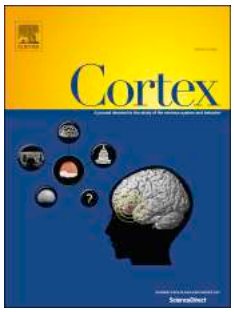


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PII: S0010-9452(21)00173-8

DOI: https://doi.org/10.1016/j.cortex.2021.04.013

Reference: CORTEX 3238

To appear in: *Cortex*

Received Date: 10 April 2020

Revised Date: 31 August 2020

Accepted Date: 28 April 2021

Please cite this article as: Hoofs V, Park HRP, Vermeylen L, Boehler CN, Krebs RM, Neural underpinnings of valence-action interactions triggered by cues and targets in a rewarded approach/ avoidance task, *CORTEX*, https://doi.org/10.1016/j.cortex.2021.04.013.

# Neural underpinnings of valence-action interactions triggered by cues and targets in a rewarded approach/avoidance task

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- Incentive-valence-action biases were absent if all information was cue-bound
- Win/loss cues increased activity in a wide network in line with previous work
- Win vs. no-incentive approach cues activated anterior cingulate cortex
- Target activity in loss vs. win approach trials was enhanced across ROIs/cerebellum
- Uncued win/loss targets featured valence and action main effects, but no interaction

**Abstract**

Incentive-valence signals have a large impact on our actions in everyday life. While it is intuitive (and most often beneficial) to approach positive and avoid negative stimuli, these prepotent response tendencies can also be maladaptive, as exemplified by clinical conditions such as overeating or pathological gambling. We have recently shown that targets associated with monetary incentives can trigger such valence-action biases (target condition), and that these are absent when valence and action information are provided by advance cues (cue condition). Here, we explored the neural correlates underlying the abolition of the behavioral bias in this condition using fMRI. Specifically, we tested in how far valence and action information are integrated at all in the cue condition (where no behavioral biases are observed), assessing activity at the moment of the cue (mainly preparation) and the target (mainly implementation). The cue-locked data was dominated by main effects of valence with increased activity for incentive versus no-incentive cues in a network including anterior insula, premotor cortex, (mostly ventral) striatum (voxel-wise analysis), and across five predefined regions of interest (ROI analysis). Only one region, the anterior cingulate cortex, featured a valence-action interaction, with increased activity for win-approach compared to no-incentive-approach cues. The target-locked data revealed a different interaction pattern with increased activity in loss-approach as compared to win-approach targets in the cerebellum (voxel-wise) and across all ROIs. For comparison, the uncued target condition (target-locked data only) featured valence and action main effects (incentive > no-incentive targets; approach > avoid targets), but no interactions. The results resonate with the common observations that performance benefits after incentive-valence cues are promoted by increased preparatory control. Moreover, there is support for the idea that valence and action information are integrated according to an evolutionary benefit (cue-locked), requiring additional neural resources to implement non-intuitive valence-action mappings (target-locked).

**Keywords:** fMRI; approach/avoidance; win/loss; reward; valence-action bias

## 1. Introduction

Incentive-valence signals can substantially impact behavior in everyday life and performance in experimental tasks. In the vast majority of experimental work, these signals lead participants to improve performance in order to maximize monetary outcomes (Braver et al., 2014). However, valence-associated stimuli can also hinder optimal performance if they are in conflict with the current task goal, such as via attentional capture by previously rewarded stimulus features (for review see Anderson, 2016; Krebs & Woldorff, 2017). Another source of such conflict are inherent mappings between (incentive) valence and action tendencies (approach if positive; avoid if negative) if these are not in line with the task goal. These so-called valence-action biases[1] are characterized by response facilitation for intuitive, compatible mappings (positive-approach and negative-avoid), and response slowing or errors for non-intuitive, incompatible mappings (positive-avoid and negative-approach). This has been described for emotional stimuli (e.g., Chen & Bargh, 1999; Krieglmeyer, Deutsch, De Houwer, & De Raedt, 2010; Solarz, 1960) as well as for motivationally relevant ones, such as monetary incentives/rewards[2] (e.g., Guitart-Masip, Düzel, Dolan, & Dayan, 2014; Hoofs, Boehler, & Krebs, 2019). Although these biases have been beneficial for survival in evolutionary history, in that they globally facilitate approaching the good and avoiding the bad (Elliot, 2006), they can also trigger undesired behavior (Dayan, Niv, Seymour, & Daw, 2006), such as reaching for a tasty cookie whilst being on a diet. In such situations, counteracting an almost automatic action seems to require additional cognitive resources (Asci, Braem, Park, Boehler, & Krebs, 2019), which is reminiscent of overriding a prepotent response in classic conflict tasks such as the Stroop task, Simon task, and the Eriksen flankers task (for review see Ridderinkhof, Forstmann, Wylie, Burle, & van den Wildenberg, 2011). Strikingly, in extreme cases, individuals may not be able to regulate inherent

[1] We note that while prepotent responses to valence stimuli can be adaptive, we refer to these mappings as valence-action "bias" as they reflect an imbalance that can impair participants' performance in situations where this imbalance is not mirrored in the environment (i.e., when the response triggered by a valence stimulus is not in line with the task goal).

[2] While reward is the more common term, we will mainly use the term incentive valence (or simply valence) throughout the manuscript as reward is strongly linked to win conditions, whereas (incentive) valence seems to encompass both win and loss.

valence-action mappings, leading to maladaptive behavioral patterns such as overeating and pathological gambling, but also phobias (Boffo et al., 2018; Heuer, Rinck, & Becker, 2007; Veenstra & de Jong, 2010). These examples highlight the relevance of better understanding the neurocognitive mechanisms that underlie valence-triggered response biases and how they can be abolished. This may also be informative with regard to training procedures to counteract maladaptive response tendencies in clinical conditions, which currently focus on stimulus devaluation and establishing more adaptive stimulus-response mappings (Wiers, Eberl, Rinck, Becker, & Lindenmeyer, 2011).

Previous studies investigating the integration of incentive valence and action have mainly employed Go/NoGo paradigms (Asci et al., 2019; Freeman, Razhas, & Aron, 2014; Guitart-Masip et al., 2011). In these studies, participants learned or were instructed to respond to specific stimuli, while others required the inhibition of a response. In addition, particular stimulus features were coupled to win outcomes for correct and in-time responses, while other features were associated with avoiding loss outcomes or with no incentive. Of note, while all used the Go/NoGo task, these studies differed substantially in experimental layout. Guitart-Masip and colleagues (2011) employed valence-action cues in the form of unique stimuli (fractals), the meaning of which was established via instructions and probabilistic trial-by-trial feedback (i.e., four valence-action combinations represented by four unique fractals). Asci et al. (2019) used valence-action targets in form of colored numbers, the meaning of which was instructed before the actual task as well (i.e., valence was signaled by color, action requirement was signaled by magnitude), but here there was no incorporation of trial-based feedback. Finally, in Freeman et al. (2014), participants responded to shapes (action requirement) on a colored background (valence association), the meaning of which was established in a preceding learning phase (i.e., Pavlovian-Instrumental-Transfer), while all trials were followed by fixed feedback events. Moreover, one study included monetary win and loss trials (Guitart-Masip et al., 2011), one included monetary win and no-incentive trials (Asci et al., 2019), and one included juice reward and no-reward trials (Freeman et al., 2014). Despite differences in experiment layout, the common behavioral finding was that stimuli associated with positive valence facilitated responses in Go trials (win/loss-associated cues: Guitart-Masip et al., 2011; win-associated targets: Asci et al., 2019; sweet liquid: Freeman et al., 2014), but impaired performance in NoGo trials in the form of triggering more commission errors (Asci et al., 2019; Freeman et al., 2014).

Two of these studies assessed neural activity modulations using functional magnetic resonance imaging (fMRI), one focusing on subcortical regions of the dopaminergic system (striatum and substantia nigra/ventral tegmental area [SN/VTA]; Guitart-Masip et al., 2011, see also Guitart-Masip et al., 2012), and one considering the whole brain (Asci et al., 2019). The former study (Guitart-Masip et al., 2011) reported that action but not valence information significantly modulated activity in dopaminergic regions. This seems surprising given that motivational valence signals are known to increase dopaminergic activity (Knutson & Cooper, 2005; Schott et al., 2008). While this study was limited to subcortical regions, a related fMRI study from our group (see Asci et al., 2019) revealed that trials in which motivational valence was incompatible with the required response (i.e., win-NoGo; no-incentive-Go) elicited the highest activity in dorsolateral prefrontal cortex (dlPFC). This was considered as an index of increased cognitive demands to act in line with the task goal in the context of prepotent, but currently inappropriate, action tendencies. This notion is supported by the study by Freeman et al. (2014) combining a Pavlovian-Instrumental-Transfer paradigm with transcranial magnetic stimulation (TMS; see above). Here, the authors found that motivationally conditioned Go stimuli lead to earlier and stronger corticospinal excitation, and that successful NoGo trials feature a stronger suppression of the respective action (i.e., effector). Moreover, in follow-up work, these authors unveiled that the strength of the suppression of automatically activated motor responses furthermore depended on the level of fatigue, in that suppression of rewarded NoGo trials was associated with more commission errors after performing an effortful task. This finding suggests that the suppression of an action in NoGo directly depends on cognitive control capacities (Freeman & Aron, 2016).

Another set of studies directly focused on the function of frontal brain regions in counteracting valence-action biases, and supported the conclusion of the whole brain analysis by Asci et al. (2019). Specifically, in an EEG study employing a conceptually similar version of the cue-locked Go/NoGo paradigm as used by Guitart-Masip et al. (2011), this was reflected in strengthened functional connections of the midfrontal cortex with both lateral prefrontal and motor cortices, when incompatible actions had to be overridden (Swart et al., 2018). Further, using computational modelling, the authors inferred that this is subserved by increased theta synchrony, which promotes a more conservative decision threshold (see also Cohen et al., 2009 for a non-rewarded Go/NoGo task). This notion has been recently extended by relating inter-individual differences in counteracting such biases and structural connectivity in the

amygdalofugal pathway (Bramson et al., 2020). Finally, another research group showed that transcranial direct current stimulation over prefrontal cortex diminished valence-action biases (Ly et al., 2016; see also Ly, Huys, Stins, Roelofs, & Cools, 2014). Together, these findings underline the importance of incorporating frontal brain regions within the scope of neural investigations of valence-action biases.

While the previously mentioned studies focused on mechanisms that modulate valence-action biases ad-hoc, we recently explored whether preparatory, pro-active control mechanisms would help participants to act in line with the task goal. In a behavioral study, participants performed approach (push) and avoid (pull) movements in win (reward), loss, or no-incentive trials of a joystick manikin paradigm (Hoofs, Boehler, & Krebs, 2019). In this task, approach and avoid joystick responses were followed by manikin movements towards and away from the target stimulus, respectively (adapted from Mogg, Bradley, Field, & De Houwer, 2003; see also Hoofs, Carsten, Boehler, & Krebs, 2019). Importantly, incentive valence and required action were both either signaled by advance cues (cue-informative condition) or by targets themselves (target-informative condition). These different incentive-valence manipulations have been adopted to different task domains in the past (Jimura, Locke, & Braver, 2010; Kostandyan et al., 2020; Schevernels et al., 2015), and are considered to broadly map on to two different cognitive control modes, i.e., pro-active and re-active control, respectively (for a review on the Dual Mechanisms of Control see-Braver, 2012). Specifically, while advance incentive cues allow participants to allocate attention and control in anticipation of the targets, the processing of uncued incentive targets relies on more re-active mechanisms[3] (Braver et al., 2014; Krebs, Hopf, & Boehler, 2015; Krebs & Woldorff, 2017). Importantly, due to the lack of preparation and/or mere time, performance is likely more affected by inherent valence-action mappings in the re-active context (i.e., target-informative condition). Like in our previous study (Asci et al., 2019), valence and action were signaled by orthogonal stimulus features (here, color and shape), and the respective mappings were instructed before the experiment (Hoofs, Boehler, & Krebs, 2019). We

[3] Pro-active and re-active incentive manipulations are not entirely independent. For example, the pro-active mode (cue-based) will likely be accompanied by re-active adjustments depending on the upcoming target, and the re-active mode (target-based) can be influenced by sustained pro-active mechanisms (e.g. attentional set for certain target features; see Krebs et al., 2016; Krebs & Woldorff, 2017).

observed valence-action biases in the target-informative condition (with facilitation in the form of faster and more accurate responses for win-approach vs. loss-approach trials and loss-avoid vs. win-avoid trials), and global response facilitation regardless of action in the cue-informative condition (faster responses in both win and loss vs. no-incentive trials). The facilitation effect of valence cues resonates with numerous incentive-valence cuing paradigms across different task domains that did not involve an approach/avoid dimension (as reviewed in Braver et al., 2014; Krebs & Woldorff, 2017; Oldham et al., 2018; Xue et al., 2013), and is typically assigned to preparatory control allocation in anticipation of the target. In the present paradigm, this is further promoted by the fact that the correct action is also already known at the moment of the cue, which allows participants to focus more on the incentive-valence dimension of the task and the higher-order goal of maximizing the outcome.

With the present fMRI study we aimed to explore the neural correlates underlying the differential behavioral effects in the cue as compared to the target condition. We were especially interested in whether valence and action information are integrated at all during cue presentation or whether incentive-valence cues lead to enhanced preparatory control regardless of action, and how this would affect action implementation at the target level in turn. A preparatory control benefit of incentive-valence cues would be signified by a main effect of valence in regions commonly associated with attention and cognitive control (Braver et al., 2014; Krebs, Boehler, Roberts, Song, & Woldorff, 2012; Padmala & Pessoa, 2011), while interactions between valence and action would speak for their integration. Here, higher activity for valence-compatible actions (win-approach, loss-avoid) mappings could be interpreted in terms of increased value of evolutionary predominant mappings, while higher activity for valence-incompatible mappings (win-avoid, loss-approach) may be indicative of increased control allocation to counteract a predominant mapping. In addition, we assessed neural activity in the uncued target condition, which does not allow for advance preparation, hence providing a conceptual replication of our previous work (Asci et al., 2019). Of note, the cue-informative condition allows to explore neural modulations at different processing stages (cue-locked: mainly preparation vs. target-locked: mainly implementation), providing additional insights into *when* valence and action information are integrated (if at all). In the target-informative condition, different cognitive processes are much more intermixed by design as there is only one onset (target) to sample from. We note,

however, that even in the cue-informative condition, there is no clear-cut line between these processes.

Behaviorally, we expected to replicate the finding of our previous study (see Hoofs, Boehler, & Krebs, 2019), in particular the absence of valence-action biases in the cue-informative condition. In keeping with the above considerations regarding the underlying neurocognitive mechanisms, our fMRI analysis focused on frontal brain regions that have been implicated in cognitive control and response selection, especially in the context of conflict, i.e., anterior cingulate cortex (ACC), pre-supplementary motor area (pre-SMA), and dlPFC (Garavan, Ross, Kaufman, & Stein, 2003; Liebrand, Pein, Tzvi, & Krämer, 2017; Miller & Cohen, 2001; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Rushworth, Walton, Kennerley, & Bannerman, 2004). A second focus was on regions sensitive to incentive valence, i.e., the ventral striatum (vSTR) and SN/VTA (Braver et al., 2014; Knutson & Cooper, 2005; Schott et al., 2008). Of note, the delineation into cognitive control and valence regions is not clear-cut in that e.g., the ACC is also known to be involved in value-based decision making (e.g., Rushworth, Kolling, Sallet, & Mars, 2012; Shenhav, Cohen, & Botvinick, 2016), while the SN/VTA has also been associated with cognitive effort allocation (e.g., Boehler et al., 2011; Krebs et al., 2012).

## 2. Material and methods

### *2.1 Participants*

Below, we report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures included in the study. The sample size was established prior to the data analyses, and was set at between 30-35 participants to be included in the analyses. This number is slightly higher than the last fMRI projects of our lab that also used a within-subject design in a motivational context (Park, Kostandyan, Boehler, & Krebs, 2018; Park, Kostandyan, Boehler, & Krebs, 2019) due to a higher number of conditions in the present study. All recruitment criterions, as well as data quality screening procedures for the behavioral and fMRI data were established prior to the data analysis. Participants were recruited through the online recruiting website of Ghent University. In addition to the typical screening criteria for participation in MR experiments (e.g., no ferromagnetic metal implants, no previous brain

surgery, no irremovable piercings, permanent make-up or metal ink tattoos), the prerequisites for participation were age between 18-35 years, right-handedness, normal color perception, normal or corrected-to-normal vision, and no (history of) diagnosed mental disorders. The data from the first eleven participants were excluded from the analyses due to suboptimal scan settings resulting in severe signal drop out, especially in subcortical brain regions (i.e., flip angle of 90° instead of 68°, pre-scan normalization off instead of on). One additional participant (female) was excluded due to vertigo during the functional scans, two more (females) due to difficulties with performing switches between block types (> 10% responses before target presentation), and two (females) due to technical issues (severe ghosting artefact, unsuccessful co-registration procedure). For all remaining participants, error rates were within the range of three standard deviations from the group mean (averaged across conditions). The final sample consisted of 35 participants (23 females, mean [*M*] age ± SD: 21.8 ± 2.2 years, age range 19-28 years). After the experiment, participants received a base reimbursement of 35 euro for the 110-minute session (60 minutes in the MR scanner) and an additional bonus based on their performance in the win and loss trials (*M* = 13.52 euro). All experimental procedures were approved by the Ghent University Hospital Ethics Committee and in line with the Declaration of Helsinki from 1964 and its later amendments. Written informed consent was obtained from each participant upon arrival at the scanning facility.

### *2.2 Paradigm and procedure*

In both the practice and the experimental runs, stimulus presentation and assessment of the joystick responses were controlled by Presentation software (version 20.2; Neurobehavioral Systems, Inc., Berkeley CA, USA). The task structure is illustrated in Figure 1 and translated task instructions are provided in the Supplementary material. Participants were instructed that they are represented by a small manikin on the screen (based on Krieglmeyer et al., 2010), and should envision that *they* are moving towards/away from a target stimulus by performing push/pull joystick movements. Push movements would lead to a reduction in target-self distance, while pull movements would increase the target-self distance. Whether they were required to push/approach or pull/avoid was signaled by the orientation of particular cue/target stimuli in each trial (see below). Participants started with two practice runs outside the MR scanner (80

trials each) to get familiar with the task. Note, however, that the practice did not include any incentive-valence manipulation yet. The practice runs (and the actual experiment) included two possible trial types, i.e., cue-informative and target-informative trials. In cue-informative trials, the orientation of a rectangular cue signaled the required action. In target-informative trials, the orientation of an oval target signaled the required action. For both the informative cues (rectangles) and targets (ovals), one orientation (vertical vs. horizontal) was associated with push and one with pull joystick responses, counterbalanced across participants. Moreover, informative cues and targets were colored (orange/blue/pink/green), but these colors were not informative at this stage of the experiment. The meaning of these colors, i.e., incentive valence, was only instructed after the practice run (see below). Finally, the respective non-informative trial event had no specific orientating and no distinct color, hence merely providing temporal information, but no information about action or valence. Specifically, targets in the cue-informative trials (gray circles) signaled the moment of response execution, while cues in the target-informative trials (gray squares) signaled the start of the trial. Cues were displayed for 800 ms, and targets for a maximum of 800 ms or until a response was given. These trial events were separated by a varying stimulus onset asynchrony (SOA) between 1500 and 3000 ms. Cue-informative and target-informative trials were presented in blocks of 20 trials, and were preceded by an instruction screen indicating the upcoming block type ("informatieve-cues blok", in Dutch meaning: informative cues block; "informatieve-targets blok", i.e., informative targets block; displayed for 1500 ms). For the practice run, responses were given via a standard gaming joystick with the same general characteristics as the MR-compatible joystick used inside the MR scanner (i.e., same sensitivity and re-centering springs). In contrast to the fixed joystick position in the subsequent MR experiment (see below), participants were free to position the joystick at a desired position between themselves and the laptop. During the practice runs, movement-congruent feedback (i.e., manikin movement towards or away from the target) was provided immediately upon correct and in-time responses in form of a moving manikin on the screen (see Hoofs, Boehler, & Krebs, 2019). In case of erroneous, too-late, or responses before target onset, participants saw the words "fout" (meaning: error), "te laat" (i.e., too late) or "te vroeg" (i.e., too early), respectively, instead of a manikin movement.

In order to create comparable performance expectations across participants, positive feedback (i.e., manikin movements signaling correct and in-time responding) was presented in

80% of all trials within each condition. The feedback in the other 20% of the trials was related to response errors, responses before target onset, and too-late responses (i.e., response time > response time-out). To achieve the overall percentage of 20% of negative feedback in each condition, we used a continuous staircase procedure adjusting the response time-out dynamically (for a similar procedure, see Hoofs, Boehler, & Krebs, 2019). Each practice run ended with feedback stating the percentage of correct and in-time responses of that run (based on the staircase procedure).

After additional instructions about the meanings of cue and target colors (see below), participants entered the MR scanner to perform four experimental runs (160 trials each). In contrast to the practice runs, target duration was fixed and no performance feedback was provided to avoid contributions from feedback-related activity modulations when assessing hemodynamic responses at target onset. Responses were administered by means of an MR-compatible joystick (Hybridmojo, San Mateo CA, USA) that was fixed on the right upper leg using Velcro strips. A pillow was placed under both legs, and additional pillows supported the right elbow. This promoted both a comfortable body posture, as well as enabling responses with minimal overall movement. During all trial events, a white fixation cross and a white place holder were visible in the upper half of a black screen. Like in the practice runs, each trial contained a cue (rectangle shape) and a target (oval shape) that were displayed for 800 ms each (Fig. 1). All event onsets were separated following a pseudo-exponential distribution of 1 (70%), 2 (15%), 3 (10%), or 4 (5%) TRs, resulting in an average SOA of 2250 ms (SOA range: 1500-6000 ms; Hinrichs et al., 2001). This approach helps to ameliorate differential overlap in the hemodynamic signal in tasks featuring multiple events within a trial. Dependent on the current block type (cue-informative/target-informative blocks), either cues or targets provided information regarding valence prospect and action requirement in the current trial. Specifically, while shape color signaled valence (win; no-incentive; loss), shape orientation signaled the required action (approach; avoid).

Participants were informed that they could earn bonus money based on the color of cue and target stimuli in the main experiment. These stimulus colors were drawn from a set of four colors (i.e., orange RGB = 238, 91, 18; blue RGB = 50, 138, 255; pink RGB = 230, 10, 200; green RGB = 27, 158, 23). For each participant, one color was introduced as “win”, one as

"loss", and two as "no-incentive" colors. We introduced two no-incentive colors to yield a balanced ratio between salient incentive and no-incentive trials (50:50), while preventing for low-level habituation effects in that all colors occurred with similar probability (for similar procedures see Hoofs, Boehler, & Krebs, 2019). Color-incentive mappings were counterbalanced across participants. Participants were instructed that correct and fast enough responses would lead to winning and avoid losing money in the win and avoid-loss trials, respectively. The amount at stake was 12 ct per incentive trial. Although there were no wins/avoid-losses following suboptimal performance in the no-incentive trials, participants were requested to respond as fast and accurate as possible in these trials as well. The trial event that did not convey valence and action information, i.e., cues in target-informative blocks and targets in cue-informative blocks, was always presented in gray (RGB = 139, 139, 139). Like in the practice phase, this event only provided temporal information in that cues in target-informative blocks signaled the start of the trial, and targets in cue-informative blocks signaled the moment of response execution. In order to promote accurate action representations (i.e., push = approach; pull = avoid), a manikin was presented below the placeholder during target presentation, although this manikin did not move upon response execution (unlike in the practice phase). Participants were explicitly informed that there would be no trial-by-trial feedback in form of manikin movements inside the MR scanner, and that targets now had a fixed duration. Nonetheless, they were instructed to take into account that there would still be a strict time out under which responses had to be given, certainly before target offset (i.e., response time < 800 ms). Global feedback was provided at the end of each run in the form of a 12-second screen stating the amount of money won in win trials, the amount lost in loss trials, and the total amount of money gained in the current run. To ensure comparable outcome expectancies across participants, but also allow some variation to prevent suspicion, the amount of money was calculated in a pseudorandom fashion (mimicking the staircase procedure during practice). Each correct and in-time response in win and loss trials had a 20% chance to be considered as too-late for bonus money calculations; this percentage was dynamically adjusted upon the percentage of actual errors, too-late, and too-early responses. Importantly, independent of this, all trials with responses within the pre-set response window of 150-1400 ms were considered for the behavioral and fMRI analyses. Within each of the four experimental runs, the different block types alternated every 20 trials, and were preceded by an instruction screen indicating the

upcoming block type (similar to the practice runs). Block order ('ABAB…' or 'BABA…') was counterbalanced across runs and participants. After each run, participants were offered a short break before the start of the next run. No part of the study procedures was pre-registered prior to the research being conducted.

[Please add Fig. 1 around here]

*2.3 Image acquisition and preprocessing*

MR images were collected using a 3T Magnetom Prisma$^{fit}$ MR scanner system (Siemens Medical Systems, Erlangen, Germany) with a 64-channel radio-frequency head coil. Prior to the functional scans, T1-weighted MP-RAGE volumes were acquired using a 3D magnetization-prepared rapid acquired gradient echo sequence (TR = 2250 ms, TE = 4.18 ms, TI = 900 ms, base resolution = 256, field of view (FoV) = 256 mm, flip angle = 9$^{o}$, voxel size = 1 x 1 x 1 mm), as well as geometric distortion sensitive field map volumes (TR = 474 ms, TE 1 = 4.92 ms, TE 2 = 7.38 ms, base resolution = 64, FoV = 192 mm, flip angle = 60$^{o}$, voxel size = 3 x 3 x 3 mm). For each of the four functional runs (corresponding to one experimental run), T2*-weighted echo-planar imaging (EPI) volumes were acquired (TR = 1500 ms, TE = 29 ms, multiband acceleration factor = 2, base resolution = 64, FoV = 192 mm, flip angle = 68$^{o}$, voxel size = 3 x 3 x 3 mm). Additionally, T2-weighted structural scans were acquired at the end of the test session (TR = 11.87 s, TE = 88 ms, base resolution = 256, FoV = 220 mm, flip angle = 120$^{o}$, voxel size = 0.9 x 0.9 x 1.2 mm). The complete scan protocol was about 60 minutes long and included a localizer scan, a structural T1 scan, a field map scan, four functional T2* runs, and a structural T2 scan.

Images were preprocessed and further analyzed using SPM12 (v. 7219; Penny, Friston, Ashburner, Kiebel, & Nichols, 2007), which operated in the Matlab environment (version R2016B; MathWorks, Inc., Natick, Massachusetts, USA). After excluding the first four EPI scans of each run to reach steady magnetization, the fMRI data were realigned and field map-based unwarped to reduce signal drop-out and spatial distortion due to magnetic field inhomogeneities. Next, the data underwent the remaining preprocessing steps, i.e., slice timing correction of the EPI scans, coregistration of the structural and functional scans, segmentation

and normalization of the coregistered images to the Montral Neurological Institute (MNI) space, reslicing of the EPIs to a voxel size of 2 x 2 x 2 mm, and spatial smoothing with a Gaussian smoothing kernel of 6 by 6 by 6 mm.

*2.4 Behavioral analysis*

The behavioral data were first cleaned by excluding trials with responses before and within 150 ms from target onset. This cut-off was based on the data cleaning procedures used in related approach/avoidance studies (e.g., Hoofs, Boehler, & Krebs, 2019; Hoofs, Carsten, et al., 2019; Krieglmeyer et al., 2010; Krieglmeyer, De Houwer, & Deutsch, 2011; Reichardt, 2018a, 2018b) and should prevent inclusion of trials with premature responses that are not actually triggered by target presentation (Samson, 2017). Next, trials in which no responses were registered (misses) were excluded from the dataset. The remaining data were assigned to the response time (correct trials) and error rate (all trials) repeated-measures analyses of variance (rANOVAs), with within-subject factors Valence (win; no-incentive; loss), Action (approach; avoid), and Block type (cue-informative; target-informative). Greenhouse-Geisser corrections were applied when the sphericity assumption was violated. JASP software (version 0.9.1.0; JASP Team, 2018) was used for all behavioral analyses. In keeping with our previous behavioral study, our main interest was the three-way interaction between Valence, Action, and Block type, which signifies differences in the expression of valence-action biases between cue-informative and target-informative blocks. If this higher-order interaction is significant, significant embedded two-way interactions are directly discussed as part of the higher order interaction. In case of significant interactions, post hoc contrasts are performed to assess the nature of the interaction. Importantly, since F-tests and t-tests alone cannot be used to quantify the magnitude of effects, we provide additional measures on weight of evidence i.e., effect sizes for all tests, point estimates of the contrasted conditions (*M* and within-subject standard deviation [*wSD*]), and 95% confidence intervals (CI) for the post hoc tests that serve the crucial exploration of which conditional differences are driving the effects of interest. The reported combination of F-tests, t-tests and CIs, even in case they put forward overlapping inferences, serves to facilitate between-study comparisons (see Lecoutre, Poitevineau, & Lecoutre, 2005). The *wSDs*, which are optimized for reporting variability in within-subject designs, have been calculated as advised by Cousineau (2005), and

corrected with Morey's corrections for providing more accurate representations (see O'Brien & Cousineau, 2015). Please note that these values are useful estimates but should not be used for any statistical inference (Cousineau, 2005). To avoid common misunderstandings on CIs for mean differences (Hoekstra, Morey, Rouder, & Wagenmakers, 2014), we highlight that a range not encompassing the 0-value is illustrative of a significant difference (Braitman, 1991). In order to preserve readability while presenting all relevant information, in-text reporting is based on the guidelines proposed by Louis and Zeger (2009; *wSDs* in brackets following mean estimates, $M_{(wSD)}$; lower and upper bound of the 95% CIs for mean differences are surrounding the between-conditions mean difference, $_{\text{lower bound}}\text{Mean difference}_{\text{upper bound}}$).

*2.5 fMRI analysis*

On the individual level (i.e., first level analysis), hemodynamic responses based on the blood oxygen level dependent contrast (BOLD) were modelled with delta functions at stimulus onsets, and then convolved with a standard hemodynamic response function. A high-pass filter with a cut-off frequency of 128 s was used to remove low-frequency noise (Ashburner & Friston, 1999), and serial autocorrelations were estimated using an AR(1) model (Glaser & Friston, 2003). Next, scan onsets corresponding to cues and targets of trials with correct and in-time responses (RT > 150 ms and < 1400 ms) were assigned to a total of 24 condition-specific regressors (formed by Valence, Action, Event type [cue onset; target onset], and Block type) of a general linear model (GLM; Friston et al., 1994) for each participant. Both the cue and target onsets of trials with suboptimal performances (i.e., errors, misses, too-late or premature responses), as well as scan onsets corresponding to instruction and feedback screens were assigned to a separate regressor of no interest. Last, six motion regressors derived from the realignment procedure were included as additional regressors of no interest.

At the group level (i.e., second level analysis), activity maps from each participant and each condition were submitted to a whole brain voxel-wise analysis in the form of a flexible factorial model with factors Valence (win; no-incentive; loss), Action (approach; avoid), Event type (cue onset; target onset), and Block type (cue-informative; target-informative). Of note, to answer our research question regarding the role of advance preparation in overcoming maladaptive response tendencies, the analysis is mostly focused on cue-informative blocks which

did not feature valence-action biases at the behavioral level. Nevertheless, the target-informative condition provides a conceptual replication of a previous rewarded Go/NoGo study (see Asci et al., 2019) and will be compared to the cue-informative condition (but see *1. Introduction* for inherent limitations). Moreover, this condition was needed to match our previous task structure (see Hoofs, Boehler, & Krebs, 2019) and to verify whether valence-action biases are triggered in this modified version of the task (which did not feature trial-by-trial feedback).

For the estimation of Valence main effects, we employed two different contrasts, one testing for Global Valence (unsigned) effects where no-incentive trials act as a baseline with a weight of -1 ([win + loss] vs. no-incentive), and one testing for Absolute Valence (signed) where no-incentive trials are ignored (win vs. loss). While the former contrast captures commonalities between incentive trials in terms of goal-directed motivation (cf. Oldham et al., 2018; Xue et al., 2013), the latter is sensitive to differences between win and loss conditions, which is relevant with regard to potential valence-action interactions (Guitart-Masip et al., 2011). Moreover, we assessed Action main effects (approach vs. avoid) and the interaction between factors. Activations were considered significant if they survived a cluster-level family-wise error (FWE) correction of $p = .05$, with a cluster-forming voxel-wise threshold of $p < 0.001$, which is considered sufficiently conservative for inferences at cluster level (Flandin & Friston, 2019). Moreover, we used a contiguity threshold of five voxels as a precaution against type-1 errors (Forman et al., 1995). For significant main effects and interactions (F-tests), we created post hoc contrasts (t-tests) to unveil the directionality of these effects. Subtle differences in the activity maps between F-tests and t-tests, arise from these tests being two-sided and one-sided in SPM, respectively. Coordinates are in the standard stereotaxic reference space of the Montreal Neurological Institute system (x, y, z), and local maxima labelling is performed with the Automated Anatomical Labelling atlas (AAL, Tzourio-Mazoyer et al., 2002).

To complement the whole brain voxel-wise analysis, we performed additional analyses in pre-defined anatomical regions of interest (ROIs), i.e., dlPFC, ACC, pre-SMA, vSTR, and SN/VTA. We used MRIcron version 2MAY2016 to create the masks (Rorden & Brett, 2000), and Marsbar Toolbox version 0.44 to extract and average the respective parameter estimates (beta; Brett, Anton, Valabregue, & Poline, 2002). Cortical masks were created based on anatomical labeling and in accordance with common findings in the cognitive control literature.

The ACC mask encompassed the bilateral rostral and caudal cingulate zone with the following boundary coordinates (MNI x y z, left/right: x = -10/10, posterior/anterior: y = 0/45, ventral/dorsal: z = 5/45). The pre-SMA mask included left and right hemisphere of the anterior medial part of Brodman area 6 (x = -12/13, y = 0/20, z = 46/60). For dlPFC, two spherical masks were created in left and right hemisphere separately in the vicinity of Brodmann areas 46 and 9 (left: x = -49/-29, y = 12/32, z =19/38; right: x = 29/49, y = 12/32 z = 19/38). Furthermore, we created masks for vSTR and SN/VTA based on the group-averaged T1-weighted (vSTR) and T2-weighted (SN/VTA) scans. Specifically, for the vSTR mask we followed Mawlawi and colleagues (2001; here, with trimmed white matter structures; Gawryluk, Mazerolle, & D'Arcy, 2014; see also Asci et al., 2019). For the SN/VTA mask we employed the procedures as described in an earlier study (see Krebs, Heipertz, Schuetze, & Düzel, 2011), albeit based on the anatomical T2 scan instead of a proton density scan (see also Asci et al., 2019 for a similar approach). Schematic representations of these masks are depicted in the *3.2.2 ROI results* section (vSTR: see Fig. 4J, K, L; SN/VTA: see Fig. 4M, N, O). Next, these ROIs were converted to an SPM-compatible format and used for parameter estimate extraction using the Marsbar Toolbox. The extracted parameter estimates of each ROI were averaged across runs, and submitted to three separate rANOVAs with factors Valence (win; no-incentive; loss), Action (approach; avoid), and ROI (ACC; pre-SMA; dlPFC; vSTR; SN/VTA). The inclusion of ROI as additional within-subject factor allowed to formally compare neural signatures across the brain (for similar procedures see e.g., Helfrich, Becker, & Haarmeier, 2013; Knoll, Obleser, Schipke, Friederici, & Brauer, 2012; Schubotz, Friederici, & Yves Von Cramon, 2000). Analogous to the whole-brain analysis, separate rANOVAs were performed for cue onsets in cue-informative blocks, target onsets in cue-informative blocks, and target onsets in target-informative blocks. These rANOVAs were performed in JASP, and Greenhouse-Geisser corrections were applied when the sphericity assumption was violated. Post hoc tests were again performed for in-depth exploration of significant effects of interest. To provide measures on weight of evidence, we again report effect sizes, conditional point estimates (*M* and *wSD*), and 95% CIs for mean differences. Again, *wSDs* are reported in brackets following mean estimates: $M_{(wSD)}$, and the lower and upper bound of the 95% CIs for mean differences are surrounding the between-conditions mean difference: $_{\text{lower bound}}\text{Mean difference}_{\text{upper bound}}$. No part of the study analyses was pre-registered prior to the research being conducted.

## 3. Results

### 3.1 Behavioral results

3.1.1 Response times

Response speed was affected by Valence ($F(2, 68) = 23.49$, $p < .001$; $\eta^2_p = .409$), with faster responses in win ($M = 445.38_{(8.97)}$ ms; $t(34) = -6.32$, $p < .001$; $d = -1.069$; $_{-21.58}-16.33_{-11.08}$) and loss trials ($M = 450.27_{(9.63)}$ ms; $t(34) = -4.22$, $p < .001$ ; $d = -.713$; $_{-16.96}-11.45_{-5.93}$) when compared to no-incentive ones ($M = 461.71_{(11.87)}$ ms), as well as faster responses in win compared to loss trials ($t(34) = -2.47$, $p = .019$; $d = -.417$; $_{-8.91}-4.89_{-0.86}$). Responses were faster in avoid ($M = 447.40_{(15.19)}$ ms) compared to approach trials ($M = 457.51_{(15.19)}$; Action: $F(1, 34) = 7.75$, $p = .009$; $\eta^2_p = .186$), and also in cue-informative ($M = 365.18_{(37.37)}$ ms) compared to target-informative blocks ($M = 539.73_{(37.37)}$ ms; Block type: $F(1, 34) = 381.84$, $p < .001$; $\eta^2_p = .918$). We observed multiple interactions, i.e., Valence x Block type ($F(1.56, 53.08) = 11.55$, $p < .001$; $\eta^2_p = .254$), Valence x Action ($F(2, 68) = 8.88$, $p < .001$; $\eta^2_p = .207$), and a higher-order interaction between Valence x Action x Block type ($F(2, 68) = 8.41$, $p < .001$; $\eta^2_p = .198$; Fig. 2A). The only remaining F-test, i.e., Block type x Action, was non-significant ($p > .9$). The three-way interaction is reflective of a significant differential impact of valence information on the required action in target-informative blocks (Valence x Action: $F(2, 68) = 13.31$, $p < .001$; $\eta^2_p = .281$), which was absent in cue-informative blocks ($p > .8$). Further exploration of this interaction in target-informative blocks revealed faster responses in win ($M = 528.50_{(20.08)}$ ms) compared to loss ($M = 549.02_{(27.42)}$ ms; $t(34) = -4.28$, $p < .001$ ; $d = -.723$; $_{-30.27}-20.52_{-10.77}$) and no-incentive trials ($M = 557.15_{(22.84)}$ ms; $t(34) = -6.86$, $p < .001$ ; $d = -1.160$; $_{-37.14}-28.66_{-20.17}$) in the approach condition, with no difference between loss and no-incentive trials ($p > .1$). The analogous contrasts in the avoid condition of target-informative blocks were non-significant (all $p > .5$). Moreover, instead of a Valence x Action interaction, cue-informative blocks featured response facilitation in both win and loss trials compared to the respective no-incentive-approach ($M = 382.49_{(16.41)}$ ms) and no-incentive-avoid trials ($M = 373.63_{(15.65)}$ ms; win-approach: $M = 364.19_{(14.76)}$ ms; $t(34) = -4.78$, $p < .001$; $d = -.808$; $_{-26.09}-18.31_{-10.52}$; win-avoid: $M = 354.50_{(12.41)}$ ms; $t(34) = -5.74$, $p < .001$; $d = -.970$; $_{-25.90}-19.13_{-12.35}$; loss-approach: $M = 363.72_{(14.27)}$ ms; $t(34) = -5.04$, $p < .001$; $d = -.852$; $_{-26.34}-18.78_{-11.21}$; loss-avoid: $M = 352.54_{(14.63)}$ ms; $t(34) = -5.53$, $p < .001$; $d = -.934$; $_{-28.84}-21.09_{-13.33}$), with no difference between win and loss trials (all $p > .5$). In

sum, the response time data are in line with our previous behavioral study in that valence information biased specific actions only in target-informative blocks (i.e., valence-action biases), while facilitating responses regardless of action type in cue-informative blocks. An overview of the response time data distribution (Figure S1) and the significant response time results (Table S1) can be found in the Supplementary material.

3.1.2. Error rates

We observed a main effect of Valence ($F(2, 68) = 4.15$, $p = .020$; $\eta^2_p = .109$), resulting from significantly more errors in win ($M = .040_{(.014)}$%; $t(34) = 3.06$, $p = .004$; $d = .517$; $_{.003}.009_{.015}$) and loss ($M = .039_{(.016)}$%, $t(34) = 2.38$, $p = .023$; $d = .402$; $_{.001}.008_{.015}$) when compared to no-incentive trials ($M = .031_{(.012)}$%), but there were no differences between win and loss trials ($p > .8$). Moreover, avoid responses ($M = .032_{(.017)}$%) were more accurate than approach responses ($M = .041_{(.017)}$%; Action: $F(1, 34) = 5.20$, $p = .029$; $\eta^2_p = .133$), and responses in cue-informative blocks ($M = .011_{(.030)}$%) were more accurate than in target-informative blocks ($M = .062_{(.030)}$%; Block type: $F(1, 34) = 52.23$, $p < .001$; $\eta^2_p = .606$). These main effects were accompanied by multiple interaction effects, i.e., Valence x Action ($F(2, 68) = 7.36$, $p = .001$; $\eta^2_p = .178$), Valence x Block type ($F(1.41, 48.05) = 6.28$, $p = .008$; $\eta^2_p = .156$), and a higher-order interaction between Valence x Action x Block type ($F(2, 68) = 5.27$, $p = .007$; $\eta^2_p = .134$; Fig. 2B). The three-way interaction resulted from a significant differential impact of valence information on the required action in target-informative blocks (Valence x Action: $F(2, 68) = 6.86$, $p = .002$; $\eta^2_p = .168$), which was absent in cue-informative blocks ($p > .1$). Further exploration of this interaction in target-informative blocks revealed that win ($M = .079_{(.055)}$%; $t(34) = 5.22$, $p < .001$; $d = .882$; $_{.029}.048_{.067}$) and loss trials ($M = .060_{(.048)}$%; $t(34) = 3.29$, $p = .002$; $d = .556$; $_{.012}.031_{.049}$) triggered more errors as compared to the no-incentive condition ($M = .030_{(.027)}$%) in the avoid condition, with no difference between win and loss-avoid trials ($p > .1$). The respective contrasts in the approach condition of target-informative blocks were non-significant (all $p > .1$). For completion, the Action x Block type interaction was non-significant ($p > .5$). Together, similar to the response time data, interactions between incentive valence and action were exclusively observed in target-informative blocks. An overview of the error rate data distribution (Figure S1), and the significant error rate results (Table S2) can be found in the Supplementary material.

[Please add Fig. 2 around here]

### 3.2 fMRI results

3.2.1 Whole brain voxel-wise fMRI results

We assessed the main effect of Valence (both Global and Absolute; see *2.5 fMRI analysis*), the main effect of Action, and the interaction between factors, for cue and target events in cue-informative blocks, and for target events in target-informative blocks, separately. Significant activity modulations are illustrated in Figure 3 and detailed in Tables 1-3 (Table 1: Global Valence; Table 2: Action, Table 3: Absolute Valence x Action)[4].

*Cue-informative blocks - Cue-locked activity.* The Global Valence contrast ([win+loss] vs. no-incentive) and the respective post hoc contrast ([win+loss] > no-incentive) revealed increased activity in a network including caudate, pallidum, thalamus, anterior insula, SMA and pre-SMA, as well as the inferior temporal lobe and the cerebellar vermis for incentive compared to no-incentive cues. The opposite post hoc contrast (no-incentive > [win +loss]) yielded increased activity in a single cluster located in the hippocampus (Fig. 3A; Table 1A). The Absolute Valence contrast (win vs. loss) did not reveal any significant activations. The Action contrast (approach vs. avoid) and the associated post hoc test revealed that approach actions elicited higher activity in superior/medial frontal gyrus (motor cortex) when compared to avoid actions, while the opposite contrast revealed activations in parahippocampal gyrus and inferior temporal lobe (Fig. 3D; Table 2A). There were no significant interaction effects between Valence (Global and Absolute) and Action at cue onset at the conservative FWE-corrected threshold.

[4] It may be the case that significant activations in the midbrain have been missed due to commonly reduced signal strength in the midbrain for gradient-echo EPI-based BOLD imaging (Düzel et al., 2015). In the present study, this may apply to the whole brain voxel-wise results (based on inspection of the second level map of included voxels), while the ROI results remain relatively unaffected (based on the observed overlap between averaged EPI and ROI).

*Cue-informative blocks - Target-locked activity.* The Global Valence contrast ([win+loss] vs. no-incentive) and the respective post hoc test ([win+loss] > no-incentive) revealed increased activity

in inferior parietal cortex, caudate, and cerebellum in incentive when compared to no-incentive trials. The other post hoc contrast (no-incentive > [win +loss]), did not return any activations (Fig. 3B; Table 1B). The Absolute Valence contrast (win vs. loss) did not yield any significant modulations. The Action contrast (approach vs. avoid) and the respective post hoc test yielded increased activity for approach actions within cerebellum, postcentral gyrus, and posterior insula, while the opposite contrast (avoid vs. approach) revealed no activations (Fig. 3E; Table 2B). Finally, an interaction between Absolute Valence and Action was observed in a cluster in the cerebellum, encompassing parts of the vermis and lobe 4_5 (Fig. 3G; Table 3B). To explore the nature of this interaction, we extracted the average parameter estimates from this cluster for the different experimental conditions. The interaction reflects differential activity increase for targets requiring an approach response following loss compared to win cues, and the reverse (albeit numerically weaker) difference for targets that required an avoid response. There were no significant interaction effects between Global Valence and Action at target onset anywhere in the brain at the conservative FWE-corrected threshold.

*Target-informative blocks - Target-locked activity.* The Global Valence contrast ([win+loss] vs. no-incentive) and the respective post hoc test ([win+loss] > no-incentive) revealed increased activity in right caudate and bilateral inferior parietal cortex (Fig. 3C; Table 1C). There were no significant modulations based on the Absolute Valence contrast (win vs. loss). Differential Action modulations were observed in the precentral gyrus, cerebellum, and operculum. Direct contrasts revealed increased activity for approach versus avoid actions (with one additional cluster emerging in the paracentral lobe; Fig. 3F; Table 2C). In this block type, there were no significant interactions between Valence (Global and Absolute) and Action anywhere in the brain at the conservative FWE-corrected threshold.

[Please add Fig. 3 around here]

**Table 1.** Whole brain voxel-wise activations based on the Global Valence contrast ([win+loss] vs. no-incentive). Significant main effects and relevant post hoc contrasts are reported for cue (A) and target onsets (B) in cue-informative blocks, and target onsets in target-informative blocks (C).

| A. Cue-informative blocks - cue onsets | | | Coordinates (MNI) | | | | |
|---|---|---|---|---|---|---|---|
| Main effect | H | Brain region | X | y | z | F-value | k |
| Global Valence contrast [win+loss] vs. no-incentive | R | Caudate head | 12 | 6 | 2 | 53.39 | 106 |
| | R | Anterior insula | 34 | 22 | 4 | 43.04 | 162 |
| | R | Thalamus | 12 | -12 | 6 | 40.26 | 74 |
| | | | 6 | -20 | -2 | 29.77 | |
| | | | 12 | -14 | -2 | 26.43 | |
| | R | Vermis 3 | 2 | -48 | -20 | 34.79 | 38 |
| | L | Thalamus | -10 | -18 | 6 | 33.22 | 62 |
| | | | -4 | -22 | 0 | 29.10 | |
| | L | Anterior insula | -30 | 24 | 0 | 32.67 | 41 |
| | R | (Pre-)Supplementary motor area | 6 | 2 | 56 | 30.87 | 96 |
| | L | Pallidum | -10 | 6 | 0 | 30.63 | 14 |
| | L | Inferior temporal gyrus | -46 | -62 | -10 | 30.06 | 36 |
| Post hoc contrasts | | | | | | T-value | |
| [win+loss] > no-incentive | R | Caudate head | 12 | 6 | 2 | 7.31 | 127 |
| | R | Anterior insula | 34 | 22 | 4 | 6.56 | 185 |
| | R | Thalamus | 12 | -12 | 6 | 6.34 | 100 |
| | | | 6 | -20 | -2 | 5.46 | |
| | | | 12 | -14 | -2 | 5.14 | |
| | R | Vermis 3 | 2 | -48 | -20 | 5.90 | 49 |
| | L | Thalamus | -10 | -18 | 6 | 5.76 | 86 |
| | | | -4 | -22 | 0 | 5.39 | |
| | L | Anterior insula | -30 | 24 | 0 | 5.72 | 55 |
| | | | -34 | 16 | 0 | 4.88 | |
| | R | (Pre-)Supplementary motor area | 6 | 2 | 56 | 5.56 | 131 |
| | L | Pallidum | -10 | 6 | 0 | 5.53 | 18 |
| | L | Inferior temporal gyrus | -46 | -62 | -10 | 5.48 | 52 |
| | R | Inferior temporal gyrus | 44 | -58 | -12 | 5.07 | 9 |
| | R | (Pre-)Supplementary motor area | 14 | 6 | 68 | 4.93 | 5 |
| no-incentive > [win+loss] | R | Hippocampus | 28 | -10 | 18 | 5.17 | 5 |
| B. Cue-informative blocks - target onsets | | | Coordinates (MNI) | | | | |
| Main effect | H | Brain region | X | y | z | F-value | k |
| Global Valence contrast [win+loss] vs. no-incentive | L | Cerebellum crus 2 | -14 | -76 | -34 | 31.74 | 33 |
| | R | Cerebellum 8 | 24 | -58 | -42 | 29.04 | 25 |
| | L | Cerebellum crus 2 | -30 | -68 | -44 | 27.91 | 24 |
| | | | -36 | -64 | -40 | 25.05 | |
| | L | Cerebellum 6 | -6 | -82 | -16 | 27.81 | 47 |
| | L | Cerebellum crus 2 | -2 | -82 | -30 | 26.76 | |
| | R | Inferior parietal lobe | 54 | -40 | 52 | 26.42 | 22 |
| | | | 50 | -48 | 54 | 24.99 | |
| | L | Cerebellum 8 | -22 | -68 | -46 | 26.08 | 6 |
| | R | Caudate | 10 | -4 | 14 | 25.82 | 5 |
| Post hoc contrasts | | | | | | T-value | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| [win+loss] > no-incentive | L | Cerebellum crus 2 | -14 | -76 | -34 | 5.63 | 123 |
| | | | -6 | -82 | -16 | 5.27 | |
| | | | -2 | -82 | -30 | 5.17 | |
| | | Cerebellum 8 | 24 | -58 | -42 | 5.39 | 40 |
| | | Cerebellum crus 2 | -30 | -68 | -44 | 5.28 | 89 |
| | | | -22 | -68 | -46 | 5.11 | |
| | | | -36 | -64 | -40 | 5.01 | |
| | | Inferior parietal lobe | 46 | -54 | 54 | 5.24 | 49 |
| | | | 54 | -40 | 52 | 5.14 | |
| | | Thalamus | 10 | -4 | 14 | 5.08 | 10 |
| | | Thalamus | 2 | -10 | 14 | 5.05 | 8 |
| | | Middle frontal gyrus | 42 | 42 | 18 | 5.00 | 28 |
| | | Caudate | -18 | -6 | 22 | 4.93 | 5 |
| | | Inferior frontal gyrus | 54 | 14 | 18 | 4.88 | 15 |
| no-incentive > [win+loss] | | | | | | | |
| C. Target-informative blocks - target onsets | | | Coordinates (MNI) | | | | |
| Main effect | H | Brain region | X | y | z | F-value | k |
| Global Valence contrast | R | Caudate body | 10 | 2 | 4 | 33.24 | 26 |
| [win+loss] vs. no-incentive | L | Inferior parietal lobe | -32 | -62 | 44 | 32.86 | 232 |
| | | | -42 | -50 | 58 | 32.63 | |
| | | | -38 | -50 | 48 | 32.32 | |
| | R | Caudate body | 12 | 2 | 16 | 27.63 | 12 |
| | R | Inferior parietal lobe | 46 | -42 | 50 | 26.23 | 5 |
| Contrasts | | | | | | T-value | |
| [win+loss] > no-incentive | R | Caudate body | 10 | 2 | 4 | 5.77 | 59 |
| | | | 12 | 2 | 16 | 5.26 | |
| | L | Inferior parietal lobe | -32 | -62 | 44 | 5.73 | 308 |
| | | | -42 | -50 | 58 | 5.71 | |
| | | | -38 | -50 | 48 | 5.69 | |
| | R | Inferior parietal lobe | 46 | -42 | 50 | 5.12 | 15 |
| | L | Precentral gyrus | -40 | 6 | 34 | 4.99 | 9 |
| | L | Inferior parietal lobe | -48 | -38 | 44 | 4.98 | 11 |
| | R | Inferior parietal lobe | 38 | -48 | 44 | 4.86 | 7 |
| no-incentive > [win+loss] | | | | | | | |

*Notes.* H = hemisphere (L = left, R = right); k = cluster size. Brain regions labels represent local maxima. Only clusters surviving an FWE-corrected threshold of $p$ = .05, and consisting of at least five voxels are shown.

**Table 2.** Whole brain voxel-wise Action effects. Significant main effects and relevant post hoc contrasts are reported for cue (A) and target onsets (B) in cue-informative blocks, and target onsets in target-informative blocks (C).

| A. Cue-informative blocks - cue onsets | | | Coordinates (MNI) | | | | |
|---|---|---|---|---|---|---|---|
| Main effect | H | Brain region | X | y | z | F-value | k |
| Action contrast approach vs. avoid | L | Superior frontal gyrus | -18 | -30 | 64 | 49.45 | 347 |
| | L | Superior frontal gyrus | -16 | -20 | 72 | 35.46 | |
| | L | Medial frontal gyrus | -8 | -22 | 60 | 30.50 | |
| | R | Precentral gyrus | 24 | -26 | 64 | 34.49 | 62 |
| | L | Parahippocampal gyrus | -34 | -12 | -24 | 31.07 | 16 |
| | L | Inferior temporal gyrus | -42 | 2 | -32 | 29.86 | 6 |
| Post hoc contrasts | | | | | | T -value | |
| approach > avoid | L | Postcentral gyrus | -18 | -30 | 64 | 7.03 | 409 |
| | L | Superior frontal gyrus | -16 | -20 | 72 | 5.95 | |
| | L | Medial frontal gyrus | -8 | -22 | 60 | 5.52 | |
| | L | Precentral gyrus | 24 | -26 | 64 | 5.87 | 87 |
| avoid > approach | L | Parahippocampal gyrus | -34 | -12 | -24 | 5.57 | 19 |
| | L | Inferior temporal gyrus | -42 | 2 | -32 | 5.46 | 6 |
| | L | Parahippocampal gyrus | -26 | -10 | -14 | 4.98 | 6 |
| B. Cue-informative blocks - target onsets | | | Coordinates (MNI) | | | | |
| Main effect | H | Brain region | X | y | z | F-value | k |
| Action contrast approach vs. avoid | R | Cerebellum 8 | 26 | -44 | -52 | 44.56 | 72 |
| | L | Postcentral gyrus | -24 | -38 | 72 | 33.86 | 29 |
| Contrasts | | | | | | T-value | |
| approach > avoid | R | Cerebellum 8 | 26 | -44 | -52 | 6.68 | 86 |
| | L | Postcentral gyrus | -24 | -38 | 72 | 5.82 | 39 |
| | L | Postcentral gyrus | -16 | -38 | 78 | 5.20 | 6 |
| | - | Vermis 6 | 0 | -70 | -10 | 5.18 | 7 |
| | L | Posterior insula | -38 | -22 | 22 | 5.09 | 14 |
| avoid > approach | | | | | | | |
| C. Target-informative blocks - target onsets | | | Coordinates (MNI) | | | | |
| Main effect | H | Brain region | X | y | z | F -value | k |
| Action contrast approach vs. avoid | L | Precentral gyrus | -26 | -28 | 58 | 29.09 | 16 |
| | R | Vermis 6 | 4 | -62 | -22 | 28.60 | 19 |
| | R | Cerebellum 8 | 24 | -46 | -54 | 28.00 | 12 |
| | L | Rolandic operculum | -38 | -22 | 20 | 27.45 | 8 |
| Contrasts | | | | | | T -value | |
| approach > avoid | L | Precentral gyrus | -26 | -28 | 58 | 5.39 | 25 |
| | R | Vermis 6 | 4 | -62 | -22 | 5.35 | 31 |
| | R | Cerebellum 8 | 24 | -46 | -54 | 5.29 | 19 |
| | L | Rolandic operculum | -38 | -22 | 20 | 5.24 | 13 |
| | L | Paracentral lobe | -8 | -32 | 50 | 4.97 | 8 |
| avoid > approach | | | | | | | |

*Notes.* H = hemisphere (L = left, R = right); k = cluster size. Brain regions labels represent local maxima. Only clusters surviving an FWE-corrected threshold of $p$ = .05, and consisting of at least five voxels are shown.

**Table 3.** Whole brain voxel-wise interaction between Absolute Valence (win vs. loss) and Action. Significant interaction effects and relevant post hoc contrasts are reported for cue (A) and target onsets (B) in cue-informative blocks, and target onsets in target-informative blocks (C).

| A. Cue-informative blocks - cue onsets | | | Coordinates (MNI) | | | | |
|---|---|---|---|---|---|---|---|
| Interaction effect | H | Brain region | X | y | z | F-value | k |
| Absolute Valence x Action | | | | | | | |
| **B. Cue-informative blocks - target onsets** | | | **Coordinates (MNI)** | | | | |
| Interaction effect | H | Brain region | X | y | z | F-value | k |
| Absolute Valence x Action | L | Vermis 3 | -2 | -44 | -12 | 28.95 | 16 |
| | L | Cerebellum 4_5 | -6 | -50 | -4 | 26.20 | 8 |
| Post hoc contrasts | | | | | | T-value | |
| [win-approach - win-avoid] > [loss-avoid - loss-approach] | | | | | | | |
| [loss-approach - loss-avoid] > [win-avoid - win-approach] | L<br>L | Vermis 3<br>Cerebellum 4_5 | -2<br>-6 | -44<br>-50 | -12<br>-4 | 5.38<br>5.12 | 42 |
| **C. Target-informative blocks - target onsets** | | | **Coordinates (MNI)** | | | | |
| Main effect | H | Brain region | X | y | z | F -value | k |
| Absolute Valence x Action | | | | | | | |

*Notes.* H = hemisphere (L = left, R = right); k = cluster size. Brain regions labels represent local maxima. Only clusters surviving an FWE-corrected threshold of $p = .05$, and consisting of at least five voxels are shown.

### 3.2.2 ROI results

In addition to the whole brain voxel-wise analysis, we performed more targeted anatomy-based ROI analyses (Astrakas & Argyropoulou, 2010) across five pre-defined ROIs (i.e., ACC, pre-SMA, dlPFC, vSTR, SN/VTA; for details see *1. Introduction* and *2.5 fMRI analysis*). We assessed main effects of Valence and Action as well as their potential interaction. In case of a higher-order interaction with the factor ROI, follow-up tests were performed in individual ROIs. Note that we did not explore the main effect of ROI as this is not relevant for the current research question, and, more importantly, global activity differences between these brain regions are not considered meaningful. The results of the cue-informative blocks (cue-locked and target-locked) and target-informative blocks (target-locked) are detailed in the subsequent paragraphs and illustrated in Figure 4 (cue-informative blocks: cue onsets: left column, target onsets: middle column; target-informative blocks: right column). An overview of significant results can be found in Table S3 (cue-informative blocks - cue locked), S4 (cue-informative blocks - target locked), and S5 (target-informative blocks - target locked) of the Supplementary material, along

with data distributions (Figure S2). For a comprehensive data overview, the statistical output of the ROI analysis (including exact p-values of non-significant tests), can be found on the Open Science Framework page (https://osf.io/yaf4n/).

*Cue-informative blocks - Cue-locked ROI activity (Fig. 4, left column).* The analysis revealed a main effect of Valence ($F(2, 68) = 6.68$, $p = .002$; $\eta^2_p = .164$), with increased activity for win ($M = -.290_{(.269)}$; $t(34) = 3.29$, $p = .002$, $d = .556$; $_{.091}.239_{.386}$) and loss ($M = -.379_{(.246)}$; $t(34) = 2.21$, $p = .034$, $d = .374$; $_{.012}.150_{.288}$) as compared to no-incentive trials ($M = -.529_{(.311)}$), but no difference between win and loss trials ($p > .1$). Moreover, we observed a significant Action x ROI interaction ($F(3.10, 105.51) = 4.47$, $p = .005$; $\eta^2_p = .116$), which was further qualified by a significant interaction encompassing all factors (Valence x Action x ROI; $F(3.55, 41.98) = 2.88$, $p = .022$; $\eta^2_p = .078$). Based on these interactions with ROI, the main effect of Action as well as the Valence x Action interaction were assessed within individual ROIs. In ACC (Fig. 4A), we found no main effect of Action ($p > .9$), but a significant Valence x Action interaction ($F(1.68, 57.02) = 4.18$, $p = .026$; $\eta^2_p = .110$), reflecting a significant activity increase for win-approach cues ($M = -.615_{(.510)}$) as compared to no-incentive-approach cues ($M = -.993_{(.497)}$; $t(34) = 3.28$, $p = .002$; $d = .555$; $_{.144}.378_{.612}$). Further, activity for no-incentive-approach cues was significantly lower compared to no-incentive-avoid cues ($M = -.728_{(.405)}$, $t(34) = -2.35$, $p = .025$; $d = -.397$; $_{-.496}-.266_{-.036}$). The remaining post hoc tests in this comparison were non-significant (all $p > .06$). The same analysis in the pre-SMA (Fig. 4D) revealed that both the main effect of Action and the Valence x Action interaction were non-significant (all $p > .3$). In vSTR (Fig. 4J), we found a main effect of Action ($F(1, 34) = 12.95$, $p = .001$; $\eta^2_p = .276$), with increased activity for avoid ($M = -.718_{(.296)}$) compared to approach cues ($M = -.973_{(.296)}$). The interaction between Valence and Action was non-significant in this region ($p > .06$). In SN/VTA (Fig. 4M), the main effect of Action and the Valence x Action interaction were non-significant (all $p > .2$). Finally, the dlPFC ROI featured no significant activity modulations (all $p > .9$; Fig. 4G). For completion, the remaining F-tests for cues in cue-informative blocks were non-significant (Action: $p > .3$; Valence x Action: $p > .1$; Valence x ROI: $p > .09$).

To summarize, during cue processing, we observe global activity increases across ROIs for incentive valence as compared to no-incentive trials. One region, the ACC, displayed a

valence-action interaction, which was mainly driven by increased activity for win-approach cues as compared to no-incentive-approach cues.

*Cue-informative blocks - Target-locked ROI activity (Fig. 4, middle column).* Across ROIs, we observed a Valence x Action interaction ($F(2, 68) = 3.25$, $p = .045$; $\eta^2_p = .087$), arising from a differential activity increase for loss-approach ($M = .645_{(.426)}$) as compared to both loss-avoid ($M = .405_{(.483)}$; $t(34) = 2.17$, $p = .037$; $d = .366$; $_{.015}.241_{.466}$) and win-approach trials ($M = .381_{(.410)}$; $t(34) = 2.77$, $p = .009$; $d = .468$; $_{.070}.264_{.458}$). In contrast, no-incentive avoid trials ($M = .361_{(.403)}$) elicited the lowest activity (as compared to loss-approach: $t(34) = -2.78$, $p = .009$; $d = -.470$; $_{-.493}$-$.285_{-.077}$). The remaining post hoc tests in this comparison were non-significant (all $p > .05$). Moreover, the analysis revealed an Action x ROI interaction ($F(2.89, 98.13) = 3.62$, $p = .017$; $\eta^2_p = .096$), which related to significantly increased activity for approach relative to avoid trials in ACC ($M = .154_{(.293)}$; Fig. 4B) compared to pre-SMA ($M = .030_{(.241)}$; Fig. 4E; $t(34) = 2.39$, $p = .022$; $d = .405$; $_{.019}.124_{.229}$) and dlPFC ($M = -.006_{(.269)}$; Fig. 4H; $t(34) = 2.82$, $p = .008$; $d = .477$; $_{.045}.161_{.276}$), as well as in vSTR ($M = .276_{(.442)}$; Fig. 4K) as compared to pre-SMA ($t(34) = 2.73$, $p = .010$; $d = .462$; $_{.063}.246_{.429}$) and dlPFC ($t(34) = 3.05$, $p = .004$; $d = .516$; $_{.094}.282_{.470}$). The remaining post hoc tests in this comparison were (including SN/VTA; Fig. 4N), were non-significant (all $p > .1$). For completion, the remaining F-tests for targets in cue-informative blocks were non-significant (Valence: $p > .4$; Action: $p > .08$; Valence x ROI: $p > .3$; Valence x Action x ROI: $p > .1$).

Taken together, during target presentation, we observed a relative activity increase for loss-approach targets. Although the data pattern seemed to differ across ROIs based on visual inspection (with a more pronounced Valence x Action interaction in ACC, vSTR, and SN/VTA), there was no significant higher order interaction with ROI (Valence x Action x ROI). We hence consider this interaction pattern as a fairly global response across the selected ROIs.

*Target-informative blocks - Target-locked ROI activity (Fig. 4, right column).* We observed an interaction between Valence and ROI ($F(5.02, 170.77) = 2.73$, $p = .021$; $\eta^2_p = .074$) and hence assessed the effect of Valence within individual ROIs. In ACC (Fig. 4C), win trials ($M = 1.008_{(.408)}$) were associated with higher activity as compared to no-incentive trials ($M = .749_{(.412)}$;

$t(34) = 2.43$, $p = .020$; $d = .411$; $_{.042}.259_{.475}$) and loss trials ($M = .801_{(.279)}$; $t(34) = 2.64$, $p = .012$; $d = .477$; $_{.048}.207_{.365}$), with no differences between loss and no-incentive trials ($p > .5$). In dlPFC (Fig. 4I), both win ($M = .637_{(.386)}$) and loss trials ($M = .519_{(.355)}$) were associated with higher activity as compared to no-incentive trials ($M = .348_{(.338)}$; win vs. no-incentive: $t(34) = 3.32$, $p = .002$; $d = .561$; $_{.112}.290_{.467}$; loss vs. no-incentive: $t(34) = 2.16$, $p = .038$; $d = .365$; $_{.010}.172_{.333}$). There was no difference between win and loss trials ($p > .2$). There were no significant differences between win, loss, and no-incentive trials within pre-SMA (Fig. 4F), vSTR (Fig. 4L) or SN/VTA (Fig. 4O; all $p > .06$). Moreover, we found an interaction between Action and ROI, which resulted from increased activity for approach versus avoid responses in ACC ($M = .108_{(.266)}$) compared to dlPFC ($M = -.048_{(.319)}$; $t(34) = 2.30$, $p = .028$; $d = .389$; $_{.018}.156_{.293}$), and in SN/VTA ($M = .203_{(.325)}$) compared to both pre-SMA ($M = .038_{(.241)}$; $t(34) = 2.60$, $p = .014$; $d = .440$; $_{.036}.165_{.293}$) and dlPFC ($t(34) = 3.11$, $p = .004$; $d = .526$; $_{.087}.251_{.415}$). The remaining post hoc tests were non-significant (all $p > .1$). For completion, the remaining F-tests for targets in target-informative blocks were non-significant (Valence: $p > .06$; Action: $p > .2$; Valence x Action: $p > .6$; Valence x Action x ROI: $p > .7$).

In sum, at the target onsets of target-informative blocks, two ROIs (ACC and dlPFC) featured increased activity for win as compared to loss and/or no-incentive trials (irrespective of action), and two ROIs (ACC and SN/VTA) featured increased activity for approach compared to avoid trials (irrespective of valence).

*Comparisons between event and block types.* The results of an exploratory analysis across different trial events and block types can be found in the Supplementary material. First, this analysis provides support for differential processing of valence and action information at cue versus target onsets within cue-informative blocks in that neural modulations were more region-specific at cue as compared to target onset. Second, we observed a significant valence-action interaction at target onset across both block types (cue-informative and target-informative), suggesting that the interaction pattern is similar (albeit only significant in cue-informative blocks; see main analysis). That said, we note that a formal comparison between these different event types is problematic based on inherent design differences. While informative cues and informative targets overlap with regard to relevant information, they differ in terms of trial

position and the processes triggered (at least task preparation vs. action implementation). Moreover, informative targets and non-informative targets overlap in terms of trial position, but are still entirely different in that one is merely a go signal while the other one is containing relevant valence-action information. In this regard, it is even more interesting that target events in the different block types seem to feature a common valence-action interaction pattern.

[Please add Fig. 4 around here]

## 4. Discussion

Incentive-valence signals can bias our behavior in that positive and negative stimuli map onto approach and avoidance actions, respectively, similar to emotional valence stimuli (Asci et al., 2019; Chen & Bargh, 1999; Freeman et al., 2014; Guitart-Masip et al., 2011; Phaf et al., 2014; Solarz, 1960). Specifically, across emotional and motivational manipulations it has been shown that participants are faster to initiate actions in general (Go trials), and in particular to perform approach movements, to positive/appetitive stimuli. Conversely, participants are better at withholding actions (NoGo trials), or performing avoid movements, when faced with negative/aversive stimuli. In turn, when the task requires an action that is incompatible with the presented stimulus valence (Go/approach-negative; NoGo/avoid-positive), performance is relatively impaired, which speaks to the notion of an automatic integration of valence and action information that can undermine goal-directed behavior. We recently showed that action biases triggered by incentive valence in an approach-avoidance task (win-approach; loss-avoid) are abolished when all the relevant information is provided by a cue before actual action implementation (Hoofs, Boehler, & Krebs, 2019). We interpreted this finding in terms of increased preparatory control during the cue-target interval. With the present fMRI study, we aimed to confirm this idea, and moreover explore whether valence and action information are still integrated on the neural level in this cuing context in terms of inherent valence-action mappings. The behavioral data alone (featuring mainly performance benefits for incentive-valence cues regardless of action) provide little insights into putative valence-action integration. And we note that previous related studies *have* reported behavioral valence-action biases triggered by pre-cues (e.g., Fini, Fischer, Bardi, Brass, & Moors, 2020; Hoofs, Prével, & Krebs,

2020). Here, we assessed neural activity modulations (both whole-brain voxel-wise and ROI approach) during cue and target processing in the cue-informative condition, and in comparison with the uncued target-informative condition. In accordance with neurocognitive mechanisms associated with incentive-valence cuing paradigms (reviewed in Braver et al., 2014), as well as those reported by earlier studies on valence-action biases (e.g., Asci et al., 2019; Guitart-Masip et al., 2011; Ly et al., 2016; Swart et al., 2018), our analysis was focused on regions implicated in cognitive control and response selection as well as those associated with incentive-valence processing - which are also partly overlapping. The behavioral data closely replicated our previous study[5] (Hoofs, Boehler, & Krebs, 2019), with valence-action biases in the target-informative condition (with benefits for valence-compatible actions and costs for valence-incompatible actions), but not in the cue-informative condition. The latter featured global facilitation by incentive-valence cues (win and loss), regardless of the required action.

### 4.1 Neural activity modulations triggered by valence-action cues

Whole brain voxel-wise analyses revealed that cues signaling incentive valence (win and loss) as compared to no incentive activated a network including the (mostly ventral) striatum (i.e., caudate head and pallidum), thalamus, anterior insula, and premotor cortex (SMA and pre-SMA). These modulations are well in line with previous studies using incentive cues (e.g., Braver et al., 2014; Krebs et al., 2012; Padmala & Pessoa, 2011), and indicative of ramping up cognitive resources in anticipation of the target onset. Similar incentive-valence effects were observed in the ROI analysis, with significantly increased activity for both win and loss trials when compared to no-incentive trials across all ROIs (i.e., main effect of valence, but no interaction with ROI). Based on these observations, it seems that the general motivational impact

[5] Although not directly relevant for the effects of interest, there is one global difference between the previous (Hoofs, Boehler, & Krebs, 2019) and the current behavioral data. While the closest related experimental variant of the former study featured similar performance for approach and avoid responses, the current data showed facilitation for avoid responses. This could possibly be explained by differences in joystick position. That is, while the joystick was placed horizontally in the behavioral lab context, it was positioned somewhat tilted in the MR scanner (fixated to upper leg that rested on a pillow). Consequentially, pull responses were now facilitated by gravity pulling at the joystick, while push responses needed overcoming of this.

of win and loss prospect is, to a large extent, comparable in the present task (Oldham et al., 2018; Xue et al., 2013). With regard to the mechanism, the widespread activity increase for incentive cues likely reflects a mixture of preparatory control and response selection processes. Specifically, considering that all relevant information is provided by the cue, and given the fairly short cue-target interval in most trials, participants will likely immediately prepare the action and get ready to respond (but see *4.2 Neural activity modulations triggered by targets following valence-action cues* for further qualification). In addition to these incentive valence effects, we found that anticipating and preparing approach actions (i.e., pushing the joystick forward) elicited higher premotor cortex activity (superior/medial frontal gyrus), while preparing avoid actions (pulling the joystick back) was associated with higher inferior temporal and parahippocampal activity. This pattern could be reflective of a generally lower (motor) control demand for avoid compared to approach actions considering that the latter regions have been linked to the default-mode network (Raichle, 2015).

The conservative whole brain analysis revealed no interaction between valence and action type during cue processing, suggesting that preparatory mechanisms to maximize incentive outcome are fairly independent of action type. However, the more targeted ROI analysis provided some evidence for the integration of valence and action information, above and beyond a shared motivational impact of win and loss cues. Specifically, in the ACC, activity was differentially increased for win-approach cues, and in particular when contrasted with no-incentive-approach cues. The ACC has, among other functions, been associated with value-based decision making (Rushworth et al., 2012; Shenhav et al., 2016; Ullsperger, Danielmeier, & Jocham, 2014; Wallis & Kennerley, 2011). Hence, the differential increase for win-approach trials might reflect the added value of evolutionary beneficial mappings (in that an approach action is more likely to garner reward). Although only speculative, this predominant coding of compatible valence-action mappings might be the driving factor of the behavioral bias observed in the uncued target-informative condition (for further discussion see *4.3 Neural activity modulations in target-informative blocks*). This notion also resonates with a recent observation that incentive stimuli directly increase response vigor, which is not always beneficial (Oudiette, Vinckier, Bioud, & Pessiglione, 2019).

Together, these data provide support for increased preparatory control triggered by incentive-valence cues regardless of action requirements, but also for an integration of valence and action information consistent with an evolutionary benefit during cue processing.

### 4.2 Neural activity modulations triggered by targets following valence-action cues

The present paradigm allowed us to assess neural activity modulations triggered by the subsequent targets, i.e., when the actions had to be implemented. Importantly, the target event in the cue condition merely served as response prompt and did not convey any additional information. In the whole brain analysis, targets following incentive cues when compared to no-incentive cues elicited higher activity in inferior parietal cortex, caudate, and cerebellum, with no substantial differences between the win and loss trials. Action-related activity modulations were mostly restricted to the cerebellum, with multiple dissociable clusters for approach (push towards) and avoid (pull away) actions. Intriguingly, this voxel-wise analysis revealed an interaction cluster in the vermis region of the cerebellum. Further inspection based on the extracted parameter estimates showed that this interaction was driven by differentially increased activity for loss-approach as compared to win-approach actions, and the reverse pattern for avoid actions. Although we did not have specific predictions regarding the cerebellum, this is an interesting observation. Contemporary views of the cerebellum postulate a modulatory role in motor processes, and in particular the flexible initiation and termination of actions (Miall, 2013; Miquel, Nicola, Gil-Miravet, Guarque-Chabrera, & Sanchez-Hernandez, 2019). Relatedly, the cerebellum has been linked to impulsivity and response inhibition, inspired by research on attention deficit hyperactivity disorder. Specifically, it seems that reduced engagement of the cerebellum (together with prefrontal regions) is related to deficits in inhibitory control and executive functioning in general (Miquel et al., 2019; Stevens, Pearlson, Calhoun, & Bessette, 2018). Based on these views and previous observations, the activation pattern in the cerebellum might be related to inhibiting the predominant action triggered by win and loss stimuli and promoting the non-dominant action.

In addition, the ROI analysis in key regions implicated in cognitive control and incentive-valence processing revealed a similar interaction between valence and action, and in particular a differential increase for loss-approach actions. Intriguingly, although there were numerical

differences in this pattern between ROIs, there was no higher-order interaction with ROI (Valence x Action x ROI), signifying a fairly global response, and we will hence not discuss specific functional contributions from the different regions (numerically, it was most apparent in ACC, vSTR, and SN/VTA). Very generally, this pattern is in line with the idea that valence-incompatible actions require more neural resources compared to intuitive, valence-compatible actions, in that it parallels activity in (re-active) conflict resolution paradigms where more cognitive resources are needed in the face of conflicting inputs and/or responses (Garavan et al., 2003; Miller & Cohen, 2001; Ridderinkhof, Van Den Wildenberg, Segalowitz, & Carter, 2004). This is striking given that in this context (cue condition), participants are able to fully prepare their action before the target onset - and a substantial part of the cuing data is indicative of increased preparatory activity for incentive trials (regardless of action). Together, these modulations indicate that the absence of behavioral valence-action biases in the current paradigm is not a consequence of passing time and/or preparatory control processes alone (cue-locked), but that ad-hoc adjustments at the moment of action implementation may contribute to goal-directed behavior (target-locked). The observation that the interaction across ROIs is mainly driven by loss-approach versus win-approach trials is interesting and was not predicted. We speculate that this might be related to differences in global action invigoration in terms of behavioral activation versus inhibition (Carver & White, 1994) - in addition to the actual direction. Specifically, negative valence signals can trigger avoid responses (which include action invigoration), but also inaction. In contrast, positive valence is thought to invigorate actions globally, and approach actions in particular. Hence, it is possible that it requires more neural resources to perform a loss-approach action, not only because of the non-intuitive direction, but also because it is not intuitive to perform an action at all.

The observation of increased neural resource allocation for valence-incompatible as compared to valence-compatible actions also resonates with previous studies investigating valence-induced conflicts. For instance, Aupperle and colleagues found increased activity in a network including ACC, dlPFC, and caudate when participants were faced with high compared to low conflict decisions in an approach-avoidance conflict task (Aupperle, Melrose, Francisco, Paulus, & Stein, 2015). Further, in a paradigm in which reward prospect was signaled by emotional facial expressions, we found increased ACC activity when participants had to respond to incompatible reward-emotion mappings (Park et al., 2018).

### 4.3 Neural activity modulations in target-informative blocks

The analysis of the uncued target condition revealed main effects only - both in the whole brain voxel-wise as well as within the ROIs. Incentive versus no-incentive targets, and in particular win targets, were associated with increased activity in dorsal striatum, inferior parietal lobe (voxel-wise analysis), as well as ACC and dlPFC (ROI analysis), which is consistent with increased attention to reward-related target stimuli (Asci et al., 2019; Krebs, Boehler, Egner, & Woldorff, 2011). Moreover, approach as compared to avoid actions elicited significantly higher activity compared to avoid actions in premotor regions and the cerebellum (voxel-wise analysis), as well as ACC and SN/VTA (ROI analysis). This latter finding is in line with two previous related studies (Asci et al., 2019; Guitart-Masip et al., 2011) that mainly observed main effects of action in this region.

The absence of any interaction between valence and action in the target-informative condition is surprising, given that this is the context in which we observed valence-action biases at the behavioral level. The most likely reasons for the absence of an interaction in the present target condition are lack of power and the intermixing of different neural signatures. First, the complex design with many conditions may have reduced the probability of observing an interaction, especially at the conservative whole-brain level (see also *4.4 Limitations*). Importantly, however, the valence-action interaction in the ROI analysis is observed across target onsets of both block types (see *Supplementary Material*), indicating that neural modulations triggered by targets in target-informative condition are similar to the cue-informative condition, albeit not significant. Second, the target condition suffers from a stronger intermixing of different processes as initial evaluation of incentive valence coincides with action implementation. And if a region is involved in multiple processes, the neural signatures could average out if they go in opposite directions. To provide two examples, ACC and SN/VTA have both been associated with valence processing and resource allocation in general, and display opposite patterns for cue and target events in the cue condition. In addition to these issues, it is important to consider why we observed a valence-action interaction in our previous related study (Asci et al., 2019), despite similar intermixing of different processes. The most feasible explanation is that the Go/NoGo task emphasizes valence-action compatibility effects as it is contrasting response activation with response withholding, while the approach avoidance task

contrasts actions that both require action initiation. Incompatible trials in the former would hence be more demanding, leading to a stronger, observable interaction at the neural level (above and beyond other involved processes).

All this being said, the observation of valence-action interactions at the neural level in the target condition is in our view not a prerequisite for the interpretation of the cue condition (the main research question). First and foremost, the behavioral data clearly shows evidence for a valence-action bias in one condition and not in the other, we do not see a convincing alternative explanation for the performance pattern in the target condition. And related to this, we do find indications of valence-action compatibility (a "neural bias" if you will) in the cue condition itself. The particular interaction at cue level in ACC (with increased activity for win-approach trials) is in line with the predominant coding of valence-compatible actions (in terms of a higher reward probability from an evolutionary perspective), which is the assumed reason for behavioral valence-action biases in the first place.

### 4.4 Limitations

Considering the data of the voxel-wise analysis and the ROI analysis together, it seems that the design might have been slightly underpowered. Indeed, the design entails many conditions, and we potentially sacrificed power for the analysis of the cue condition (main focus) by including the target-informative blocks. However, this was necessary to assess the presence versus absence of valence-action biases in the present paradigm (target-informative condition serving as a baseline) and replicate the task context of the precursor study which likely has an influence on how participants approach the task globally.

Another issue is the interpretation of the no-incentive trials. In some data, they form the baseline for incentive effects, while at other times they end up in the middle between win and loss (interaction between Absolute Valence and Action), or behave more like loss trials, probably due to a negative connotation in the context of win. And more technically, while the voxel-wise analysis entails one test that includes no-incentive trials (Global Valence contrast) and one that ignores them (Absolute Valence contrast), the ROI analysis includes all possible valence and interaction effects in one model due to the different nature of statistical testing.

Last, we emphasize that the current inferences on the involvement of (pro-active and re-active) control mechanisms are based on neural correlates and may not reflect causal relationships (neither between neural data and behavior, nor between neural modulations of different regions). Effective connectivity approaches, such as Dynamic Causal Modeling (DCM; Friston, Harrison, & Penny, 2003), would help to address this common problem in neuroimaging research. However, the current design with multiple conditions, multiple trials events, different block types, and many involved brain regions features an enormous number of degrees of freedom in model creation. A simplified experiment with clear hypothesis about effective connectivity based on the current data would make for an interesting follow up experiment but is beyond the scope of the present study. That said, even if the current data does not allow to verify different mechanistic alternatives, the observed interaction patterns in the cue condition in the least provide evidence for an integration of valence and action information.

### 4.5 Conclusion and integration

Above and beyond global preparatory activity across a wide network triggered by incentive cues, we found differentially increased activity for compatible win-approach cues as compared to no-incentive approach cues in ACC, as well as for targets following incompatible loss-approach cues relative to win-approach cues in the cerebellum and across all ROIs. This compatibility effect at target level is intriguing, especially given that all information is already provided by the cue. With regard to our research question, these data seem to suggest that behavioral facilitation in incentive trials is not merely the result of passing time and/or preparation, but that additional neural resources are allocated during the implementation of valence-incompatible actions. This is striking considering that participants only need to execute an already planned action. Moreover, the differential activity for valence-compatible actions during cue processing is indicative of an integration in terms of a predominant coding of valence-compatible actions (win-approach) based on an evolutionary benefit (which may be the very basis of valence-action biases in the first place). In general, the observation of neural valence-action interactions in the cue condition goes beyond the conclusions based on the behavioral data, which featured behavioral facilitation in incentive trials, regardless of the required action. In addition to these basic insights, the present observations may be relevant for real-life behavior in that even in a situation in which a

person is well prepared to e.g., resist an appetitive (but maladaptive) behavior, the appropriate action (e.g., avoidance response) still requires extra resources. In other words, the data show that the effort does not stop with the decision process, but extends to action implementation.

In contrast to previous related studies, the present paradigm (and especially the cue condition) allows a more fine-grained dissociation of different processes on a temporal scale - which is in contrast to previous related studies (Asci et al., 2019; Guitart-Masip et al., 2011). While the latter study (Guitart-Masip et al., 2011) did not assess neural activity during action implementation (or no-action) and focused on subcortical regions, the former (Asci et al., 2019) could not dissociate between evaluative processes and action implementation since all information was presented at the moment of the target (i.e., no cues). Moreover, both previous studies employed a Go/NoGo task, which is different from the present approach/avoidance paradigm which requires matched action involving opposing directions (e.g., pull/push) rather than probing execution versus withholding of an action. Hence, it is not surprising that the main effect of action (vs. no action) is much more pronounced in the previous studies, and may partly overshadow other more, subtle effects. That said, given the similarities in the behavioral data between the present study and the previous ones using Go/NoGo manipulations, compatibility effects between incentive valence and action tendencies seem to arise regardless of how approach and avoidance are framed exactly (approach/Go; avoid/NoGo). What differs, however, is that avoid actions do not only need to be "prepared" (if at all, see Schevernels, Bombeke, Krebs, & Boehler, 2016 for further discussion), but also executed, which renders them more comparable to approach responses in terms of action invigoration. Finally, the target condition, in which valence-action biases impair task performance, did not reveal indications for valence-action integration on the neural level. As discussed above, this could well be due to a lack of power in combination with intermixed neural processes that might cancel each other out on average. For an exploratory comparison across cue and target conditions and trial events, see the Supplementary material.

## 5. Funding

This study was supported by a starting grant of the European Research Council (ERC) under the Horizon 2020 framework (grant No. 636116 awarded to RMK).

## 6. Competing interests

The authors have no competing interests to declare.

## 7. Acknowledgements

We wish to thank two anonymous reviewers for their constructive comments on our manuscript.

## 8. Data availability

The de-identified behavioral and fMRI data, analysis scripts, and other study materials are available via the Open Science Framework page: https://osf.io/yaf4n/

## 9. Supplementary material

The Supplementary material includes task instructions, detailed overviews of the statistical output of the behavioral (Tables S1 and S2) and ROI analyses (Tables S3-S5), data distribution plots of the behavioral (Figure S1) and ROI data (Figure S2), and the results and discussion of an exploratory analysis comparing the different block types and onset types.

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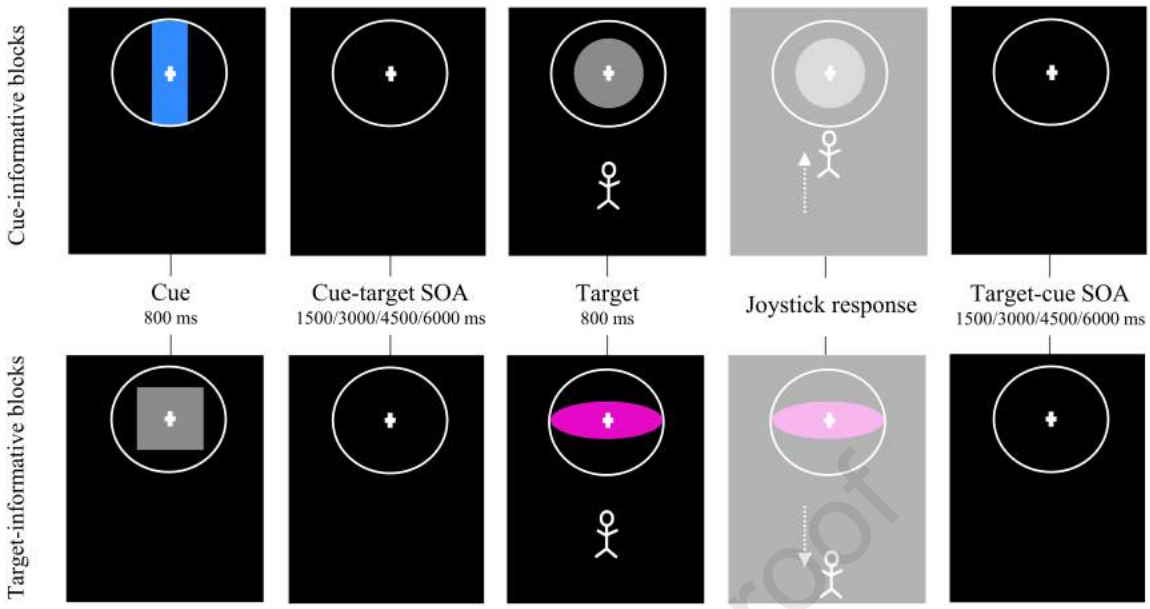
## Figure legends

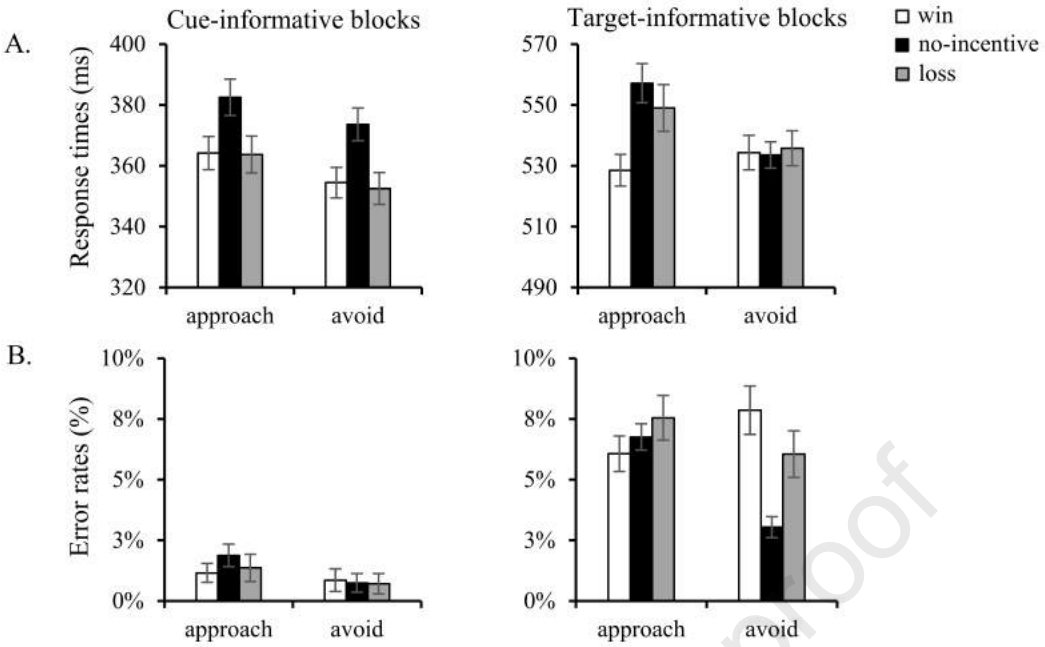
**Figure 1.** Schematic depiction of trials in cue-informative (top) and target-informative blocks (bottom). Both valence (stimulus color) and action information (stimulus orientation) were linked to either the cues or the targets in discrete blocks of 20 trials. The respective other event (in gray) only provided temporal information in that targets in cue-informative blocks signaled the moment of response execution, while cues in target-informative blocks signaled the start of the trial. The action-congruent manikin movement of the approach/avoid responses (indicated by gray shading) was only presented during the practice runs but not during the actual experiment inside the MR scanner to avoid contributions from explicit feedback processing to the target-locked neural activity.

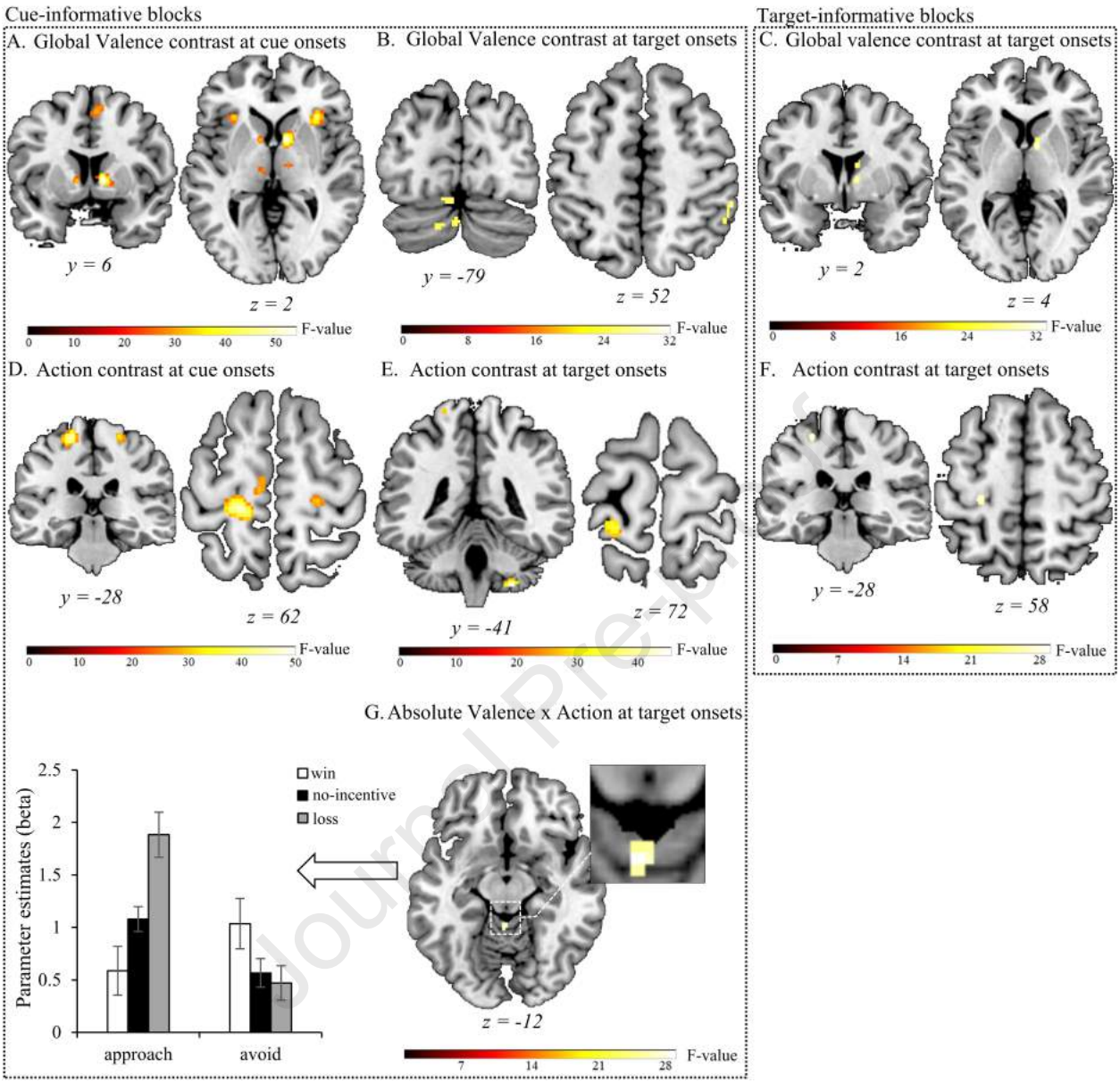
**Figure 2.** Response times (A) and error rates (B) corresponding to the cue-informative blocks *(left)* and target-informative blocks *(right)* for the different types of Valence (win; no-incentive; loss) and Action (approach; avoid). Note that due to the strong main effect of Block type on RT, the y-axis range differs between block types for better visibility of the within-block effects. *Error bars* indicate ± one within-subject standard error (Cousineau-Morey method, for more information see O'Brien & Cousineau, 2015).

**Figure 3.** Results of the whole brain voxel-wise analysis (FWE corrected at cluster level $p < .05$). Slices are selected to illustrate the most relevant activation clusters. For a detailed overview, see Tables 1-3. *Error bars* indicate ± one within-subject standard error.

**Figure 4.** Estimated activity modulations of the cue (left) and target onsets (middle) in cue-informative blocks, and the target onsets in target-informative blocks (right) within three ROIs implicated in cognitive control and response selection (ACC, pre-SMA, dlPFC), and two ROIs implicated in valence processing (vSTR and SN/VTA). Within each plot, the different bars correspond to the types of Valence (win; no-incentive; loss) and Action (approach; avoid). All masks are displayed on the generic ch2better template, except for the enlarged SN/VTA region which is superimposed on the group-averaged T2 scan for better anatomical localization. *Error bars* indicate ± one within-subject standard error.






Cue-informative blocks
Target-informative blocks
A. Global Valence contrast at cue onsets
B. Global Valence contrast at target onsets
C. Global valence contrast at target onsets
y = 6
z = 2
y = -79
z = 52
y = 2
z = 4
F-value
0 10 20 30 40 50
0 8 16 24 32
D. Action contrast at cue onsets
E. Action contrast at target onsets
F. Action contrast at target onsets
y = -28
z = 62
y = -41
z = 72
y = -28
z = 58
0 10 20 30 40 50
0 10 20 30 40
0 7 14 21 28
G. Absolute Valence x Action at target onsets
Parameter estimates (beta)
2.5
2
1.5
1
0.5
0
win
no-incentive
loss
approach
avoid
z = -12
7 14 21 28