



## Habit strength is predicted by activity dynamics in goal-directed brain systems during training



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### ABSTRACT

Previous neuroscientific research revealed insights into the brain networks supporting goal-directed and habitual behavior, respectively. However, it remains unclear how these contribute to inter-individual differences in habit strength which is relevant for understanding not only normal behavior but also more severe dysregulations between these types of action control, such as in addiction. In the present fMRI study, we trained subjects on approach and avoidance behavior for an extended period of time before testing the habit strength of the acquired stimulus-response associations. We found that stronger habits were associated with a stronger decrease in inferior parietal lobule activity for approach and avoidance behavior and weaker vmPFC activity at the end of training for avoidance behavior, areas associated with the anticipation of outcome identity and value. VmPFC in particular showed markedly different activity dynamics during the training of approach and avoidance behavior. Furthermore, while ongoing training was accompanied by increasing functional connectivity between posterior putamen and premotor cortex, consistent with previous assumptions about the neural basis of increasing habitualization, this was not predictive of later habit strength. Together, our findings suggest that inter-individual differences in habitual behavior are driven by differences in the persistent involvement of brain areas supporting goal-directed behavior during training.

When we learn that a certain behavior in a specific stimulus context leads to specific consequences, an association is built between the response and the outcome in the respective context (R-O), which constitutes the prerequisite for goal-directed behavior. This knowledge enables us to purposefully choose this response when the consequence is desired. At the same time, an association can be formed between the stimulus and response (S-R), building the basis for habitual, stimulus-driven behavior which is independent of the outcome. It is assumed that both response selection processes, goal-directed and habitual, are simultaneously involved when we choose an action, but with variable contributions depending on the circumstances (Lee, Shimojo, & O'Doherty, 2014): When stimulus-response-outcome contingencies and the desirability of the outcome are stable, then after sufficient repetition, behavior becomes increasingly habitual (Dickinson, 1985), rendering responses faster and less resource demanding but also inflexible (Seger and Spiering, 2011).

To test whether behavior is indeed controlled by S-R associations in contrast to R-O associations, outcome devaluation or contingency degradation procedures are typically employed (Dickinson, 1985): By either making the outcome undesirable or removing the contingency

between response and outcome, it can be tested to what degree subjects adjust their response frequency, indicating goal-directed, outcome-controlled behavior, or continue to perform the habitual response.

On the neural level, goal-directed and habitual behaviors are assumed to be supported by separate, albeit interacting, networks. A large body of research has demonstrated that goal-directed behavior relies on several key regions, notably the ventromedial prefrontal cortex (vmPFC) (de Wit et al., 2009; Noonan et al., 2011; Wunderlich et al., 2012), inferior parietal lobule (Gläscher, Daw, Dayan, & O'Doherty, 2010; Liljeholm, Dunne, & O'Doherty, 2015; Zwosta et al., 2015) and the (anterior) caudate nucleus (Balleine et al., 2009; Brovelli et al., 2011; Liljeholm, Tricomi, O'Doherty and Balleine, 2011; Ruge and Wolfensteller, 2013; Yin et al., 2005). On the other hand, the formation of S-R-associations as well as habitual responding are assumed to be related to the (posterior) putamen (Brovelli et al., 2011; Tricomi, Balleine, & O'Doherty, 2009; Wunderlich et al., 2012) connected to the premotor and motor cortices (de Wit et al., 2012; Yin and Knowlton, 2006).

The most convincing evidence for this functional dissociation between caudate and putamen comes from animal studies which showed

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that lesions or chemical deactivation of rodent homologues of caudate nucleus and putamen led to reductions in goal-directed and habitual behavior, respectively (Yin et al., 2004; Yin et al., 2005). For humans, however, evidence is correlational and more ambiguous as the reported training-related changes in putamen activity are heterogeneous across studies: In a variety of different paradigms with different training lengths, putamen activity was sometimes found to increase during training (Brovelli et al., 2011; Tricomi et al., 2009) and sometimes to decrease (Gillan et al., 2015; Liljeholm et al., 2015).

Furthermore, it remains open how changes in brain activity during training are actually related to habit strength expressed in overt behavior. A previous study has found evidence for a negative correlation of interindividual differences in habitual behavior with structural caudate-vmPFC connectivity and a positive correlation with structural putamen-premotor connectivity (de Wit et al., 2012). However, these correlations could also be driven by processes occurring at the stage of testing rather than during training, i.e. reflecting inter-individual differences in the ability to flexibly suppress habits.

Several studies investigating the neural correlates of factors leading to increased habitual behavior found that they were related to an impairment of the goal-directed system rather than the habitual system. For example, the pharmacological manipulation of stress hormones, which was accompanied by stronger habitual behavior, selectively impaired goal-directed systems during training (Schwabe et al., 2012). Furthermore, patients with obsessive compulsive disorder, who displayed increased habitual behavior, showed changes in the goal-directed system (Gillan et al., 2015). An animal study, which found that lesions in the infralimbic cortex rendered behavior more goal-directed, led to the hypothesis that habitual behavior is actually characterized by a suppression of the goal-directed system (Coutureau and Killcross, 2003). Together, these studies raise the question whether the expression of habitual behavior might mainly be predicted by changes in the goal-directed system rather than the habitual system.

Hence, the present study aimed at investigating the neural processes during extended training of behavior and their predictive value for habit strength as expressed during a consecutive test phase. So far, the vast majority of studies investigating the transition of goal-directed into habitual behavior focused on approach, i.e. rewarded behavior, while avoidance behavior has gained far less attention. Moreover, it has been mostly studied in respect to neural processes underlying its initial acquisition (e.g. Cox et al., 2015; Jocham et al., 2014; Kim, Shimojo, & O'Doherty, 2006; Palminteri et al., 2012; Schlund et al., 2011) rather than extended training (but Gillan et al., 2015) and habitual approach and avoidance behavior have not been directly compared yet. This leads to the open question whether previous findings are specific for approach behavior or also apply to avoidance behavior.

We extensively trained subjects on actions which were either rewarded or not punished while neural processes were measured with fMRI. Consecutively, habit strength was tested by assessing how strongly these habits interfered with the selection of goal-directed actions, acquired for the same stimuli in a preceding learning session prior to the training session.

Given the findings of previous studies mentioned above, inter-individual differences in habit strength could be due to the differential contributions of two complementary mechanisms. At the outset of training, behavior is assumed to be strongly controlled by the goal-directed system, that is, by processes linking S-R associations and (the anticipation of) reward or the absence of punishment. Across practice, the evolution of inter-individual differences in habit strength might in part be due to differences in how much the goal-directed system's involvement is decreasing and in part it might be due to increasing S-R strengthening itself supported by the habitual system.

## Materials and methods

### Subjects

The sample consisted of 53 subjects (29 female, 24 male; mean age: 23.5 years, range 19–32 years). All subjects were right-handed, neurologically healthy and had normal or corrected vision including normal color vision. The experimental protocol was approved by the Ethics Committee of the Technische Universität Dresden. All subjects gave written informed consent prior to taking part in the experiment and they were compensated with 8€ per hour in addition to the money they gained during the experiment.

### Experimental procedure

The experimental paradigm consisted of three consecutive phases. During the first phase, which was performed outside of the scanner, goal-directed behavior was established. In the second phase, which was performed inside the MRI scanner, habits were induced. Finally, in the third phase, habits and goal-directed behavior were put into competition in order to test habit strength.

*Phase 1: Establishment of goal-directed behavior.* The first part of the experiment was performed outside of the MRI scanner and aimed at establishing a representation of hierarchical R-O associations as the foundation of goal-directed behavior. The task was based on a modified version of a previously established experimental protocol (Zwosta et al., 2013), such that R-O contingencies for one type of stimuli were inverted for the other type of stimuli in order to prevent the formation of habits.

Ten stimuli grouped into five “artificial” and five “natural” stimuli were used. The stimuli were black-and-white, vertically symmetrical icons of different objects (natural stimuli: tree, snowflake, cow, mushroom, lungs; artificial stimuli: scissors, computer mouse, car, cupboard, ball). Responses were made using a keyboard, by pressing the key “D” with the left index finger or the key “K” with the right index finger. Responding to a stimulus from one group of stimuli (e.g. artificial) with the right key led to a blue outcome color and responding with the left key led to an orange outcome. This R-O association was inverted for the other group of stimuli (e.g. natural), such that pressing the right key led to an orange outcome and pressing the left key led to a blue outcome (see Fig. 1A). This particular task setup was chosen in order to minimize habituation processes during this phase. Thus, for each stimulus each of the two responses was equally often correct (and reinforced by the absence of error feedback) and hence, only the combination of the intended goal (i.e., the anticipated color outcome) together with the stimulus determined the response.

The assignment of the R-O contingencies to the groups of stimuli as well as the order in which the groups were instructed was counter-balanced across subjects.

Phase 1 started with an instruction screen depicting all stimuli belonging to each group and the R-O relationships assigned to them. Afterwards, the task was explained by text and illustrations. The experimenter stayed with the participant during the instruction phase and an additional 20 practice trials, answering potential questions, in order to make sure the participant had understood the instructions.

The first phase consisted of a total of 240 trials. Examples for the trial procedure are depicted in Fig. 1A. Each trial started with the presentation of a cue containing either the German words for “change” or “maintain”. This word was framed by a colored square displaying the present outcome color that was produced in the previous trial (or a random color in the first trial). After 1200 ms the cue was replaced by one of the ten stimuli. The subjects' task was now to press the key that would either change or maintain the current outcome color for the group the displayed stimulus belonged to. The response window was set to 2000 ms. As soon

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