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Automatic motor activation in the executive control of action

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Although executive control and automatic behavior have often been considered separate and distinct processes, there is strong emerging and convergent evidence that they may in fact be intricately interlinked. In this review, we draw together evidence showing that visual stimuli cause automatic and unconscious motor activation, and how this in turn has implications for executive control. We discuss object affordances, alien limb syndrome, the visual grasp reflex, subliminal priming, and subliminal triggering of attentional orienting. Consideration of these findings suggests automatic motor activation might form an intrinsic part of all behavior, rather than being categorically different from voluntary actions.

Keywords: action, cognitive control, response inhibition, unconscious, volition

It is widely believed that human cognition and behavior is governed by both voluntary and automatic processes. Voluntary "executive control" mechanisms are assumed to direct behavior in goal-directed ways through use of explicit knowledge and expectations. On the other hand, accumulating research has revealed that perceptual processing of visual stimuli can automatically and unconsciously modulate motor responses (see e.g., Eimer and Schlaghecken, 2003; Sumner, 2007). Traditionally, the processes underpinning automatic and unconscious triggering of actions have been considered separate from the processes underpinning voluntary action planning and control. Embedded in this concept of separate functional pathways is the idea that automatic processes are unconscious, fast, and rigid whereas voluntary action planning and control were considered to be conscious, and flexible (see e.g., Schneider and Shiffrin, 1977; Shiffrin and Schneider, 1977, 1984). However, several lines of evidence, briefly reviewed previously by Sumner and Husain (2008), challenge this traditional distinction.

In this review we consider recent empirical findings and discuss how they provide evidence that voluntary and automatic control of action might not in fact be so distinct. We suggest that many "automatic" mechanisms can in fact be surprisingly flexible, quite unlike the traditional, inflexible view of these processes. We begin by reviewing evidence that even simple, flashed visual stimuli can automatically modulate on-going motor responses. Then we discuss how automatically primed responses might affect interactions with real objects in the world around us, focusing on the subject of object affordance. Finally we turn to the issue of how such primed activity might be controlled, and to what extent such control could be automatic. Throughout the review, we draw on evidence from three converging approaches: using subliminal priming paradigms to show that unconscious motor activation can also be reversed unconsciously; using traditional "conscious inhibition" paradigms to show that such inhibition can also be triggered automatically; using the two types of paradigm together to see if they interact. The demonstration of flexible control over automatic processes suggests an intricate link between these historically distinct processes.

EVIDENCE FOR AUTOMATIC ACTIVATION OF MOTOR RESPONSES

Perceptual processing of a visual stimulus can result in motor responses even when the observer does not intend to act. One of the most well-studied of these phenomena is the "visual grasp reflex", where an observer makes a fast, reflexive eye movement (saccade) toward a suddenly appearing—and irrelevant—visual stimulus, despite their intention to look elsewhere (e.g., Theeuwes et al., 1998; Irwin et al., 2000). Even when irrelevant distractors do not fully succeed in capturing gaze they may nevertheless have a remarkable influence on on-going motor activity. For example, saccades can curve whilst in flight toward an irrelevant distractor on the way to correctly landing on the target (e.g., McPeek and Keller, 2001; Godijn and Theeuwes, 2002; McPeek et al., 2000, 2003). But as response latencies increase, saccades are more likely to curve *away* from a distractor (e.g., Walker et al., 2006), revealing an inhibitory mechanism acting to suppress unwanted motor activity toward the irrelevant stimulus (e.g., Sheliga et al., 1995).

Saccades toward targets can also be slowed when an irrelevant distractor is presented simultaneously—or nearly simultaneously—with the target (the saccade distractor effect; e.g., Walker et al., 1995, 2000). Furthermore, transient changes to the scene during saccade planning in simple tasks, reading, or visual search produce a characteristic "dip" in the frequency of saccades made around 90–100 ms after the change (saccadic inhibition effect; e.g., Reingold and Stampe, 1999, 2000, 2002, 2003; Buonocore and McIntosh, 2008; Edelman and Xu, 2009; Bompas and Sumner, 2011). These dips provide highly robust evidence for rapid modulation of on-going motor commands by visual information. Manual reaching responses too are affected by irrelevant non-target stimuli. Like saccades, reaches can be slowed (e.g., Tipper et al., 1997), curve toward (e.g., Tipper et al., 1997) or away from (e.g., Howard and Tipper, 1997) non-target stimuli in flight. These findings suggest that both manual and oculomotor responses can be automatically modulated by irrelevant visual inputs.

Although not often considered in this context, such effects of irrelevant stimuli might in fact be related to a long-established view that simply visually processing an object can automatically evoke action plans appropriate for interacting with it. Gibson (1979) described "affordances" as properties of the environment that automatically prime the observer to act in such a way. According to this view, seeing a coffee cup with its handle to the right *affords*—or facilitates—a reaching movement with the right hand to grasp the cup. Recently there has been renewed interest in affordances, and their effects have been examined using functional imaging as well as behavioral methods. For example, motor regions of the brain—such as those within the dorsal medial frontal cortex—are activated when observers merely look at a graspable object (e.g., Grèzes and Decety, 2002), even when they do not intend to act. In other tasks that require arbitrary responses to pictures of graspable objects (such as squeezing a trigger to indicate whether the object is man-made), the response is facilitated when it is congruent with the action afforded by the object (e.g., Tucker and Ellis, 1998; see **Figures 1A** and **B** for examples of typical affordance stimuli and their effects on response times). Findings such as these suggest that the brain has learnt to associate objects with actions appropriate to "capture" them, and these actions can be (partially) activated by visual processing of the object.

However, there has been some debate about whether object affordance effects genuinely arise from visual objects automatically eliciting motor plans. Anderson et al. (2002) observed that the most visually salient part of the objects used in many affordance studies were also often the graspable part of the object. They demonstrated that response times were faster whenever the side of the response corresponded with whichever side of the object was most visually salient, even when the object was not graspable (e.g., left hand responses to a picture of an analog clock showing a time of quarter to nine). Therefore, affordance-like behavioral effects do not necessarily arise from possibilities for action *per se*, but instead can stem from congruence between the required response and this shift of attention.

But this is not to say all affordance effects are perceptual. Object orientation was irrelevant in most other affordance experiments (e.g., Tucker and Ellis, 1998), but by contrast it was the response-defining property of the object in Anderson and colleagues' task. They also used line-drawings of common objects which may have evoked qualitatively different responses than those evoked by the photographs or images of 3D models used elsewhere (e.g., Tucker and Ellis, 1998; Phillips and Ward, 2002; McBride et al., 2012). Furthermore, perceptually lateralized stimuli that do not afford actions do not necessarily produce affordance effects (e.g., Buccino et al., 2009). Finally, object affordance effects have recently been shown with stimuli and responses that are not lateralized, and instead rely on compatibility between object size and response (pinch or power grasp) to produce affordance effects (e.g., Ellis and Tucker, 2000; Tucker and Ellis, 2001; Derbyshire et al., 2006; Ellis et al., 2007). These considerations suggest that there are good reasons to believe perceptual processing of graspable objects can automatically evoke motor responses associated with them.

ALIEN HAND SYNDROME AND UTILIZATION BEHAVIOR

Some of the most striking evidence that visual objects can indeed automatically generate responses comes from studies of some unusual neurological cases. Patients with alien hand syndrome spontaneously and involuntarily grasp objects—even other people—in their environment as if magnetically drawn to them (for a review see Scepkowski and Cronin-Golumb, 2003). These individuals are aware of their hand making these movements, but report that they are not controlling them, and instead feel the movements are being controlled by an external agent. In a related syndrome, patients who display *utilization behavior* automatically grasp and use objects placed within their reach, even when the objects are not needed. For example, they may grasp and begin to peel an apple placed within their reach, even though they are not hungry, do not want to eat the apple, and know that it doesn't belong to them (e.g., Boccardi et al., 2002).

Alien limb and utilization behavior are rare neurological syndromes, and so case reports and experimental studies on patients with them have been correspondingly few. Some of the most detailed investigation comes from Riddoch and her colleagues (Riddoch et al., 1998; Humphreys and Riddoch, 2000). They showed that patients with an alien right hand can correctly pick up a cup with the left hand as long as the cup's handle is also on the left. However, when the handle is on the right the patients are more likely to grasp the cup with the right hand, despite instructions to the contrary. These "interference" errors were reduced when the task was to point to the object, rather than grasp, and also when the objects were inverted. Therefore, it seems that these patients responded according to well-learnt affordance-action associations rather than according to the instructions they were given. The action afforded by the object was disrupted when the object was inverted, or when the action required was not the one usually made to the object (pointing instead of grasping), so fewer interference errors were reported under these conditions.

Alien limb and utilization syndromes are most often associated with focal lesions to the medial frontal lobes (particularly the supplementary motor area; SMA e.g., Lhermitte, 1983; Boccardi et al., 2002), but have also been associated with damage to the corpus callosum (e.g., Biran and Chatterjee, 2004), as well as patients with parietal lesions following posterior cerebral artery stroke (e.g., Coulthard et al., 2007; Bartolo et al., 2011). Increasingly, they are recognized in patients with corticobasal degeneration (CBD), a slowly progressive neurodegenerative condition which affects cortical regions as well as the basal ganglia (e.g., Murray et al., 2007; Tiwari and Amar, 2008).

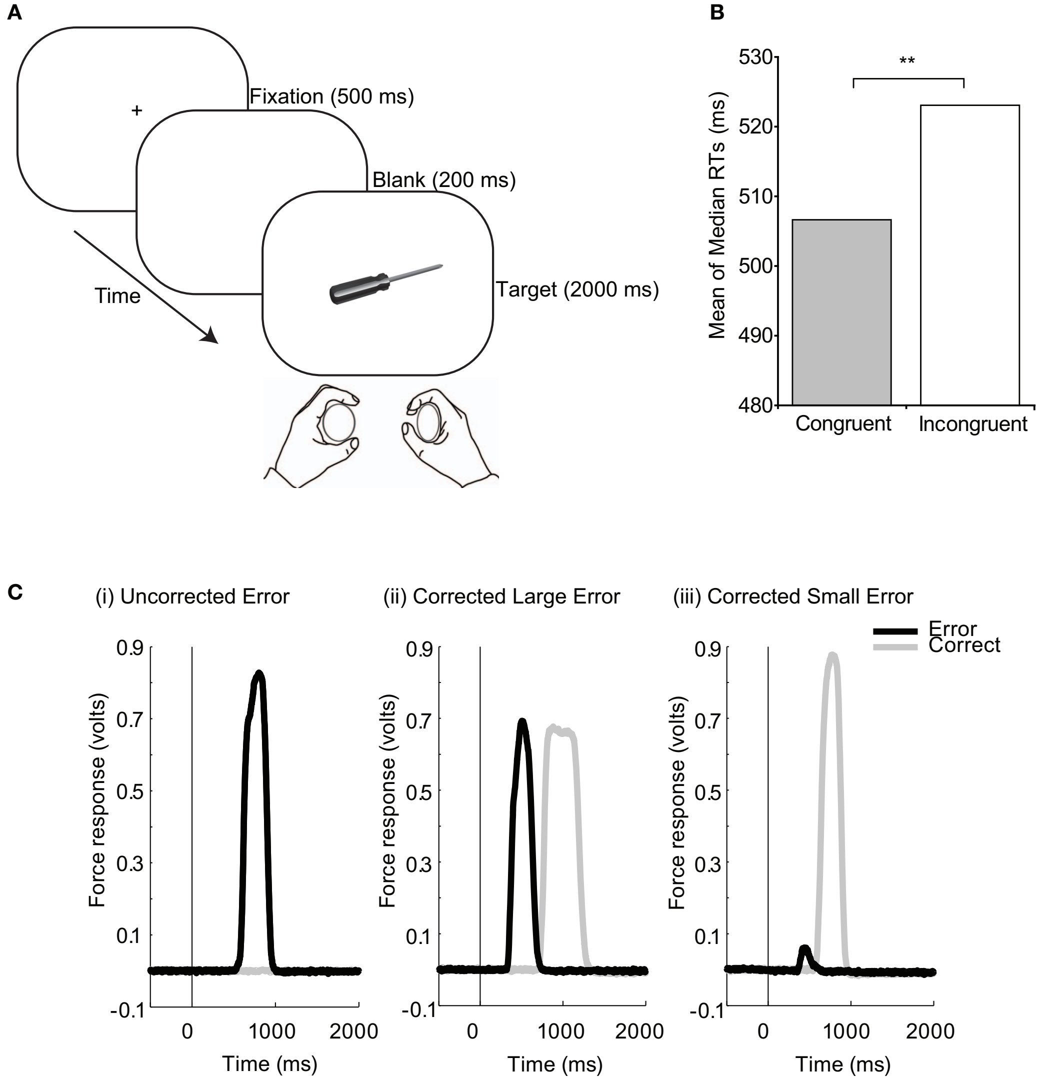

FIGURE 1 | McBride et al. (2012) studied automatic priming of motor responses by visual objects in an object affordance task. Here, participants made speeded squeeze responses with either their left or right hand according to whether the object presented on each trial belonged in a kitchen or a toolbox (see **A** for task details). The objects could also afford a grasping action with either the left or right hand. Although object affordance was irrelevant to the task, it still modulated responses so that they were faster when the object afforded a congruent response than an incongruent one **(B)**. Furthermore, partial squeeze responses (see **C(ii)** and **C(iii)** for examples of the responses recorded on individual trials) were made significantly more often on incongruent than on congruent trials—indicating that the afforded response had been activated and at least partially executed on incongruent trials. These figures are adapted with permission from Taylor and Francis and were originally published in McBride et al. (2012), *Q. J. Exp. Psychol. 65,* 13–24, www.tandfonline.com.

In a recent functional imaging study, Schaefer et al. (2010) examined the neural correlates of unwanted movements in a patient with alien limb syndrome with CBD. They reported that voluntary and alien movements activated similar brain regions, including motor and parietal cortices. However, the right inferior frontal gyrus (rIFG), which has been associated with inhibitory control of motor responses (e.g., Swann et al., 2009, 2012; Hampshire et al., 2010; Verbruggen et al., 2010; see also Aron, 2007), was activated only during alien movements. Such activation may reflect unsuccessful attempts to inhibit alien movements. Taken together, these studies highlight the impact of automatically afforded actions, and suggest that alien limb patients might find them particularly difficult to inhibit.

EVIDENCE FOR AUTOMATIC MOTOR ACTIVATION FROM "PARTIAL" ERRORS

Another line of evidence that potentially reveals the automatic effects of visual stimuli on actions comes from investigation of erroneous responses. Typically, most evidence for automatic motor priming by visual objects has been gleaned indirectly by measuring the eventual outcome of this process on reaction times, usually for manual button presses. Such responses are an all-or-nothing, binary measure: either the response made is of sufficient magnitude to trigger a button press, or it isn't. However, it is possible that small amounts of force applied (erroneously) to a button might be insufficient to trigger a measurable response and thereby escape detection.

With this in mind, there has recently been revived interest in employing continuous and sensitive measures of motor response to more directly investigate processes of automatic motor activation on a trial-by-trial basis. McBride et al. (2012) employed such a measure to investigate object affordances. They asked participants to classify object stimuli by squeezing one of two devices placed in their left and right hands (see **Figure 1A**) while measuring the force applied by either hand. Consistent with object affordance effects, responses were faster on trials where the object afforded an action with the same hand that was required to make the response (congruent trials), compared to the opposite hand (incongruent trials). But continuous, simultaneous force recordings also revealed that participants made small erroneous responses when there was conflict between the response afforded by the object and the response required by the task, i.e., when the stimulus afforded a response that was incongruent to the response required by the task. Such errors were later corrected (**Figure 1C**). These partial erroneous responses provide compelling evidence that viewing an object activates motor plans appropriate for interacting with that object, sometimes going far enough to produce a partial response.

Electromyography (EMG) has also been used to demonstrate "sub-threshold" erroneous responses on incompatible compared to compatible trials in a variety of paradigms including Eriksen flanker (e.g., Coles et al., 1985; Eriksen et al., 1985), and Simon (e.g., Burle et al., 2002) tasks. For example, continuous measurement of EMG from both arms of participants performing a flanker task has demonstrated that correct button-press responses on incompatible trials are frequently accompanied by some muscle activity in the opposite hand, i.e., for the response associated with the irrelevant flanker stimuli (Eriksen et al., 1985). Thus, response-related muscle activity measured by EMG could be measured in the absence of a "full" button-press response.

Such increased erroneous response activity on incongruent trials provides strong evidence that an irrelevant stimulus—or part of a stimulus—can automatically activate responses associated with it. These responses are not merely partially activated somewhere in the brain; the response can be measured in the muscles or in small hand movements with force transducers. These "partial" responses are not captured by current the models of decision-making, which instead assume that actions are either executed wholly once the threshold for accumulated evidence is reached, or not executed at all (see Smith and Ratcliff, 2004 for a review of commonly used models and their characteristics). These models assume that evidence in favor of particular action possibilities is accumulated until a certain threshold of evidence is reached. Models differ in how evidence accumulates. Some (e.g., random-walk) assume that evidence is accumulated as a single total so that evidence in favor of one response is necessarily evidence counter to alternative responses (e.g., Link and Heath, 1975), whereas others (e.g. accumulator models e.g., Usher and McClelland, 2001) assume that evidence in favor of competing responses is accumulated separately, often with mutual inhibition between the separate accumulators.

Importantly, all these decision models share the assumption that once the accumulated evidence reaches a "threshold," the response is executed. This all-or-nothing property of decision models does not allow any gradation of the response. Either the evidence accumulating for a particular response reaches the decision threshold and the response is made, or it does not reach threshold and no response is made. We anticipate that investigations of partial responses evoked by automatic activation of motor responses will provide interesting constraints for future work in decision-making.

INVISIBLE INFLUENCES

Thus far, in the evidence we have reviewed, the automatic nature of motor priming has been inferred from interference effects: if the participant or patient is engaged in a particular task and stimuli interfere with that task, we infer that responses to the task-irrelevant stimulus (or part of a stimulus) were not volitional. Another way to study automatic influences is to investigate the effects that *invisible* stimuli have on motor behavior. If an observer is unaware of a stimulus, then traditionally it is concluded that any response made to it cannot have been evoked voluntarily and must, therefore, have been made automatically.

One way to present a stimulus subliminally is to use the *backwards masking* technique (e.g., Ögmen and Breitmeyer, 2006). Using this technique, participants are usually required to make a manual button press as quickly as possible to a target stimulus (often a left or right pointing arrow). This target is preceded by a "prime" stimulus for a very short duration (say, 20 ms) which is followed by an overlapping (or surrounding in the case of metacontrast masking) stimulus—or "mask." This technique renders the prime stimulus imperceptible to the observer. Even when the participants cannot discriminate the identity of the prime under forced choice, responses are generally faster and more accurate when the prime stimulus was associated with the same response as the target stimulus (compatible trial) compared to when the prime was associated with the opposite response (incompatible trial; e.g., Leuthold and Kopp, 1998). Thus, manual responses can be partially activated automatically by visual stimuli even when they cannot be consciously discriminated.

Subliminal stimuli can also prime a shift of attention (e.g., McCormick, 1997; Ivanoff and Klein, 2003; for a review see Mulckhuyse and Theeuwes, 2010) so that observers respond more quickly and accurately to stimuli presented at the cued location relative to an un-cued location. For instance, McCormick (1997) manipulated the luminance of cues so that some were visible and others were not. The cues were mostly *invalid* so the target was most likely to appear at the opposite location to the cue. When participants perceived the cue they were faster to respond to a target presented at the location opposite the cue, suggesting that they had *volitionally* moved their attention to the most appropriate (i.e., statistically predicted) location. However, when participants were not aware of the cue they were faster to respond to targets at the cued, relative to un-cued, location. This provides evidence that the invisible cue produced an *automatic* and *involuntary* shift of attention to the cued location.

Cues do not have to be based on low-level differences in visual salience in order to produce reliable effects. Socially relevant eye-gaze can also direct attention exogenously. Responses are faster to target stimuli that have been preceded by a non-predictive face (or schematic drawing of a face) with the eyes gazing in the direction of the target (e.g., Friesen and Kingstone, 1998, 2003; Driver et al., 1999; but see Tipples, 2002). These so-called "gaze cueing effects" have been shown following cues that have been backwards-masked to render them invisible to the participant (Sato et al., 2007). In summary, shifts of attention and motor responses can be automatically and unconsciously triggered by visual stimuli. Effects of non-perceived stimuli such as these have provided key evidence that visual stimuli can automatically prime the observer to act.

INHIBITION OF PRIMED ACTIONS

In the above section, we have reviewed evidence from parallel domains that visual stimuli can automatically generate actions. These automatically generated actions can interfere with the intended or task-relevant response, and can be triggered by stimuli that are not consciously perceived, potentially facilitating responses to them. But an important question that arises is how such automatically primed responses might be controlled to allow flexible, goal-directed, behavior. For it would not be useful to respond to every object that we see. Thus, it is necessary to consider how brain systems inhibit or override responses that have been triggered automatically by the environment and are not relevant to our current goals.

"Cognitive control" over simultaneously activated competing motor plans has been extensively studied using "conflict" tasks such as such as the Eriksen flanker task described above (see Eriksen and Eriksen, 1974), the Stroop color-word naming task (e.g., Stroop, 1935) and the Simon task (for a review see Lu and Proctor, 1995). In these tasks, multiple responses can be simultaneously activated and in conflict: one response according to the task instruction and one evoked automatically by the irrelevant stimulus (or irrelevant property of the target stimulus). Typical theoretical frameworks for the congruency effects shown in conflict tasks suggest that stimuli are simultaneously processed by two routes which converge at the level of response programming (e.g., dual route model by Kornblum et al., 1990; activation suppression model by Ridderinkhof, 2002; see **Figure 2A**).

Processing by the fast, *direct processing route* is automatic, and occurs irrespective of task instructions. For example, the spatial location of a target stimulus in a Simon task would be processed quickly and automatically via the direct processing route. At the same time, processing of the task-relevant target attribute (e.g., target color in a Simon task) proceeds via a slower *indirect processing route*. On congruent trials, the same response is activated by both the direct and the indirect processing routes, producing fast, correct responses. On incongruent trials, however, the direct processing route and the indirect processing route activate different responses which results in increased error rates, and slower response times as the conflict between competing responses is resolved.

Importantly, models of information processing in conflict tasks often include an active inhibition mechanism which acts to selectively suppress inappropriate response activation resulting from the direct processing route. Evidence for such control over automatically activated responses can be gleaned by studying the temporal dynamics of interference effects—for example, by plotting the accuracy of responses as a function of response speed as a *Conditional Accuracy Function* (CAF, see van den Wildenberg et al., 2010 for a review; see **Figure 2B**).

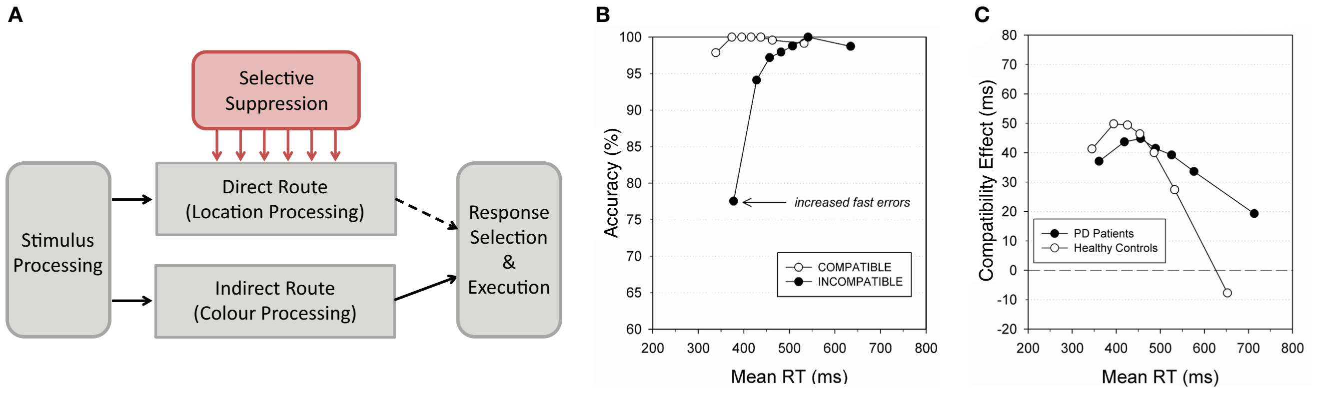

FIGURE 2 | (A) Information processing during a Simon task as modelled by the Activation-Suppression model [e.g., Ridderinkhof (2002)]. The relevant stimulus dimension (color in the Simon task) is processed via the slow, indirect, processing route. Simultaneously, irrelevant stimulus location is processed via the fast, direct, processing route. Activation of the location-based response activation is inhibited by selective suppression (shown here in red), which facilitates execution of the correct, color-based, action. The selective suppression takes time to develop, which results in a relatively high proportion of fast erroneous (location-based) responses on incongruent trials, with near-perfect response accuracy when responses are slower as the inappropriate responses have been suppressed. These effects seen by plotting response accuracy as a function of response time in a Conditional Accuracy Function (CAF) as shown in **(B)**. Furthermore, the interference on incongruent trials would be expected to reduce as unwanted responses are suppressed as RTs increase. This effect can be seen in the negative slope of a delta plot, as shown in **(C)**. Delta plots can reveal individual and group differences in motor activation and suppression that cannot be seen in average measures of RT. Panels **(B)** and **(C)** were originally published in van den Wildenberg et al. (2010). *Front. Hum. Neurosci.* 4:222. doi: 10.3389/fnhum.2010.00222. Panel **(B)** was modified after Wylie et al. (2009), with permission from Elsevier. Panel **(C)** was modified after Wylie et al. (2010).

In conflict tasks, accuracy for compatible trials is near-perfect, while fast responses on incompatible trials are often near (e.g., Wylie et al., 2009) or below (e.g., Stins et al., 2007) chance level. This pattern of erroneous responses is unlikely to be purely a result of fast-guessing, which would be expected to result in similar accuracy levels for both incompatible and compatible trials. Instead, these findings are consistent with the suggestion that erroneous responses are activated quickly via the direct processing route, before being selectively suppressed by an inhibitory control mechanism.

How response activation and suppression change as a function of response speed can also be seen in a *delta plot* (e.g., Burle et al., 2002; Ridderinkhof, 2002; Ridderinkhof et al., 2005; Wylie et al., 2010). This shows the size of the compatibility effect (RT on compatible trials subtracted from the RT on incompatible trials) as a function of RT (see **Figure 2C**). The plots make use of the whole RT distribution, rather than relying on a single measure of the central tendency, and therefore, they can reveal differences in the dynamics of response activation and suppression across individuals or groups even when mean RTs are not reliably different. Delta plots in traditional conflict tasks typically show initial positive effects that level off, or even become negative, as response times increase (e.g., de Jong et al., 1994; see also van den Wildenberg et al., 2010 for a review). This leveling-off is consistent with suppression of the unwanted stimulus-triggered response activation. As this suppression takes time to develop, a pattern of facilitation followed by inhibition is shown in the RT delta plot. Note however, that it is not necessary to postulate the existence of an active inhibitory mechanism which acts to selectively suppress inappropriately activated responses to explain the temporal dynamics of interference effects: the patterns shown in CAFs and delta plots may instead be produced by early activation of the inappropriate response which spontaneously decays over time (but see Burle et al., 2002 for evidence against this suggestion).

PRE-STIMULUS VS. POST-STIMULUS COGNITIVE CONTROL

Control mechanisms that can override inappropriate response plans which have been automatically evoked by the environment not only act to inhibit responses *after* they have been evoked by the stimulus. *Pre-stimulus* control mechanisms also seem to play a role. Thus, task set and previous experience can modulate conflicting response tendencies in a *preparatory* manner. Indeed, there is good evidence that pre-stimulus inhibitory mechanisms play a role in controlling responses in many contexts, including stop-signal (e.g., Verbruggen and Logan, 2009b), the anti-saccade (e.g., Everling and Munoz, 2000; Munoz and Everling, 2004), and reaction time tasks incorporating warning signals (e.g., Boulinguez et al., 2008).

The effects of pre-stimulus control have also been reported in traditional "conflict" tasks. Thus, the size of the congruency effect on the current trial in a conflict task can be modulated by (1) a pre-cue indicating whether the upcoming trial will be congruent or incongruent (e.g., Logan and Zbrodoff, 1982); (2) the ratio of congruent and incongruent trials in a block or experiment (e.g., Logan and Zbrodoff, 1979); and (3) whether the immediately preceding trial was congruent or incongruent (the so-called "Gratton effect" e.g., Gratton et al., 1988, 1992).

The Gratton effect has in particular been subject to much investigation. While some have suggested that it arises from repetition priming of exactly the same stimulus-response links from previous trials (e.g., Mayr et al., 2003), others have reported that it can occur without exact stimulus-response repetitions (e.g., Kerns et al., 2004; Akçay and Hazeltine, 2007). An influential *conflict monitoring hypothesis* proposed that following the response conflict experienced on an incongruent trial, cognitive control mechanisms which resolve this conflict are boosted for the next trial, in turn leading to reduced interference if the subsequent trial is also incongruent (e.g., Botvinick et al., 2001). This suggestions is supported by several observations that performance on incongruent trials is improved if they are preceded by another incongruent trial relative to a congruent trial (e.g., by Gratton et al., 1992 using Eriksen flankers; McBride et al., 2012 using object affordance; and by Stürmer et al., 2002 using the Simon task). However, this pattern has not consistently been reported and several researchers have documented selective benefits for compatible trials when the previous trial was also compatible (e.g., Kunde and Wühr, 2006; Akçay and Hazeltine, 2007; van Gaal et al., 2010a; Schlaghecken and Martini, 2011).

Schlaghecken and Martini (2011) recently accounted for these discrepant findings by suggesting that the effects of trial history on cognitive control were driven by a mechanism which responds to the previous experience of *both* the presence and the absence of conflict, arguing that the mechanism is one of *context* adaptation, rather than *conflict* adaptation. Whatever the mechanisms are that produce pre-stimulus control effects, it is clear that task set, instruction, and previous experience can modulate the apparently automatic priming of motor responses by visual objects.

UNCONSCIOUS CONTROL OVER UNWANTED RESPONSES

Traditionally, cognitive control mechanisms resulting in response inhibition have been considered as tightly coupled to consciousness (e.g., Schneider and Shiffrin, 1977; Shiffrin and Schneider, 1977, 1984), just as for voluntary control over actions. The logic behind this view is that observers need to be aware of the interfering, control-evoking, stimulus in order for control mechanisms to be implemented and for unwanted motor responses to be suppressed. Such a suggestion is supported by evidence from studies showing that inhibition of primed responses only operates when stimuli are presented above—and not below—the threshold required for conscious awareness (e.g., Merikle et al., 1995 using the Stroop task).

However, there is now increasing evidence that some forms of cognitive control can be executed entirely automatically, without conscious awareness—or volition. Some of the most compelling evidence for the automatic inhibition of unconsciously triggered motor priming comes from several experiments by Eimer and Schlaghecken (for reviews, see Eimer and Schlaghecken, 2003; Sumner, 2007). In their paradigm, participants typically made a speeded button-press response according to the direction of a target arrow, which was preceded by a masked (subliminal) prime. When the interval between mask and target was short (e.g., 20–40 ms), participants showed the expected speeding of responses when prime and target were compatible relative to when they were incompatible (positive compatibility effect, PCE). However, when the interval between prime and mask was extended beyond around 100–150 ms, incompatible trials produced faster responses than compatible trials. In other words, the usual priming effect had *reversed*.

This *negative compatibility effect* (NCE) has now been widely reported with button-press responses, foot responses, and eye movements (e.g., Eimer and Schlaghecken, 1998, 2002, 2003; Schlaghecken and Eimer, 2000, 2002; Eimer et al., 2002; Aron et al., 2003; Schlaghecken et al., 2003; Seiss and Praamstra, 2004; Sumner et al., 2007; Boy et al., 2008; Hermens et al., 2010), as well as in electroencephalogram recordings (e.g., Eimer and Schlaghecken, 1998, 2003; Praamstra and Seiss, 2005). They can also bias free-choice responses (e.g., Klapp and Hinkley, 2002; Schlaghecken and Eimer, 2004; Klapp and Haas, 2005), and have been shown both with familiar stimulus response mappings—such as arrows—and also when stimuli have been arbitrarily mapped to responses (e.g., Boy et al., 2008; Sumner, 2008).

Many researchers have suggested that this reversed priming results from an inhibitory mechanism in the motor system which acts to suppress sub-threshold motor activation evoked by the prime (e.g., Eimer and Schlaghecken, 1998; Klapp and Hinkley, 2002; Schlaghecken and Eimer, 2002; Schlaghecken et al., 2006). The most recent evidence suggests that such inhibition is triggered by the arrival of new stimuli—that the appearance of a second stimulus after the prime (normally the mask) automatically elicits an "emergency brake" that cancels any motor activation initiated by the prime (Jaśkowski and Przekoracka-Krawczyk, 2005; Lleras and Enns, 2006; Jaśkowski, 2007, 2008; Boy et al., 2008).

However, there has been considerable debate over whether the NCE genuinely reflects an inhibitory mechanism rather than arising from a purely perceptual process, or alternatively, from positive priming (PCE) of a motor response associated with elements of the mask stimulus. Perceptual accounts suggest that the NCE occurs because perceptual processing of the target stimulus is slower following a compatible prime, due to habituation-like processes such as "repetition blindness" or an attentional refractory period (Bavelier et al., 2000; Huber, 2008; Sohrabi and West, 2008; see also van Leeuwen and Lachmann, 2004, also discussed in Lleras and Enns, 2005 alongside the object updating theory; Hochhaus and Johnston, 1996; Huber et al., 2001, 2002; Johnston et al., 2002; Sohrabi and West, 2009). Such perceptual processes may play a role in producing some reversed priming effects, but they cannot account for more recent findings. For example, Boy and Sumner (2010) found that when participants learned novel sensorimotor associations in a masked priming task, and those response mappings were suddenly switched, both positive and negative priming effects temporarily reversed (see **Figure 3**)—indicating that the old response mappings continue to be primed until the participants learn the new mappings sufficiently well. Perceptual accounts of inverse priming cannot explain this finding.

Alternatively, perceptual interactions between the prime and the mask could end up causing motor priming in the opposite direction to that expected from the prime. This idea has been variously termed "object-updating," "active mask," or "mask-induced priming" (Lleras and Enns, 2004; Verleger et al., 2004; see Sumner, 2007 for review). Many early experiments used masks that were constructed by superimposing features in the alternative primes. In this case the most visually salient features of the mask could be those that were new onsets in the stimulus sequence—i.e., those that were not in the prime. Thus, the prime-mask sequence could actually prime the response opposite the one associated with the prime. Object updating may play a strong role in producing the NCE when masks are constructed from prime features, but they cannot account for the NCE in other cases where masks do not contain elements of possible primes (e.g., Sumner, 2008).

Overall, therefore, reversed priming effects can be caused in several ways. For the purposes of this review, the most interesting one is a form of automatic motor inhibition, which can be revealed with appropriate stimuli. Finding the NCE with subliminally presented primes provides evidence that the mechanisms at its origin are deployed automatically. If the observer is not aware of the prime, then presumably they cannot volitionally suppress any motor response associated with it. However, note that the prime does not necessarily need to be subliminal for the NCE to occur (e.g., Klapp and Hinkley, 2002; Klapp, 2005; Lleras and Enns, 2005; Mattler, 2005; Sumner et al., 2006; Schlaghecken et al., 2008).

AUTOMATIC INHIBITION IN THE AFFORDANCE PARADIGM

If the NCE shown in masked priming genuinely reflects an automatic control mechanism to suppress sub-threshold activation of an unwanted motor response (see above), one might expect to see evidence of an NCE in other paradigms where visual stimuli automatically evoke motor responses. Vainio and colleagues have recently reported that the positive stimulus-response compatibility effects usually shown in object affordance tasks can become *negative* if the object stimulus is presented briefly and then removed (e.g., Vainio, 2009; Vainio et al., 2011; see also Vainio and Mustonen, 2011).

This NCE-like effect was reported even when the prime stimulus (e.g., a cup) was not relevant to the on-going task (respond to direction of a subsequently presented target arrow), quite unlike the masked prime paradigm where primes typically need to contain elements relevant to the task for NCEs to be observed (e.g., Eimer and Schlaghecken, 1998). To account for this discrepancy, Vainio and colleagues suggested that even though the cup primes in their experiments were irrelevant to the participants' task, a small degree of motor activation occurred due to the relatively long stimulus duration (compared to the primes in previous NCE studies), and the fact that the response association is highly over-learnt (compared to the semi-arbitrary correspondence between simple arrows or lines and a response). However, the associated motor activation was still sub-threshold, and thus able to be reversed by inhibition when perceptual support for that response was interrupted (producing the observed NCE). Overall, these studies suggest that actions which have been automatically primed by object affordances may also be subject to automatic control.

AUTOMATIC TRIGGERING OF "ENDOGENOUS" CONTROL

In the masked prime paradigm, the participants are not actually instructed to employ response inhibition—it just appears to occur

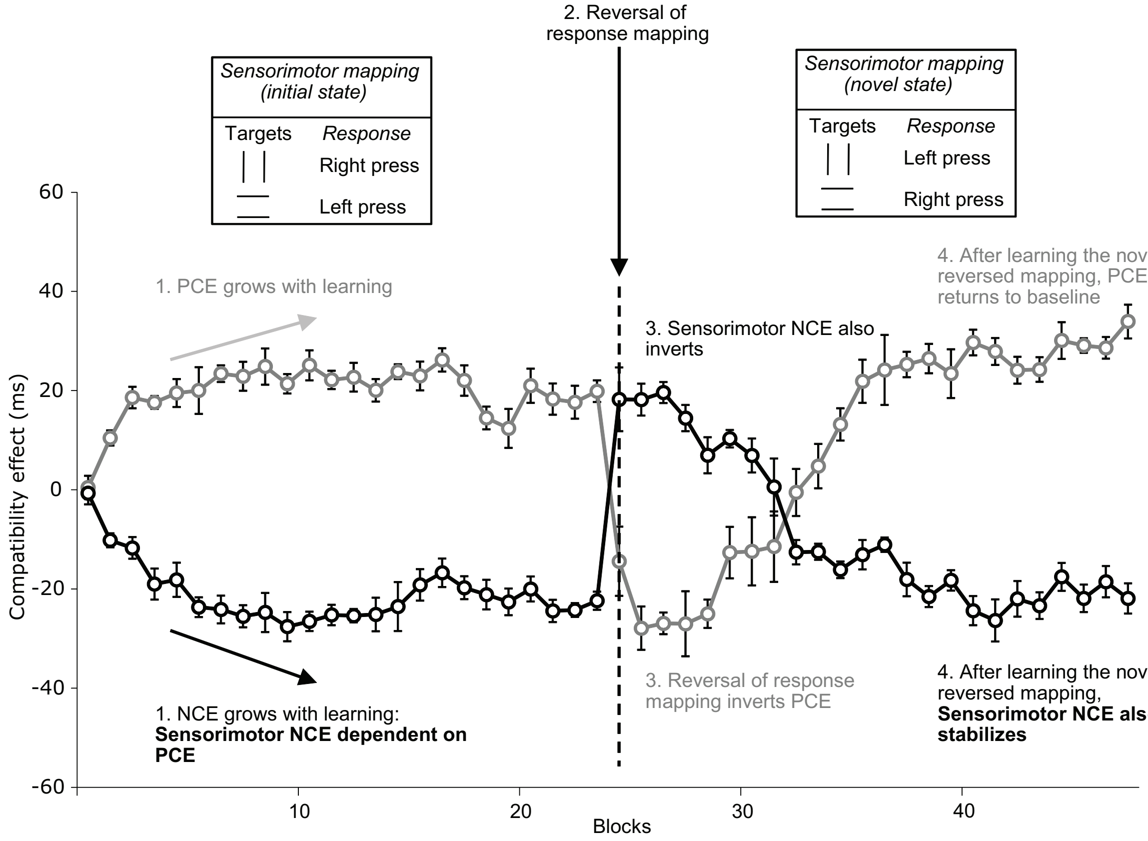

FIGURE 3 | Evolution of Positive and Negative Compatibility Effects following the sudden reversal of the response mapping in the paradigm used by Boy and Sumner (2010, Experiment 4). Participants were trained to respond to targets in a masked prime paradigm alternating short and long mask-target intervals by blocks of five trials. Figure adapted with permission from Boy and Sumner (2010). *J. Exp. Psychol. Hum. Percept. Perform.* 36, 892–905, originally published by the American Psychological Association.

automatically following the prime and mask. In other paradigms, participants are specifically asked to *endogenously* inhibit their planned motor responses when cued to do so, for example in the go/no-go task and stop signal task (e.g., Logan, 1994). In both tasks, participants are instructed to respond as quickly as possible to go-signals, but to withhold their response when other (“stop”) stimuli occur.

Traditionally, such endogenous response inhibition has been thought to depend on the *conscious* detection of stop signals (e.g., Eimer and Schlaghecken, 2003). However, recent work suggests that endogenous suppression of pre-potent responses can also be primed or evoked unconsciously and automatically (e.g., Verbruggen and Logan, 2009a; van Gaal et al., 2008, 2009, 2010a,b). For example, van Gaal et al. (2009, 2010b) examined whether inhibition of a response could be triggered unconsciously by a *masked* stop-signal. They reported that although participants did not completely withhold their responses on unconscious (strongly masked) stop trials, they were significantly slowed relative to go trials, indicating there was some (incomplete) suppression of responses triggered by the imperceptible stop signal. Thus, the control processes involved in suppressing responses can be—at least partially—evoked by signals that are not consciously perceived.

AUTOMATIC PRE-STIMULUS CONTROL

In the case of both the NCE and the “endogenous inhibition” paradigms discussed above, inhibitory control processes appear to be evoked to deal with motor activation after it has been elicited. Is it also possible that pre-stimulus preparatory types of control can be elicited automatically? Many researchers have suggested that observers must consciously experience conflict in order for the pre-stimulus control mechanisms to be deployed (e.g., Kunde, 2003; Mayr, 2004; Ansorge et al., 2011). However, recent evidence from van Gaal et al. (2010a) suggests that some pre-stimulus control can be evoked automatically, without conscious awareness (see **Figure 4**). They used a meta-contrast masking paradigm to manipulate awareness of conflict-inducing stimuli. Conflict between co-activated responses was either conscious (weakly masked primes) or unconscious (strongly masked primes). The largest conflict adaptation effects occurred when both the current and the previous trial were weakly masked (visible). Importantly, a small but statistically significant conflict adaptation effect was evident when primes on trial *n* and trial *n–1* were both presented below the threshold required for conscious awareness (strongly masked condition). This is consistent with the suggestion that unconsciously presented stimuli can automatically evoke these pre-stimulus conflict adaptation mechanisms,

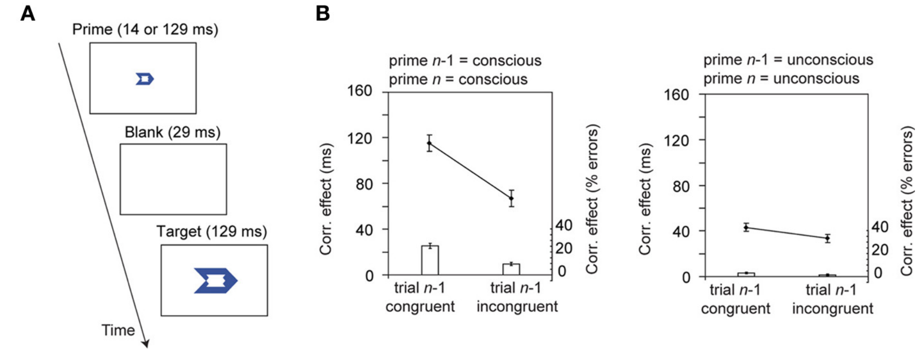

FIGURE 4 | Automatic (unconscious) conflict adaptation effects as shown in van Gaal et al. (2010a). Observers responded to the direction of a target arrow stimulus that had been preceded by a backwards (meta-contrast) masked prime that either corresponded with the response required to the target (as shown in **A**), or was non-corresponding. The prime stimulus was either conscious (presented for 129 ms) or unconscious (presented for 14 ms). Correspondence effects (non-corresponding—corresponding) on trial *n* were modulated by whether trial *n*–1 was corresponding or not. These effects were largest when both trial *n* and trial *n*–1 had visible primes **(B)**, but were still significant when both trial *n* and trial *n*–1 contained invisible primes. These figures were originally published in van Gaal et al. (2010a). *PLoS One* 5:e11508. doi: 10.1371/journal.pone.0011508.

and can modulate the effects of subsequent conflicting stimuli. However, this result should be interpreted cautiously because responses are typically faster following fast responses (congruent trials), and slower following slow responses (incongruent trials; see e.g., Laming, 1979). If this effect were more apparent on fast (congruent) trials than on slow (incongruent) trials then it might entirely account for the small Gratton effect observed with non-conscious stimuli.

OVERLAP BETWEEN BRAIN AREAS RESPONSIBLE FOR AUTOMATIC AND VOLUNTARY CONTROL

The traditional distinction drawn between automatic and voluntary cognitive control is not only being challenged by behavioral studies. Lesion and imaging studies have also revealed substantial overlap between brain regions traditionally associated with "voluntary" control and those active during automatic control. Brain areas in medial frontal cortex such as the SMA and anterior cingulate cortex (ACC) have traditionally been considered to be important for *voluntary* control (for a review, see Nachev et al., 2008). However, they also seem to be involved in mediating *automatic* motor activation and suppression of unwanted action plans (e.g., D'Ostilio and Garraux, 2011, 2012). For example, Sumner et al. (2007) used a masked prime paradigm to reveal that two extremely rare patients with microlesions of the SMA and/or the adjacent supplementary eye field (SEF) showed normal PCEs but failed to show NCEs, unlike healthy matched controls. These data are consistent with the view that the SMA and SEF may play causal roles in producing the *automatic* motor inhibition indexed behaviorally by the NCE. Thus, areas involved in the voluntary control of action might play a crucial role in automatic inhibition of unwanted actions (in this case, evoked by the subliminal prime).

There is also evidence from healthy observers that the SMA and nearby pre-SMA are involved in producing the unconscious NCE in healthy observers. Recent research from van Gaal et al. (2011b), found that individual differences in pre-SMA gray matter density were correlated with participants' ability to correctly respond to a target that had been preceded by a strongly masked (invisible) incompatible prime. Furthermore, Boy et al. (2010a) found that the fMRI signal was modulated by (invisible) prime compatibility in the SMA. Moreover, by studying normal participants' *in vivo* neurochemistry through magnetic resonance spectroscopy (MRS), Boy et al. (2010a) found that for a region including the SMA, the measured concentration of gamma-aminobutyric acid (GABA)—the main neurotransmitter responsible for neuronal inhibition—was correlated with the magnitude of the NCE.

There is also overlap between "voluntary" and "automatic" neural mechanisms involved in more conventional inhibition tasks such as go/no-go, and stop signal paradigms. van Gaal et al. (2010b) found that the amplitude of a fronto-central N2 event-related potential (ERP) component was reliably correlated with successful stopping on weakly masked (conscious) stop trials, and with the amount of slowing on strongly masked (unconscious) stop trials (as measured by the stop signal reaction time; SSRT). Thus, the size of this N2 component correlated with behavioral measures of both conscious and unconscious suppression of response. In addition, functional imaging has shown that strongly masked no-go signals activate much of the same brain areas that are activated by weakly masked no-go signals, particularly the pre-SMA and inferior frontal cortex (van Gaal et al., 2010b). The strength of activation in these areas was positively correlated with the amount of slow-down on strongly masked no-go trials—which supports the suggestion that this activity may be functional and have a direct effect on stopping behavior.

Taken together, these findings challenge the traditional assumption that voluntary control and involuntary mechanisms occur through distinct pathways in the brain. Rather, there is considerable overlap between the brain regions which are active during consciously and unconsciously triggered action control.

DISSOCIATIONS IN AUTOMATIC AND VOLUNTARY CONTROL

Recent work from Boy et al. (2010b) suggests that the important distinction is not between control that is automatic compared

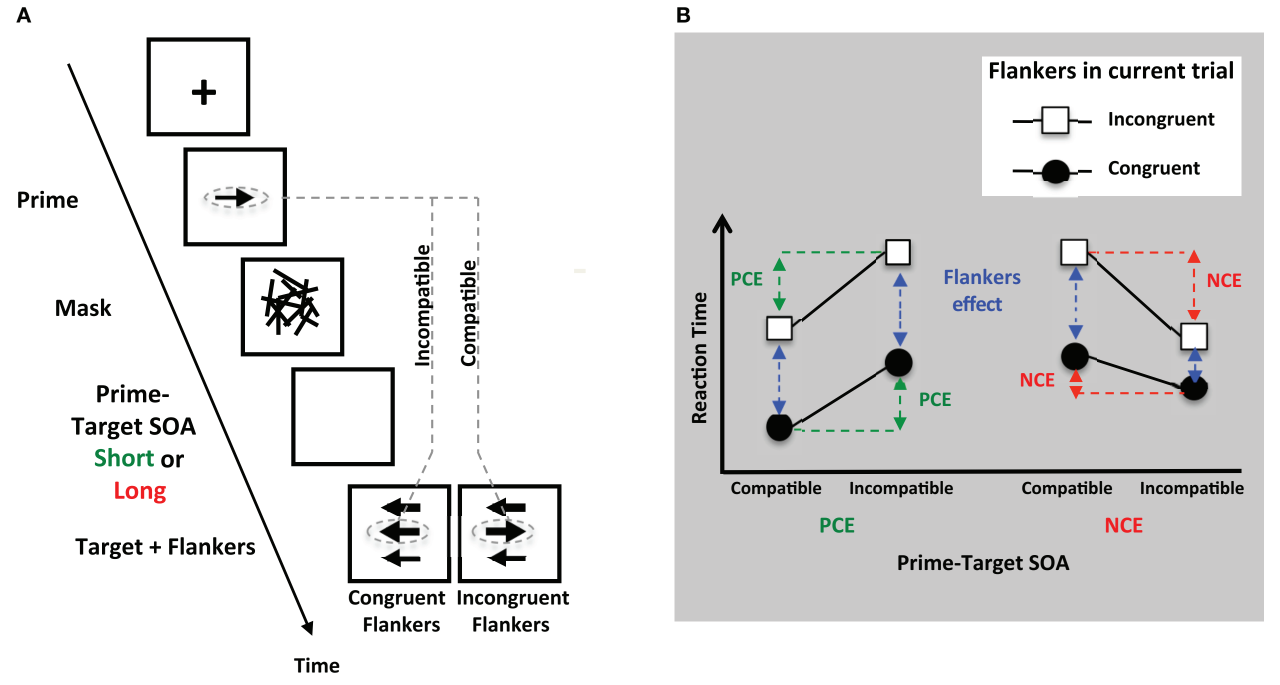

FIGURE 5 | (A) Schematic illustration of the task in Boy et al. (2010b), which combines subliminal priming and flanker interference. If the stimulus onset asynchrony (SOA) between prime and target (response) cue is short (70 ms), a PCE in response times is found (green arrows in **B**). If the SOA is longer (180 ms), an NCE is found (red arrows in **B**). Compatibility refers to whether the direction of prime arrow and target (response) arrow is the same (compatible) or different (incompatible). Targets are flanked by arrows. If the flankers are congruent with the target, then response times are shorter than if flankers are incongruent (the flanker interference effect; blue arrows in **B**). 4-B. Results: for positive priming (PCE), the priming effect was additive with the effect of flanker interference. For the NCE, which measures subliminal inhibition, there was an interaction with flanker interference. This interaction did not occur for pre-stimulus control [data not shown here, see Boy et al. (2010b)].

to control that is voluntary, but rather between *pre-* and *post-stimulus* control (see discussion above on pre- vs. post-stimulus control). These investigators used a hybrid task which integrated masked priming into an Eriksen flanker paradigm (see **Figure 5A**). They showed an interaction between the *post-stimulus* inhibitory influences caused by prime-mask sequence (the NCE) and the post-stimulus control of flanker interference. Thus, these processes presumably share some common mechanisms (see **Figure 5B**). However, when examining the influence of the previous trials' flankers on performance in the current trial (the Gratton effect, see section on pre-stimulus control), no such interaction was found with the NCE. This suggests that pre-stimulus control mechanisms did not share processes with the NCE, and thus are distinct from post-stimulus mechanisms.

FLEXIBLE AUTOMATICTY

Automatic and unconscious processes are traditionally regarded as inflexible (e.g., Schneider and Shiffrin, 1977; Shiffrin and Schneider, 1977, 1984), quite distinct in quality from the flexible nature of "voluntary" processes. However, there is increasing evidence that automatic and subliminal processes can in fact be modulated by "top-down" processes of attention, intention ("task set" or current goals) and expectation. For example, Kentridge and colleagues (e.g., Kentridge et al., 1999, 2004, 2008) have reported a series of studies in which attention modulates apparently subconscious processing, both in a "blindsight" patient, GY, and in normal participants. Focussing attention in time (e.g., Naccache et al., 2002) and in space (Lachter et al., 2004; Sumner et al., 2006; Marzouki et al., 2007) can also modulate the effects of masked primes on motor responses. For example, positive and negative compatibility effects in a masked prime task can be enhanced by exogenously pre-cueing prime location (Sumner et al., 2006), and in such a way that was not simply explained by an attentional boost to the perceptual strength of the prime. This suggests that attention does not only enhance perceptual processing, but can also modulate sensori-motor linkages.

Task set-up and instruction can also modulate many of the effects of visual stimuli on motor responses and control. As noted above, prime stimuli in masked priming tasks generally only affect responses when they share task-relevant elements with the target stimuli (e.g., Eimer and Schlaghecken, 1998; see also Huang et al., 2011). For example, Eimer and Schlaghecken (1998) found no NCE when participants responded to letter targets that had been preceded by masked arrow primes, even though arrow primes reliably prime responses when targets are also arrows. Moreover, recent evidence shows that object affordance effects are also dependent on the goals of the observer. Bub and Masson (2010) demonstrated that the handle of a mug only produced reliable affordance effects on reach and grasp responses, not when the response was made via a speeded button press.

Unconscious "endogenous" control over responses also depends on task instruction. Wokke et al. (2011) tested participants with a go/no-go task in which a masked (unconscious) prime stimulus preceded an unmasked (conscious) target. One of two possible targets was presented on each trial, but unlike other studies, stimuli were not consistently paired with either a "go" or a "no-go" response across a testing session. Instead, which of the possible targets required a "go" or a "no-go" response was cued on a trial-by-trial basis. Response inhibition rates were improved when a "no-go" target was preceded by an invisible "no-go" cue. As the instruction cue manipulation eliminated any long-term associations being built up between stimulus and response, it seems that control processes evoked by unconsciously presented stimuli can be triggered in a flexible manner according to task instruction.

Finally, pre-stimulus, conflict adaptation effects such as the Gratton effect can also be modulated, seemingly by reward (van Steenbergen et al., 2009). For example, van Steenbergen and colleagues (2009) showed that the conflict adaptation effect in a flanker task can be reduced by reward, even though rewards were given arbitrarily and were unrelated to the task. In fact Botvinick (2007) has recently suggested that conflict might be experienced as a negatively reinforcing event. As such, it is possible for the effects of conflict (a negative stimulus) to be counteracted by a positive stimulus (reward)—an example of possible flexible control over an automatic response.

Taken together, these findings indicate that seemingly "automatic" response activation and control can be implemented flexibly—quite unlike the traditionally inflexible view of automatic processes.

CONCLUSION

The evidence described in this review demonstrates that stimuli can automatically prime specific, purposeful actions. Simple stimuli can capture eye movements, produce activity in motor-related brain areas, and can trigger the actions afforded by an object. Because observers are constantly bombarded by a complex set of visual stimulations, such automatic activation of potential responses is likely to be important, either in facilitating responses or requiring inhibition so other responses can be made. While their effects might not be obvious in healthy adults, the effects of such automatic activation of motor programs can be dramatically revealed following brain damage (e.g., in alien limb syndrome or utilization behavior).

A necessary pre-requisite for flexible, goal-directed action is the ability to inhibit inappropriate, competing, responses even when those competing responses have been activated automatically. Cognitive control has traditionally been seen as tightly coupled to awareness, it has been suggested that an observer must be aware of a stimulus in order to inhibit motor activation evoked by that stimulus. Many of the findings reviewed here challenge this assumption and instead suggest there is substantial overlap between the mechanisms supporting conscious and unconscious control of responses. Thus, we suggest that while there may be differences between automatic and voluntary control, they may not be entirely distinct in the brain, that automatic processes may play a role in all behavior, and that we must revise traditional views that couple cognitive control to consciousness and automaticity to inflexibility.

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