

Unconscious inhibition separates two forms of cognitive control

Frederic Boy^a, Masud Husain^b, and Petroc Sumner^{a,1}

^aSchool of Psychology, Cardiff University, Cardiff CF10 3AT, United Kingdom; and ^bUCL Institute of Cognitive Neuroscience and UCL Institute of Neurology, University College, London WC1N 3AR, United Kingdom

Edited by Dale Purves, Duke University Medical Center, Durham, NC, and approved May 7, 2010 (received for review February 18, 2010)

In the human brain, cognitive-control processes are generally considered distinct from the unconscious mechanisms elicited by subliminal priming. Here, we show that cognitive control engaged in situations of response conflict interacts with the negative (inhibitory) phase of subliminal priming. Thus, cognitive control may surprisingly share common processes with nonconscious brain mechanisms. In contrast, our findings reveal that subliminal inhibition does not, however, interact with control adaptation—the supposed modulation of current control settings by previous experience of conflict. Therefore, although influential models have grouped immediate cognitive control and control adaptation together as products of the same conflict detection and control network, their relationship to subliminal inhibition separates them. Overall, these results suggest that the important distinction lies not between cognitive or top-down processes on the one hand and nonconscious priming mechanisms on the other hand but between responsive (poststimulus) mechanisms that deal with sensorimotor activation after it has occurred and preparatory (prestimulus) mechanisms that are modulated before stimulus arrival.

automatic | executive | negative compatibility | voluntary | flanker task

A hallmark of cognitive control is the ability, under conditions of conflict and uncertainty, to select a required response among competing alternatives. Such control has been extensively investigated with tasks that contain situations of potential response conflict, such as the influential Eriksen flanker task (1). In this task, a target stimulus is flanked by stimuli that are either associated with the same response (congruent) or with another response (incongruent). Responses are normally slower with incongruent flankers because of coactivation of conflicting responses to flankers and target. Such conflict is assumed to be minimized by a control process that is sensitive to task demands and attempts to ensure that the correct response is made (1, 2). Moreover, this control process is thought to be adaptive so that, after a conflict situation, the system is better prepared for the next instance of conflict (3–8).

A paradigmatic example of unconscious mechanisms, however, is subliminal priming (9). In this case, stimuli are masked so that they are not consciously perceived, but such masked primes nevertheless affect subsequent responses. Investigations have also revealed an important oscillation in the priming effect (10). Initially, the prime unconsciously activates the response associated with it so that responses are sped up for subsequent targets that require the same (compatible) response and slowed down if prime and target are associated with different (incompatible) responses. This is referred to as a positive compatibility effect (PCE). However, if the delay between prime and target is extended, the priming effect reverses, producing a negative compatibility effect (NCE): primes now facilitate incompatible responses and slow down compatible responses (11, 12).

There is now a wealth of evidence that this reversal is caused by a nonconscious inhibitory mechanism that suppresses the initial, subthreshold motor activation evoked by the prime (11, 13–19). The rationale for such inhibition in everyday life is that priming of the motor system that does not lead to an immediate action needs to be suppressed so that other actions can be made.

In the laboratory setting, a delay between priming and response cues of ~200 ms is long enough to observe such inhibition being deployed. Oscillations of motor priming such as this must arise entirely automatically when the participants cannot consciously report the primes.

Here, we ask whether goal-directed cognitive control is entirely distinct from such oscillation of motor priming, although the latter is automatic, unconscious, and blind to the goal-directed response. To probe their relationship, we combine a masked-priming paradigm with the flanker interference task. If they are distinct, the flanker effect and the priming compatibility effect are predicted to be additive. In other words, both would be present in the data, and their effects would simply add up in their influence on the final response time (Fig. 1 prediction box). However, if the inhibitory mechanisms involved in masked priming and flanker paradigms are overlapping, the effects would be expected to interact, such that when the unconscious mechanism swings into the inhibitory phase, it becomes especially difficult to inhibit flankers that do not coincide with the direction of unconscious inhibition.

Results and Discussion

Flanker Interference Interacts with Automatic Inhibition. We combined the flanker paradigm with two versions of the masked-prime paradigm (Fig. 1 and Fig. S1). One of these used a short stimulus onset asynchrony (SOA) of 70 ms between prime and target (the response cue), which previous studies have shown to produce a positive priming effect (PCE). The other paradigm used a longer SOA of 180 ms, by which time priming has reversed to produce the NCE (11, 19). In both tasks, we could examine the effects of flankers being congruent or incongruent with the direction of the target. Thus, we used a 2 × 2 study design that allowed us to examine the effects of compatible/incompatible primes and the effects of congruent/incongruent flankers. Importantly, in all experiments, we ascertained that the prime stimuli were not consciously perceived (all forced choice identification rates were between 46.5% and 51.9%; comparison with 50%: all had $t < 1.3$ and $P > 0.2$).

In the PCE block, the incongruent flankers and incompatible subliminal primes both prolonged responses, as expected, and their effects were simply additive (Fig. 2A): the flanker effect is simply the vertical displacement between the two lines [$F(1, 9) = 9.3$; $P = 0.014$; $\eta^2_p = 0.5$], whereas the priming effect is the slope of the lines [$F(1, 9) = 23.7$; $P = 0.001$; $\eta^2_p = 0.72$]. Additivity is indicated by the lines being parallel [interaction is not significant; $F(1, 9) < 1$].

Author contributions: F.B., M.H., and P.S. designed research; F.B. performed research; F.B. and P.S. analyzed data; and F.B., M.H., and P.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

¹To whom correspondence should be addressed. E-mail: sumnerp@cardiff.ac.uk.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1001925107/-DCSupplemental.

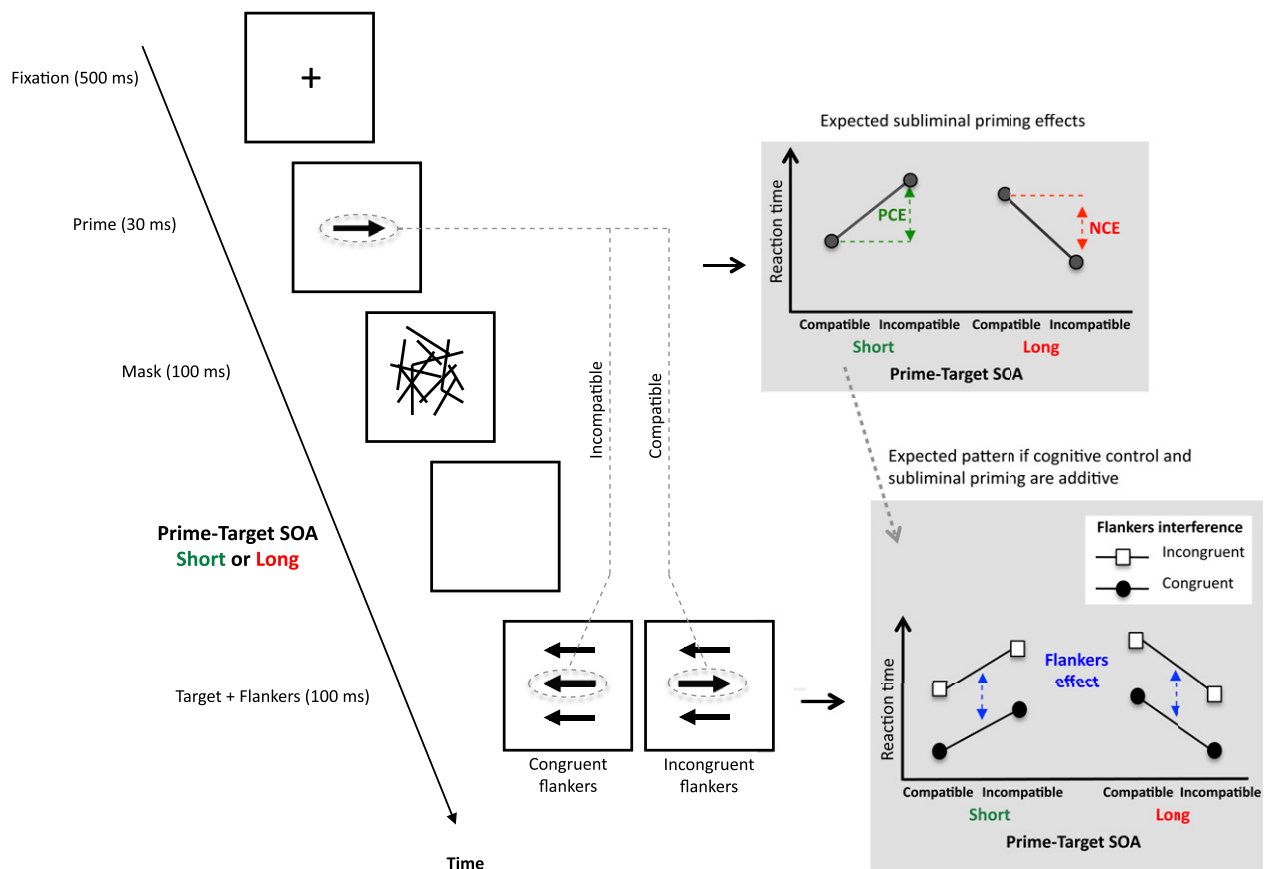


Fig. 1. Schematic illustration of the task, which combines subliminal priming and flanker interference. If the stimulus onset asynchrony (SOA) between prime and target (response) cue is short (70 ms), a PCE in response times is found (green). If the SOA is longer (180 ms), an NCE is found (red). Compatibility 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 plot). The question is whether these effects interact. The stimuli represent the ones used in most experiments, but they are schematic. The sequence illustrated is that for the long SOA condition. In the short SOA condition, there was no blank screen between mask and target, and the mask (always 100 ms in duration) was still on the screen when the target-flanker set appeared (Fig. S1). For this reason, in both conditions, the target-flanker set was actually presented at a random position in a virtual annulus around the mask locus (Fig. S1).

However, in the NCE block where the priming effect is negative, we found a clear interaction with flanker interference (Fig. 2B): $F(1, 9) = 27.8$; $P = 0.001$; $\eta_p^2 = 0.75$; main effect of flankers conflict: $F(1, 9) = 9.52$; $P = 0.013$; main effect of priming: $F(1, 9) = 51.1$; $P < 0.001$. In other words, the key finding was that the effect of the flankers depends on the effect of the subliminal primes. Incongruent flankers had little or no additional costs compared with congruent ones when primes were incompatible with target cues. However, when primes were compatible with targets, the presence of incongruent flankers increased response times. Because this interaction might be considered surprising, we replicated it two times with different sets of stimuli, and we confirmed that, relative to neutral flankers, it is the incongruent, not congruent, flankers that are the source of the interaction (Figs. S2 and S3).

In turn, these findings suggest that the inhibitory process involved in controlling flanker interference is not independent from automatic inhibition in subliminal priming. When the unconscious mechanism swings into the inhibitory phase, it becomes relatively easy to inhibit flankers that coincide with the direction of unconscious inhibition. For example, if a left prime is followed by a right target flanked by leftward arrows, there is no significant cost of these incongruent flankers. Because the flankers are in the direction of the prime, it seems that the system already has a head start in inhibiting them. However, if the flankers do not coincide

with the direction of unconscious inhibition (for example, when a right prime is followed by a right target with leftward flankers, as in Fig. 1), then it is much more difficult to inhibit these flankers [evidence that there is a hindering effect as well as a helping effect comes from a supplementary study involving neutral primes; the flankers effect for compatible primes was increased with respect to the neutral ones, $t(11) = 2.8$ and $P < 0.017$ (one-tailed), and also, the flankers effect for incompatible primes was decreased with respect to that of neutral primes, $t(11) = 2.5$ and $P < 0.028$ (one-tailed)]. Importantly, the effect that the prime has on the difficulty of dealing with the flankers is over and above the additive effect that would be expected if their mechanisms were separate (compare Fig. 2A, showing an additive effect, to Fig. 2B, showing the interaction). Instead, the attempt to inhibit flanker interference seems to critically depend on the direction of subliminal inhibition that has been evoked. Thus, we conclude that conflict control and subliminal inhibition share essential neural machinery.

The interaction we measure must stem from the process of controlling flanker interference after it arises (i.e., poststimulus) rather than changing the amount of motor activation caused by the flankers in the first place (e.g., through perceptual priming of the flanker stimuli or facilitating motor activation by the flankers). This is because, for flanker activation, it should not matter whether the flankers are congruent or incongruent with the target—all flankers are expected to activate their associated action plans, and

such as flankers. Such slowing did not occur in our data (if anything, the reverse occurred) (Fig. 3).

Alternatively, prestimulus control could be caused by narrowing of spatial attention around the expected target location. However, in our case, the targets occurred anywhere in an annulus around the prime and mask location so that their location could not be predicted. Still, it may be that prestimulus control acts in a way akin to spatial attention in that it modulates the degree to which flankers cause motor activation in the first place rather than attempting to control that activation after it has happened (Fig. 4). Thus, the distinction between poststimulus control, which interacts with subliminal inhibition, and prestimulus control, which does not, may be most parsimoniously attributed to mechanisms that inhibit motor activation in the former case and mechanisms that modulate perceptual processing in the latter case (37). Note that this is an important departure from models in which a single control mechanism is put in place to deal with interfering stimuli (whether on the motor or perceptual side), and prestimulus control operates through that same mechanism (3, 5).

We can then ask how the prestimulus control process is modulated by previous conflict and whether conscious awareness is necessary. Mayr and Awh (8) discuss four alternative ways in which modulation could occur: explicit feedback from conflict detection (3, 5), passive carryover of control settings (38), learned associations between stimulus arrangement and control state (39), or a deliberate prestimulus regulatory process. In their basic form, the first three of these all envisage that the previous trial effect comes from changing the state or settings (by different means) of the same control process that deals with incongruent flankers when they occur. Thus, they predict that subliminal inhibition should have interacted with both (or neither) the flanker effect and the previous trial effect.

However, on one hand, these ideas could be adapted to a model in which prestimulus control and poststimulus control are separate, but the former is still modulated within a trial and affects the next trial. On the other hand, previous data seem most consistent with deliberate prestimulus control. Mayr and Awh (8) found that the previous trial effect was most prominent only in the first 200 or so trials of testing, after which, it declines. Although this decline may not be present in all data [it is not present in ours—previous trial effects for first and last 200 trials were 20 ms and 17 ms; $t(19) = 1.45$; $P =$ not significant], its occurrence in any data is difficult to explain in terms of the first three explanations listed above, which would expect it to stay the same throughout (feedback loop or passive carryover) or grow (instance-based learning). More persuasively perhaps, Kunde (25) reported that control adaptation occurs only with conscious awareness of conflict and not for conflict induced by subliminal primes (40, 41).

In sum, our data indicate that prestimulus control is distinct from poststimulus (stimulus-evoked) control, with only the latter being related to subliminal inhibition. Previously, there has been

an intuitive tendency to group subliminal and reflexive mechanisms together on the one hand and cognitive, goal-directed processes together on the other hand. However, our results suggest that this is the wrong conceptual distinction. We suggest a more neuronally meaningful segregation should be drawn on other lines between prestimulus control and poststimulus inhibitory mechanisms (Fig. 4B). Note that prestimulus control must be general, because the direction of the target and flankers is not known before they appear, but both poststimulus control and automatic inhibition share the essential feature that they are evoked to inhibit a specific (directional) response. Thus, it is not too speculative to suppose that neural machinery can be shared between subliminal inhibition and voluntary, top-down control (42).

Methods

Participants. A total of 34 individuals from Cardiff University (21 females; age: 18–35 y) participated in the experiments reported here for payment or course credit. All were right-handed, had normal or corrected-to-normal vision, and were naïve to the purpose of the experiments.

Apparatus (All Experiments). Stimulus presentation was performed by a personal computer-controlled Cambridge Research Systems (CRS) Visage connected to a 21-in Sony GDM-F520 Trinitron monitor placed at a viewing distance of 70 cm. Stimulus presentation was synchronized with the screen refresh rate of 100 Hz, and timings were controlled and measured by the CRS clock and thus, were not subject to the errors produced by normal PC operating systems. Manual responses were collected using a CRS-CB6 button box.

Stimuli and Procedure. In the main experiments reported above, participants had to make speeded responses with a left- or right-hand key press to the orientation of arrows targets ($1.8^\circ \times 0.5^\circ$), which occurred in random order and were located at 3.5° from fixation in a random direction from fixation. These targets were flanked by two other arrows, appearing at 1° at the top and the bottom (Fig. 1 and Fig. S1). The direction of the two could be congruent or incongruent with the target. At the beginning of the trial, a fixation cross was visible at the center of the screen. After a brief blank (100 ms), primes were briefly presented (30 ms) that were identical to either one of the possible targets and appeared within 0.5° of fixation (i.e., in the same vicinity as the target but not in an identical location on any trial). The prime was followed by a mask of $3^\circ \times 3^\circ$ and constructed of 45 randomly orientated lines, excluding any orientation closer than $\pm 5^\circ$ to the vertical or the horizontal ($0^\circ / 90^\circ$). A new mask was constructed on each trial but appeared always in the same place, centered on fixation. We used two timing conditions: one with mask-target SOA of 40 ms and the other with a long SOA of 150 ms. These are known to produce PCE and NCE, respectively. In the first main experiment, 400 trials were presented in each condition with brief breaks every 50 trials. In the second main experiment, there was double that number. Participants carried out the two conditions in counterbalanced order with a pause of about 20 s between each condition. Figs. S1–S5 show details of the supplementary experiments.

ACKNOWLEDGMENTS. We thank Jamie Ballard for assistance with some data collection and Chris Chambers, Frederick Verbruggen, Aline Bompas, and Jen McBride for comments. The Wellcome Trust and the Wales Institute of Cognitive Neuroscience (WICN) supported this work.

- Eriksen BA, Eriksen CW (1974) Effects of noise letters upon the identification of a target letter in a nonsearch task. *Percept Psychophys* 16:143–149.
- Shiffrin RM, Schneider W (1977) Controlled and automatic human information-processing. 11. Perceptual learning, automatic attending, and a general theory. *Psychol Rev* 84:127–190.
- Botvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD (2001) Conflict monitoring and cognitive control. *Psychol Rev* 108:624–652.
- Ullsperger M, Bylsma LM, Botvinick MM (2005) The conflict adaptation effect: It's not just priming. *Cogn Affect Behav Neurosci* 5:467–472.
- Kerns JG, et al. (2004) Anterior cingulate conflict monitoring and adjustments in control. *Science* 303:1023–1026.
- Verbruggen F, Notebaert W, Liefvoeghe B, Vandierendonck A (2006) Stimulus- and response-conflict-induced cognitive control in the flanker task. *Psychon Bull Rev* 13:328–333.
- Mayr U, Awh E, Laurey P (2003) Conflict adaptation effects in the absence of executive control. *Nat Neurosci* 6:450–452.
- Mayr U, Awh E (2009) The elusive link between conflict and conflict adaptation. *Psychol Res* 73:794–802.
- Neumann O, Klotz W (1994) Motor-responses to nonreportable, masked stimuli—where is the limit of direct parameter specification. *Attention and Performance XV: Conscious and Nonconscious Information Processing*, eds Umiltà C, Moscovitch M (MIT Press, Cambridge, MA), pp 123–150.
- Eimer M, Schlaghecken F (1998) Effects of masked stimuli on motor activation: Behavioral and electrophysiological evidence. *J Exp Psychol Hum Percept Perform* 24:1737–1747.
- Eimer M, Schlaghecken F (2003) Response facilitation and inhibition in subliminal priming. *Biol Psychol* 64:7–26.
- Sumner P (2007) Negative and positive masked-priming—implications for motor inhibition. *Advances in Cognitive Psychology* 3:317–326.
- Schlaghecken F, Eimer M (2006) Active masks and active inhibition: A comment on Lleras and Enns (2004) and on Verleger, Jaskowski, Aydemir, van der Lubbe, and Groen (2004). *J Exp Psychol Gen* 135:484–494.

14. Sumner P, et al. (2007) Human medial frontal cortex mediates unconscious inhibition of voluntary action. *Neuron* 54:697–711.
15. Sumner P (2008) Mask-induced priming and the negative compatibility effect. *Exp Psychol* 55:133–141.
16. Sumner P, Brandwood T (2008) Oscillations in motor priming: Positive rebound follows the inhibitory phase in the masked prime paradigm. *J Mot Behav* 40:484–489.
17. Jaśkowski P (2009) Negative compatibility effect: The object-updating hypothesis revisited. *Exp Brain Res* 193:157–160.
18. Jaśkowski P (2008) The negative compatibility effect with nonmasking flankers: A case for mask-triggered inhibition hypothesis. *Conscious Cogn* 17:765–777.
19. Boy F, Sumner P (2010) Tight coupling between positive and reversed priming in the masked prime paradigm. *J Exp Psychol Hum Percept Perform*, 36(4): doi:10.1037/a0017173.
20. Verleger R, Jaśkowski P, Aydemir A, van der Lubbe RH, Groen M (2004) Qualitative differences between conscious and nonconscious processing? On inverse priming induced by masked arrows. *J Exp Psychol Gen* 133:494–515.
21. Lleras A, Enns JT (2004) Negative compatibility or object updating? A cautionary tale of mask-dependent priming. *J Exp Psychol Gen* 133:475–493.
22. Gratton G, Coles MGH, Donchin E (1992) Optimizing the use of information: Strategic control of activation of responses. *J Exp Psychol Gen* 121:480–506.
23. Hommel B, Proctor RW, Vu KP (2004) A feature-integration account of sequential effects in the Simon task. *Psychol Res* 68:1–17.
24. Egner T (2008) Multiple conflict-driven control mechanisms in the human brain. *Trends Cogn Sci* 12:374–380.
25. Kunde W (2003) Sequential modulations of stimulus-response correspondence effects depend on awareness of response conflict. *Psychon Bull Rev* 10:198–205.
26. Naccache L, Blandin E, Dehaene S (2002) Unconscious masked priming depends on temporal attention. *Psychol Sci* 13:416–424.
27. Kunde W, Kiesel A, Hoffmann J (2003) Conscious control over the content of unconscious cognition. *Cognition* 88:223–242.
28. Sumner P, Tsai P-C, Yu K, Nachev P (2006) Attentional modulation of sensorimotor processes in the absence of perceptual awareness. *Proc Natl Acad Sci USA* 103: 10520–10525.
29. Lau HC, Passingham RE (2007) Unconscious activation of the cognitive control system in the human prefrontal cortex. *J Neurosci* 27:5805–5811.
30. Verbruggen F, Logan GD (2009) Automaticity of cognitive control: Goal priming in response-inhibition paradigms. *J Exp Psychol Learn Mem Cogn* 35:1381–1388.
31. Cohen JD, Servan-Schreiber D, McClelland JL (1992) A parallel distributed processing approach to automaticity. *Am J Psychol* 105:239–269.
32. Schlaghecken F, Bowman H, Eimer M (2006) Dissociating local and global levels of perceptuo-motor control in masked priming. *J Exp Psychol Hum Percept Perform* 32: 618–632.
33. Schlaghecken F, Klapp ST, Maylor EA (2009) Either or neither, but not both: Locating the effects of masked primes. *Proc Biol Sci* 276:515–521.
34. Boulinguez P, Ballanger B, Granjon L, Benraiss A (2009) The paradoxical effect of warning on reaction time: Demonstrating proactive response inhibition with event-related potentials. *Clin Neurophysiol* 120:730–737.
35. Jaffard M, et al. (2008) Proactive inhibitory control of movement assessed by event-related fMRI. *Neuroimage* 42:1196–1206.
36. Lo CC, Boucher L, Paré M, Schall JD, Wang XJ (2009) Proactive inhibitory control and attractor dynamics in countermanding action: A spiking neural circuit model. *J Neurosci* 29:9059–9071.
37. Egner T, Delano M, Hirsch J (2007) Separate conflict-specific cognitive control mechanisms in the human brain. *Neuroimage* 35:940–948.
38. Gilbert SJ, Shallice T (2002) Task switching: A PDP model. *Cognit Psychol* 44: 297–337.
39. Logan GD (1988) Toward an instance theory of automatization. *Psychol Rev* 95: 492–527.
40. Dehaene S, et al. (2003) Conscious and subliminal conflicts in normal subjects and patients with schizophrenia: The role of the anterior cingulate. *Proc Natl Acad Sci USA* 100:13722–13727.
41. Mayr U (2004) Conflict, consciousness, and control. *Trends Cogn Sci* 8:145–148.
42. Sumner P, Husain M (2008) At the edge of consciousness: Automatic motor activation and voluntary control. *Neuroscientist* 14:474–486.