequently than the less rewarded option in every block ( $F_{2.66}$ =74.9, p<0.001). For example in the 0.8/0.2 block left hand responses were most likely, whereas in the 0.2/0.5 block right hand responses dominated (Fig.6.2A). A mixed ANOVA including group as a factor revealed no differences between BD and GD groups in any of the relevant comparisons indicated above (all ps>0.68). Figure 6.2B depicts the evolvement over time of participants' choices, showing that people quickly learn the difference between the reward conditions, in an unbiased way.



**Figure 6.2.** Choice frequencies according to prime-response congruence and reward probability. (A) Mean probability of each decision for each prime-response condition (the four different colored lines), for each underlying left/right reward probability (plotted on the x-axis). (B) Probability of choices across trials in a block. Error bars and shaded area around each line represent SEM.

Next we tested whether the prime-target congruency also affects reaction times. We performed a three-way ANOVA on participants' reaction times on their free choices with the factors prime direction, response direction and reward probability. **Figure 6.3** depicts the reaction times associated with participants' choices. As expected, participants were faster (more fluent) when pressing the same direction as the one indicated by the prime ( $F_{1,33}$ =36.46, p<0.001) and this effect was modulated by the reward condition, since the choices were even faster when pressed in accordance to the most probable reward condition ( $F_{2,66}$ =21.98, p<0.001). A mixed ANOVA including group as a factor revealed no difference between the BD and GD group in the comparisons indicated before (all *ps*>0.07).



*Figure 6.3. Reaction times for free choices. Mean reaction times for each of the prime-response combinations, plotted as a function of probability condition. Error bars indicate SEM.* 

#### Metacognitive confidence

Next we analyzed the impact of primes on participants' confidence in free choice trials. A three-way ANOVA was performed with the factors prime direction, response direction and reward probability. Figure 6.4A shows that, overall, participants were not equally confident in each block. They were the least confident in the 0.2/0.5 blocks and were more confident for the first two probability conditions ( $F_{2.66}$ =28, p<0.001). Moreover, there was an interaction between probability condition and response direction ( $F_{2.66}$ =66.96, p<0.001), indicating that participants were more confident when their choices were in accordance with the most probable reward option. Interestingly, prime direction did not impact participants' confidence in receiving a reward ( $F_{1,33}$ =1.9, p=0.18), nor did it interact with any of the other factors (all ps>0.05). A mixed ANOVA including group as a factor revealed no difference between the BD and GD group in the comparisons indicated before (all ps>0.39). Figure 6.4B shows that participants rated confidence according to the probability conditions at stake and that there was no bias towards a response option over trials.



**Figure 6.4. Confidence rating. (A)** Mean confidence as a function of prime direction, response direction and reward probability. **(B)** Mean confidence as a function of prime direction, response direction and reward probability condition evolving across all trials in each block. Error bars and shaded area around each line indicate SEM.

Finally, we analyzed participants' performance on questions presented at the end of a block in which they estimated the probability that the left/right side was rewarded. A two-way ANOVA with the factors side and probability condition was performed. **Figure 6.5** shows that, overall, participants keep

track of the estimated probabilities along the blocks (interaction between side and probability condition:  $F_{2,66}$ =95.7, p<0.001) meaning that, in general, left side estimations are higher than right side estimations when left rewards more often, but that this patterns reverse when the right side is most often rewarded (this interaction was absent for the confidence estimations:  $F_{2,66}$ =2.2, p=0.13).



*Figure 6.5. Estimated probability of reward for the left and right response. Error bars indicate SEM.* 

#### Discussion

In the present study we investigated the effects of masked cues on both performance and metacognition in a reward learning task. Participants aimed to attain as much reward as possible by freely deciding between which of two (left or right) responses was most often rewarded. Specifically, the masked cues (pointed arrows) either pointed in the same or opposite direction of the more rewarding response, creating, on some trials, internal conflict, depending on the congruency between the prime direction and the most probable reward direction. Questions aimed at evaluating metacognitive insight were presented on trials in which participants were free to choose. We found that primes influenced behavioral performance, but did not influence metacognitive confidence. First we discuss the results relating to performance in more detail.

Overall we observed a raise in the frequency of choosing the option that was in accordance with the direction of the masked prime. Also, these choices were faster compared to choices incongruent to the prime direction. This work is in line with previous evidence showing that human decisions are influenced by subliminal cues in a free choice decision task. For example, in one study, participants' free choices between a left or right response were consistently biased by a left or right pointing arrow such that participants' choices were more likely to be congruent with the direction of the prime arrow (Schlaghecken & Eimer, 2004). In masked priming tasks as used here, performance effects seem to rely on the fact that masked primes can be processed efficiently enough to directly affect the motor system (e.g. Dehaene et al., 1998; Leuthold & Kopp, 1998; Neumann & Klotz, 1994). If responses on congruent trials are already primed, participants would have a benefit in performance. On the other hand, when responses on incongruent trials conflict with the primed response direction, an "internal conflict" would be generated, impacting performance.

In contrast to performance measures, it is possible that confidence measures rely less on the strength of the stimuli, but more so on the ability to detect the secondary effects that these stimuli may generate. For instance, people may show a slowing of their response as a consequence of the incongruency between the subliminal prime and the target response, which may trigger internal conflict and hence some metacognitive awareness of this incongruency. In line with this, Marti and colleagues have observed that participants are indeed capable of accurately introspecting their speed of responding (Marti et al., 2010). A recent study directly tested this hypothesis by disrupting post response confidence without altering visual discrimination performance. Participants were asked to make a difficult perceptual decision by reporting the direction of a grating superimposed on noise. Next, they had to provide a confidence rating in their discrimination. By stimulating the premotor cortex associated with the unchosen response (using transcranial magnetic stimulation), participants' confidence in their decision was reduced, suggesting that action-specific activity contributes to perceptual confidence (Fleming et al., 2015). In our experiment, however, although participants were faster when pressing the same response as the direction indicated by the prime, these subtle motor related-factors seemed not to be sufficient to influence participants' confidence in receiving a reward. So, we observed a clear dissociation between the impact of masked cues on performance and on metacognition.

#### Dissociations between performance and metacognition

There are many studies that indicate important dissociations between performance and metacognition. Blindsight is considered a classical example of a dissociation between performance and visual awareness. Patients with brain damage to the occipital lobe manage to discriminate stimuli when forcedchoice procedures are used, while claiming not knowing why they score so high

on these tests (Morten Overgaard, 2011). Clearly, in this situation, conscious awareness, or metacognition, and performance are dissociated. In healthy participants, a similar question regarding dissociations between action selection and sense of control was addressed by Wenke and collaborators (2010). In their study, participants rated their sense of control when responding to cued or free targets that were primed by a briefly presented congruent or incongruent arrow. Depending on participants' selected action, their choices were compatible or incompatible with the preceding masked prime and different colors were displayed as a consequence of this congruency. Participants then rated how much control they experienced over the occurrence of the different colors presented after each decision. The results indicated that participants felt more control over colors that followed prime compatible actions than over colors that followed prime-incompatible actions. It seemed that, although subjects could not see the primes, some metacognitive information was accessible from participant's rates of control (Wenke et al., 2010). Again, this illustrates that awareness of stimuli can be dissociated from the metacognitive effects these stimuli have.

More recently, Charles and colleagues (2014) investigated participants' ability to detect their own errors on consciously and subliminally primed decisions (Charles, King, & Dehaene, 2014; Charles et al., 2013). They hypothesized that some monitoring processes could be sufficiently automatized to unfold nonconsciously. To test this, participants were shown briefly displayed numbers followed by masks with different Stimulus Onset Asynchronies (SOAs), generating strongly/weakly masked numbers. Participants were instructed to make a fast forced-choice number comparison, reporting whether the target number was smaller or larger than 5, and whether they saw it or not. Participants were then asked to report whether they thought they had committed an error or not in the previous trial. Participants managed to detect their errors at above-chance levels, a measure of metacognitive insight, on trials on which they reported not having seen the number and could not discriminate whether it was larger/smaller than 5. This study again shows that there is information potentially retrieved from metacognitive estimations, even in the absence of perception.

Dissociations between performance and metacognition might be due to variations in task design. In our task, the reason why primes influenced performance, but not metacognition, could be related to the short life-time of unconscious information processing, typically thought to be around 500 ms (Kiefer, 2002; Sergent, Baillet, & Dehaene, 2005; van Gaal et al., 2014).

Therefore, potential interference caused by the primes might have died out while participants had to respond to the confidence question.

In our study, action fluency, the better performance when prime and target were congruent, was not translated into higher confidence rates in receiving a reward. There could be several reasons for the fact that participants were not aware of their performance bias. For instance, in our experiment, the prime was not informative about the direction of the reward and therefore could be fully ignored. It may be that manipulating the task relevance would leverage the impact of primes on metacognition (see van Gaal, de Lange, & Cohen, 2012). It might be that unconscious primes could influence confidence estimations if participants were offered real incentives, therefore boosting participants' motivation. Another way to boost action fluency relevance would be to ask participants to bet on their choices, instead of merely asking for confidence in receiving reward, before the feedback is given. Future studies are necessary to address which conditions are necessary and sufficient to promote metacognitive assessment of a person's decision bias.

## 7. Summary and discussion

In this thesis we explored the role of stimulus awareness, neuromodulation and metacognition in perceptual and cognitive decision making in human participants. In doing so, we manipulated external variables that may contribute to people's decisions, such as stimulus strength (e.g. by masking stimuli), and we monitored (internal) fluctuations in the brain's arousal state and the accuracy of metacognitive decision evaluation in the lab. Moreover, we employed EEG recordings, pupil responses, behavioral measures and computational modeling in our studies to unravel the mechanisms underlying perceptual and cognitive decision making (for a graphical summary of all the experiments see **Figure 7.1**).

Specifically, using the combination of experimental approaches we aimed to answer three specific research questions in this thesis:

- 1. How does the level of awareness of decision outcomes modulate the way people learn, decide and monitor their own behavior? (Chapters 2-3).
- 2. How do stimulus evoked fluctuations of the brain's arousal state affect perceptual awareness and metacognitive evaluation of decision accuracy? (Chapter 4).
- 3. What is the role of metacognition in monitoring and updating our decisions? (Chapters 5-6).



*Figure 7.1. Overview of the main questions addressed in the different chapters of this thesis. The role of awareness, neuromodulation and metacognition for perceptual and cognitive decision* 

making were studied. Behavioral, physiological, electrophysiological and computational analyses were performed.

#### Summary of the main findings

In the following sections I will briefly summarize and interpret the obtained results regarding each of these three questions. For an elaborate discussion and interpretation of the results of each of the questions we refer to the specific chapters.

Q1. How does the level of awareness of decision outcomes modulate the way people learn, decide and monitor their own behavior?

Recent studies have reported that reward cues that are masked from awareness can still influence performance on tasks in the lab (Aarts et al., 2008; Bijleveld, Custers, & Aarts, 2012; Capa at al., 2013; Pessiglione et al., 2007). The neural mechanisms allowing for this kind of decision adjustments based on rewards at different levels of awareness were examined in our first experimental chapter. Specifically, we aimed to unravel whether, and if so how, people can learn from and integrate reward information at different levels of feedback awareness during decision formation.

We observed that participants switched their responses after both unmasked and masked unfavorable outcomes more often than after favorable outcomes, suggesting that humans can learn to update the value of the available options from probabilistic rewards, even when the decision outcomes were not fully consciously perceived. However, degrading the visibility of the reward increased participants' tendency to repeat previous choices (perseveration), suggesting that awareness of decision outcomes is necessary for optimal decision making strategies. Our best fitting model parameters included perseveration and indicated that this parameter was significantly positive for both the visibility modules, although perseveration was smaller for the fully conscious module. Such a finding is relevant for our mixed design task (various levels of feedback awareness along the task). Here, repeating previous choices can constitute the implementation of a higher-level strategy, by ignoring irrelevant negative rewards, sticking to their decision strategy. This could be done based on the integration of information over a longer sequence of trials, when full conscious awareness of the outcome was (often) lacking. Additionally, by analyzing electroencephalographic (EEG) recording in combination with computational modeling we dissociated electrophysiological signatures evoked by the reward-based learning processes from those elicited by the reward-independent repetition of previous choices and showed that
these neural activities were significantly modulated by reward visibility. Speculatively, the presence of feedback-related-negativity (FRN) component for both masked and unmasked feedback may reflect a fast feedforward and nonconscious high-level "fast-alarm" response (as suggested recently by Ullsperger et al (2014), whereas the P3 component may reflect more conscious, and longer lasting neural responses, potentially dependent on recurrent interactions and necessary for behavioral adaptations (Del Cul, Baillet, & Dehaene, 2007; Sergent & Dehaene, 2004). It remains an open question however how subtle differences in early error detecting (as reflected in the FRN), are not fully "used" for adapting future decisions when decision outcomes are masked. This is matter of future experimentation.

Overall, in this chapter we shed new light on the neural computations underlying reward-based learning and decision-making and we highlighted that, although clearly beneficial, reward awareness is not strictly necessary for the trial-by-trial adjustment of decision-making strategies, though highlighting a beneficial role of reward awareness in adjusting decision-making strategies.

After having demonstrated how awareness played a role in feedback processing in Chapter 2, we further investigated the role of participants' expectation on being correct or not in their decision (Fleming & Lau, 2014) on a trial-by-trial basis (based on single trial confidence reports). For that, we used a challenging perceptual decision-making task in which half of the veridical feedback was masked and the other half was not. We observed that EEG and pupil signals were sensitive enough to reflect differences in reward valence and in people's ongoing expectations, even when outcomes were subjectively reported as not seen. However, there seemed to be more complex cognitive functions that required conscious awareness of the feedback to unfold. When we analyzed pupil and brain signals after fully conscious feedback we observed that only in this condition, both the P3 ERP component and pupil dilation measures mirrored a prediction error signal, reflecting an integration of feedback correctness, which was modulated by the confidence in the previous decision (Nieuwenhuis, Aston-Jones, & Cohen, 2005). Feedback at lower levels of awareness did not show this pattern of results, but showed effects separately for feedback correctness (pupil) and confidence (P3 ERP). Therefore, the results of chapter 3 suggest that confidence modulations of outcomeevoked stimulus processing depend on feedback awareness. We tentatively suggest that this may reflect the involvement of the catecholamine system (e.g. dopamine, noradrenaline) promoting belief updating (Colizoli et al., 2018; Jepma et al., 2016). It is therefore possible that awareness is needed for the

integration of performance outcomes with confidence estimates to update and optimize future decisions.

Overall we showed in chapter 2 and 3 that the evaluation of decision outcomes can be tracked using EEG and pupil measures, regardless of (full-blown) feedback visibility. Overall visual awareness seems crucial for the emergence of fully integrated performance monitoring mechanisms, which are associated with flexible value updating and trial-by-trial decision adjustments.

## **Q2.** How do stimulus-evoked fluctuations of the brain's arousal state affect perceptual awareness and metacognitive evaluation of decision accuracy?

Next we addressed the question how the brain's arousal state may account for variation in our perceptual decisions even in the presence of the same external stimulation (Glimcher, 2005; Gold & Shadlen, 2007; Shadlen et al., 1996; Newsome, 2005; Sugrue, Corrado, & Wvart & Koechlin. 2016). Neuromodulation is a source of internal variation in the brain's arousal state that may partly explain differences in decision making performance and it has been shown previously that these internal fluctuations can be tracked by proxies, such as pupil dilation and the P3 event-related component (Aston-Jones & Cohen, 2005; de Gee et al., 2017; de Gee, Knapen, & Donner, 2014; Nieuwenhuis, Aston-Jones, & Cohen, 2005).

In chapter 4, we showed that stimulus-evoked pupil dilation (preceding participants' response) could, on average, differentiate between correct and incorrect perceptual decisions. This result, that under larger pupil dilation participants have a better discrimination sensitivity (d') may indicate that stimuli that are difficult to perceive are better encoded under high phasic arousal, possibly related to increased fine tuning of attentional mechanisms (Aston-Jones & Cohen, 2005). This interpretation is in line with a recent pharmacological study that showed that modulation of the level of noradrenaline induced by Reboxetine/Clonidine leads to altered Gabor discrimination (Gelbard-Sagiv, Sharon, & Nir, 2018). However, interestingly, in our study, stimulus-induced higher arousal states (as reflected by larger pupils) were associated with worse metacognitive performance (reduced metacognitive sensitivity: meta-d' efficiency). In chapter 4 we have argued that this may reveal that an increased brain arousal state facilitates bottom-up stimulus processing, but at the same time may detriment top-down processes, as has been suggested previously (Aston-Jones & Cohen, 2005; de Gee et al., 2017; Eldar et al., 2013). Such an inverse modulatory effect of neuromodulation on bottom-up and top-down information processing is in line with a recent

study which showed that lower arousal levels, induced by noradrenergic blocking by propranolol, were associated with improved metacognitive performance, but had no significant impact on first-order task performance (d') (Hauser et al., 2017).

Overall, and more generally, the results of Chapter 4 show how stimulusevoked neuromodulatory changes may affect perception and metacognition in opposite ways. This is in line with the neural gain hypothesis, which claims that noradrenaline (gain in arousal) may amplify strong evidence, i.e. bottom up signals, and may diminish weaker signals, as top down metacognitive evaluations of performance (Aston-Jones & Cohen, 2005; Donner & Nieuwenhuis, 2013).

As for the role of neuromodulation in stimulus detection and the metacognitive evaluation of the accuracy of perceptual decisions, we showed that the pupil is a good proxy for explaining variance in people's decision accuracy. However, and despite finding similar results with other studies (Hauser et al., 2017; Urai et al., 2017), it remains a topic for further research to understand why improvements in perception accompanied by stimulus driven (phasic) arousal responses (see also Gelbard-Sagiv et al., 2018) are accompanied by worse metacognitive assessment of such sharpened perceptions. Finally, because we focused here on stimulus induced pupil measures, future studies should also focus on pre-stimulus fluctuations in pupil size and how these relate to stimulus processing, sensitivity and metacognitive accuracy, as phasic responses of brainstem arousal systems can account for a significant source of responses' variability (Lima et al., 2011; Zagha et al., 2013), as has been observed mainly in mice (McGinley et al., 2015).

## **Q3.** Are conscious awareness and/or metacognition necessary for monitoring our decision biases or updating our behavior?

It has repeatedly been established that subliminal primes have a clear impact on people's decisions (Dehaene et al., 1998; Klotz & Neumann, 1999; Pessiglione et al., 2008; Pessiglione et al., 2007; Vorberg et al., 2003). A robust example of this is the conflict effect, which refers to worse performance and slower reaction times to an incongruent prime-target pair compared to a congruent prime-target pair in a masked priming experiment (Jiang et al., 2013; Jiang, Zhang, & van Gaal, 2015; van Gaal, Lamme, & Ridderinkhof, 2010). Besides this direct influence of incongruency on behavior, conflict adaptation over trials can also be observed. Conflict adaptation reflects the phenomenon that previously experienced conflict diminishes the conflict effect on the current trial, probably related to increased cognitive control triggered by the conflicting information on the previous trial (Gratton, Coles, & Donchin, 1992; Ullsperger, Bylsma, & Botvinick, 2005; van Gaal, Lamme, & Ridderinkhof, 2010). Interestingly, it has been observed that even this high-level cognitive process can be triggered by incongruent subliminal prime-target pairs (Desender, Van Lierde, & Van den Bussche, 2013; Huber-Huber & Ansorge, 2017; Jiang, Zhang, & van Gaal, 2015b; Reuss et al., 2014; van Gaal, Lamme, & Ridderinkhof, 2010), although evidence is mixed (Frings & Wentura, 2008; Greenwald, Draine, & Abrams, 1996; Jiménez & Méndez, 2013).

What is challenging about the possible existence of "unconsciously triggered conflict adaptation" is the hypothesis that some of the observed conflict adaptation effects might in fact be driven by metacognitive awareness of the conflict, and therefore are related to conscious conflict experience after all (Desender et al., 2016; Desender, Van Opstal, & Van den Bussche, 2014; Questienne, Opstal, & Dijck, 2016). It could be that, even without being aware of the primes due to heavy masking, participants could experience a "feeling of conflict" (Desender et al., 2014), due for example to reduced fluency of their responses (e.g. slower reaction times). We followed this reasoning and, in chapter 5 of this thesis, we described a series of experiments in which we studied whether conflict adaptation, triggered by masked primes, could be due to metacognitive access to conflict information ("feeling the conflict"). We found that current trial conflict effects were always present, irrespective of conflict experience on that trial, whereas conflict adaptation was only present on trials that were not previously interrupted by metacognitive questions about conflict experience. We argued that these intervening questions may have disrupted ongoing, but fragile, conflict processing. It has been argued that unconscious stimuli decay rapidly while progressing up in the cortical hierarchy (Greenwald et al., 1996; Mattler, 2005) and recently Duthoo and colleagues (2014) showed that the conflict adaptation effect decreases with increasing inter-trial-intervals. Although we did not find evidence for subjective conflict experience in cognitive control after masked conflict primes, in a more extensive study that followed up on the present results with 64 participants performing a similar task (Jiang et al., 2018), we found that the subjective experience of conflict elicited behavioral adaptation, but, crucially, this was also the case when conflict was present, but not experienced. This demonstrated that conflict adaptation probably does not depend on conflict experience (see also Huber-Huber et al 2017), but that conflict experience may be associated with increased cognitive control, because trials on which conflict is strongly triggered are also the trials on which participants often experience conflict (see Abrahamse & Braem, 2015).

Finally, in the sixth chapter of this thesis, we explored whether people could metacognitively detect unconscious biases of their decisions, following previous findings showing that unconscious primes can affect "free" decisions (Kiesel et al., 2006; Schlaghecken & Eimer, 2004). We measured the behavioral and metacognitive impact of subliminal primes that were presented just before a target stimulus. Targets were always preceded by prime arrows that could either be congruent or incongruent with the most rewarded response option in a block (some responses were more often rewarded than others). Participants were sometimes cued to make a specific response and sometimes they were "free" to decide which response they preferred (the latter were the trials of interest). On each trial, subjects were asked about the confidence in receiving a reward based on their previous response. We showed that prime direction affected participants immediate decisions, so when participants were free to decide, they chose more often congruently with the direction of the prime. However, prime and response congruency did not influence participants' confidence in receiving a reward, suggesting that participants were unaware that their decisions were biased. We therefore observed a dissociation between performance and metacognitive assessment.

Overall, in chapters 5 and 6, we found that masked stimuli affected ongoing behavior and simple decisions, but these effects were not necessarily translated into metacognitive awareness, or metacognitive evaluation did not have a clear impact on evolving control processes. We will discuss possibilities for future research aimed at addressing our main question 3 below.

It has recently been observed that confidence estimates can be disrupted without altering visual discrimination performance (Fleming et al., 2015). Fleming and colleagues stimulated the premotor cortex associated with the unchosen response (using transcranial magnetic stimulation) in a perceptual decision-making task and showed that participants' confidence in their decision was reduced under these conditions. This suggests that action-specific motor activity contributes to perceptual confidence estimations. Further, Wenke and collaborators (2010) showed that subjects experienced increased control over decision outcomes that were associated with responses that were congruently primed with masked prime arrows, suggesting that subjects experience more control over "fluent actions". Finally, Charles and collaborators (Charles et al., 2014) found that metacognitive monitoring processes could be sufficiently automatized to unfold based on unconsciously presented stimuli. In our study, however, although participants were faster when pressing the same response

as the direction indicated by the prime, these subtle motor related-factors seemed not to be sufficient to influence participants' confidence in receiving a reward. Dissociations between performance and metacognition might be due to variations in task design. In our task, the reason why primes influenced performance, but not metacognition, could be related to the short life-time of unconscious information processing (Kiefer, 2002; Sergent, Baillet, & Dehaene, 2005; van Gaal et al., 2014). Therefore, potential interference caused by the primes might have died out while participants had to respond to the confidence question. In sum, in this experiment, people seemed metacognitively unaware of the choice bias that was induced by subliminal primes (Fleming & Dolan, 2014).

Why did we not observe confidence modulations by masked primes? We found that masked primes affected free choices, but note that primes were not predictive of the reward probability on that trial per se. Therefore, it is possible that the bias the primes introduced was not relevant for the task type and, therefore, could not be metacognitively accessed, since it was not informative of the reward probability at stake. This is not unfamiliar in the literature: a previous study showed that subliminal primes could not activate prefrontal control networks when they were task irrelevant (van Gaal et al., 2008) but did so when they were meaningful. Also, Ansorge & Neumann (2005) showed that task-relevant prime features (shape) affected responses to the target only when the shape dimension was response relevant, but not when this feature was task-irrelevant (when the color of the target was the required response). Such selectivity in activations was corroborated by Lau & Passingham (2007) who showed unconscious modulations of cortical networks specifically associated with the task type. They found increased or decreased activity of cortical networks specifically associated with their phonological or semantic tasks. Therefore, task-relevance is a non-negligible factor for detecting the impact of unconscious manipulations in behavioral performance and metacognition. Future studies should address task-relevance carefully in order to do so.

## General remarks and overall conclusions

Throughout this thesis we often use the terms "conscious" and "unconscious" to refer to processing of visible (or reportable, aware) and invisible (or non-reportable, unaware) stimuli, respectively. This terminology was used for convenience with the nomenclature in the literature. However, in this thesis we often did not (manage to) manipulate awareness in an "all-or-none" manner, creating conscious and unconscious stimuli, but more so we manipulated awareness in a graded manner, leading to partial or "minimal awareness" and

"full awareness". Although the graded nature of the manipulation of perceptual awareness in our studies, we have often observed qualitative differences in the effects these stimuli had on behavioral and cognitive variables. For example in chapter 3 we observed that the integration of confidence and correctness (leading to a prediction error response) was only observed when decision feedback was presented fully consciously, and not when it was heavily masked and therefore only partly conscious. Qualitative differences may suggest a clear computational difference between conscious and unconscious processes, however, we would like to acknowledge here that we do not claim that the processes that we have studied in this thesis can also unfold fully unconsciously (e.g. RL-learning from unconscious feedback), mainly because we have not tested that specifically (d' was not 0 in those studies). Therefore, future studies should be performed to test to what extent the obtained results in this thesis, regarding the masked stimuli, are similar for stimuli that can truly not be detected/discriminated above chance-level and are hence fully unconscious.

In this thesis we have described and elaborated on the role of stimulus awareness, neuromodulation and metacognitive evaluation in perceptual and cognitive decision making. In doing so, we have pointed out some potential benefits of conscious awareness for specific cognitive (control) and monitoring processes. For further progress, future research should more mechanistically address this issue because there are still many open questions. For instance, which underlying neural mechanisms are reflected in the various neural signatures that we have measured, such as the P3 ERP component (Cohen, Ranganath, 2007; Nieuwenhuis et al., 2005). Elger. & How does neuromodulation, tracked by pupil dilation, mechanistically change the way information is processed and how is that translated into changes in performance and metacognition (Hauser et al., 2017; Lempert et al., 2015)? Is there an evolutionary reason why metacognition and performance may start to dissociate under high levels of arousal? In general, Cognitive (Neuroscience) has brought us many new tools to investigate the various processes relevant for explaining our decisions. However, at present, we are only just beginning to understand how decision making is implemented in the human brain. It is my hope we have contributed to this endeavor by increasing our understanding of the role of stimulus awareness, neuromodulation and metacognition in perceptual and cognitive decision making.

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## Summary in Dutch

In dit proefschrift onderzoek ik de rol van bewustzijn in menselijke besluitvorming en cognitie en probeer ik beter te begrijpen waarom we soms bewust worden van informatie in onze omgeving en waarom soms niet. Om dat te onderzoeken, manipuleerde ik externe variabelen die het beslisproces beïnvloeden, zoals de zichtbaarheid van een visuele stimulus op basis waarvan mensen een simpele beslissing moeten maken. Ook onderzocht ik (interne) schommelingen in de staat van alertheid van de hersenen (gemeten door te kijken naar de pupilgrootte) en de nauwkeurigheid van onze beslissing en de metacognitieve evaluatie van onze beslissingen (inzicht in de accuraatheid van onze beslissingen). In onze studies hebben we metingen van gedrag, pupilgrootte en EEG (elektrische hersensignalen) gecombineerd met computationele modellen om de mechanismen te ontrafelen die ten grondslag liggen aan perceptuele en cognitieve beslissingen.

Het werk gepresenteerd in dit proefschrift richt zich op drie hoofdvragen:

1. Hoe beïnvloedt bewustzijn van de uitkomst van een beslissing de manier waarop mensen leren, keuzes maken en hun gedrag bijsturen? (Experimenten 1-2).

2. Hoe beïnvloedt de alertheidsstaat van de hersenen ons perceptueel bewustzijn en metacognitieve evaluatie over de nauwkeurigheid van ons keuzegedrag? (Experiment 3).

3. Zijn bewustzijn en metacognitie noodzakelijk voor het monitoren van onze beslisvoorkeuren, of voor het bijstellen van ons toekomstige gedrag? (Experimenten 4-5).

Samenvattend laat het werk in dit proefschrift zien dat de uitkomst van een beslissing kan worden gemeten met behulp van hersen- en pupilmetingen, ongeacht de (volledige) zichtbaarheid van prestatiefeedback (positieve of negatieve feedback). Echter lijkt het er op dat visueel bewustzijn cruciaal is voor optimale controle van onze prestatie en is het belangrijk om flexibel te leren van onze fouten en aanpassingen door te voeren van onze toekomstige keuzepatronen. Verder laten we zien dat een verhoogde alertheid van de hersenen tijdens de presentatie van informatie die relevant is voor de beslissing, onze perceptie en metacognitieve evaluatie van onze prestatie op tegenovergestelde manieren beïnvloedt. Dit heeft waarschijnlijk te maken met het vrijgeven van de neurotransmitter noradrenaline, die de verwerking van externe prikkels (stimuli) kan versterken en de verwerking van zwakkere signalen kan reduceren.
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