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Splitting Motivation: Unilateral Effects of Subliminal Incentives

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Abstract

Motivation is generally understood to denote the strength of a person's desire to attain a goal. Here we challenge this view of motivation as a person-level concept, in a study that targeted subliminal incentives to only one half of the human brain. Participants in the study squeezed a handgrip to win the greatest fraction possible of each subliminal incentive, which materialized as a coin image flashed in one visual hemifield. Motivation effects (i.e., more force exerted when the incentive was higher) were observed only for the hand controlled by the stimulated brain hemisphere. These results show that in the absence of conscious control, one brain hemisphere, and hence one side of the body, can be motivated independently of the other.

Keywords

effort, motivation, perception, reward, split-brain

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There was a time when rewards were offered for bringing in outlaws “dead or alive.” The higher the reward, the more effort bounty hunters exerted in tracking their target. The process that translates greater expected reward into more exerted effort, known as *incentive motivation*, has been widely studied in experimental economics and psychology. In the field of psychology, it is generally assumed that what is motivated by incentives is the person, who may experience a conscious desire for the expected reward and therefore voluntarily engage more effort on the imposed task (Haggard, 2008; Sheldon, Ryan, Deci, & Kasser, 2004; Wright & Brehm, 1989). In the field of economics, it is generally assumed that a person invests more resources when the offer is estimated, within the limits of bounded rationality, to be more profitable (Kahneman & Tversky, 2000; Von Neumann & Morgenstern, 1944). The amount that the individual invests is based on abstract cost/benefit calculations and should not depend on which hand is used to execute the transaction.

Long-standing neuroscience research studies have implicated limbic prefronto-subcortical circuits in the incentive motivation process (Berridge, 2004; Knutson & Cooper, 2005; Robbins & Everitt, 1996). One intriguing possibility is that the brain implements motivational processes (below subjective conscious awareness) through separate systems underpinning different degrees of motivation. One of the main divisions in brain structure separates the two hemispheres, which control

the movements of contralateral body parts (MacNeilage, Rogers, & Vallortigara, 2009). To test the possibility of subpersonal incentive motivation, we targeted subliminal incentives to either the left or the right brain hemisphere of study subjects and compared the effort exerted with the ipsilateral and contralateral hands.

We (Pessiglione et al., 2007) previously demonstrated that subjects exert greater physical effort (produce greater force) in order to receive higher monetary incentives, even when they do not perceive them consciously (i.e., they cannot report how much money is at stake). The effect of subliminal motivation on the force produced was accompanied by an elevated skin conductance response (measured on the resting hand), indicating the participation of affective brain systems. Functional neuroimaging showed that subliminal motivation was underpinned by the bilateral activation of limbic basal ganglia structures. Thus, we did not observe lateralization of motivation processes in these earlier data, which we obtained via central presentation of subliminal incentives.

In the study reported here, we modified our paradigm by presenting incentives peripherally and tested for lateralization

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of motivation effects on force production. A coin image of either one euro cent (1c) or one euro (€1) was flashed in one visual hemifield (left or right), and a scrambled coin in the other (Fig. 1). The coin display lasted for either 17 ms or 117 ms, and was preceded and followed by visual masks in both hemifields. After the incentive display, subjects were asked either to make a perceptual decision with one hand, which was positioned over a keyboard, or to exert an effort with the other hand, which was holding a power grip. In the perception control trials, subjects were asked to report which coin (1c or €1) had just been displayed, by pressing the corresponding key. In the force test trials, subjects had to squeeze the handgrip to raise the fluid level of the thermometer drawn on screen. Subjects had been told that their payoff would be proportional to both the height the fluid reached and the amount of money at stake. We compared the effects of presentation side on two dependent variables, one indicating discrimination performance (correct responses in the perception test) and the other indicating motivation effect (differential impact of incentive levels on grip force).

Method

Subjects

The study was approved by the Pitié-Salpêtrière Hospital ethics committee. Participants gave informed consent prior to participating in the experiment. Thirty-three subjects (12 males, 21 females; mean age = 24 years, $SE = 0.7$ years; all right-handed) were included. A first group of 17 subjects (3 males,

14 females; mean age = 24 years, $SE = 1.0$ years) comprised undergraduate students from Université Paris 8, who participated for extra course credit. A second group of 16 subjects (9 males, 7 females; mean age = 24 years, $SE = 1.1$ years) was recruited by public advertisement and believed that they were playing for real money. To avoid discrimination, we rounded payoffs for the second group to a fixed amount at the end of the experiment. Given that we did not observe a main effect of group on grip force or any significant interactions between group and other experimental factors (duration and side of incentive display), we pooled all subjects for most analyses.

Materials and procedure

Subjects were seated in front of a computer screen, at a 60-cm distance. They held in one hand a power handgrip, designed by Eric Featherstone and Peter Aston (Wellcome Trust Centre for Neuroimaging, London, England). The grip was made of two molded plastic cylinders (5 cm wide) that compressed an air tube connected to a transducer that converted pressure into voltage. Thus, compression of the two cylinders via subjects' isometric hand grip resulted in the generation of a differential voltage signal, which was linearly proportional to the force exerted. The signal was fed into the computer that generated the stimuli via a signal conditioner (CED 1401, Cambridge Electronic Design, Cambridge, England). Stimulus presentation was programmed with Cogent 2000 (Wellcome Department of Imaging Neuroscience, London, England). The dynamic changes in the recorded signal were used to provide subjects with real-time visual feedback (fluid level moving up

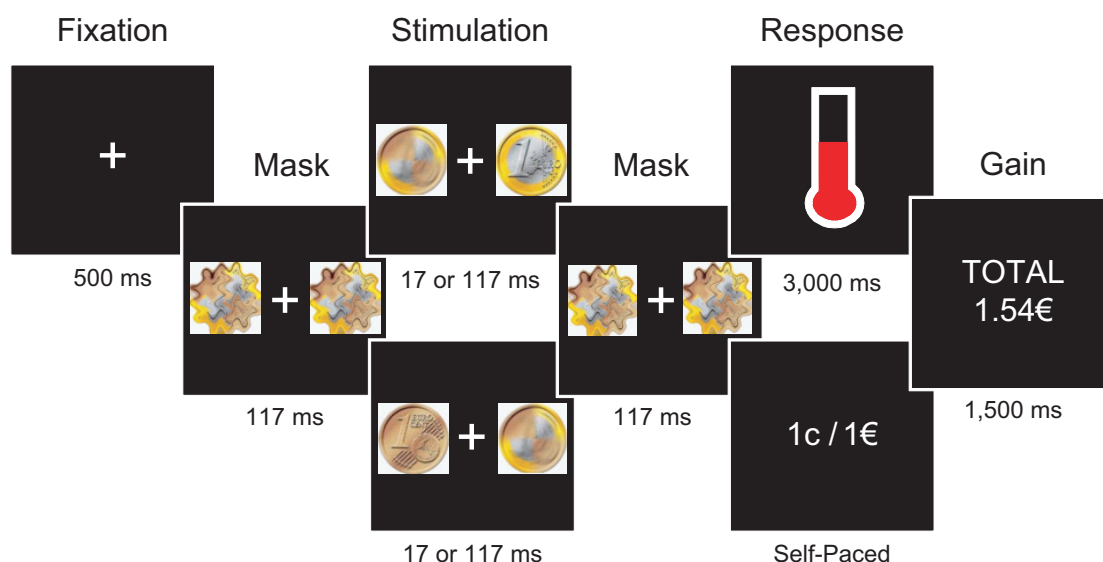


Fig. 1. Experimental procedure. Possible successive screenshots over the course of a trial are shown from left to right, along with their durations. Each trial included the following sequence: a fixation cross (500 ms), a mask (117 ms), one of two coin images presented to one visual hemifield and a scrambled image presented to the other (17 or 117 ms), another mask (117 ms), and finally a response request. On force test trials, the subjects' task was to squeeze a handgrip to raise the fluid level in the illustration of a thermometer; on perception control trials, the task was to report the value of the coin that had been shown. At trial completion, the total amount earned was displayed.

and down within a thermometer) about the force they were exerting on the grip. We first calibrated baseline ("do nothing") and maximal ("squeeze the grip as hard as you can") force. Subjects were then given the task instructions and familiarized with the coin (1c and €1) and mask images.

The experiment was divided into three sessions that differed in the duration of the incentive display: 17 ms in the first and last sessions and 117 ms in the intermediate session. Within each session, subjects performed two blocks that lasted about 10 min each and contained 10 repetitions of eight trial types, for a total of 80 trials for each block. The eight trial types corresponded to a 2 (incentive: 1c or €1) \times 2 (side: incentive display ipsilateral or contralateral to the tested hand) \times 2 (task: perceptual decision or force production) factorial design. The two levels of each factor (incentive, side and task) were equally frequent and randomly distributed over the trials. The two tasks were randomly intermixed in order to ensure that subjects were similarly attentive to the subliminal incentives, as they could not predict which task they would have to perform after the stimulation. To produce grip force, subjects used their left, nondominant hand in one block of each session and their right, dominant hand in the other. They used their free hand (i.e., the hand not holding the power grip) to press keys in the perception control trials. The order of the two blocks (i.e., assessing the left and right hand) was counterbalanced across subjects.

Each trial started with the presentation of a central cross that subjects used to fixate their gaze direction. Next, a mask-stimulus-mask sequence was displayed on each side of the fixation cross, at 6° visual angle. The stimuli were a coin image representing the incentive on one side and a scrambled coin on the other (see Fig. 1). Subjects were told that only one incentive, presented on the left or right side, would be at stake in every trial. After the mask-stimulus-mask sequence, subjects were shown on the screen either the two coin values (1c or €1), for the perceptual decision task, or the thermometer, for the incentive force task. In the perceptual decision task, subjects had to guess which incentive had been displayed and report their decision by pressing with their index or middle finger either a left key (designating 1c) or a right key (designating €1). In the incentive force task, subjects could win a fraction of the money at stake by squeezing the handgrip to make the fluid level in the thermometer rise.

Subjects were informed that reaching the top of the thermometer corresponded to obtaining the money at stake; hence, the fraction won was directly determined by the height reached. For the first group of subjects, visual feedback was calibrated such that they reached the top of the thermometer when they exerted their individual maximal force, which was measured beforehand. For the second group, visual feedback was calibrated such that the subjects reached only 75% of the thermometer height when they produced their maximal force. This method was implemented to avoid ceiling effects, which could have occurred if the maximal force was underestimated. At the end of every trial, regardless of the task completed

(perceptual decision or force production), subjects were shown a cumulative total of the money they had won.

Data analysis

Grip force was calculated for each trial as both the peak force and the total force. These two measures gave similar results; we report results for the peak value here, as it was more directly linked to the payoff. Motivation effects were calculated as the difference in grip force between the two incentive conditions (€1 – 1c). For all conditions, motivation effects were normalized by the effects obtained with a stimulus duration of 117 ms, irrespective of the side of the brain targeted. Thus, results given for the stimulus duration of 17 ms express subliminal motivation effects as a percentage of conscious motivation effects. The other dependent variable in this study was the percentage of correct responses in the perceptual decision task. Paired *t* tests were used to compare dependent variables with chance level (50% correct responses and zero motivation effects), as well as to compare dependent variables between experimental conditions. All statistical tests were conducted with the Matlab Statistical Toolbox (Matlab R2006b, The MathWorks, Natick, MA).

Results

Our crucial comparison was between intrahemispheric trials, in which incentives were displayed on the side ipsilateral to the response hand, and interhemispheric trials, in which incentives were displayed on the side contralateral to the response hand (Figs. 2a and 2b). With conscious incentives (117-ms displays), presentation side made no difference in perceptual decision (correct responses: $M = 90.8\%$, $SE = 2.1\%$, and $M = 91.5\%$, $SE = 1.8\%$) and for incentive motivation (differential grip force: $M = 102.8\%$, $SE = 8.5\%$, and $M = 97.2\%$, $SE = 8.5\%$).

In interhemispheric trials with subliminal incentives (17-ms displays), perceptual decisions were at chance ($M = 50.8\%$, $SE = 1.0\%$), and motivation effects were around zero ($M = -1.9\%$, $SE = 11.5\%$). Perceptual decisions were no better in subliminal intrahemispheric trials ($M = 52.2\%$, $SE = 1.1\%$, n.s.), but motivation effects were significantly higher ($M = 35.3\%$, $SE = 15.2\%$), $t(32) = 2.32$, $p < .05$. Intrahemispheric subliminal motivation effects were not driven by subjects who performed above chance on the perceptual task, as these effects were significantly positive even in subjects who performed below chance level on the perceptual task, $t(15) = 1.98$, $p < .05$, and there was no correlation between incentive motivation and perceptual decision performance ($r = -.021$, n.s.; Figs. 2c and 2d).

Analyses of intrahemispheric subliminal motivation effects on grip force, conducted separately for the two subject groups (see Fig. 3b), revealed that these effects were bordering significance for both the subjects tested with virtual money, $t(16) = 1.66$, $p = .058$, and the subjects tested with real money,

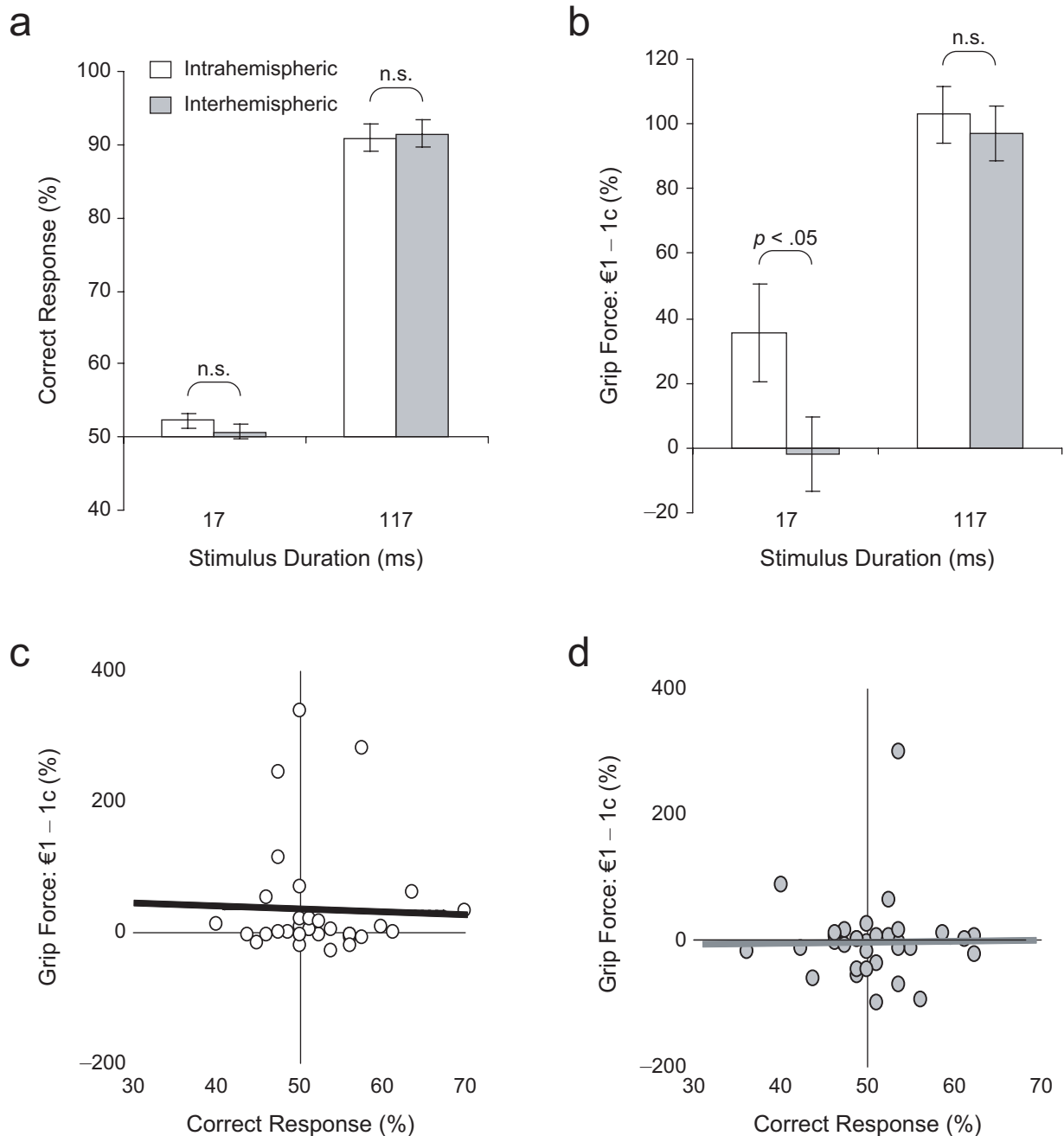


Fig. 2. Evidence for intrahemispheric subliminal motivation. The graphs in the top row show (a) the percentage of correct perceptual decision responses and (b) the difference in grip force between incentive conditions as a function of the stimulus duration, separately for intrahemispheric and interhemispheric trials. The graphs in the bottom row show the difference in grip force between incentive conditions as a function of the percentage of correct perceptual decision responses in (c) intrahemispheric and (d) interhemispheric trials. Dots represent data from individual subjects, and lines show the linear regression fit. Error bars represent intersubject standard errors of the mean.

$t(15) = 1.67, p = .058$). A comparison of the two groups showed a trend for real money to enhance these subliminal motivation effects ($M = 44.3\%$, $SE = 26.5\%$, vs. $M = 26.8\%$, $SE = 16.2\%$), but the difference was not significant. Intrahemispheric subliminal motivation effects were also significant for each of the two subliminal sessions (the first and last sessions), $t(32) = 1.84, p < .05$, and $t(32) = 1.89, p < .05$. The effects were

numerically higher in the last session ($M = 53.9\%$, $SE = 28.4\%$) than in the first session ($M = 16.7\%$, $SE = 9.1\%$), as if conscious trials had trained the response to subliminal incentives, but, again, the difference was not significant (Fig. 3d). Finally, subliminal intrahemispheric motivation effects were significant for both the left and the right hand, $t(32) = 2.06, p < .05$, and $t(32) = 1.9, p < .05$, and there was no noticeable

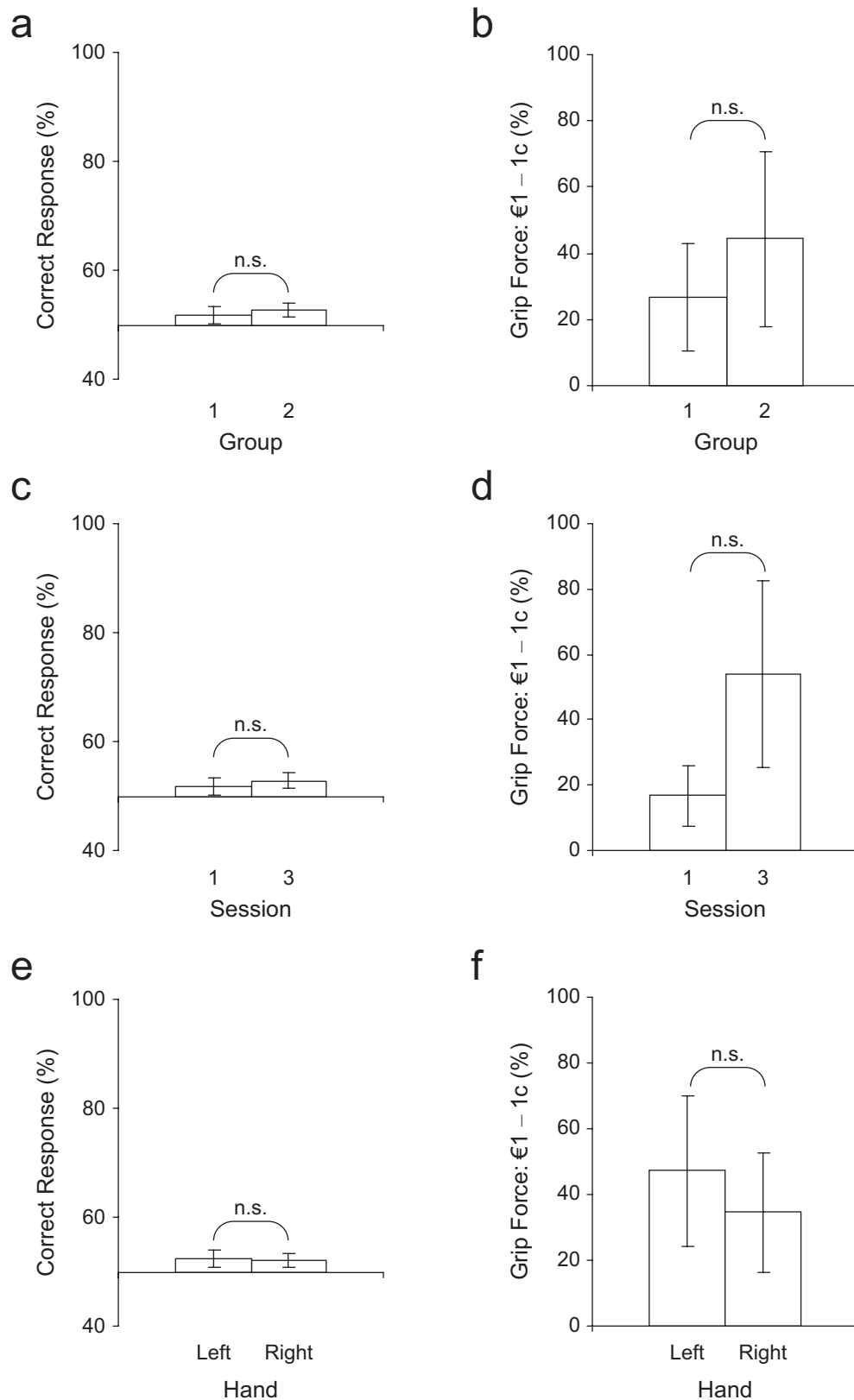


Fig. 3. Percentage of correct responses on the perceptual decision task (left column) and the difference in grip force between incentive conditions (right column) broken down by (a, b) subject group, (c, d) session, and (e, f) response hand. Error bars represent intersubject standard errors of the mean. Group 1 played for virtual money, and Group 2 played for real money. Coin images were presented subliminally in both Sessions 1 and 3, but Session 3 followed a session in which the coin images were presented supraliminally. Left and right hands were used in different blocks with each session.

difference in the effects between the two hands (Fig. 3f). In the case of perceptual decisions, the same comparisons between groups, sessions, and hands did not yield significant differences, and performance was close to chance level (correct responses: $M < 52.8\%$, $SE = 1.5\%$) in each group, in each session, and for each hand (see Figs. 3a, 3c, and 3e).

Discussion

Our first conclusion is that motivation can be subliminal. Indeed, the results of the intrahemispheric condition in our study replicated previous demonstrations of subliminal motivation obtained with centrally presented stimuli (Aarts, Custers, & Marien, 2008; Pessiglione et al., 2007). In the present data, discrimination performance was numerically, and in certain conditions significantly, above chance level. These results do not necessarily imply that incentives were consciously perceived, but may represent another case of the well-studied subliminal perception phenomenon (Kouider & Dehaene, 2007; Van den Bussche, Van den Noortgate, & Reynvoet, 2009). The converse situation is more informative: Chance-level discrimination performance is a good indicator that stimuli are not consciously perceived. Here, our linear regression analyses across subjects showed a positive motivation effect for stimuli that yielded only chance-level perceptual decision. Thus, even when unaware of what the incentive was, subjects still produced more force when this incentive was higher.

The difference between discrimination performance and the motivation effect cannot be attributed to a bias in top-down attentional processes. We surmise that subjects must have paid equal attention to subliminal stimulation in the two tasks (decision and effort) because at the time a coin image was presented, they could not predict what their task would be. Also, the result cannot be attributed to conscious training of stimulus-response associations because motivation effects were observed from the first subliminal session. That no effect was obtained in interhemispheric trials can be considered further proof that incentives were truly subliminal with a 17-ms display, as conscious incentives (in the 117-ms condition) produced similar effects on both hands. Interestingly, we observed no difference in intrahemispheric effects when the right (dominant) and left (nondominant) hands were used for response. This result suggests that, contrary to what has been shown for semantic processing (Abernethy & Coney, 1996; Diaz & McCarthy, 2007; Koivisto & Hamalainen, 2002), the two brain hemispheres are equally competent for incentive motivation.

The second conclusion we draw from our results is that motivation can be subpersonal. Subjects appeared to be more motivated (but no more conscious) when using one hand than the other. From a philosophical perspective, this finding is at odds with concepts of agents as unified entities, and accords well with theories of modularity. From a neuroscience perspective, this finding means that separate parts of the brain—in this case, the left and right hemispheres—can be differentially

motivated by subliminal incentives. This finding could be accounted for by the global-workspace theory of consciousness (Baars, 2005; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). Within this framework, conscious incentives would be processed by a large-scale prefronto-parietal network involving the two hemispheres, and hence would be able to energize any motor effectors. Subliminal incentives would be processed by local modules, probably within limbic prefronto-subcortical circuits, confined to one hemisphere and affecting only one side of the body.

This idea is consistent with a previous neuroimaging study showing that each brain hemisphere represents the reward value of the contralateral option in a binary choice task (Palmineri, Boraud, Lafargue, Dubois, & Pessiglione, 2009). In the latter study, subjects chose with their ipsilateral hand between fully visible options displayed on a screen, presented to the left and right of fixation, on the basis of their expected values. Although expected-reward representations were lateralized at the neuronal level, this was not apparent in subjects' behavior, as their choices reflected appropriate integration of the option values represented in contralateral hemispheres. In the study reported here, we have demonstrated that lateralization of expected-reward representations can lead, in the absence of conscious control, to different behaviors being expressed by the two hands.

Our data also imply that, in our experimental conditions, subconscious reward-related information failed to pass through interhemispheric neural fibers, but traveled through the entire neuronal circuit up to the motor pathways. This has been previously reported, although not consistently, for other representations, such as representations of the magnitude of numbers (Reynvoet & Ratinckx, 2004; Reynvoet, Ratinckx, & Notebaert, 2008). It is likely that our unusually short presentation duration (17 ms) reduced the capacity of the stimulus to activate neuronal representations in the ipsilateral brain hemisphere. Thus, using subliminal incentives in healthy subjects, we were able to demonstrate a phenomenon of unilateral motivation resembling that observed in split-brain patients, whose hands sometimes appear to reflect different, or even opposite, motives (Gazzaniga, 2005; Sperry, 1961).

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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