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Lateralized implicit sequence learning in uni- and bi-manual conditions

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ABSTRACT

It has been proposed that the right hemisphere (RH) is better suited to acquire novel material whereas the left hemisphere (LH) is more able to process well-routinized information. Here, we ask whether this potential dissociation also manifests itself in an implicit learning task. Using a lateralized version of the serial reaction time task (SRT), we tested whether participants trained in a divided visual field condition primarily stimulating the RH would learn the implicit regularities embedded in sequential material faster than participants in a condition favoring LH processing. In the first study, half of participants were presented sequences in the left (vs. right) visual field, and had to respond using their ipsilateral hand (unimanual condition), hence making visuo-motor processing possible within the same hemisphere. Results showed successful implicit sequence learning, as indicated by increased reaction time for a transfer sequence in both hemispheric conditions and lack of conscious knowledge in a generation task. There was, however, no evidence of interhemispheric differences. In the second study, we hypothesized that a bimanual response version of the lateralized SRT, which requires interhemispheric communication and increases computational and cognitive processing loads, would favor RH-dependent visuospatial/attentional processes. In this bimanual condition, our results revealed a much higher transfer effect in the RH than in the LH condition, suggesting higher RH sensitivity to the processing of novel sequential material. This LH/RH difference was interpreted within the framework of the Novelty-Routinization model [Goldberg, E., & Costa, L. D. (1981). Hemisphere differences in the acquisition and use of descriptive systems. *Brain and Language, 14*(1), 144–173] and interhemispheric interactions in attentional processing [Banich, M. T. (1998). The missing link: the role of interhemispheric interaction in attentional processing. *Brain and Cognition, 36*(2), 128–157].

1. Introduction

Implicit learning can be defined as the incidental learning of complex information without awareness about what it has been learned (Shanks, 2005). This phenomenon has been investigated using three main paradigms (for a review see Cleeremans, Destrebecqz, & Boyer, 1998): artificial grammar learning (Reber, 1967), dynamic systems control (Berry & Broadbent, 1984) and sequence learning (Nissen & Bullemer, 1987). Because sequencing of actions and information is a fundamental human skill that can be considered as a complex form of implicit learning, and because sequence learning experiments are easy to conduct in controlled settings, this paradigm has become increasingly popular (Clegg, Digirolamo, & Keele, 1998).

Sequence learning has been mostly studied using the serial reaction time task (SRT). In the original SRT study by Nissen and Bullemer (1987), participants were sequentially presented visual stimuli, displayed horizontally at one of several fixed locations on a computer screen. They were instructed to press as fast and as accurately as possible on the spatially compatible response key upon each appearance of the stimulus, after what the next location was displayed. Unknown to them however, stimuli were not randomly distributed but followed a repeated sequence of ten positions (e.g. 1-4-6-3-2-1-5-4-3-2, each number representing a location on the screen). Results showed that participants exposed to this structured material became gradually faster and more accurate, as compared to participants exposed to a purely random pattern of stimuli, suggesting that they had learned the sequential regularities allowing them to anticipate on the next location. Notwithstanding, they were unable to verbally describe the repeated sequence at the end of the learning session (Nissen & Bullemer, 1987). Such dissociation between a gradual increase in participants' performance and the lack of ability to consciously describe the underlying structured material was interpreted as implicit learning. In further studies, sequence learning was tested at the within-subject level by introducing a block of random trials

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or a different sequence at the end of the learning session after repeated exposure to the material, with the effect that participants' reaction times (RTs) increased when confronted to random or novel material, i.e. a transfer effect. Response slowing in this context was interpreted as reflecting participant's sensitivity to the violation of learned regularities in the unstructured or different material (e.g. Cohen, Ivry, & Keele, 1990; Reed & Johnson, 1994). Transfer effects reflecting successful sequence learning have been investigated in many different conditions including aging (e.g. Cherry & Stadler, 1995; Curran, 1997; Howard & Howard, 1989), childhood (Meulemans, Van der Linden, & Perruchet, 1998; Thomas & Nelson, 2001; Thomas et al., 2004), brain damage (e.g. Smith, Siegert, McDowall, & Abernethy, 2001; Vandenberghe, Schmidt, Fery, & Cleeremans, 2006) and psychopathology (Brown, Aczel, Jimenez, Kaufman, & Grant, 2010).

Whether and to what extent sequence learning is implicit can be disputed if the assessment of awareness is based solely on verbal reports (Shanks & St. John, 1994). The lack of sensitivity of such measures has prompted the use of more sophisticated methods to evaluate participants' awareness (for a review see Destrebecqz & Peigneux, 2005). For instance, recognition tasks in which participants must decide whether sequential fragments (e.g. chunks of three successive elements) belong or not to the learned sequence have been used as a better estimate of conscious sequential knowledge (e.g. Perruchet & Amorim, 1992). Alternatively, some authors have also advocated using generation tasks (e.g. Jimenez, Mendez, & Cleeremans, 1996; Shanks & Johnstone, 1999), in which participants are asked to generate the learned sequence, or what they think it was, instead of merely reacting to the displayed stimuli. In this case, generation of learned sequence chunks above chance level can be taken as an index of conscious knowledge. The results of such sensitive tests have been generally suggestive that sequence learning involves largely conscious knowledge. However, such generation task cannot be taken to constitute exclusive tests of conscious knowledge. Rather, they can also involve familiarity, and hence implicit knowledge. Thus, a participant may successfully generate the successor of a sequence fragment but claim that he was merely guessing. Generation tasks, therefore, involve a mixture of implicit and explicit knowledge, and probably overestimate the extent of conscious knowledge. This contamination problem can be solved by adapting the Process Dissociation Procedure (PDP, see Jacoby, 1991) to sequence generation tasks (Destrebecqz & Cleeremans, 2001). The rationale behind the PDP is that during a classical generation task in which participants must reproduce the learned sequence (an "inclusion" condition), both explicit and implicit knowledge of the sequence contribute to performance and generation of learned chunks. However, if participants are requested to generate a different or the inverse sequence than the learned one (i.e. an "exclusion" condition), then conscious knowledge should allow them to avoid producing any learned element. If, on the contrary, they continue to generate learned chunk elements above chance level, one can then conclude that these responses depend on the influence of implicit processes that cannot be controlled by conscious knowledge, thus demonstrating implicit sequence learning (Destrebecqz & Cleeremans, 2001; Destrebecqz & Peigneux, 2005).

To the best of our knowledge, cerebral hemispheric specialization has never been investigated in the context of implicit sequence learning. This is all the more surprising since specific, testable assumptions concerning the role of the left (LH) and right (RH) hemispheres during learning of novel material can be formulated in this context. Indeed, according to the *Novelty-Routinization* model (Goldberg & Costa, 1981; see also Goldberg & Podell, 1995; Goldberg, Podell, & Lovell, 1994), the RH should be crucial in the initial acquisition stage during learning, when exploratory processing of new cognitive situations is necessary and preexisting cognitive strategies and representations are not yet firmly established. On the other hand, LH processing would favor preexisting representations and well-routinized cognitive strategies. Nevertheless, the model has so far not been thoroughly tested (for a short review see Dien, 2008, p. 296). In line with this prediction however, RH dominance in a commissurotomized patient performing an implicit visual statistical learning task has been recently reported (Roser, Fiser, Aslin, & Gazzaniga, 2011). In this study, the patient was unwittingly exposed to scenes composed of random combinations of fixed pairs of shapes. After a phase of incidental exposition, the patient was asked to make a two-alternative forced-choice and to decide which pair of shapes had appeared together during the familiarization phase. The two shapes were briefly presented either within the left (LVF) or right (RVF) visual fields, thus primarily targeting the patient's RH or LH, respectively. Results in this split-brain patient showed above-chance shape discrimination only when the RH was stimulated. Additionally, he was unable to explicitly describe the relations between the different pairs of shapes. Given that callosotomy impairs interhemispheric cortical transfer, this study suggests that visual implicit statistical learning may be established at first within the RH.

RH predominance in hippocampus and caudate nucleus activation was also observed using fMRI in healthy participants performing the same statistical learning task (Turk-Browne, Scholl, Chun, & Johnson, 2009). It should be noted that these specific regions also participate in sequence learning (e.g. Albouy et al., 2008; Destrebecqz et al., 2005; Peigneux et al., 2000). In addition, the Novelty-Routinization model (Goldberg & Costa, 1981) makes the prediction of an initial RH dominance during the acquisition of a novel material, shifting toward a LH dominance when the material is sufficiently integrated. Accordingly, preferential RH activation was found in a functional neuroimaging study (Seger et al., 2000) when healthy participants learned to distinguish between exemplars of two categories made of variations of different unseen prototype stimuli, and LH activations were found at the end of the learning session in participants showing the best performance.

In this context, the aim of the present study was to study the influence of hemispheric specialization on implicit sequence learning. In line with the Novelty-Routinization model (Goldberg & Costa, 1981), we hypothesized that transfer effects reflecting sequence learning would be observed at first in the RH after a relatively short, unique training session on the SRT task. To probe this hypothesis, participants were tested using a divided visual field, lateralized version of the SRT to ensure preferential unihemispheric processing, either in the LVF (i.e. RH stimulation) or in the RVF (i.e. LH stimulation). Moreover, to maximize interhemispheric differences, LVF and RVF groups performed the lateralized SRT task with the hand ipislateral to the stimulated visual field, thus promoting both visual perception and motor response related to sequence learning prioritized in the same hemisphere (Bourne, 2006; Gazzaniga, 2000). Finally, after the learning session, participants performed a generation task in both inclusion and exclusion conditions using reversible sequences (Pasquali, 2009) to evaluate their degree of conscious knowledge of the incidentally learned sequence.

2. Study 1

2.1. Method

2.1.1. Participants

Twenty-four young healthy right-handed volunteers participated in this experiment. Twelve participants were assigned to the left visual field (LVF) group (1 male) and the remaining to the right visual field (RVF) group (2 males). Mean age did not differ