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Research report

Volitional action as perceptual detection: Predictors of conscious intention in adolescents with tic disorders

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ABSTRACT

Voluntary actions are accompanied by a distinctive subjective experience, so that they feel quite different from physically similar involuntary movements. However, the nature and origin of this experience of volition remain unclear. Voluntary actions emerge during early childhood, in parallel with reduction of involuntary movements. However, the available markers of the experience of volition, notably Libet's mental chronometry of intention, cannot readily be used in young children. In Gilles de la Tourette syndrome (GTS), however, involuntary tic movements may coexist with voluntary control into adulthood. Therefore, adolescents with GTS could potentially confuse the two classes of movement. We have measured the temporal experience of voluntary action in a well-characterised group of adolescents with GTS, and age-matched controls. We replicated previous reports of a conscious intention occurring a few hundred milliseconds prior to voluntary keypress actions. Multiple regression across 25 patients' results showed that age and trait tic severity did not influence the experience of conscious intention. However, patients with stronger premonitory urges prior to tics showed significantly later conscious intentions, suggesting that the anticipatory experience of one's own volition involves a perceptual discrimination between potentially competing pre-movement signals. Patients who were more able to voluntarily suppress their tics showed significantly earlier conscious intention, suggesting that the perceptual discrimination between different action classes may also contribute to voluntary control of tics. We suggest that the brain learns voluntary control by perceptually discriminating a special class of internal 'intentional' signals, allowing them to emerge from motor noise.

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1. Introduction

Human societies assume that individuals voluntarily control their actions, yet the neurobiological basis of volitional control is hardly understood. Voluntary control emerges gradually with the development and maturation of cortical motor structures: newborn infants move continually, but seem to have little voluntary control over their movements (Piaget, 1952). Societies recognise this progressive development of voluntary control by defining ages of criminal responsibility, although the specific age point shows notable cultural variations. These biological and social notions of volition are based not only on physiological facts about the motor system, but also on descriptions of the *subjective experience* of voluntary action. The mental life of healthy adults includes a continuous and coherent experience of agency related to future, present and past actions (James, 1890). This sense of voluntary control over one's actions is essential in order to accept responsibility. In contrast, involuntary movements (reflexes, spasms) are classed as "automatisms" that are not under an individual's voluntary control.

The developmental trajectory from unstructured, involuntary motor acts to dominance of volitional actions and conscious self-control has been described by developmental psychologists (Piaget, 1952). However, experimental data are scarce, because the critical changes occur in early life, before formal testing and subjective report are possible. Acquiring voluntary control over one's own bodily actions presumably involves a form of instrumental learning. Experiences of volition and motivation are repeatedly paired with goal-directed body movements, and with rewarding outcomes (Balleine, 2011; Fetz, 1969, 2007). In contrast, other, involuntary movements simply occur, without any associated experience of volition. Learning associations between a feeling of volition, a body movement, and a subsequent external event would allow one to learn to be voluntary (Haggard, Clark, & Kalogeras, 2002).

In developmental tic disorders, however, this progressive dominance of voluntary action over involuntary movement is altered. Gilles de la Tourette's syndrome (GTS), for example, affects approximately 1% of children and adolescents (Robertson, Eapen, & Cavanna, 2009). It is characterised by tics, involuntary, patterned and repetitive exaggerated movements and vocalisations misplaced in context and time with a mean onset around the age of 7 years (Robertson et al., 2009). This disorder provides a valuable opportunity for studying the emergence of volition at a critical stage. In GTS, movements that may be behaviourally similar become classified as voluntary actions, or as involuntary tics. The main evidence for this classification is often a parent or caregiver's judgement regarding whether a movement is 'appropriate' (inappropriate implies involuntary) and how often it is repeated (voluntary actions are often quite sporadic, while involuntary movements are often repetitive). Since children appear to lack a strong phenomenal awareness of all their actions, both voluntary and involuntary, this classification is generally third-person rather than first-person in origin.

Indeed, tics in GTS have features of both volitional and involuntary movements: they are generated by the brain's voluntary motor pathways (Bohlhalter et al., 2006), yet they are experienced as involuntary or unwanted. We hypothesised that the presence of tics might lead to blurring of the normal boundaries between voluntary and involuntary movement, and an impaired perception of the different subjective experiences accompanying these two distinct kinds of action. For example, many GTS patients are able to suppress their tics voluntarily, yet report the tic itself as involuntary or imposed (Ganos et al., 2012). GTS patients often report "premonitory urges" prior to tics. These may resemble somatic sensations such as itches (Jackson, Parkinson, Kim, Schüermann, & Eickhoff, 2011), but may also resemble the experience before voluntary action – for example they may be accompanied by Readiness Potentials (Karp, Porter, Toro, & Hallett, 1996; van der Salm, Tijssen, Koelman, & van Rootselaar, 2012). These features set tics apart from other extra movements in children, e.g., transient postural chorea, that are perceived as completely automatic and uncontrollable. Tics are thus located in the borderland between voluntary and involuntary action. Patients often report partial control for some time until urges become irresistible and they are forced to tic. One recent study offers some direct support for the hypothesis that tics might mask normal volition. Moretto et al. showed that adults with GTS have an altered experience of their own volition (Moretto, Schwingenschuh, Katschnig, Bhatia, & Haggard, 2011), using Libet's paradigm for reporting "W judgements" – the perceived time of intentions preceding voluntary action (Libet, Wright, & Gleason, 1983).

The relation between voluntary and involuntary movement in GTS could also clarify the bases of "conscious free will" in the healthy brain. On one view, intention to act is a perception-like experience that occurs when activity within frontal motor networks exceeds a threshold level (Fried, Mukamel, & Kreiman, 2011; Hallett, 2007; Matsuhashi & Hallett, 2008). On this view, the increased level of "motor noise" in GTS might require a more conservative threshold for detecting volition, in order to avoid excessive sensitivity to noise. This increased threshold would in turn produce delays in the perceived urge to move (Hallett, 2007) (see Fig. 1). This view therefore predicts that tic parameters should correlate with mean W judgement.

Studies of developmental tic disorders could therefore potentially clarify the processes whereby voluntary control emerges from the wider noise of involuntary sensorimotor activity, and becomes a characteristic cognitive and phenomenological event. In particular, we speculated that the experience of volition in GTS could resemble a perception-like signal detection process, rather than a post hoc explanation of actions. Investigating this hypothesis would also provide an important window into the learning process assumed to underlie the normal development of capacity for voluntary action. We therefore tested the experience of volition in 27 adolescents with GTS, and 30 healthy volunteers, using a cross-sectional design. We hypothesised that high levels of tics would be associated with delays in the normal experience of volition, because the characteristic neural activities that signal one's own volition would be lost in motor noise, delaying awareness of one's own intentions. As a control for non-specific features of the task unrelated to volition, patients and controls also judged the perceived time of the keypress action itself.

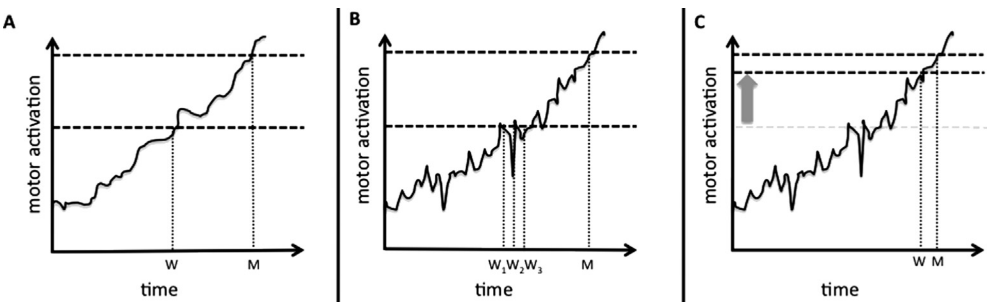

Fig. 1 – A simple model of conscious intention as a signal detection problem. A. Experience of intention (W) occurs when motor activation exceeds a first threshold level. Actual movement onset (M) occurs when motor activation reaches a second, higher threshold. B. Motor noise produces a wide range (W1–W3) during which experience of intention could occur, possibly more than once C. Increasing the threshold level for experience of intention (grey arrow) prevents extensive sensitivity to noise but delays experience of intention.

2. Methods

2.1. *Clinical evaluation*

Twenty-seven adolescents (21 male) diagnosed with GTS aged between 10 and 17 years (mean age 13.7 years ± 2.3 SD) were recruited from the GTS outpatient clinic in the Department of Neurology, University Medical Center Hamburg-Eppendorf (clinical characteristics given in Supplementary Table 1). In two cases we were unable to collect scores on all clinical tests, so only 25 patients could be included in correlation analyses. The control group comprised 30 age-matched healthy control subjects (16 male, mean age 13 years ± 2.2 SD; range 10–17). All subjects and their parents gave their written informed consent prior to study participation. The study was performed in accordance with the Declaration of Helsinki and was approved by the local ethics committee (PV4049).

All subjects underwent a thorough clinical assessment (A.M., C.G.) based on a semi-structured neuropsychiatric interview adapted from Robertson and Eapen (Robertson & Eapen, 1996). DSM-IV-TR criteria were used for a diagnosis of GTS (American Psychiatric Association, 2000). Tic severity was determined using the Yale Global Tic Severity Scale (YGTSS) (Leckman et al., 1989) and the Modified Rush Video Scale (MRVS) (Goetz, Pappert, Louis, Raman, & Leurgans, 1999). The potential to voluntarily inhibit tics was assessed by asking patients to maximally suppress their tics for 2 × 2.5 min while being videotaped [head and shoulders and whole body view, respectively; previously described (Ganos et al., 2012)]. Tic inhibition potential (IP) was calculated as follows: $IP = (RF - RI)/RF$, where RF (Rush Free) and RI (Rush Inhibition) were MRVS-based tic scores during "free ticcing" and tic inhibition respectively. Video sequences of healthy controls were also screened for the presence of tics by medical students trained in tic recognition (L. A., J. B.). No tics were noted in healthy controls.

The Tourette syndrome Diagnostic Confidence Index (DCI) was used to assess lifetime GTS-associated symptoms (Robertson et al., 1999). Premonitory urges were assessed using the validated German version of the Premonitory Urge for Tics Scale (PUTS) (Rössner, K, & Neuner, 2010; Woods, Piacentini, Himle, & Chang, 2005).

All participants were screened for major comorbidities as follows. For Attention Deficit Hyperactivity Disorder (ADHD), the "Fremdbeurteilungsbogen für Aufmerksamkeits/Hyperaktivitätsstörungen" (FBB-ADHS) from the "Diagnostik-System für Psychische Störungen nach ICD 10 und DSM-IV für Kinder und Jugendliche II (DISYPS-II) (Döpfner, Görtz-Dorten, & Lehmkuhl, 2008) was used. This is a 20-item questionnaire (final score 0–3) reflecting both DSM-IV and ICD-10 diagnostic criteria commonly employed in German paediatric population with good reliability and content validity (Döpfner et al., 2008). The items were completed by participants' parents. Obsessive-compulsive symptoms were captured by the Children's Yale-Brown Obsessive Compulsive Scale (CY-BOCS) (Goodman et al., 1989; Scahill et al., 1997). The CY-BOCS is a clinician-rated scale that assesses symptom severity as well as type of obsessive-compulsive symptoms. Ten of the 19 items of the scale comprise the total score which ranges from 0 to 40. Finally, the German version of the Children's Depression Rating Scale -Revised (CDRS-R) (Keller et al., 2011), a 17-item semistructured clinician-based interview, was employed to capture the presence and severity of depressive symptoms in participants. Clinical data are presented in Supplementary Table 1.

2.2. *Behavioural task*

We used Libet et al.'s method (Libet et al., 1983) to measure the experiences associated with voluntary action. Briefly, participants viewed a small clock hand rotating within a dial every 2560 msec. They were instructed to make a simple keypress action at a time of their own choosing, noting the position of the clock hand when they first detected the intention to "move now" (cf. "feel the urge to move", in Libet's original words). Patients with GTS were given no particular instruction regarding ticcing during this task. The mean time between conscious intention and keypress is typically a few hundred ms, and has been used as an index of the strength of volition. For example, judgements of intention are delayed in adults with GTS (Moretto et al., 2011), patients with parietal lesions (Sirigu et al., 2004), and in patients with psychogenic tremor (Edwards et al., 2011), suggesting they provide a valuable indication of the experience of volition. The standard deviation of repeated judgements provides an additional, independent measure of experience, akin to phenomenal clarity and precision. For example, vague and variable phenomenology of volition should produce a high standard deviation of intention judgements, while a clear experience that reliably precedes actions by a fixed latency should produce a lower standard deviation. As a control for non-specific aspects of the Libet task, including using the rotating clock hand as a chronometric device for timing subjective experiences, we asked participants to perform an additional block of trials in which they judged the time of their actual keypress, rather than the intention that caused it. Trial order was counterbalanced between the two judgement conditions. The means and standard deviations of 40 intention judgements and of 40 action judgements were estimated for each subject.

2.3. *Multiple regression analysis*

To investigate the relation between tic behaviour and experience of volition, we used a multiple regression model to predict the mean time of intention across participants. We used a range of predictor variables covering two main domains: First, we included three tic-related predictors: overall actual tic severity (RF), premonitory urges (PUTS scores), and capacity for intentional suppression of tics (IP). In addition, we included two general, non-tic-related factors likely to influence conscious intention. These were the degree of attention deficit (FBB-ADHS), and the reliability of each individual's W judgement (SD W), which partly reflects the criterion used to judge the onset of intention. The detailed justification for each of these predictors is given in Supplementary Text 1.

Finally, in order to assess, whether GTS has a specific effect on perception of intentions, without generally altering time estimation or perceptual judgement about other motor events such as actions, a separate regression was performed for judgements of the keypress action (M-judgement), using the same regression model as for judgements of intention.

3. Results

3.1. *Between group analyses*

The experience of intention (mean of Libet's W judgement) occurred at a similar time in patients (mean −184 msec ± 147 SD) and controls (mean −185 msec ± 97 SD). Also, the estimated time of the keypress (M-judgement) was comparable between patients (mean −56 msec ± 56) and controls (mean −68 ± 46). Comparison of volition measures between GTS patients and healthy volunteers yielded no significant effect of group ($F_{1,55} = .094$, NS). There was an expected difference between the perceived time of intention and the perceived time of action ($F_{1,55} = 72.536$, $p < .001$), but no interaction with group ($F_{1,55} = .124$, NS). Thus, in this group of adolescents we did not replicate the delayed experience of volition found previously in GTS adults (Moretto et al., 2011). Given the relatively large size of our study compared to previous studies, this is unlikely to reflect lack of statistical power.

3.2. *Multiple regression analysis within the patient group*

The overall model fitted the data well ($F_{5,19} = 7.996$, $p = .0003$), explaining 82.3% of the variance. The contributions (beta weight values) of each variable in predicting mean time of intention are shown in Fig. 2. The correlation matrix and partial regression test table are shown in Supplementary Table 2. Regarding specific tic-related factors, we found that tic severity was unrelated to W judgements. Greater capacity for intentional tic suppression was associated with earlier W judgements. Stronger premonitory urges were associated with later W judgements. Regarding general non tic-specific factors, higher ADHD ratings were associated with later W judgements. Greater trial-to-trial variability in judgements of intention (SD W) was associated with earlier W judgements.

3.3. *Judgements of keypress actions*

We fitted the same regression model to the patients' judgements of the keypress action (M judgements). We did not find

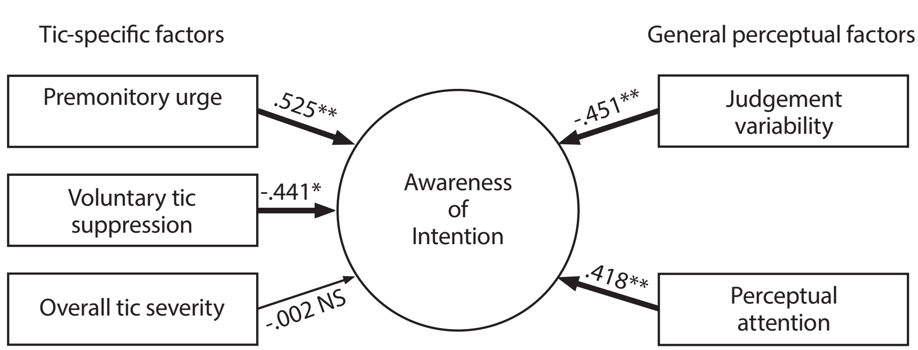

Fig. 2 – Regression model for predicting time of conscious intention (W judgement) in the GTS group. Numbers indicate beta weights. Negative coefficients indicate that a higher score on that measure is associated with earlier intention. Thin lines indicate non-significant terms included in the model for theoretical completeness. * = p < 0.05; ** = p < 0.01. See text for explanation.

any significant associations, and the overall model was far from significant (F5,19 = 0.823, p = .549, r^2 = .178: see Supplementary Table 3). This suggests that the associations reported for conscious intention reflect the specific perceptual ambiguities of volition, rather than interactions between tics and general features of the task, such as using the rotating clock. Interestingly, judgements of keypress actions did not show the significant relation between mean and standard deviation that had previously been found for judgements of intentions. We suggest that the association between the mean and standard deviation of judgements using the Libet method may reflect individual differences in setting perceptual criteria. For a clear and unambiguous signal such as a keypress, choice of criterion may be more straightforward, and more consistent across individuals. When judging events with a more tenuous phenomenology such as volition, choosing a more liberal criterion will produce an earlier but more variable W judgement.

3.4. *Control group*

We could not use the same regression model to predict conscious intention in the control group, because they had no scores on the clinical measures. However, our hypothesis that individual differences in criterion setting produce a relation between mean and standard deviation of intention judgements could be tested also in the control group. A simple linear regression confirmed a significant relation in the same direction as for the patients (F1,28 = 4.518, p = .0425). However, this regressor explained around half as much variance (13.9%) as in the patient group (27.9%). This result suggests that the relation between mean and standard deviation of time of intention is driven by a general factor present in both groups. This factor may not be specifically related to tics, although the presence of tics may make its expression stronger. Indeed, the standard deviation of W judgement was both nonsignificantly greater and more variable across individuals in the patient group, compared to controls [mean 205 msec, SD 171 msec for patients, mean 161 msec SD 142 msec for controls: t-test on mean of SDs: $t(55) = 1.07$, p = .289].

4. Discussion

4.1. *Volition in adolescent and adult GTS populations*

We found no difference in the average time of conscious intention between GTS patients and controls in our group of adolescents. A previous study had reported a delay in conscious intention in adults with GTS relative to controls (Moretto et al., 2011) but this result was not replicated in our younger and larger sample. The absence of delay in adolescence combined with delayed experience of volition in adults with GTS suggests that adults may *learn* the experience of volition. In healthy adults, the normal experience of intention prior to voluntary action may reflect prolonged perceptual learning at discriminating the internal signals that characterise volition. Persistent co-occurrence of voluntary and involuntary movement in GTS could make this discrimination problem harder. Therefore, patients with GTS may show delayed learning about their own volition, or may extinguish such learning after it has occurred, as a result of prolonged tic behaviour. Adults have prolonged experience of their own voluntary action, and may have learned the discriminative perceptual markers of volition. However, for an adult with GTS, frequent tics may have made this discrimination harder, leading to a more conservative criterion for detecting the signal among noise. GTS adults may thus lack the normal anticipatory awareness of intentional action. In our adolescent sample, the two groups do not yet diverge in this way. That is, we suggest that the delayed experience of volition in adult GTS represents a failure of perceptual learning for volition-related signals, due to masking by tics and tic-related factors, such as premonitory urges. Some possible factors are discussed in the next section.

4.2. *Factors affecting volition in GTS*

GTS is characterised by tics. Our results showed several influences of ticcing on the experience of *voluntary* action. These results are consistent with the broad theory that the experience of volition involves learning a *perceptual discrimination* between the distinctive internal states and signals corresponding to preparation of voluntary actions, and other, involuntary body movements. For example, a striking result of our regression analysis was that *subjective* experiences linked to involuntary tic movements (measured by the PUTS) provided the single strongest predictor of volition. Participants who experienced strong premonitory urges prior to tics had a later perception of the intention preceding voluntary action. Stronger premonitory urges preceding involuntary movements could impair detection of the distinctive experience of volition, since urges to tic would constitute perceptual noise masking actual intentions. In contrast, the *objective* occurrence of tic behaviours, measured by the established Rush video scoring method, did not predict the experience of volition. More generally, our results suggest that both voluntary and other types of movements are accompanied by subjective experiences, each with their own perceptual characteristics. The perceptual ability to distinguish between these experiences, and process and control each class of movement accordingly, lies at the heart of the capacity for volition.

Patients with GTS are widely stated to have intact voluntary action (Moretto et al., 2011), with the presence of parallel involuntary movements being the main pathology. However, the co-occurrence of these two classes of movement introduces a perceptual problem in distinguishing between them. Involuntary movements constitute a perceptual learning challenge. During normal development, children may learn to recognise the signals corresponding to the desires, preparations and goals that drive voluntary actions, despite the constant presence of general motor noise arising from other, involuntary movements of the body. One consequence of such motor noise is a variability in judging *when* a phenomenally-thin event, such as intention to act, occurs within the motor system. Indeed, we found that the mean perceived time of an event was positively correlated with the variability in timing judgements, in both GTS and control groups. In GTS, this perceptual learning problem may be exacerbated by three factors. First, the level of this noise is unusually high: tics occur spontaneously and repetitively. Second, tics may be difficult to discriminate from voluntary actions, because they involve the same neural motor circuits, and often have the same physical form as a voluntary action. Third, tics are noted and commented on by others including parents and peers. There are often implicit or explicit requests to stop ticcing. This may foster a process of attending to tics. Increased attention may in turn produce strong subjective experiences associated with tic generation processes, masking the experience of voluntary action generation. Thus, the child with GTS may have particular difficulty in discriminating the internal signals corresponding to their truly voluntary actions, in the presence of this ongoing activity.

4.3. *Volition as a signal-in-noise problem*

We therefore suggest that the experience of one's own volition, as measured by the perceived time of intentions to perform a simple voluntary action, begins as a *perceptual* problem of detecting signals in noise. The individual must detect a specific internal motor signal of volition in the presence of ongoing, background motor noise. This problem is most acute in early childhood, where involuntary movements are relatively frequent. Our view strongly contrasts with alternative accounts suggesting that conscious intention is a retrospective inference to account for actions after they have occurred. According to retrospective theories, the ‘experience’ of intention should depend largely on retrospective construction of an apparent mental cause of our actions (Wegner, 2002), and not on the nature, or noise context, of internal signals that preceded the action. In contrast, the signal-in-noise view suggests that experience of volition occurs when an internal signal exceeds a criterion value, or crosses a threshold. Patients with GTS vary in the level of motor noise associated with tics, and also in the perceptual awareness and intentional controllability surrounding their tics. Our results show that these latter factors strongly influence the experience of volition in GTS. Therefore, patients with GTS may face a greater difficulty than controls in the crucial *perceptual* computation to separate one's own volitional actions from other movements.

Could a retrospective, inferential account of intention also explain the results in GTS patients? Retrospective accounts would suggest that experiences of volition are inserted post hoc, whenever a patient moves. In GTS, this process would occur both after voluntary actions, and also after tics. This retrospective insertion might potentially explain some premonitory urges – although many urges build up over a much longer timescale than the subsecond timescales associated with retrospective insertion of intentions.Crucially, however, a retrospective account of GTS action awareness would suggest that a patient who strongly reconstructs urges should also strongly reconstruct intentions. In our dataset, high PUTS scores should then be associated with early W judgements. In fact, we found a strong effect in the *opposite* direction. Therefore, our results seem more consistent with the idea of perceptual learning of a premotor signal, rather than a general inferential mechanism for retrospective insertion of intentions.

4.4. *Threshold-setting and judgements of conscious intention*

A recent computational model rejected the notion of volition as a hierarchical top-down control of the motor system, and suggested instead that random fluctuations of a motor readiness signal could be sufficient to explain the initiation of voluntary actions (Schurger, Sitt, & Dehaene, 2012). Our result is consistent with the view that people also *experience* an intention to act when an internal signal exceeds an individual's threshold level (Hallett, 2007). The choice of threshold leads to a relation between the average time of conscious intention, and its trial-to-trial variability. We verified this prediction in both GTS and the control group. Setting a suitable threshold level for the neural signals that produce the thin and ambiguous experience of volition is a perceptual challenge. Setting a low threshold will regularly produce false positives. These individuals would show early detection of intention on average, but their judgements would be highly susceptible to motor noise. In contrast, an individual who chooses a high threshold would be less susceptible to noise. However, the high threshold would be crossed only late in the motor preparation sequence, leading to a delayed experience of volition. We show that this idiosyncratic variation exists in the general population, as well as in GTS. However, this factor has a stronger influence in GTS, perhaps reflecting the greater challenge of threshold-setting in this group for whom motor noise levels are unusually high.

4.5. *Relation to self-control and voluntary initiation of action*

We have studied the subjective experience of volition, rather than the objective capacity to initiate and control voluntary action. Nevertheless, our results suggest an interesting link between subjective experience of volition and capacity for voluntary control. Voluntary control is classically thought to be unaffected in pure GTS (Ganos et al., 2014; Ganos, Roessner, & Munchau, 2013; Jung, Jackson, Parkinson, & Jackson, 2012), and our patients were indeed able to perform the voluntary action task successfully. However, we found a strong relation in our patients between a *negative* aspect of voluntary control, i.e., the capacity to suppress tics, and the capacity to experience the intentional signals preceding initiation of voluntary action. Specifically, participants who were able to suppress their tics reported earlier experiences of volition that those who did not. Importantly, these two measures were obtained independently, in separate experimental tests – no particular instruction was given regarding tic inhibition during the voluntary action task.

This result suggests that the capacity to discriminate signals for volition from signals related to other involuntary movements is directly related to successful voluntary self-control. The capacity to inhibit involuntary movements could cause a stronger experience of volition, by reducing the background motor noise within which signals related to voluntary action are embedded. This would improve the landscape for perceptual learning. However, we cannot exclude the possibility that causation might run in the opposite direction. Patients who have early experiences of volition might be better able to control voluntary suppression of other, involuntary movements that lacked this marker. Our result establishes, for the first time, an association between perception of volition, and voluntary self-control, although it cannot prove the direction of causation. Irrespective of directionality, the association between experience of volition and voluntary self-control may have important implications for movement disorder therapies. For example, training that focuses on perception of internal volitional signals rather than on noise related to tics could potentially increase voluntary self-control.

4.6. *Implications for development of volition*

The ability to perceive the signals associated with volition, and to discriminate them from other internal motor events, is a crucial first stage in developing the capacity for voluntary control. Humans might acquire volition using mechanisms similar to reinforcement learning of operant actions in animals (Fetz, 1969). A gradual, implicit learning process would favour motor outputs that influenced the level of a specific class of sensations, associated with drives, desires and motivations – such as reducing hunger or inducing pleasure. People may *learn* to be voluntary, by the same general principles that biofeedback training uses to allow voluntary control over heart rate, and other autonomic processes (Lehrer et al., 2003). Learning may be delayed or compromised if the signals that cause voluntary action cannot be successfully identified or discriminated from background noise generated by movements that are not so readily controlled.

We began this paper by distinguishing between perceptual theories of volition based on detection of internal preparatory signals (Fried et al., 2011; Hallett, 2007; Matsuhashi & Hallett, 2008), and retrospective theories based on inferences about the causes of one's own actions (Dennett, 1991; Wegner, 2002). If our suggestion of volition as developmental perceptual learning is correct, then the contrast between perceptual and inferential theories appears rather contrived. We speculate that infants would be retrospective inferentialists: they learn in early life that particular internal sensations of wanting and striving are associated with particular motor actions, and that these actions influence the corresponding internal sensations. That is, the infant would learn by repeated Hebbian association that some particular sensory states were under voluntary control. To learn this association, the developing brain must extract the correlation between an internal premotor signal or premotor sensation, and the resulting body movement. Social rewards for particular movements, such as smiling, act as powerful reinforcers for learning this association. With repetition, the infant comes to perceive the special relation between those specific internal signals and their external consequences. Because associations support predictions, the infant will begin to perceive volition before the action itself. Adults can develop novel methods of voluntary control through neurobiofeedback training (Fetz, 1969; Hatsopoulos & Donoghue, 2009; Lebedev & Nicolelis, 2006). We suggest that basic control of voluntary body movements begins with a similar process, of learning to perceive internal signals. By learning to discriminate and consciously perceive signals that correspond to development of motor action, individuals may acquire fine voluntary control over their actions. In GTS, the child is faced with multiple well-formed movements that do not correspond to their intentions. In our GTS group, we showed that individuals' experience of intention could be explained because of the difficulty of discriminating intentional actions from this involuntary motor noise.

4.7. *Limitations and future directions*

Finally, we point out several limitations with our study. First, our suggestions regarding the role of development in learning volition are rather speculative, because they are based on a cross-sectional, rather than a longitudinal study. Longitudinal studies with GTS could be particularly valuable for studying the relation between motor noise and experience of volition, because tic disorders often spontaneously resolve in children with GTS. Our model predicts that these naturally-occurring changes in levels of motor noise should be followed by changes in the experience of voluntary action. Second, our study is relatively small [though larger than previous experimental studies of volition in GTS (Moretto et al., 2011)]. Further, some patients had to be excluded from the crucial correlation analysis, because some measures were unavailable. Future studies with a larger sample would be better placed to investigate whether comorbid OCD and depression influence the experience of volition. Larger studies might also fruitfully use factor analysis methods. We have shown how a range of dependent measures is associated with the experience of volition. Factor analysis may help to reveal whether these can be reduced to a smaller number of factors, each reflecting the contribution of a specific neural substrate.

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Supplementary data

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