

# **From affective blindsight to affective blindness: When cortical processing suppresses subcortical information**

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**Some patients with a lesion to their primary visual cortex (V1) show a phenomenon called ‘affective blindsight’: they can correctly guess the emotional expression of a face presented to their blind field. This ability has been attributed to an evolutionary old subcortical route for processing of emotional information. Neuroimaging studies show that this route is also functioning in normal observers: emotional faces, made invisible using backward masking, still elicit responses of the amygdala via a subcortical pathway. However, contrary to blindsight patients, normal observers cannot overtly identify the expression of unseen emotional faces. In this chapter, I will introduce and discuss a model describing the relation between conscious and unconscious processing that explains this discrepancy.**

## ***Introduction***

Visual processing and visual awareness are not the same: recent advances in the cognitive neurosciences have made it clear that what we consciously perceive is in fact only a tip of the iceberg of the vast amount of information that is processed by the brain. This seems especially the case for emotional stimuli, such as emotional facial expressions: every time we perceive a face, an extensive network of interacting brain areas processes different aspects of that face, such as identity, gender, age, and emotional expression (Vuilleumier and Pourtois, 2007). We use this information to guide our behaviour, for example to initiate an approach reaction towards a happy person, or avoid someone when there is a clear expression of anger on her or his face. Even more basic responses, such as fight or flight reactions can be triggered by facial expressions: an expression of fear, for example, may signal that there is a potential threat imminent, and it may be a good idea to prepare to run away (Ohman and Soares, 1993; LeDoux, 1996).

Generally, we believe that we are in control of our actions, and that we guide our behaviour by what we consciously perceive. In the example above, we may think we base our decision to avoid a friend who looks extremely angry on the fact that we have consciously perceived his facial expression. But is this true? Studies in patients with a lesion to the primary visual cortex (V1) show that these patients have the ability to correctly identify the emotional expressions of faces that are shown to them, even though these patients are blind. This is called 'affective blindsight'. Affective blindsight is thought to be mediated by an evolutionary old subcortical pathway that processes visual information independently of the cortical face processing areas that are necessary of conscious awareness (Morris, Ohman, and Dolan, 1999). This pathway activates the amygdala, a structure responsible for the regulation of emotional behaviour. Apparently, blindsight patients are able to use the information processed in this pathway in order to discriminate between different emotional expressions. Since even patients with fairly recent lesions show affective blindsight, it is not likely that this ability is the result of structural changes in the brains of these patients (Pegna, Khateb, Lazeyras, and Seghier, 2005). The subcortical pathway mediating affective blindsight has projections to the parietal somatosensory association cortex. Activations in this area have been demonstrated to correlate with subjective feelings of emotional experience in absence of visual awareness in patients showing affective blindsight (Anders, Birbaumer, Sadowski, Erb, Mader, Grodd, and Lotze, 2004). According to some researchers, affective blindsight shows that we in fact are 'blindly led by our emotions' when responding to emotional expressions: our reactions are guided by unconsciously processed information; conscious perception is just a slow epiphenomenon (DeGelder, Vroomen, Pourtois, and Weiskrantz, 1999; DeGelder, Vroomen, Pourtois, and Weiskrantz, 2000; Heywood and Kentridge, 2000).

Indeed there is ample evidence that the emotional significance of facial expressions is processed by a subcortical pathway involving the amygdala in normal observers (Morris, Ohman, and Dolan, 1999). Even when facial expressions cannot be consciously identified, the amygdala shows differential responses to emotional expressions of fear, anger, sadness, and happiness (Whalen, Rauch, Etcoff, McInerney, Lee, and Jenike, 1998; Kilgore and Yurgelun-Todd, 2004). Apparently, the same pathway that mediates

blindsight is doing exactly the same in normal observers: processing information about emotional expressions of faces, and activate the amygdala, suggesting that evolution has equipped us with a backup route for processing of emotions (LeDoux, 1996). However, there is an interesting discrepancy between the work on affective blindsight and the work on unconscious emotion processing in normal observers: the very definition of ‘unconscious emotion processing’ seems to be conflicting with the notion of ‘affective blindsight’. In virtually all studies on the neural correlates of unconscious emotion processing in normal observers, unawareness of the faces used is assessed by asking an observer to report the emotional expression of the faces used in the experiment. If the observer is unable to do so, this is taken as evidence of unawareness, and indeed, even though the observer cannot tell the difference between a neutral and a fearful expression, his amygdala can (e.g. Whalen *et al.*, 1998). However, in affective blindsight, we see the opposite: these patients are not able to consciously perceive facial expression shown to them, yet they can discriminate between different emotional expressions, an ability shown to be associated with differential activations of the amygdala (Morris, De Gelder, Weiskrantz, and Dolan, 2000; Pegna *et al.*, 2005). How can we explain this paradoxical situation, where the same pathway seems to support successful emotion discrimination in patients, but not in normal observers?

In this chapter I will lay out a hypothesis explaining this discrepancy, based on my work on transcranial magnetic stimulation induced blindsight in normal observers (Jolij and Lamme, 2005). In short, I propose that the information in the fast but crude subcortical pathways is often ignored or even actively inhibited by the executive areas of the brain: the executive systems show a strong preference for cortically processed information when generating a response. Only when the quality of cortically processed information is compromised over a longer period of time, the brain’s executive systems take subcortically processed information into account.

### ***Subcortical processing of emotional expressions: fast... but crude***

The idea that emotional content of visual stimuli is processed in a subcortical pathway is not new. In his famous two route model of emotion processing, LeDoux (1996) proposes that potentially threatening elements in a visual scene (for example, a snake, or a fearful face) can be detected in two ways: first, it could be that the object sensitive areas in cortical visual system identify the object and activate the amygdala. This route, however, can be quite slow: although latencies of object sensitive neurons in the temporal cortex have been shown to be in the range of 100 – 110 ms (e.g. Kiani, Esteky, and Tanaka, 2005), latencies of 200 – 300 ms have been reported for basic visual processes, such as scene segmentation, and visuomotor transformations (e.g. Heinen, Jolij, and Lamme, 2005; Jolij, Van Gaal, Scholte, and Lamme, *in press*), especially under non-optimal viewing conditions. That may be too slow if a tiger is looming in the jungle: by the time the cortical visual system has identified the blur coming at you as a tiger, it may be too late. LeDoux theorizes that evolution has equipped the brain with a shortcut to rapidly analyze potentially threatening elements in a visual scene. This so-called subcortical route involves the superior colliculi, the pulvinar, and the amygdala, and can detect stimuli that potentially require a fight or flight response, such as snakes, spiders, and fearful faces. Because of the tuning properties of the neurons in this pathway, it is less

sensitive to fine details (Sahraie *et al.*, 2003), but it is faster, and can activate the amygdala without requiring the extensive processing of the cortical system. This allows an organism to prepare or even initiate a fight or flight reaction more rapidly. It is believed that this very direct perception-action system in fact is a very old evolutionary system, and may have been a forerunner of the more advanced cortical visual system.

LeDoux's (1996) model is quite generally accepted, but direct anatomical evidence of a subcortical processing route for emotional information processing in humans is rare. The recent neuroimaging studies on unconscious processing of emotional expressions do seem to confirm the existence of this route, however. In most studies on the neural correlates of unconscious processing of facial expressions, a backward visual masking paradigm is used to prevent conscious identification of pictures of faces with an emotional expression. There is evidence that masking derives its effectiveness from interfering with cortical processing of the masked stimulus: either the mask 'catches up' with the masked stimulus (Breitmeyer and Ogmen, 2000; Macknick, 2006), or interferes with cortico-cortical interactions (Lamme, Zipser and Spekreijse, 2002; Fahrenfort, Scholte, and Lamme, 2007), and prevents the masked stimulus from being processed up to a level of conscious awareness. It is therefore assumed that any residual processing of masked emotional faces must be restricted to subcortical areas. A consistent finding in neuroimaging studies of unconscious emotion processing is that unseen fearful faces activate the amygdala, or more specifically, the right amygdala. Left amygdala activations are reported when faces are consciously perceived by the observers (Pessoa, 2005). Studies in blindsight patients seem to confirm the role of particularly the right amygdala in unconscious emotion detection (Morris *et al.*, 2000; Pegna *et al.*, 2005). Unconscious detection of fear is not just based on configural processing of a face. Apparently, presentation of a pair of fearful eyes is enough to evoke an amygdala response even the eyes are masked (Whalen *et al.*, 2004). Finally, the amygdala is not just capable of detecting fearful stimuli, but also shows differential responses to happy and sad expressions, suggesting that unconscious processing of facial expressions is not just limited to fear (Kilgore and Yurgelun-Todd, 2004).

More direct evidence of a subcortical pathway to the amygdala has been provided by Morris, Ohman, and Dolan (2000): they observed increased connectivity in this pathway when the amygdala showed an increased response to fearful expression, but for unseen faces only, a finding corroborated by Lidell *et al.* (2005), using completely undetectable stimuli, and Morris *et al.* (2000) in a blindsight patient. As is to be expected from the neurophysiological characteristics of the neurons in this pathway, the subcortical pathway mediating unseen emotions is sensitive to specifically the lower spatial frequency components of faces, containing the coarse details of a face, mainly the eyes and the mouth – elements that play a critical role in signalling emotional expression. Finer details, such as wrinkles are processed by areas in the neocortex (Vuilleumier, Armony, Driver, and Dolan, 2003; Winston, Vuilleumier, and Dolan, 2003).

Summarizing, even when visual stimuli such as faces with an emotional expression are masked, and not processed by the cortical visual system, the amygdala receives input via a network of subcortical structures signalling the coarse details of the unseen stimulus.

Apparently, this information is sufficient to allow the amygdala to differentiate between different emotional expressions.

### ***Affective blindness or affective blindsight?***

Even though normal observers cannot overtly discriminate between masked facial expression while the information necessary to make such discriminations is present in the brain, unseen emotional expressions do affect behaviour. For example, unseen fearful expressions can increase the galvanic skin response, a measure of autonomic nervous activity associated with acute stress, indicating that even an unseen fearful expression may trigger a fight/flight reaction (Ohman and Soares, 1993). An even more compelling demonstration of how unseen facial expressions can subtly influence behaviour has been provided in a classical study by Murphy and Zajonc (1993). In this study, observers had to rate Chinese characters they were unfamiliar with as either positive or negative. Critically, pictures of either positive or negative facial emotional expressions were presented very briefly, preventing conscious discrimination of the facial expression, right before presentation of the Chinese character. It turned out that unseen negative emotional expressions resulted in a more negative evaluation of Chinese characters, while positive emotions resulted in a more positive evaluation. It is not unlikely that these subtle effects are mediated by the same subcortical pathways mediating affective blindsight.

Apparently, observers are not as blind to unseen facial expressions as they seem. Could it be that the assessment of unawareness of emotional expressions in studies of unconscious neural processing may have been not sensitive enough to pick up residual emotion processing? A recent study by Pessoa, Japee, Sturman and Ungerleider (2005) seems to suggest so: as in other studies on unconscious emotion processing, Pessoa *et al.* measured neural activity evoked by masked expressions of fear. However, they found that some of the masked faces were perceived by their participants, particularly by a sub-population of 'over-achievers'. When this was factored in the analysis of the fMRI data, it turned out that the amygdala only showed a response to these 'seen' trials. Since earlier studies did not use a trial-by-trial analysis, Pessoa *et al.* suggest that the 'unconscious' processing of emotional expression may not be so unconscious after all. Apparently, there are large inter- and intra-individual differences in the detection of the emotion at near-threshold presentation conditions (Pessoa, Japee, and Ungerleider, 2005; Pessoa and Padmala, 2005; Szczepanowski and Pessoa, 2007). It may be that the alleged unconscious perception of emotions may in fact be an example of 'weak conscious processing', and that the remarkable inability of normal observers to discriminate between masked facial expressions may be due to the fact that unconscious effects can only be revealed if consciously processed information is completely absent in stead of reduced (Snodgrass, Bernat, and Shevrin, 2004; Snodgrass and Shevrin, 2006).

Especially this latter point is important. It may potentially explain the discrepancy between affective blindsight in patients and affective blindness in normal observers: if normal observers perform at a level of 'weak conscious processing', this residual processing may override unconsciously processed information – a phenomenon that has been demonstrated in unconscious semantic priming (Snodgrass, Bernat, and Shevrin, 2004; Snodgrass and Shevrin, 2006). To really make sure that any residual processing

can only be attributed to purely unconscious processing, and can actually be measured, one needs to make sure that stimuli are presented below the threshold of objective awareness, that is, participants must be at chance level in a stimulus *detection* task instead of on a *discrimination* task in order to properly assess unawareness: participants should not only be unable to tell the emotion of a masked face (that is, they are subjectively unaware of a facial expression); they should even be unable to report that a face has been presented *at all* – something called objective unawareness (Snodgrass, Bernat, and Shevrin, 2004).

In most of the work on unconscious processing of emotions, masking of stimuli has prevented conscious discrimination of stimuli instead of conscious detection of stimuli. It might be that this has allowed some conscious effects on emotion processing in subcortical structures, and potentially interfered with subtle effects of unconscious processing on overt behaviour. However, even in blindsight there are some reports of residual visual awareness, which, though unlikely, may mediate weak conscious processing of unseen signals of fear (Sahraie, Weiskrantz, Barbur, Simmons, Williams, and Brammer, 1997; Silvanto, Cowey, Lavie, and Walsh, 2007). In the first study on affective blindsight, indeed patient GY, who has unilateral damage to his primary visual cortex, did report to be aware of the on- and offset of stimuli, even though he reported not to consciously perceive the emotional expressions (DeGelder *et al.*, 1999). This finding shows that it is hard to meet the criteria of objective unawareness, even in patients with cortical damage, though these patients still show effects of unconsciously processed information on overt behaviour.

However, Liddell *et al.* (2005) have demonstrated that even with undetectable stimuli a brainstem-amygdala-cortical network is activated in normal observers, despite the objective unawareness of the stimuli; furthermore affective blindsight has been reported in patients with bilateral destruction of the primary visual cortex, excluding the possibility that contralesional cortical visual pathways contribute to their residual visual processing, as has been hypothesized in the case of unilateral patients such as G.Y. (Hamm, Weike, Schupp, Treig, Dressel, and Kessler, 2003; Pegna *et al.*, 2005; Sahraie *et al.*, 1997). These studies demonstrate that even in cases of objective unawareness, emotion processing still occurs in a subcortical pathway, and, more importantly, still show the same paradoxical pattern where normal observers cannot discriminate between unseen facial expressions (Liddell *et al.*, 2005), but patients can (Pegna *et al.*, 2005).

Recently, we have published a study in which we report both affective blindsight and affective blindness in normal observers (Jolij and Lamme, 2005). In this study, we let observers discriminate between happy and sad schematic faces, while we stimulated the early visual cortex on different moments after stimulus presentation, ranging from 50 to 300 ms after stimulus onset. We replicated the basic finding that TMS of the occipital pole suppresses perception of visual stimuli when applied around 100 ms after stimulus onset (Amassian, Cracco, Maccabee, Cracco, Rudell, and Eberle, 1989; Corthout, Uttl, Ziemann, Cowey, and Hallett, 1999), as assessed with both localization and detection tasks, but despite objective unawareness of the stimuli, observers were still able to guess the emotion of schematic faces above chance level in those trials in which TMS

successfully suppressed the conscious percept of the stimuli. However, when we increased the presentation time of our stimuli from 17 ms to 33 ms, we still were able to successfully suppress conscious awareness of the stimuli when TMS was applied around 100 ms after stimulus onset, but in this condition the observers' ability to successfully report the emotional expression of the schematic faces was suppressed as well.

This seems rather counterintuitive. With longer presentation times, one would expect that the signal in the subcortical pathways would be stronger, leading to even better unconscious recognition of affect, instead of the reverse effect we report. A further analysis revealed that a similar effect was present in the later trials of the short presentation time condition: after prolonged exposure to the task, unconscious recognition of emotional expression diminished. Disappearance of the blindsight effect seemed to covary with how well the observers performed in the approximately five out of every six trials in which TMS was not effective in suppressing the visual stimulus because of the stimulus-TMS interval: when overall performance on the emotion detection and stimulus localisation tasks was around 70% in these unsuppressed trials, TMS around 100 ms resulted in suppression of conscious awareness of the stimulus, but not in suppression of emotion recognition. However, when performance on both tasks in unsuppressed trials was 90% or higher, TMS around 100 ms did not only suppress conscious awareness, but also emotion recognition (Jolij and Lamme, 2005). We replicated this finding in two observers by manipulating stimulus luminance, with the same effect (Jolij, unpublished data).

Apparently, observers can only respond unconsciously processed emotions in quite specific circumstances. There seems to be an interaction between overall state of certainty about a given task, and the ability to respond to unconsciously processed information: the better one performs, the more likely one is to respond to what one consciously perceives, and ignore unconsciously processed information. However, if a task is particularly hard, unconsciously processed information might be taken into account when making a response (Jolij and Lamme, 2005). But how does this interaction work? How does the brain decide which type of information to use? And why would the brain's executive systems ignore unconsciously processed information?

### ***Repression of unconscious information by conscious processing: a model***

Our study (Jolij and Lamme, 2005) suggests an interaction between conscious perception, or better, task accuracy, and unconscious processing in emotion recognition: only in certain circumstances observers take into account unconsciously processed emotional information when responding to unseen stimuli. This may potentially explain the paradoxical finding that blindsight patients can report the emotional expression of unseen emotional faces, while normal observers cannot. In the remainder of this chapter, I will lay out a basic model of this interaction between conscious and unconscious processing.

I will take the dual route model of emotional face processing as a starting point (Johnson, 2005; Ledoux, 1996; Vuilleumier, Armony, Driver, and Dolan, 2003; Vuilleumier and Pourtois, 2007). According to this model, the emotional expression of a face is processed in parallel by both cortical areas, and subcortical areas. Processing in the cortical areas is

necessary for conscious perception of the face (though not all cortical processing will result in conscious awareness; cf. Lamme, 2003), while on the other hand processing in the subcortical areas cannot support visual awareness of the face.

The accuracy of the cortical processing route under normal viewing conditions is near perfect: performance on emotion discrimination tasks of unmasked facial expressions is near 100% (cf. Jolij and Lamme, 2005). Obviously, there is a large number of factors that can strongly impair the accuracy of cortically processed information: in our experiment, shortening presentation times yielded a performance drop of almost 25% to 75%, but masking or lowering luminance of stimuli will also degrade a conscious percept, leading to a lower accuracy of the cortical pathways. The subcortical pathways are less accurate even under optimal viewing conditions. If we assume that the performance of blindsight patient GY is based on subcortically processed information only, accuracy of subcortically processed information should be around 60% - 80% for optimally presented stimuli such as videos of about 3s (De Gelder *et al.* 1999). Interestingly, our results seem to indicate a similar performance under far less optimal viewing conditions: accuracy on emotion discrimination of briefly presented, low contrast stimuli in fully suppressed trials in our experiments was around 65% - 70%. A safe estimate of the accuracy of the subcortical processing route for facial expressions would therefore be about 70%, but apparently accuracy of this route is not as sensitive to decreases in stimulus visibility as the cortical processing route, as neuroimaging studies indeed do suggest (cf. Killgore and Yurgelun-Todd, 2004; Lidell *et al.*, 2005; Morris, Ohman, and Dolan, 1998, 2000; Whalen *et al.*, 1998).

Both the cortical and subcortical processing routes project to the executive areas in the prefrontal cortex (Morris, Ohman, and Dolan, 2000; Anders *et al.*, 2004; Haxby, Gobbini, Furey, Ishai, Schouten, and Pietrini, 2001), and we may safely assume that both cortically and subcortically contribute to visually guided behaviour. Which of both signals is used in order to initiate a response is most likely to be determined by the nature of the response required: interpreting someone's emotional expression in a social context requires accuracy (misinterpreting someone's sad expression for a happy expression could be very awkward in social interactions), while initiating a flight reaction in response to a fearful face may require a quick response – a false alarm in this scenario may not be as harmful as waiting until it is too late to respond to a potential threat. So, how does the brain select which information to use in order to initiate a response? One potential mechanism may be that unconsciously processed information is only used in response to signals indicating threat or fear. However, the literature does not seem to support this hypothesis: normal observers cannot respond to unconsciously processed fear, indicating that simple presence of a signal of fear in the subcortical pathways is not sufficient to initiate an overt response, even though some physiological responses are initiated (Morris *et al.*, 2000; Ohman and Soares, 1993; Whalen *et al.*, 1998).

Our study on TMS induced blindsight suggest that overall viewing conditions play a role in determining which type of information processing (cortical or subcortical) drives a visually guided response, something that probably relates to the difference in sensitivity for visibility reduction in the cortical and subcortical pathways. As stated above, under

optimal viewing conditions, there is a large discrepancy between the accuracy of cortically (accuracy around 100%) and subcortically processed information (accuracy around 70%). However, when visibility decreases, this discrepancy is reduced, and may even reverse: in blindsight patients, the subcortical pathways are clearly more accurate than the damaged cortical pathways.

Assuming that the brain uses the most accurate source of information to generate a response could potentially explain the discrepancy between affective blindness in normal observers and affective blindsight in patients, or the paradoxical disappearance of the affective blindsight experiment in our experiment: if viewing conditions *in general* are good, cortically processed information provides the most accurate information, and is therefore used to generate a response. However, determining whether source of information is the most accurate is not a matter of trial-by-trial evaluation. Our work suggests that general visibility (that is, visibility of stimuli over a longer period of time) is used to determine which source of information to use; even if that means that in some instances performance will suffer. It is important here to realize that ‘visibility’ should be interpreted in a real-world sense: in the work on unconscious face processing, the emotional faces were masked using neutral faces. The visibility of these neutral faces was good – subjects could clearly see them. It is not unlikely that this good visibility of neutral faces may have triggered the executive systems of the brain to use cortically processed information. After all, the brain has not evolved for laboratory experiments with masked stimuli. In order to explain why normal observers cannot respond to unconsciously processed information, we need to assume that generating a visually guided response is not simply a matter of accumulating evidence from the cortical and subcortical pathways: if that were the case, observers should be able to respond to subcortically processed information in all cases. In stead, it appears that subcortically processed information is actively ignored or repressed.

A possible reason for this may be that this avoids response conflict: if we assume that cortically processed information has a near-perfect accuracy under normal viewing conditions, but subcortical have an accuracy of around 70%, these different pathways come up with conflicting outputs on average one out of every three to four occasions. Repressing the least accurate source of information in stead of integrating when preparing a response may potentially speed up processing because the conflict does not need to be resolved. However, when overall visibility decreases, subcortically processed information becomes relatively more accurate, and may be used to generate responses as well. In our TMS experiment, even unsuppressed stimuli in the one frame condition were relatively hard to see, simulating a more realistic situation of poor visibility of emotional facial expressions, possibly explaining why we did find effects of unconscious processing in our study.

One key assumption of this model is that the brain is somehow capable of evaluating its own accuracy. Research on error monitoring and awareness indicates that that is indeed the case: when an error is made, specific error related signals are generated in the anterior cingulate cortex, and in the temporal areas of the brain. These signals have been shown to play a role in adapting behaviour and learning (Ridderinkhof, Van Den Wildenberg,

Segalowitz, and Carter, 2004; Wills, Lavric, Croft, and Hodgson, 2007). Moreover, in a recent study by Lau and Passingham (2006), areas in the dorsolateral prefrontal cortex have been identified which seem to signal the subjective quality of visual information regardless of task performance: participants were engaged in a visual discrimination task, and had to indicate whether they had clearly seen the stimulus or whether they had guessed when making a response. Lau and Passingham identified two stimulus-mask intervals at which performance on the discrimination task was equal, but the subjective experience of the stimuli (i.e. the number of 'seen' versus 'guessed' responses) was different. Functional imaging revealed that the dorsolateral prefrontal cortex signalled this difference in subjective quality. Summarizing, it appears that there indeed are neural circuits capable of evaluating performance (Ridderinkhof *et al.*, 2004; Wills *et al.*, 2007), and even areas that signal the subjective quality of visually presented information (Lau and Passingham, 2006): it is quite likely that the brain *is* capable of evaluating its own accuracy.

Taking all the above into account, a formal model of how consciously and unconsciously processed information interact in the processing of emotional facial expressions is represented in figure 1. Information about a face (here a schematic face) is processed in parallel in both cortical and subcortical areas. Under normal viewing conditions, the cortical areas have near-perfect accuracy, while the accuracy of the subcortical pathways is capped at 70%. Both pathways project to the executive areas of the brain, responsible for response generation. Information in the subcortical pathways is actively ignored, or repressed, if the accuracy of cortically processed information exceeds that of subcortically processed information to avoid response conflict (figure 1b). However, if in this situation on cortical information processing is disrupted, for example by masking or by a TMS pulse, the executive systems of the brain do not have access to any information about a stimulus: subcortically processed information is ignored, and cortical information is compromised. This situation leads to the affective blindness observed in normal subjects (figure 1c). However, when the accuracy of the cortical pathways is deteriorated over a longer period of time, and approaches that of the subcortical pathways (such as in low visibility conditions, or cortical damage), subcortically processed information may contribute to visually guided behaviour (figure 1d). If in this case cortically processed information is disrupted by masking or TMS there is information available to base a response on, resulting in affective blindsight. Areas involved in error monitoring such as the anterior cingulate cortex or the dorsolateral prefrontal cortex may play a role in the hypothesized repression of subcortically processed information.

A mechanism like this clearly has its benefits: it assures that we are *not* blindly led by emotions. Misinterpreting an emotional expression may have severe consequences for social beings like humans, and apparently the need for accurate identification outweighs the need for fast fight or flight responses. Still, this mechanism allows for such responses if circumstances change. Moreover, covert responses based on subcortically information are not repressed. These covert responses may speed up an overt response when needed, thus sacrificing relatively little on speed, while gaining in accuracy. The model described above fits the data published thus far about unconscious emotion processing and is able to

explain the paradoxical discrepancy between affective blindsight observed in patients and the affective blindness of normal observers.

### **Conclusion**

There is no doubt that emotional facial expressions can be processed in total absence of awareness, and that these unconsciously processed emotions can modulate behaviour and even result in emotional feelings (Anders *et al.*, 2004; DeGelder *et al.*, 1999; Murphy and Zajonc, 1993; Ohman and Soares, 1993; Pegna *et al.*, 2005; Whalen *et al.*, 1998). However, this does not mean that we are blindly led by emotions (Heywood and Kentridge). The accuracy of unconsciously processed information is limited (DeGelder *et al.*, 1999; Jolij and Lamme, 2005), and guiding responses purely based on this information may have serious disadvantages for social beings like humans: an inappropriate response to a wrongly interpreted facial expression may lead to awkward social situations. Therefore, in stead of guiding responses by unconsciously processed information, the brain guides its responses by consciously processed information when possible, and represses unconsciously processed information to avoid response conflicts. Only when the accuracy of consciously processed information is compromised over a longer period of time, the brain changes its strategy and takes unconsciously processed information into account when generating overt responses.

Obviously, this model remains to be tested empirically, and a lot of questions remain unanswered. Exactly when does the brain switch from ‘conscious processing’ to ‘unconscious processing’? Are there interpersonal differences in strategy? And, what does ‘conscious’ exactly mean? Recent empirical and theoretical work on visual awareness suggests that there may be a distinction between ‘phenomenal awareness’ (the actual qualitative experience) and ‘access awareness’ (the contents of awareness we can report upon) (Block, 2005; Lamme, 2003; Snodgrass, Bernat, and Shevrin, 2004). Are ‘consciously’ guided responses based on phenomenal awareness or on access awareness? And, finally, can this model be generalized to other types of visually guided behaviour? Not only emotional stimuli are processed unconsciously – in fact, unconscious processing has been demonstrated for a vast array of different stimuli (e.g. Dehaene *et al.*, 1998; Lau and Passingham, 2007). Yet, direct demonstrations of overt responses to unconsciously processed stimuli in normal observers are rare and not entirely undisputed (Boyer, Harrison, and Ro, 2005; Jolij and Lamme, 2005; Kolb and Braun, 1995; Meeres and Graves, 1990; Morgan, Mason, and Solomon, 1998), while blindsight in patients has been demonstrated for a wide variety of stimulus attributes, such as colour, form, and motion (Weiskrantz, 2003). Could a same model explain this discrepancy as well? We are currently working on behavioural and neuroimaging experiments in our lab to test this model, and find an answer to the questions posed above.

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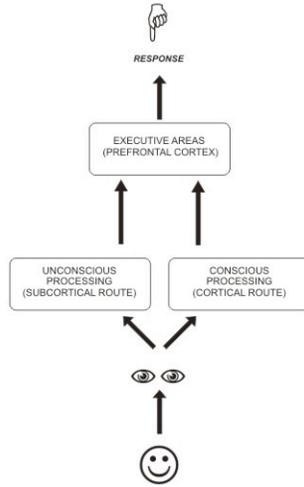
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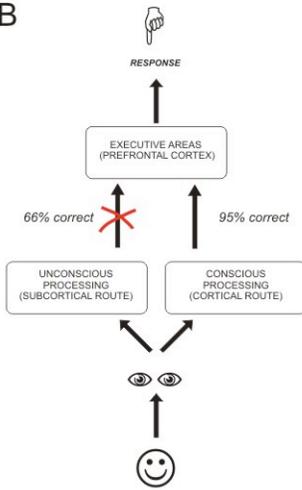
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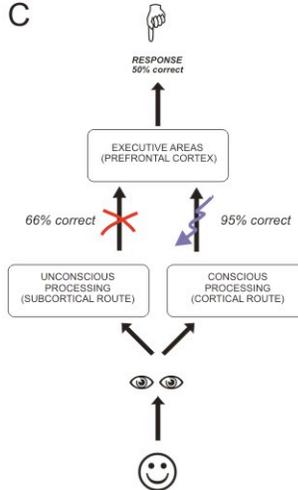
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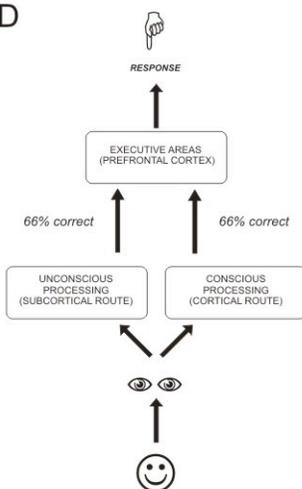
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