How emotion context modulates unconscious goal activation during motor force exertion

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A B S T R A C T

Priming participants with emotional or action-related concepts influences goal formation and motor force output during effort exertion tasks, even without awareness of priming information. However, little is known about neural processes underpinning how emotional cues interact with action (or inaction) goals to motivate (or demotivate) motor behaviour. In a novel functional neuroimaging paradigm, visible emotional images followed by subliminal action or inaction word primes were presented before participants performed a maximal force exertion. In neutral emotional contexts, maximum force was lower following inaction than action primes. However, arousing emotional images had interactive motivational effects on the motor system: Unpleasant images prior to inaction primes increased force output (enhanced effort exertion) relative to control primes, and engaged a motivation-related network involving ventral striatum, extended amygdala, as well as right inferior frontal cortex. Conversely, pleasant images presented before action (versus control) primes decreased force and activated regions of the default-mode network, including inferior parietal lobule and medial prefrontal cortex. These findings show that emotional context can determine how unconscious goal representations influence motivational processes and are transformed into actual motor output, without direct rewarding contingencies. Furthermore, they provide insight into altered motor behaviour in psychopathological disorders with dysfunctional motivational processes.

1. Introduction

The notion that performance is influenced by motivational factors has long been a focus of psychology and neuroscience (Jeannerod 1997; Skinner 1953). Motivating effects have most often been demonstrated using extrinsic rewards (e.g., monetary gain) and can affect a wide range of domains related to cognition, motor control, decision making, memory and so on (Zedelius et al., 2014). Another approach is to expose (prime) participants to conceptual constructs (with intrinsic motivational value), which activate goal representations to influence subsequent behaviour. Thus behaviour is not only guided by reward pursuit that requires conscious information processing. For instance, implicit priming of the concepts 'action' and 'inaction' (e.g., using words primes such as active, go or rest, stop) can facilitate or impede, respectively, motor and cognitive processes in a variety of behaviours such as eating, drawing and even political participation (Albarracín et al., 2008; Albarracín et al., 2009; Noguchi et al., 2010). Here, action

and inaction constructs were defined as "motivational end states that regulate the pursuit of high-effort, active behaviour versus low-effort, inactive behaviour" (Albarracín et al., 2011). These findings suggest that activation of action-inaction concepts partly determines the amount of effort engaged in subsequent behaviour and goal pursuit. Interestingly, these effects may occur in an automatic manner, unconsciously (i.e., even when the participants are unable to report the goal or motivation underlying the behaviour) or implicitly (i.e., when the participant has another task-relevant goal).

A related line of investigation on goal pursuit shows that implicit emotional priming can also modulate the engagement of goal-directed behaviour (Aarts et al., 2008; Custers and Aarts 2005; 2010; Marien et al., 2012). Of particular interest, Aarts et al., (2008) demonstrated enhanced effort exertion (increased grip-force production) following combined priming of subliminal exertion words (e.g., vigorous) and consciously visible positive words (whose meaning was unrelated to exertion, e.g., good), compared to priming with either exertion or

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positive words alone. Thus, when tagging action concepts with affect, positive stimuli appear to act as a reinforcing/rewarding signal to promote the mobilization of physical resources for goal attainment, even in the absence of conscious awareness and without any extrinsic reward.

Other studies have also shown that positively valenced stimuli facilitate motor behaviour by acting as a source of motivation, including enhanced force output by pleasant emotional images (Coombes et al., 2008; Coombes et al., 2011; Naugle et al., 2010) and monetary reward (Pessiglione et al. 2007; Schmidt et al. 2009; Schmidt et al. 2012). Conversely, negative affect can diminish goal priming effects and motivation (Aarts et al., 2007). Given that emotions may be associated with different action tendencies (Frijda 2009), it is plausible emotional valence (i.e., positive or negative affect) itself conveys information related to action and inaction representations, which might influence goal pursuit and motor performance in different ways. Emotional arousal (i.e., the 'intensity' of psychological and physiological alertness) also modulates motor behaviour; for instance, greater force output is produced in response to high relative to low arousing emotional stimuli (Coombes et al., 2008; Schmidt et al., 2009). However, how emotional processes modulate the activation of action representations and subsequent behaviour remains poorly understood.

Here we therefore specifically aimed to test how emotional information (visual scenes) influences the activation of action-inaction goal concepts and their impact on subsequent motor force production (as an index of motivation and effort exertion). Understanding how motivation and effort exertion are influenced by (intrinsically motivating) affect and action priming may not only illuminate mechanisms linking emotion with action and goal pursuit systems, but also have implications for health and disease. Advertising campaigns often seek to implicitly motivate people to be more active and positive, yet global inactivity tends to increase rapidly (Ng and Popkin 2012), with physical exertion and perceived effort representing important barriers to many activities (Lovell et al., 2010). Moreover, deficits in motivation and motor poverty are key features of several psychopathological disorders including depression and apathy (Bonnelle et al., 2016; Cléry-Melin et al., 2011).

Behaviourally, interactive effects between emotion and goal formation have been demonstrated, though not consistently. For instance, action priming combined with positive mood induction facilitated performance to a similar extent as inaction priming following negative mood induction (Albarracín and Hart 2011); while reward expectations increased the effect of negative emotion cues (angry face expressions) on the degree of effort exertion (Aarts et al., 2010, experiment 2). In contrast, no interaction between emotional stimuli and motivational cues on force output was observed in a task where monetary reward depended on the magnitude of force produced (Schmidt et al., 2009). At the physiological level, recent work by Gendolla and colleagues (see Gendolla, 2012 for a review) indicates that both emotion and goal concept priming manipulations induce changes in the cardiac pre-ejection period (a sympathetic nervous system marker of effort mobilization). These data have led to the implicit-affect-primes-effort (IAPE) model (Gendolla, 2012), according to which the degree of effort mobilized is proportional to the level of subjective task demands. Implicit emotional primes are thought to automatically activate mental representations determining the subjective experience associated with task demands. For example, implicit sadness primes promotes the subjective experience of task difficulty, while happiness primes are associated with ease (Gendolla and Silvestrini, 2011; Silvestrini and Gendolla, 2011b). Together, these studies support the general premise that action-inaction concepts and emotional signals can encourage goal pursuit and modulate effort exertion.

However, the neural substrates mediating these effects remain unclear. Despite a growing interest in the impact of action concepts and emotion on motor performance, brain pathways responsible for their motivating (or demotivating) influences on force output have not been systematically studied. Previous research indicates that the basal ganglia (ventral striatum [VS] and pallidum) play an instrumental role in motivation, driving force output in a reward-context (Pessiglione et al., 2007; Schmidt et al., 2009; Schmidt et al., 2012); yet different neural pathways involving the inferior frontal gyrus (IFG) and primary motor cortex appear to be associated with general emotional arousal effects on maximum force (Schmidt et al., 2009). This raises the question of whether VS activity also drives the motor system to facilitate effort exertion following implicit action-inaction priming, without any extrinsic rewards. If so, this would support the hypothesis that VS activity not only reflects incentive motivation (the energizing of behaviour by rewards) but also performance motivation, where goals of pursuing states of activity or inactivity are translated into effort exertion.

Here we directly examined how emotion signals may interact with action goals and influence effort exertion when the goal concepts are covertly activated by subliminal primes. We designed a novel functional neuroimaging experiment that combined two complementary streams of research on emotion and action priming. Extending the work of Albarracín and Hart (2011) to the motor domain, we adapted the incentive force task used in previous MRI studies (Pessiglione et al., 2007; Schmidt et al., 2009), enabling the integration of emotional and subliminal conceptual priming together with motor behaviour within a single trial. A visible high arousing (pleasant or unpleasant; matched for arousal) or low arousing (neutral) visual scene was presented, followed by a subliminal word prime related to either action or inaction or had no such meaning (control word). We chose to present the action concept priming subliminally rather than the emotion priming to avoid explicit demand effects due to the visible action meaning, and to maintain consistency with previous concept priming paradigms (e.g., Aarts et al., 2008; Gendolla and Silvestrini, 2010). Following the subliminal word prime, participants generated a maximal force contraction by pressing on a force device using a precision-grip. Neither visual feedback nor rewards were provided. Importantly, the action and inaction word stimuli were specifically related to motor features reflecting the concepts of effort exertion and force generation. This design maximised perception-action links as well as processes related to motivation and goal attainment (Custers and Aarts, 2005).

Unlike many behavioural priming studies, we used a within-subjects design, similar to previous studies (e.g., Pessiglione et al., 2007; Schmidt et al., 2009), where each participant was exposed to all emotion and action concept priming conditions. Our paradigm makes it possible to directly test the notion that pleasant and unpleasant affective cues may influence the impact of implicit priming of action and inaction goal concepts, leading to motivating but possibly also demotivating effects on the motor system on a single-trial level.

Based on previous behavioural work reviewed above, we predicted that if conceptual and emotional priming share features with extrinsic reward (Zedelius et al., 2014), then positive affect paired with action concepts may activate common goal representations (see for example, Aarts et al. (2007); Aarts et al. (2008)), so as to enhance motivational value and maximal force output, relative to negative affect paired with inaction concepts, even without conscious awareness of the action-inaction primes. At the brain level, such effects should be accompanied by increased recruitment of emotion, reward, and motor circuits (including amygdala, basal ganglia, ventrolateral PFC, and possibly upper brainstem structures). Alternatively, if negative affect is paired with inaction concepts (and thus associated with subjective experience of task difficulty), then maximal force output should be greater than for positive affect paired with action concepts, in line with the IAPE model (Gendolla, 2012).

2. Material and methods

2.1. Participants

Twenty-four healthy native French speaking volunteers (26 ± 6 years; 12 females) participated in this study. All participants were right-handed (mean laterality quotient=83%; Oldfield, 1971) and included if they had no upper limb pain or injuries, no prior or current neurological or psychiatric disorder, no history of drug use, normal hearing and speech, normal or corrected-to-normal vision and no contraindications to MRI scanning. Scores on the Hospital Anxiety and Depression Scale (Zigmond and Snaith, 1983) were within normal limits (anxiety, 5.5 ± 2.8; depression, 3.8 ± 2.7). Participants provided written informed consent to all procedures and received monetary compensation. The study was approved by the Geneva University and Hospital ethics committee, in accordance with the Declaration of Helsinki.

2.2. Apparatus and visual stimuli

Participants produced maximal precision-grip contractions by pinching an MR-compatible force-measuring device between their thumb and index finger following the presentation of emotional images and subliminal conceptual priming (see Supplementary material for further details). The visual stimuli were presented using the Matlab toolbox Cogent, displayed through a LCD projector onto a screen (1024×768 resolution; 75 Hz refresh rate) and viewed via a mirror positioned above the participants' eyes. Participants viewed a total of 270 images selected from the International Affective Picture System (IAPS; Lang et al., 2008), comprising three emotional conditions (pleasant, unpleasant, neutral) based on their normative valence and arousal ratings (where 1=pleasant/low arousal; 9=unpleasant/high arousal). Each condition contained 90 unique images (1024×768 pixels), depicting an equal number of social and non-social scenes with varied content. Valence was significantly differentiated ($p < .001$) across each condition (pleasant, 2.8 ± 0.5; unpleasant, 7.7 ± 0.5; neutral, 4.9 ± 0.4), while arousal was matched between the pleasant and unpleasant conditions, but significantly differed ($p < .001$) from the neutral condition (pleasant, 5.8 ± 0.7; unpleasant, 5.9 ± 0.8; neutral, 3.0 ± 0.5). Each condition and block of trials was exactly matched for luminance, contrast, and spatial frequency (Delplanque et al., 2007).

Subliminal stimuli consisted of words (in French) related to the concept of either action or inaction or control adjectives (three conditions). Each condition comprised five words[1] that were selected based on a pilot study in which an independent sample of native French participants (n=35; 21 female; 32 ± 7 years) rated 44 French adjectives. Participants rated the extent to which each word related to the concepts of strength and exertion on a 7-point scale ranging from strong/maximum effort (-3) to weak/minimum effort ($+3$) (McCulloch et al., 2012). The five words with the strongest relationship to each condition were chosen for the main study. The words within each condition did not differ with respect to frequency, number of letters or syllables. Words were presented in the centre of the screen (Arial 55 pt font, white) against a grey background.

2.3. Experimental design and procedure

Participants completed one experimental session that included five parts: a maximum voluntary contraction (MVC) task, an effort-priming force task, two tasks to determine subliminal thresholds, and finally subjective ratings of the emotional images.

The MVC task was used to determine the maximum isometric force that could be generated when pressing on the force device between the right thumb and index finger using a precision-grip (outside of the scanner), according to a well-established protocol (Blakemore et al., 2016; Slifkin and Newell 1999; Vaillancourt and Newell, 2003). This value was then used as a reference value to normalise the force output in the effort-priming force task (see Supplementary material).

Following the MVC task, before entering the scanner, participants completed six practice trials of the effort-priming force task, and 10 practice trials of the subliminal threshold tasks (with different target words to those used in the actual tasks). For the effort-priming task, each trial consisted of the following sequence (Fig. 1): After the presentation of a fixation cross (500 ms), participants viewed either an unpleasant, pleasant, or neutral IAPS image for 2500 ms (supraliminal emotional priming). Next, a target word (associated with the concept of action or inaction, or with a control neutral meaning) was briefly presented for 39 ms (subliminal conceptual priming), sandwiched between a random string of letters. The random letter strings served as forward and backward masks for the target word and were presented for 156 ms and 117 ms, respectively. Finally, the word "PRESSER!" appeared on the screen for 3500 ms, indicating to participants to initiate maximal force exertion until the word "PRESSER!" disappeared. These stimuli presentation durations are similar to those used in other emotion and subliminal word prime experiments (Aarts et al., 2008; Gaillard et al., 2006; Pessiglione et al., 2007; Schmidt et al., 2009; Silvestrini and Gendolla, 2013), adapted for use within an MRI environment and our screen refresh rate constraints.

The inter-trial intervals jittered between 1500–2500 ms. Participants did not receive feedback on their force output nor did they receive any monetary reward. In all trials they were simply instructed to press on the force device as hard as possible and to keep their eyes fixated in the centre of the screen. The task therefore contained nine trial types in a 3×3 factorial design: emotion context (pleasant, unpleasant, neutral) and action concept (action, inaction, control). Participants completed 270 trials as 3 blocks of 90 trials. The nine conditions were distributed equally within each block and presented randomly.

Two subliminal threshold tests (inside the scanner) were implemented to probe awareness of the masked target words. In the discrimination threshold task, participants viewed the same sequence of events for subliminal priming (a forward and backward masked target word), and were asked to report whether or not they saw the word. A descending stair-case procedure was used for stimuli presentation; the duration of the target word and backward mask varied (multiples of 13 ms; beginning with a supraliminal duration of 156 ms). The discrimination threshold was determined as the average target word duration of the last nine of 12 reversals (when participants answered '*seen*' then '*not seen*' on consecutive trials and vice versa). Mean discrimination threshold where participants could no longer perceive the prime was 93 ± 25 ms (range=59–146 ms). As these values were sufficiently above the duration of the target word in the effort-priming force task, data from all participants were retained.

In the perceptual threshold task, the subliminal priming sequence was presented (a forward and backward masked target word), followed by a four-choice forced decision requiring participants to report via button-press (within 5 s) whether they distinctly saw the word displayed (target or distractor word) or to have a guess which word was displayed. Therefore they were forced to choose one of four responses: seen target word, seen distractor word, guess target word, guess distractor word. Each of the 15 action, inaction or control words were presented four times as target words, either subliminally (39 ms) or supraliminally (156 ms) for a total of 60 trials.

Finally, subjective valence and arousal ratings of the emotional stimuli were obtained outside the scanner, using a computerised
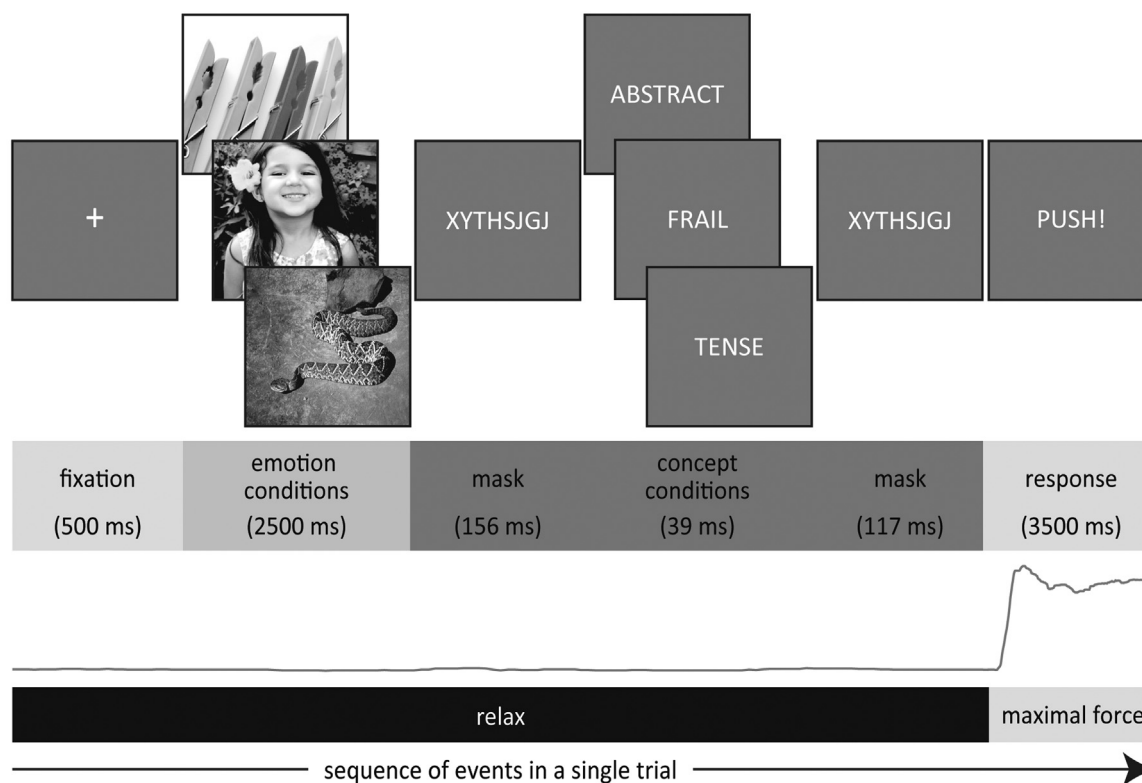
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[1] English translation in parenthesis - *Action:* énergique (active, energetic), fort (powerful, strong), puissant (strength, strong), tendu (tense), vigoureux (vigorous, strenuous). *Inaction:* faible (weak, frail), frêle (frail), immobile (still), inactif (inactive), paresseux (lazy). *Control:* abstrait (abstract), haut (high, above), neutre (neutral), profond (deep), rugueux (rough).

Fig. 1. Effort-priming force task. The sequence of screens displayed for each trial is shown from left to right. In each trial, a fixation cross was followed by a pleasant, unpleasant, or neutral IAPS image. A subliminal word was then briefly presented, corresponding to either action or inaction concepts, or to control words. The word was forward and backward masked by random letter strings. This was followed by the presentation of the word 'PUSH!', requiring the participant to initiate a maximum force production using a precision-grip. An example force trace from a single trial is shown.

version of the 9-point Self-Assessment Manikin (SAM) scale (Bradley and Lang, 1994). Following a fixation cross, each image was displayed first with the SAM-valence scale beneath. Participants rated valence by using the keyboard left and right arrow keys to move a cursor along the 9-point scale (1=pleasant, 9=unpleasant) without any time limit to answer. After confirming the rating, the valence scale was superimposed by the SAM-arousal scale; participants rated arousal in the same manner (1=low arousal, 9=high arousal), and could advance to the next trial (image) at their own pace. Ratings of the 15 word stimuli were completed in a similar manner. Participants were asked to rate the valence of the words, followed by the extent to which each word related to the concept of action or inaction (1=action, 9=inaction).

2.4. Behavioural data analysis

2.4.1. Force data

The force time-series data recorded by Matlab were digitally filtered using a one-dimensional median filter (window of 20) to remove the MR gradient interference from the signal. The maximum force reached and impulse (area under the curve) over the 3.5 s period of force production were determined for each trial and expressed as a percentage of MVC in order to eliminate individual differences in maximal force capacity (similar to other effort exertion studies; Cléry-Melin et al., 2011; Pessiglione et al., 2007; Schmidt et al., 2009; Schmidt et al., 2008; Schmidt et al., 2010). As the impulse and maximum force showed a similar pattern of results, we retained the latter to describe in the results below (see Figure S1 in Supplementary material).

For statistical analyses, we conducted a generalized linear mixed effect model (GLMM) analysis to examine the relationship underlying the effects of emotion context (pleasant, unpleasant, neutral) and action concept (action, inaction, control) on maximum force. We used lme4 package (Bates et al., 2013) within R software (v3.2.0; R Core

Team, 2014). Maximum force for each trial was modelled as a linear function of emotion context, action concept, fatigue, and their interactions as fixed effects. Participant was included as a random factor over the intercept.

Given that fatigue might develop over the course of the experiment (i.e., due to repeated motor action), we generated a fatigue term for each participant to take into account any decay in force over trials, and included this fatigue term in our statistical analyses of the force data (see below) and of the fMRI model (see Section 2.5). This term was computed by fitting, for each individual, an exponential decreasing function over the maximal force exerted for all trials irrespective of the emotion context and action concept, defined as: $f(n)=ae^{-bn}+c$, where $f(n)$=the maximal force exerted at trial n, a=difference in maximal force between the asymptote of the function and the force exerted when n=1, b=speed at which force decreases over trials, c=asymptote of the function. This function was chosen to model fatigue because exponential models have previously been used to describe muscular fatigue (Deeb et al., 1992), and it provided a better fit to our data than a linear function over trial order index (exponential function, r^2=.68; linear function r^2=.52). Note that the exponential decreasing function was fitted over all trials as we found no difference in each of the parameters of the function (a, b, c) among conditions and no interaction of emotion and concept (all p-values > 0.1). The fatigue term in the GLMM was determined from the values of this function for each corresponding trial.

An initial analysis of force output with a three-factor GLMM including emotion x concept x fatigue revealed a significant main effect of fatigue (0.23 ± 0.02, $t_{(6241)}$=13.0, p=.001), but no significant three-way interaction or two-way interactions involving fatigue. Hence although fatigue occurred over the course of the trials, it was not differentially affected by the different emotion and action word priming conditions. Our final GLMM therefore included three fixed effects

(emotion, concept, fatigue) and a single two-way interaction (emotion x concept). Where the emotion x concept interaction was significant, *p*-values are only reported for the interaction effect (Zar, 1999). The parameter estimates (beta coefficients) for force represent the force after regressing out fatigue. We present *t*-values (where the degrees of freedom within the lme4 R package are computed using Satterthwaite's approximation, and vary depending on the number of data points included within each model) and *p*-values (based on likelihood ratio tests) resulting from the GLMM analyses. All results are reported with standard error of the mean.

2.4.2. Perceptual threshold task and subjective emotional ratings

For the perceptual threshold task, three measures were obtained: percentage of correct responses (for the target words), percentage of seen responses (without guesses) and response times (including all responses). For each measure, differences between the subliminal and supraliminal conditions were analysed using a two-tailed paired *t*-test. To assess whether a participants' performance was different from chance level, a chi-square test was used at the individual level, while a two-tailed paired *t*-test was used at the group level.

For the stimuli ratings, a mean and standard deviation were calculated for emotional arousal and valence (for both the IAPS images and word primes), and for action-inaction conceptual meaning (for words), for each condition and each participant. These data were then analysed using separate one-factor repeated-measures analysis of variance to examine the effect of condition. We also tested for a relationship between the meaning and valence of words using the Pearson product-moment correlation coefficient (two-tailed).

All analyses of stimuli thresholds and subjective ratings were conducted using SPSS 22 (IBM SPSS Inc.), with the alpha set at .05. For the stimuli ratings, we used the Bonferroni degrees of freedom correction for all multiple pairwise comparisons when a significant F statistic was obtained. Only significant effects are reported.

2.5. Imaging data analysis

MRI data were acquired on a 3 T scanner and submitted to standard preprocessing (see Supplementary material). We first constructed a linear regression model (GLM1) to assess brain activity as a function of emotion and concept priming. The model contained 12 categorical regressors for each run: three conditions for the emotional primes (aligned to image onset and modelled as an event-related delta function), plus nine experimental conditions of force production (3 different emotion primes x 3 different word primes; aligned to the subliminal word onset, modelled as a boxcar function of 3.656 s to incorporate the effort exertion period). From this model, we generated parameter estimates of activity at each voxel, and the associated statistical parametric maps (SPM) for each condition relative to rest. A group analysis was performed on the 12 contrast images generated from the categorical regressors for each participant using a flexible factorial model.

From GLM1, we identified regions showing increased activity during presentation of the high arousing images compared with neutral images (pleasant+unpleasant > neutral). The resulting whole-brain t-maps were corrected for multiple comparisons ($p < .05$; FWE) and all significant clusters contained a minimum of 10 voxels. We also examined main effects of action concept by comparing activations elicited across the emotional conditions (see Supplementary material).

Next, we determined regions underlying the change of force output in the action and inaction conditions following presentation of unpleasant and pleasant images using exclusive masking procedures, which reveals the voxels showing increased response in one contrast, in the absence of any effect (even at trend level) in another contrast. Because we were specifically interested in the emotional influences exerted on action or inaction-related activity, our exclusive masking procedure allowed us to remove more general differences produced by

pleasant or unpleasant visual stimuli alone. We focused on the following two contrasts of interest: (1) To determine the influence of positive affect on action goals, we tested for a greater differential response to the comparison "pleasant-action > unpleasant action", while masking out those voxels showing significant emotion effects in the contrast "pleasant-control > unpleasant-control" ($p < .05$, exclusive masking). (2) To identify the influence of negative affect on inaction goals we then tested for a greater differential response to the comparison "unpleasant-inaction > pleasant-inaction", masked exclusively ($p < .05$) by the main emotion effect "unpleasant-control > pleasant control". Please note that the more liberal the exclusive mask threshold, the more conservative the masking procedure.

This exclusive masking approach was employed because the whole formal interaction contrasts, i.e., [(pleasant-action > unpleasant-action) − pleasant-control > unpleasant-control)], do not allow isolating activations uniquely sensitive to the action or inaction word primes, as they actually identify voxels active in both the pleasant-action and unpleasant-control conditions, relative to the unpleasant-action and pleasant control conditions (using this example). This is because mathematically [(PA-UA)−(PC-UC)]=[(UC-UA)−(PC−PA)]. Similar analyses with exclusive masking procedures have been used in other incentive motivation studies (Dixon and Christoff, 2012; Elward et al., 2015; Pochon et al., 2002). Significant activations in the contrast to be masked that survived a threshold of $p < .001$ (uncorrected) were retained, with significant clusters containing a minimum of 50 voxels ($p < .05$; FWE corrected at the cluster level).

To confirm how BOLD activity varied among the different action concept conditions, for the highly arousing emotional conditions, we conducted regions of interest (ROI) analyses on clusters of interest identified from these two main contrasts during effort exertion (see Table 2). Beta coefficients from these regions were extracted and averaged from an 8 mm diameter sphere centred on the corresponding activation peak at the second-level, and analysed using a GLMM (lme4 package within R software). Emotion context (2 levels: pleasant, unpleasant) and action concept (3 levels: action, inaction, control) were included as fixed effects, and participant was included as a random effect.

We conducted a second analysis to examine brain regions modulated by subjective ratings and force output. This model (GLM2) included two categorical regressors for each run, modelling only two distinct events in each trial corresponding to the image prime onset (with a delta function) and the subliminal word onset (with a boxcar function of 3.656 s), respectively (see Schmidt et al. (2009); Schmidt et al. (2012)). The first categorical regressor was modulated by parametric factors coding for the subjective valence and arousal ratings of the image prime. The second regressor was modulated by parametric indices representing force output (% MVC). Linear regression coefficients were computed at each voxel for each modulator and each participant. Second-level analyses were conducted on these contrast images using one-sample t-tests. Significant activations surviving a threshold of $p < .001$ (uncorrected) were retained, with significant clusters containing a minimum of 50 voxels ($p < .05$; FWE corrected at the cluster level). For both GLMs, all aforementioned regressors were convolved with a standard hemodynamic response function.

In all first-level linear regression models, we implemented physiological noise modelling to remove noise in the fMRI signal arising from respiratory fluctuations (Brooks et al., 2013). Nuisance regressors were created from the respiration data (see Supplementary material) using RETROICOR (Glover et al., 2000) and Respiration Volume per Time (Birn et al., 2006; Birn et al., 2008). Nuisance variables for each run therefore included six parameters for head motion estimated during realignment, nine respiration regressors, and one additional regressor modelling Fatigue (defined above in Section 2.4.1).
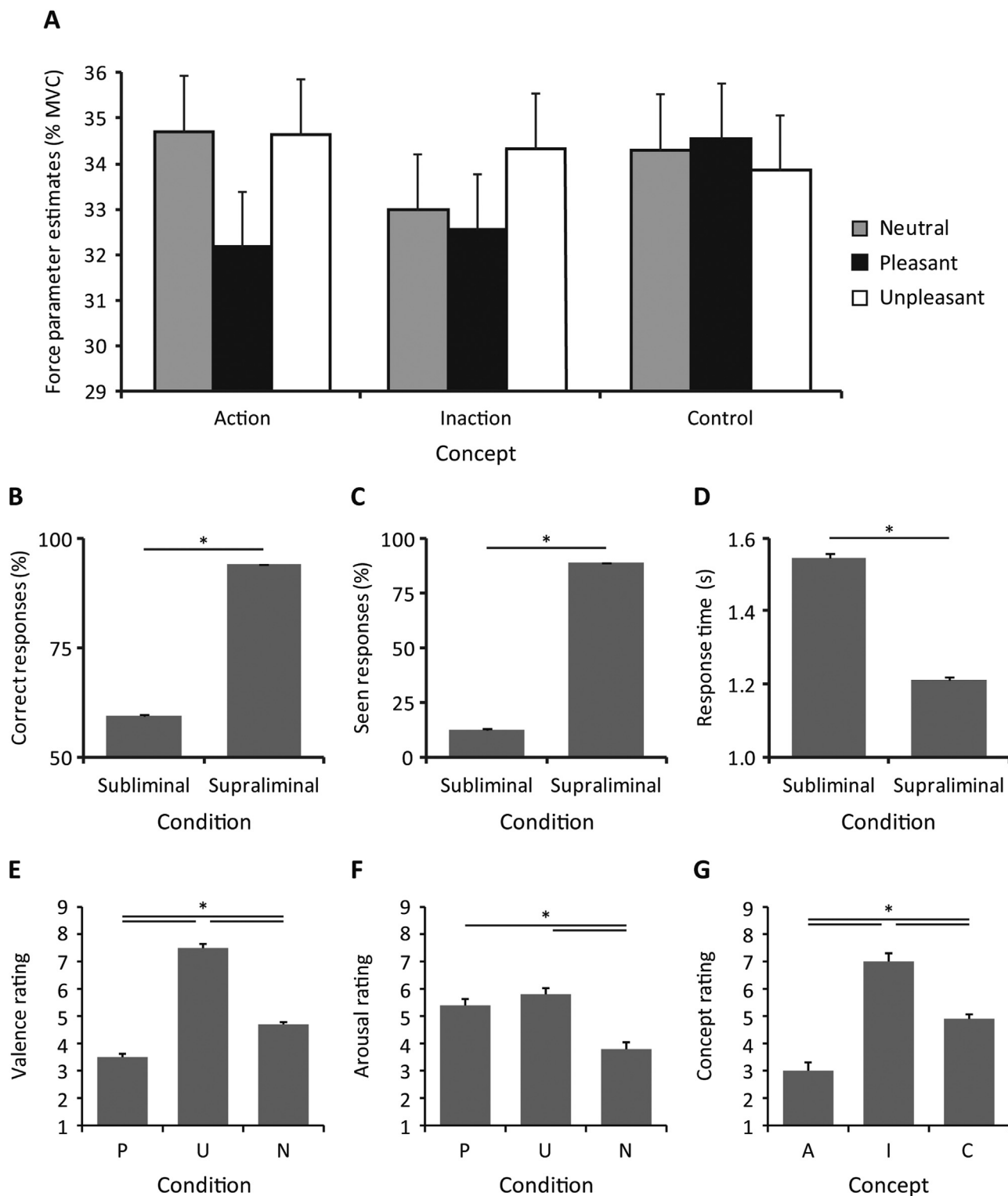
Fig. 2. Behavioural data. **A,** Force parameter (beta) estimates (expressed as % MVC; obtained from the GLMM) reflecting effort exertion in the effort-priming force task for each action concept (action, inaction, control) condition and each emotional (neutral, pleasant, unpleasant) condition. **B–D,** Responses for subliminal and supraliminal stimuli in the perceptual threshold task. Possible responses were 'seen target word', 'guess target word', 'seen distractor word', 'guess distractor word'. **E,** Mean subjective valence and **F,** mean subjective arousal ratings for each emotional condition (P, pleasant; U, unpleasant; N, neutral). **G,** Mean subjective concept ratings for each concept condition (A, action; I, inaction; C, control). Error bars in each graph represent standard error, *$p < .001$.

3. Results

3.1. Behavioural

3.1.1. Emotional ratings

In keeping with the normative IAPS ratings, a significant effect of condition was found for judgements of emotional valence ($F_{(1,31)}$=220.6, p=.001) and arousal ($F_{(1,29)}$=19.1, p=.001) of our images. Participants rated unpleasant images (7.5 ± 0.7) as more negative than neutral and pleasant images, and pleasant images as more positive than neutral images ($p < .001$; Fig. 2E). The pleasant and unpleasant images were rated as more arousing ($p < .001$) than the neutral images, but not different from each other (Fig. 2F).

Ratings of word stimuli regarding their relation to action and inaction concepts also accorded with those obtained in our pilot study. A significant effect of condition was found for both concept ($F_{(1,29)}$=43.5, p=.001) and valence ($F_{(2,46)}$=68.9, p=.001) ratings. Action words were indeed judged as evoking significantly more action-related concepts, and inaction words more associated with inaction concepts, while control words were not related to either action or inaction ($p < .001$; Fig. 2G). In addition, action words were rated as more pleasant (3.8 ± 0.6), inaction words as more unpleasant (6.2 ± 0.9), but control words rated as neutral (4.6 ± 0.7; $p < .001$). Additionally, a significant positive correlation was found between the action-relatedness and the valence of words (r =.761, p =.001); i.e., action words were generally judged as more positive.

3.1.2. Perceptual subliminal threshold

To assess whether participants could discriminate the words presented under masked conditions, we compared percentages of correct responses (Fig. 2B) and "seen" responses (Fig. 2C) as well as response times (Fig. 2D) for subliminally and supraliminally presented stimuli in the perceptual threshold task. Correct guessing was significantly lower ($t_{(23)}$=11.6, p=.001), and participants reported fewer "seen" words ($t_{(23)}$=15.2, p=.001) for subliminal compared with supraliminal stimuli. Performance on both measures for subliminal stimuli was not different from chance at the individual ($p > .07$ for all participants, chi-square test) or group (p=.223, paired t-test) levels. The average discriminability index (d'=0.18 ± 0.34) was also not different from zero. Moreover, participants responded slower ($t_{(23)}$=6.8, p=.001) for subliminal than for supraliminal stimuli.

3.1.3. Maximum force

The maximum force generated (expressed as % MVC) during the response window represents the degree of effort engaged by participants. Using a GLMM to compare the nine conditions (see methods), we found a significant emotion by action priming interaction on motor effort. As illustrated in Fig. 2A, when first exposed to neutral emotional images, maximum force was significantly lower following the subliminal presentation of inaction words compared with both action ($t_{(2104)}$=3.0, p=.003) and control ($t_{(2103)}$=2.2, p=.030) words. Consistent with previous findings (e.g., Albarracín et al. (2008)), this indicates a suppressive effect of inaction primes on motor output. However, contrary to the report of enhanced motor output following primed action concepts (e.g., Aarts et al. (2008)), we found no difference in maximum force between the neutral-action and neutral-control conditions (p=.445).

Importantly, when presented with emotionally arousing images (Fig. 2A), a different pattern of results emerged depending on the valence of images and the subsequent action concept prime. First, for inaction primes, maximum force was significantly enhanced following unpleasant images relative to pleasant ($t_{(6359)}$=3.0, p=.002) and neutral ($t_{(6360)}$=2.2, p=.025) images. Thus, only the two latter conditions showed reduced force after inaction words, relative to control words, while there was no such difference for the unpleasant condition. Second, for action primes, maximum force was significantly reduced

following pleasant images, relative to both the neutral ($t_{(6358)}$=−3.5, p =.001) and unpleasant ($t_{(6358)}$=−3.9, p=.001) images.

Taken together, these results show that force output was reduced following positive emotions, regardless of priming with action or inaction cues as compared to control primes; whereas negative affect suppressed the effect of the inaction concept prime, maintaining force output at a similar level to the control and action prime conditions.

3.2. Imaging

3.2.1. Effects of emotional images

To verify our emotional manipulation engaged brain regions associated with affective processing, we examined fMRI activation evoked by the pleasant and unpleasant images compared with neutral images (GLM1). Note that our fast imaging TR (650 ms) and orthogonal manipulation of subliminal word primes ensured a reliable assessment of emotional responses prior to the words and motor force onsets. This comparison revealed significant clusters in widespread temporal-occipital visual areas and amygdala, as well as the periaqueductal gray (PAG), extending into bilateral basal ganglia and thalamus, bilateral IFG extending to precentral areas, middle cingulate, bilateral precuneus, and anterior cerebellum (Table 1).

Parametric modulation analyses of brain responses to these images based on the subjective emotional ratings (GLM2) revealed that arousal was highly correlated with activity in the brainstem, with the peak

Table 1

Effects of arousal aligned to affective image onset. Significant clusters and their MNI coordinates (centre of mass), voxels per cluster, and Z-score for **A,** whole brain voxel-wise activations[a] while viewing pleasant and unpleasant images compared with neutral images; and **B,** parametric modulation[b,c] based on subjective arousal ratings.

	MNI coordinates (mm)			Voxels	Z-score
	x	y	z		
A. Whole brain voxel-wise activations					
Pleasant+Unpleasant > Neutral					
R Periaqueductal Gray	6	−28	−5	1302	> 8
L Periaqueductal Gray	−3	−28	−8		> 8
R Thalamus	21	−31	−2		> 8
R Amygdala	24	−4	−20		> 8
L Inferior Frontal Gyrus [BA 47]	−27	11	−23	25	5.21
L Amygdala	−24	−1	−20		4.97
R Inferior Frontal Gyrus [BA 47]	30	29	−17	59	6.57
R Inferior Frontal Gyrus [BA 45]	54	38	4	564	7.37
R Precentral Gyrus	33	−1	49		7.08
R Superior Frontal Gyrus	3	62	28	11	4.77
R Supplementary Motor Area [BA 6]	9	14	64	37	5.66
L Cingulate Gyrus	0	2	34	19	5.33
L Cingulate Gyrus	−9	−25	37	10	5.03
L Precuneus [BA 7]	−9	−46	49	15	5.01
R Precuneus [BA 7]	6	−49	52	39	5.48
L Middle Temporal Gyrus	−45	−76	7	7169	> 8
R Fusiform	24	−73	−8		> 8
L Cerebellum Anterior Lobe (IX)	−3	−52	−38	43	6.09
B. Parametric modulation					
Subjective arousal					
L Periaqueductal Gray	−3	−31	−8	655	4.87
R Inferior Frontal Gyrus	54	14	28	267	4.16
R Middle Temporal Gyrus	51	−76	16	401	4.09

[a] Clusters listed had a minimum of 10 voxels ($p < .05$; FWE corrected). When a cluster also contained other significant peak-level activations ($p < .05$; FWE corrected), these were also listed below the corresponding cluster entry.

[b] Significant activations that survived a threshold of $p < .001$ (uncorrected) were retained. Clusters listed had a minimum of 50 voxels ($p < .05$; FWE corrected at the cluster level).

[c] No significant activations were found for parametric modulation analyses of subjective valence (positive or negative). BA, Brodman area; L, left; R, right.
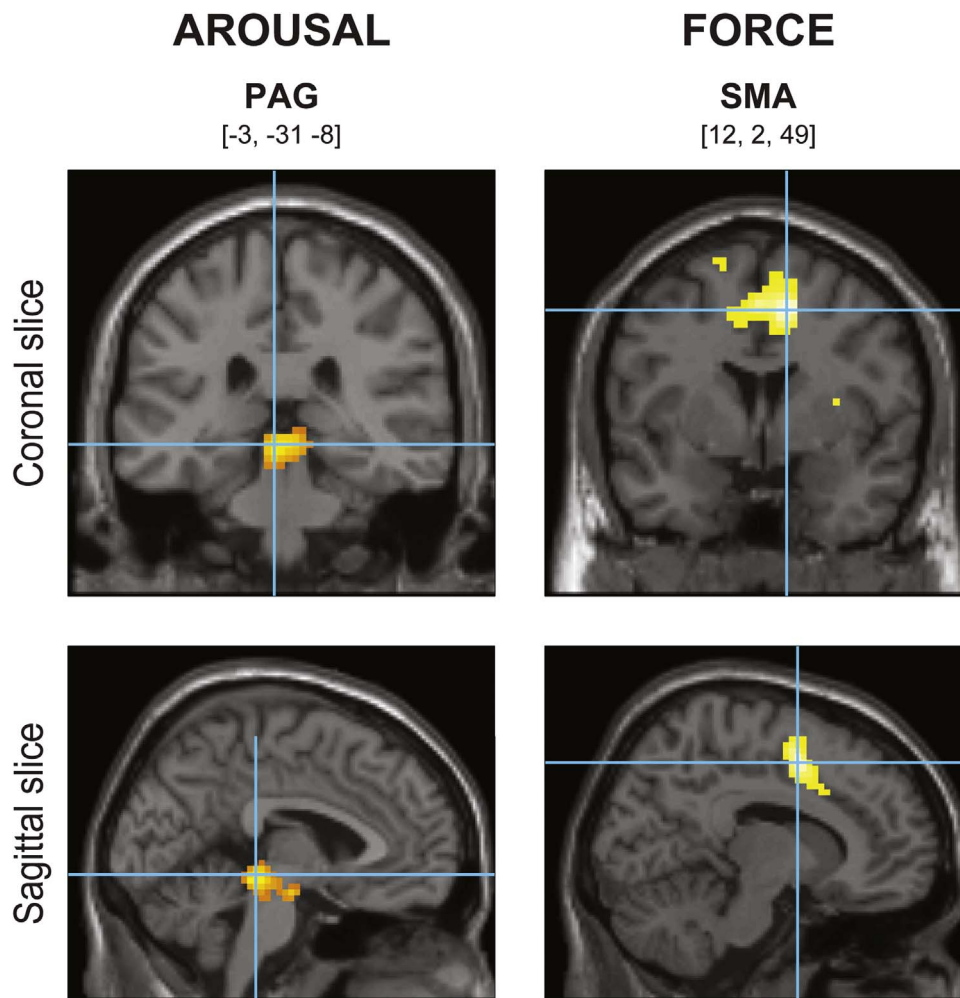
Fig. 3. Parametric modulation analyses. Left column: Neural correlates of subjective arousal ratings, aligned to the affective image onset (delta function). Right column: Neural correlates of maximum force onset, aligned to the subliminal word onset (boxcar function, including effort exertion). SPMs illustrate significant activation clusters for each parametric modulator that survived a threshold of $p < .001$ (uncorrected), with a minimum of 50 voxels ($p < .05$; FWE corrected at the cluster level). Slices are taken at the maxima of interest, with the respective MNI coordinates (x,y,z; mm).

activation centred on the PAG (possibly extending caudally into the locus coereleus; Fig. 3), but also with right IFG and posterior temporal-occipital junction (see Table 1). No clusters were parametrically modulated by valence (positive or negative), even at a liberal threshold ($p < .01$, uncorrected).

To further examine modulations of PAG activity by emotion in a non-parametric manner, beta coefficients were extracted from the three event-related regressors aligned to image onset (GLM1) and averaged across all voxels from the PAG cluster. These beta coefficients were higher for unpleasant images (-0.5 ± 1.58) compared with pleasant (-1.1 ± 1.57; $t_{(23)}=-4.7$, $p=.001$) and neutral (-2.9 ± 1.58; $t_{(23)}=-20.3$, $p=.001$) images, and for pleasant compared with neutral images ($t_{(23)}=-15.5$, $p=.001$), indicating a steeper parametric relationship with arousal in the unpleasant than other conditions. A similar pattern of results was found for rIFG ($t_{(23)} > 5.1$, $p < .001$). Taken together, this pattern accords with modulation of PAG activity by arousal but suggests greater effect of negative than positive affective contexts on the arousal response, without a linear parametric relation with valence.

3.2.2. Emotion-concept interactions during effort exertion

To delineate brain regions mediating the interactive effects between emotion and action concept priming on effort exertion, we performed two planned contrasts (see methods; GLM1). Given that our behavioural results for maximum force production revealed lower force output in the pleasant-action condition, but greater force in the

unpleasant-inaction condition, our fMRI analyses compared brain activity evoked by a given action priming condition (aligned to the subliminal word onset) in different emotion contexts.

First, we contrasted pleasant > unpleasant in the action condition, but excluding those voxels also significantly activated by pleasant > unpleasant in the control condition (exclusive mask at $p < .05$ to remove non-specific emotional effects). Results from this analysis revealed significant increases in bilateral inferior parietal lobule (IPL) and the medial surface of the superior frontal gyrus (SFG) (Table 2, Fig. 4). The reverse contrast (unpleasant > pleasant for action primes) did not reveal differential increases. To verify that the regions above were specifically activated to a greater extent in the pleasant-action condition, we also extracted the beta coefficients for each region. These data confirmed significantly greater left IPL activity for pleasant versus unpleasant images for action primes compared with both inaction ($t_{(11490)}=7.7$, $p=.001$) and control ($t_{(11490)}=10.2$, $p=.001$) primes. The same pattern of results was found for right IPL ($t_{(11200)} > 8.5$, $p < .001$) and SFG ($t_{(11480)} > 9.3$, $p < .001$). None of these areas were modulated by pleasant images on trials with inaction and control primes. This ROI analysis therefore confirms the specificity of the positive emotion effects on action prime processing in these regions.

Second, we contrasted unpleasant > pleasant in the inaction condition, now excluding those voxels significantly activated by unpleasant > pleasant in the control condition (exclusive mask at $p < .05$, again to remove non-specific emotional effects). As shown in Table 2, there were

Table 2

Effects of emotion and action concept during effort exertion aligned to subliminal word presentation. Significant clusters[a] and their MNI coordinates (centre of mass), voxels per cluster, and Z-score for whole brain voxel-wise activations for two main contrasts of interest: i) pleasant-action > unpleasant-action (masked exclusively by pleasant-control > unpleasant-control); and ii) unpleasant-inaction > pleasant-inaction (masked by unpleasant-control > pleasant-control).

		MNI coordinates (mm)			Voxels	Z-score
		x	y	z		
Whole brain voxel-wise activations						
Pleasant-Action > Unpleasant-Action						
L	Inferior Parietal Lobule	−36	−40	43	57	4.23
R	Inferior Parietal Lobule	54	−34	49	238	4.21
R	Superior Frontal Gyrus	24	44	10	364	3.97
Unpleasant-Inaction > Pleasant-Inaction						
L	Ventral Striatum	−18	−4	−2	208	4.62
R	Inferior Frontal Gyrus	51	29	−2	194	4.54
R	Extended Amygdala	21	2	−8	697	4.21
R	Middle Occipital Gyrus	36	−85	1	1256	3.34
L	Cerebellum Declive	−33	−61	−17	1404	3.28

[a] Significant activations that survived a threshold of $p < .001$ (uncorrected) were retained. Clusters listed had a minimum of 50 voxels ($p < .05$; FWE corrected at the cluster level). BA, Brodman area; L, left; R, right.

significant activations in the VS (with a peak centred on the globus pallidus but the majority of the voxels encompassing the lower putamen), as well as in the extended amygdala, rIFG, occipital cortex, and cerebellum. ROI analyses of beta coefficients of VS confirmed significantly greater increases following unpleasant versus pleasant primes for inaction primes compared with both action ($t_{(11200)} =5.7$, $p=.001$) and control ($t_{(11200)}=2.8$, $p=.006$) primes (Fig. 4). The same pattern of activation was found for rIFG ($t_{(11350)} > 7.1$, $p < .001$) and the extended amygdala ($t_{(11490)} > 2.2$, $p < .001$). None of these ROIs were modulated by unpleasant emotion during the processing of action or control primes. No significant increase was found for the reverse comparison (pleasant > unpleasant in the inaction condition).

3.2.3. Parametric modulation of force

Finally, the neural correlate of force production was examined using a parametric analysis based on force output in each trial across all conditions (i.e., irrespective of emotion and concept primes; GLM2). This revealed a significant correlation with activity in the right supplementary motor area (SMA: x=12, y=2, z=49, t =5.28, cluster size=315; see Fig. 3). This region showed increasingly higher activation with increasing force, without any difference among conditions (ROI analysis on beta coefficients from this cluster, all comparisons $p > .1$).

4. Discussion

We investigated the effects of emotional cues and action concept priming on force output to test the notion that non-rewarding but emotionally salient information can have motivating (or demotivating) influences on goal implementation and motor behaviour. As predicted, we found that inaction concepts decreased maximum force compared with action concepts when presented in a neutral emotional context, even in the absence of conscious awareness of the prime, and without extrinsic reward or punishment associated with performance. More critically, when arousing emotional cues were paired with action and inaction concepts, we found differential effects on maximum force that depended on the valence of the emotional images (positive or negative).

Pleasant images presented before action words (relative to control words) impaired maximum force output, reflecting decreased effort exertion. This effect was associated with increased activity in IPL and SFG, regions associated with the default-mode network (DMN). Conversely, unpleasant images prior to inaction word primes (relative to control words) enhanced effort exertion and increased force output. Such enhancement was associated with activity in motivation-related regions, including VS and extended amygdala, as well as rIFG. Force output itself was linearly correlated with activity in SMA, regardless of prime condition; whereas the PAG was modulated by subjective arousal across both positive and negative valence conditions.

Together, these results extend those of Albarracín and Hart (2011) and reveal interactive motivational effects on the motor system by emotionally and behaviourally relevant stimuli without direct rewarding contingencies. In particular, our data show that different emotional contexts can determine how unconscious action goal representations (activated by subliminal primes) are transformed into actual motor output. These effects were observed using a within-subjects paradigm, in which the priming conditions varied randomly from trial-to-trial. This design is not a novel approach to study subliminal motivation (or emotional priming) and force output using simultaneous behavioural and neuroimaging measures (e.g., Pessiglione et al. (2007)). It does, however, diverge from previous paradigms in psychology that investigated the effects of action concept priming on effort exertion using between-subjects designs (e.g., work by Aarts and Custers, Gendolla and colleagues). Nonetheless, we found significant modulation of motor behaviour and concomitant neural activity, thereby extending previous research to show that pleasant and unpleasant affective information can influence the impact of action and inaction goal concepts in a transient fashion, on a single trial level.

Our finding of increased maximum force following the presentation of unpleasant images and subliminal inaction words converges with prior studies showing facilitation of motor performance after exposure to negatively valenced stimuli. Such enhanced effort exertion has been related to the arousing nature of negative stimuli modulating motor areas of the ventrolateral PFC (Schmidt et al., 2009), engagement of defensive circuitry (Coombes et al., 2006; Lang and Bradley 2010), transference of affective valence adding motivational value in goal pursuit (Albarracín and Hart 2011), or access to knowledge about subjectively experienced task demands (Gendolla, 2012). However, our result cannot be attributed to the affective significance of unpleasant images only (Chiew and Braver, 2011), because there was no difference in force when unpleasant images were paired with action or control words. This suggests that the effect of negative emotion interacted with goal representations activated by the subliminal concept primes, rather than produced independent influences on motor output.

In line with the work of Gendolla and colleagues examining the effects of mood and implicit affect on effort exertion (see Gendolla (2012)), we suggest that the unpleasant-inaction condition might impact on representations signalling task difficulty and thus be experienced as more demanding than the pleasant-inaction or neutral-inaction conditions, leading to greater effort mobilisation. The IAPE model posited by Gendolla (2012) suggests that implicit emotional primes automatically activate mental representations of the corresponding affective state that contain information about task performance ease or difficulty. Access to this information influences subjective task demand and therefore regulates motivation. The IAPE model integrates principles of motivational intensity theory (Brehm and Self, 1989) to explain the conservation of energy sources, and assumes that the degree of effort mobilised is proportional to the perceived demand, as long as success is possible and justified. This theoretical principle also holds for explicit emotions via their effects on demand appraisals – that is, negative and positive moods are also associated with experienced difficulty or ease in goal conduciveness, respectively (Gendolla and Krüsken, 2002).

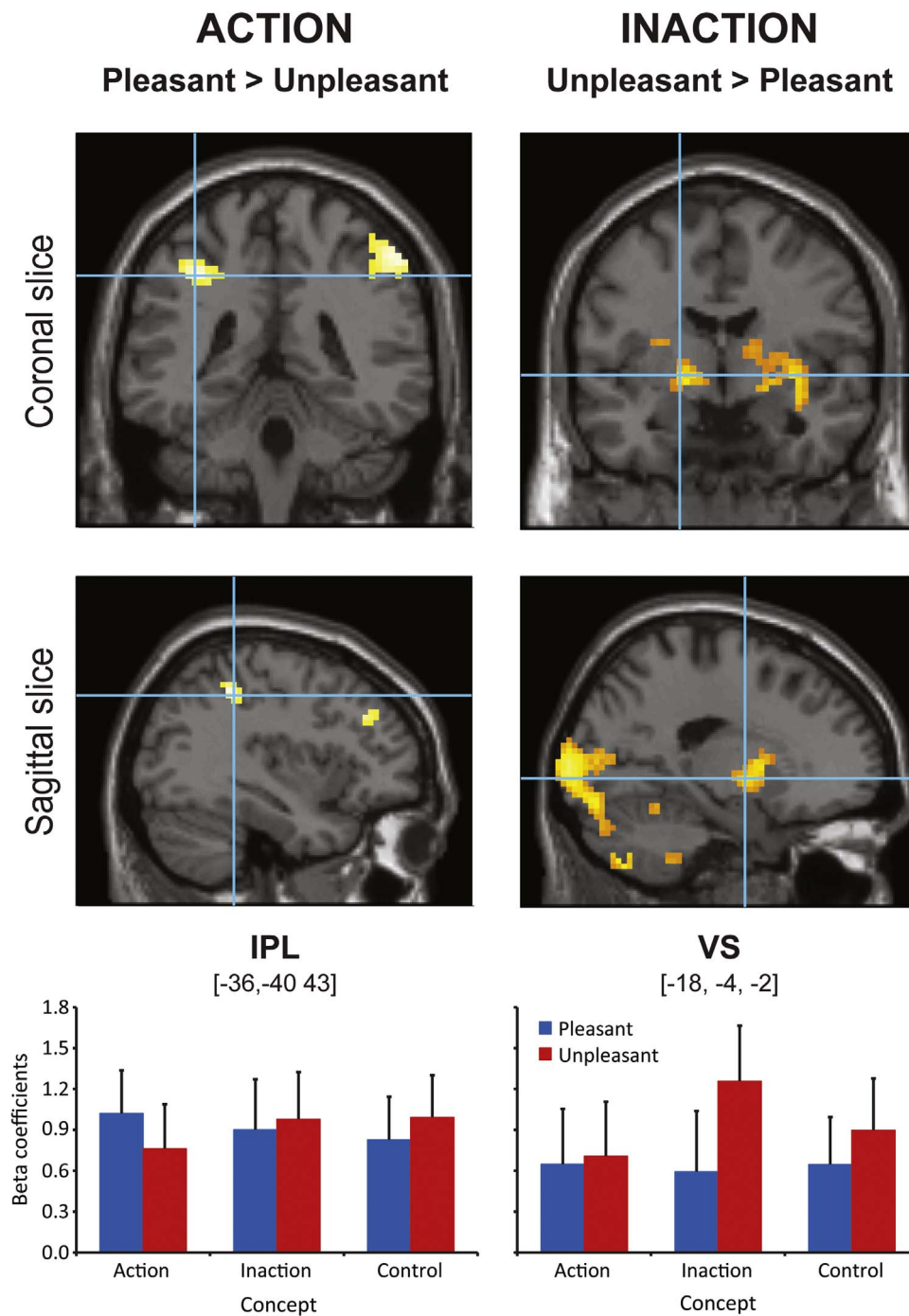It is plausible that our emotional stimuli produced similar effects on

Fig. 4. Effects of emotion context and action concept during effort exertion: Primary contrasts of interest. Left column: pleasant-action > unpleasant-action (masked exclusively by pleasant-control > unpleasant-control). Right column: unpleasant-inaction > pleasant-inaction (masked exclusively by unpleasant-control > pleasant-control). Regressors were aligned to subliminal word presentation. Top and middle rows: SPMs illustrate greatest significant activation cluster for each parametric modulator that survived a threshold of $p < .001$ (uncorrected), with a minimum of 50 voxels ($p < .05$; FWE corrected at the cluster level). Slices are taken at the maxima of interest, with the respective MNI coordinates (x,y,z; mm). The maxima cluster of interest for each contrast was used to define a functional ROI to compare activation across emotion contexts (pleasant, unpleasant) and action primes (action, inaction, control). Bottom row: Mean beta coefficients from the ROI analysis for each region illustrated. Error bars in each graph represent standard error of the mean.

subjective task demands and motivation. Although the emotional images were irrelevant to the motor task (participants were instructed to press as hard as they could on every trial), they were likely to elicit conscious affective responses as they were presented long enough to be clearly visible (Gendolla, 2012). These emotional cues could then influence effort production by modulating or gating the action representations activated by the subliminal action concepts (Gendolla and Silvestrini, 2010). Thus, trials containing inaction concepts tagged with unpleasant images were appraised as more difficult (i.e., comprising

two successive negative signals) and eventually motivated greater force production. This perceived greater difficulty induced by negative affect could therefore reverse the effect of the inaction prime by influencing the mobilization of energy resources (Gendolla, 2012) and hence increase force output (Albarracín et al., 2011), supporting the notion that automatic priming effects on behaviour are context-dependent, moderated by the present task situation and underpinned by boundary conditions (Loersch and Payne, 2011; Silvestrini and Gendolla, 2013; Wheeler and DeMarree, 2009). Such effect on perceived demand was

not too high however, as successful performance was still possible and justified; if subjective demand was too high, we would have observed low effort exertion due to disengagement (Silvestrini and Gendolla, 2011b).

In keeping with an effect of unpleasant-inaction stimuli on motivational processes regulating effort exertion, our fMRI results showed increased activity in regions known to play a role in processing incentive cues and behavioural relevance of sensory events. The ventral striatopallidal system together with the extended amygdala serve as key pathways for emotional and motivational mechanisms that guide goal-directed behaviour (Davis and Whalen, 2001; Heimer and Van Hoesen, 2006). Through an extensive network of connections, the extended amygdala acts as an interface; translating motivationally-relevant information from the amygdala, brainstem nuclei, and other sensory-receptive structures, and computing its relative value to inform the ventral striatopallidum and brainstem areas for appropriate autonomic, behavioural and somatomotor responses (for a review, see Waraczynski (2006)). The VS (and globus pallidus) is well documented to be involved in motivating effort exertion in rewarding contexts (Adam et al., 2013; Le Bouc and Pessiglione, 2013; Pessiglione et al., 2007; Schmidt et al., 2009; Schmidt et al., 2012), and effort-related decision-making in both humans and animals (Salamone and Correa, 2012). Activity of VS has shown to reflect exertion costs and cost-benefit valuations (Croxson et al., 2009; Kurniawan et al., 2010; Prévost et al., 2010), as well as anticipation of reward and high effort (Vassena et al., 2014). Here we show engagement of these basal forebrain structures (VS and extended amygdala), but importantly in the absence of explicit reward, prior knowledge of effort-action outcome contingencies, and choice (key aspects of effort-based discounting/decision-making tasks). Nonetheless, the present findings converge with previous suggestions that VS recruitment in difficult tasks reflects stimuli saliency (Schouppe et al., 2014; Zink et al., 2006), and mediates response vigour (Vassena et al., 2014). In line with endogenous activation of midbrain structures when task demands are high (Boehler et al., 2011), our findings provide novel evidence for a more general role of these areas in intrinsic motivational processes that translate goal pursuit into effort exertion and motor output. Together, this research points to the notion that the impact of unpleasant-inaction primes on goal representations could have generated stronger motivational signals and facilitated resource mobilization through recruitment of amygdala-striatal circuits to meet the enhanced task demands, which subsequently drove the motor command in SMA and motor pathways.

The SMA is also implicated in physical effort costs (Burke et al., 2013), anticipation of effort production in difficult tasks (Kurniawan et al., 2013), effort perception (Zénon et al., 2015), and is modulated by reward level (Bonnelle et al., 2016; Kurniawan et al., 2010) and emotional arousal during submaximal force maintenance (Blakemore et al., 2016). Here we found a linear relationship between SMA activity and maximal force output, highlighting a direct functional involvement of SMA in the motor command itself. Although we found no such modulation of SMA activity by emotion or action priming during effort exertion (ROI analysis; possibly due to small statistical power), the whole-brain analysis during emotion priming revealed greater SMA activity for high arousing images, consistent with previous findings (Blakemore et al., 2016).

In addition, we found concomitant activation of the rIFG that was also greatest for the unpleasant-inaction prime condition. The rIFG responds particularly strongly to stimuli at the current focus of attention when salient and relevant to motor response selection (Hampshire et al., 2009). It is also frequently activated by emotional stimuli, especially those associated with greater motivational significance and attentional capture (Ethofer et al., 2011; Sabatinelli et al., 2011). In agreement, we found a linear relationship between subjective arousal of emotional images and activity in rIFG, where responses were greatest for the most unpleasant images. Importantly, previous re-

search also found activity of rIFG to be correlated with subjective arousal in a maximal force task (Schmidt et al., 2009), and with negative emotional valence during simultaneous emotional processing and isometric submaximal force generation (Blakemore et al., 2016). Here we extend these findings to show involvement of rIFG (during effort exertion) in encoding motivational value when task demands and effort are high. It has been speculated that activity in IFG may play a role in the control of action by driving activity of the mesolimbic dopamine system (Tops and Boksem, 2011) and modulating the basal ganglia-subthalamic loop through a hyperdirect pathway (Nambu et al., 2002), both of which may act to modulate effort exertion in motor tasks. Activity of the PAG, a key midbrain structure involved in emotional processing and defensive motor behaviours (Blakemore et al., 2016; Satpute et al., 2013), was also modulated by subjective arousal. We note that our result might additionally reflect activity in the adjacent locus coereleus, as this structure is also implicated in mediating arousal (Murphy et al., 2014) and energizing behaviour (Varazzani et al., 2015). However, this remains speculative as our imaging parameters limit the ability to differentiate PAG activity from activity of surrounding brainstem nuclei (Satpute et al., 2013).

In contrast to the finding of increased effort exertion following inaction concepts tagged with unpleasant affect, we found significantly decreased force following action concepts tagged with pleasant affect, reflecting an opposite demotivating effect on effort exertion. This finding is discordant with previous research demonstrating that positive stimuli can motivate action performance by acting as reward signals due to their intrinsic motivational value (Aarts et al., 2008; Albarracín and Hart, 2011; Custers and Aarts, 2005). This discrepancy may reflect specificities of our priming paradigm, which differed from both incentive force tasks (Pessiglione et al., 2007; Schmidt et al., 2009) and priming protocols (e.g., Aarts et al. (2008); Albarracín and Hart (2011)) used in previous studies. For example, we used a within-subject design where participants were randomly exposed to all priming conditions, allowing direct comparisons of changes in behaviour and brain activity without confounding of between-group differences; the priming stimuli and behavioural response were integrated into a single trial; affective images rather than words were presented before, not after the action-inaction concepts. Nonetheless, diminished force in the pleasant-action condition does not rule out that our positive stimuli held an intrinsic motivation value. Instead, we suggest that the combined presentation of pleasant images and action concepts favoured the activation of goal representations associated with ease on a trial-by-trial basis. Thus, in accordance with the IAPE model (Brehm and Self, 1989; Gendolla, 2012), trials where action primes occurred in a pleasant context may be evaluated as easy, and therefore experienced as less demanding. This could in turn reverse the effect of the action primes on effort mobilization, attenuating force exertion.

Our fMRI results for action primes in the pleasant condition appear consistent with demotivating effects on effort exertion following activation of 'ease' concepts. We found selective activation of bilateral IPL and right SFG for pleasant versus unpleasant images in the action prime condition. Both regions are part of the default-mode network, a cortical network that deactivates in a range of active goal-directed tasks compared with baseline (Gusnard and Raichle, 2001; Raichle et al., 2001; Spreng et al., 2010). Importantly, increased DMN activity is observed in cognitive processes that do not require strong allocation of attentional resources, for example during mind-wandering, autobiographical memory, or introspection (D'Argembeau et al., 2010; Koshino et al., 2014; Schwartz et al., 2005). Thus SFG and IPL are engaged when attention is relaxed and cognitive processes are flexible, consistent with low task demands. Conversely, deactivation of the DMN occurs in tasks with high difficulty (Mayer et al., 2010) or increased processing demands (Koshino et al., 2011). The medial PFC is also reliably activated by stimuli with positive valence (Aldhafeeri et al., 2012; Sabatinelli et al., 2007) and rewarding value (Chib et al., 2009). Furthermore, positive emotions are thought to increase flex-

ibility and broaden thought-action repertoires, whereas negative emotions narrow attentional focus and promote stability (Fredrickson, 2011; Müller et al., 2007), possibly mediated by modulations of the DMN network under the influence of emotion signals (Eryilmaz et al., 2011).

Decreased goal pursuit and weaker force production when action concepts are tagged with pleasant affect might therefore reflect a broadening of attention away from the motor task when the perceived demand is low, accompanied by a default state of cortical activity that promotes inward processing and decreases motivation for outward effort. However, one should be cautious when interpreting increased activity in SFG and IPL as reflecting goal representations of low task demands, as we did not obtain subjective ratings of effort or observe extensive activations in the whole DMN. We also cannot rule out that SFG and IPL activity may be associated with other processes related to attentional disengagement. Future studies should include subjective assessments and physiological measures (e.g., cardiac pre-ejection period) to further test how modulation of reward-related and default-mode networks in the brain relate to motivational effects induced by emotion and action goal priming.

Some additional limitations of our study should be considered. Although fatigue effects were included in our analyses of force and fMRI data, fatigue may have affected the subjective ratings of the emotional images. While this is a possibility, the decay in force output over trials was not modulated by emotion or concept condition, thus one could speculate that fatigue did not differentially influence subjective emotional reactivity. It is also possible that, in the absence of covariates derived from physiological parameters, the detection of neural activity was obscured due the influence of heart rate on the BOLD response (Chang et al., 2009). Given the association between cardiovascular activity and motivation (Gendolla, 2012), future studies should implement physiological noise modelling including changes in both respiration and cardiac effort.

We also note that the IAPE model was derived from experiments using between-subject designs (Gendolla, 2012) rather than trial-by-trial manipulations of emotion and action information as used here. It could therefore be argued that motivational effects observed in these experiments are different from ours, as they depend on sustained changes in affective state. We do not believe this to be the case for several reasons. First, in the block designs of previous behavioural studies, participants were exposed to different priming contexts with non-words (Gendolla and Silvestrini, 2010; Silvestrini and Gendolla, 2013) or neutral faces (Silvestrini and Gendolla, 2011a) to control for habituation effects. Furthermore, long inter-trial intervals (2–4 s) were used to "give the implicitly activated representations of the affective states time to decay between trials" (Gendolla, 2012). Mixed presentation and similar delays between primes were used in our study. Second, increased prime frequency (presenting subliminal emotional stimuli more frequently than one third of trials) was found to diminish effort mobilization (Silvestrini and Gendolla, 2011a), suggesting that a within-subjects design should augment rather than dampen priming effects in our study. Third, there is ample evidence that physiological function (pupil dilation, electrodermal activity, heart rate variability) and modulation of brain activity by sympathetic responses (a key mechanism in the IAPE model) can occur on a single trial basis (for a review, see Critchley (2009)). Consequently, we conclude our results are in line with the IAPE model and that emotion and action primes can influence motor behaviour by altering the perceived level of experienced demand on a trial-by-trial basis. Our results therefore extend the implicit-affect-primes-effort model to the domain of conceptual action priming.

More generally, investigation into how emotions and unconscious action goal priming govern motivated goal-directed behaviour may contribute to gain insight into disorders with dysfunctional effort-related motivational processes (Salamone et al., 2016), for example apathy (Brown and Pluck, 2000; Marin, 1991), depression (Cléry-Melin et al., 2011), schizophrenia (Whitton et al., 2015), or conversely

impulsivity (Helper et al., 2012; Sebastian et al., 2014). Understanding these effects may inform development of interventions aiming to optimise motor behaviour in achievement contexts, where effort must be mobilized in order to succeed. Investigating apathy is particularly intriguing given an important feature of this syndrome is that motor poverty can be reversed by strong external incentives (Levy and Dubois, 2006). Modulation of force output in rewarding contexts have been reported in healthy individuals with high apathy traits (Bonnelle et al., 2015), and after subcortical brain damage (Schmidt et al., 2008). Whether implicit effort priming with emotional or conceptual stimuli can facilitate behaviour and concomitant activity of the mesolimbic and frontostriatal circuits in individuals with behavioural or emotional apathy remains to be elucidated.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuroimage.2016.11.002.

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