



Distinct contributions of lateral orbito-frontal cortex, striatum, and fronto-parietal network regions for rule encoding and control of memory-based implementation during instructed reversal learning



Hannes Ruge*, Uta Wolfensteller

Department of Psychology, Technische Universität Dresden, Germany

ARTICLE INFO

Article history:

Received 1 July 2015

Accepted 4 October 2015

Available online 22 October 2015

Keywords:

Instruction

Cognitive control

Working memory

Goal neglect

fMRI

ABSTRACT

A key element of behavioral flexibility is to quickly learn to modify or reverse previously acquired stimulus–response associations. Such reversal learning (RL) can either be driven by feedback or by explicit instruction, informing either *retrospectively* or *prospectively* about the changed response requirements. Neuroimaging studies have thus far exclusively focused either on feedback-driven RL or on instructed *initial* learning of novel rules. The present study examined the neural basis of instructed RL as compared to instructed initial learning, separately assessing reversal-related *encoding* processes and reversal-related *control* processes required for implementing reversed rules under competition from the initially learned rules. We found that instructed RL is partly supported by similar regions as feedback-driven RL, including lateral orbitofrontal cortex (IOFC) and anterior dorsal caudate. Encoding-related activation in both regions determined resilience against response competition during subsequent memory-based reversal implementation. Different from feedback-driven RL, instruction-based RL relied heavily on the generic fronto-parietal cognitive control network – not for *encoding* but for reversal-related *control* processes during memory-based implementation. These findings are consistent with a model of partly decoupled, yet interacting, systems of (i) *symbolic* rule representations that are instantaneously updated upon instruction and (ii) *pragmatic* representations of reward-associated S–R links mediating the enduring competition from initially learned rules.

© 2015 Elsevier Inc. All rights reserved.

Introduction

The ability to quickly learn to modify or even reverse previously acquired stimulus–response (S–R) associations is a key element of behavioral flexibility. Upon reversal, an agent faces the challenge that reward is now gained by responding to a stimulus with an action that previously did *not* yield reward in that particular stimulus context. For instance, behavioral reversal is required in social interactions that might be different depending on the current context conditions. You might have initially learned that a bow is appropriate for greeting a Japanese colleague. However, this might be true only in a group of mostly Japanese people whereas you will have to reverse to western-style handshake with the same Japanese colleague in a group of mostly European people. Learning such a reversal might be driven by a negative feedback signal (e.g., caused by a mismatch between your Japanese colleague initiating a handshake while you are initiating a bow). Alternatively, someone might have explicitly informed you beforehand about the changed rules. This illustrates two fundamentally different learning scenarios that enable both the initial learning and the reversal learning

of rules. In the feedback-driven scenario, the correct response for a particular stimulus is determined *retrospectively* depending on whether the executed response yielded reward or not. This type of ‘trial-and-error’ learning has dominated previous research both in animals and humans. By contrast, in the instruction-based scenario, verbal instruction or observation of others’ performance specifies *prospectively* which response has to be selected upon a particular stimulus to gain reward. Despite its significant role especially for learning in humans, the latter type of learning has only recently attracted more widespread interest among researchers (for overviews, see Cole et al., 2013a; Wolfensteller and Ruge, 2012) following a few earlier approaches to the issue (Duncan et al., 2008; Luria, 1973; Monsell, 1996; Noelle, 1997; Petrides, 1997).

Imaging studies on instruction-based learning have so far exclusively focused on the initial acquisition of novel rules but not on the *instructed reversal* of previously acquired rules. By contrast, imaging studies on feedback-driven learning have examined both types of learning but the vast majority of studies have focused *either* on the initial learning of novel rules (Brovelli et al., 2008; O’Doherty et al., 2004; Toni et al., 2001) *or* on the repeated reversal of rules where the alternative rules were well known after a few cycles of reversing back-and-forth between them (Cools et al., 2002; Hampshire and Owen, 2006; Kringelbach and Rolls, 2003). These studies suggest that feedback-driven rule reversal is supported by several brain regions including

* Corresponding author at: Technische Universität Dresden, Fakultät Mathematik und Naturwissenschaften, Fachrichtung Psychologie, 01062 Dresden, Germany.
E-mail address: hannes.ruge@tu-dresden.de (H. Ruge).

most prominently a region at the border of the lateral orbitofrontal cortex (IOFC), adjacent anterior insular cortex, and adjacent anterior temporal cortex (for an early review, see [Kringelbach, 2005](#)).¹ Only few imaging studies have directly compared initial feedback-driven learning with feedback-driven reversal learning. [Ghahremani et al. \(2010\)](#) showed that the posterior IOFC was more strongly engaged during deterministic reversal learning than during initial learning. However, two other studies suggest the possibility that IOFC is also relevant for the feedback-driven initial acquisition of rules ([Budhani et al., 2007](#); [Tsuchida et al., 2010](#)) – a view that is line with a recently emerging view endorsing a less specific functional role of the lateral OFC ([Stalnaker et al., 2015](#)). Besides the IOFC, previous studies also imply the dorsal striatum in feedback-driven reversal learning vs. initial learning ([Bellebaum et al., 2008](#); [Ghahremani et al., 2010](#)) and single cell recording studies suggest the possibility that other regions like the dorsolateral prefrontal cortex might exhibit differences in the precise learning dynamics between initial learning and reversal learning ([Cromer et al., 2011](#); [Pasupathy and Miller, 2005](#)).

Despite extensive previous research on reversal learning the just briefly summarized main conclusions are still limited to the one and only type of feedback-driven learning that has dominated the existing literature. Hence, the present study set out to test whether lateral OFC and dorsal striatum might also be relevant for *instructed* reversal learning and if so whether there is a difference between instructed reversal learning and instructed initial learning of novel rules. More specifically our major interest was to disentangle the neural correlates of reversal-related *encoding* processes themselves from reversal-related *control* processes that enable the subsequent memory-based implementation of the reversed rules under competition from the initially learnt rules.

To this end, we employed a paradigm comprising multiple learning episodes. A new learning episode always started with a guided phase where the correct response upon a particular stimulus was explicitly indicated by an instruction cue enabling either the rapid initial encoding of S–R rules or the rapid reversed encoding of S–R rules. This was followed by an unguided, that is, memory-based rule implementation phase in the absence of explicit instruction cues. Our primary analysis rationale was based on testing hypotheses concerning different types of relationships between reversal-related BOLD activation and reversal-related behavioral performance indices. Specifically, if reversal-related activation during the guided phase reflected instruction-based reversed rule *encoding processes* it should be associated with subsequent memory-based reversal performance during the unguided implementation phase. The unguided implementation phase, however, should no longer be dominated by instruction-based encoding processes but rather by *control processes* that enable the memory-based implementation of the reversed rules under potential competition from the initially learned rules. Following [Kane and Engle \(2003\)](#) these control processes can be assumed to serve multiple purposes reflected in different performance indices. First, the current goal to implement the reversed rule instead of the initial rule has to be maintained. Failure to do so, i.e. ‘goal neglect’, should mainly be expressed in increased reversal cost in *errors*. Such goal maintenance processes should be negligible during the guided phase as subjects can completely rely on the explicit instruction cue. A second purpose of control processes during the unguided phase is to resolve response competition arising from simultaneously active initial and reversed rules which should be mainly expressed in increased reversal cost in *response times (RT)* independently of error reversal cost. Because response competition should be a direct function of how well the reversed rules were encoded relative to the residual strength of

the initially learned rules, encoding-related brain activation during the guided phase should primarily determine RT reversal cost.

Material and methods

Subjects

Data from 34 subjects were collected. The reported analyses were based on 27 participants (13 male, mean age = 24.6 ranging between 21 and 35 years). Two subjects were excluded due to strong susceptibility artifacts in orbitofrontal and ventral striatal areas. Five subjects were excluded due to high overall mean error rates beyond 1.5 times the inter-quartile-range of the error rate distribution. Effectively this led to the exclusion of subjects with an overall error rate exceeding 15%. All subjects gave written informed consent and the procedure was approved in line with the Declaration of Helsinki by the local institutional review board.

Procedure

Subjects were required to work through 28 instructed learning blocks (see [Fig. 1](#)). In odd-numbered blocks subjects had to learn 4 novel and arbitrary stimulus–response (S–R) associations which had to be reversed during the directly following even-numbered blocks. Reversal meant that the same 4 stimuli were now pseudo-randomly assigned to different responses than in the immediately preceding initial learning phase ([Fig. 1B](#)). Hence, a total of 56 unique S–R associations were consecutively learned and reversed across the course of the experiment. Half of the blocks required *visuo-motor* learning (based on 7 unique sets of 4 arbitrary visual two-dimensional shapes) and the other half of blocks required *audio-motor* learning (based on 7 unique sets of 4 natural sounds like dog barking or bell ringing). The sequence of stimulus categories across blocks was counterbalanced across subjects. Note that the functional imaging data from visuo-motor learning and audio-motor learning blocks were not directly contrasted in the present fMRI analysis. Each learning block comprised 32 correctly performed trials, 8 for each of the 4 S–R associations. Error trials were repeated immediately. Each learning block was divided into an initial guided instruction phase (stimulus repetitions 1–3) and a subsequent unguided implementation phase (stimulus repetitions 4–8). Encoding of the novel S–R associations was to be done during the guided phase where the correct response was explicitly indicated by an additional instruction cue for each of the 4 different S–R associations ([Fig. 1D](#)). The instruction cue was different for the two stimulus categories. For visuo-motor associations, the instruction cues were the spoken words ‘one’, ‘two’, ‘three’, and ‘four’ indicating the corresponding manual response fingers (left middle, left index, right index, right middle, respectively) presented via headphones. For audio-motor associations the instruction cues were the numbers 1 to 4, visually displayed in the center of the screen. The instruction cue was presented together with a blue lined square (represented by a dotted lined square in [Fig. 1C](#)) in the center of the screen. In the subsequent unguided memory-based implementation phase (repetitions 4 through 8) only the stimulus was presented together with an *empty* blue square and thus correct responses had to be retrieved from memory ([Fig. 1D](#)).

Each block started with a 12 s visual display indicating the current block number (1 to 28), the current stimulus category, and whether initial learning or reversal learning would be required. The timing of events within a trial is depicted in [Fig. 1C](#). After a manual response (or after timeout) written feedback was displayed for 500 ms in the center of the screen (indicating correct, erroneous, or too slow responding). The duration of the inter-trial-interval (ITI) was either 800 ms, 2350 ms, or 4700 ms with longer durations being less frequent according to a geometric decay function. At the end of each block the mean performance data were displayed for 2000 ms (accuracy and speed).

¹ Interestingly, the difficulty to establish a consistent assignment to either of these adjacent regions in fact seems to reflect a tight functional and structural inter-regional relationship rather than uncertainty in functional localization ([Almashaikhi et al., 2014](#); [Wiech et al., 2014](#)).

Download English Version:

<https://daneshyari.com/en/article/6024051>

Download Persian Version:

<https://daneshyari.com/article/6024051>

[Daneshyari.com](https://daneshyari.com)