

**THE SOCIAL TRANSMISSION OF METACONTROL POLICIES:
MECHANISMS UNDERLYING THE INTERPERSONAL TRANSFER OF
PERSISTENCE AND FLEXIBILITY**

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ABSTRACT

Humans often face binary cognitive-control dilemmas, with the choice between persistence and flexibility being a crucial one. Tackling these dilemmas requires *metacontrol*, i.e., the control of the current cognitive-control policy. As predicted from functional, psychometric, neuroscientific, and modeling approaches, interindividual variability in metacontrol biases towards persistence or flexibility could be demonstrated in metacontrol-sensitive tasks. These biases covary systematically with genetic predispositions regarding mesofrontal and nigrostriatal dopaminergic functioning and the individualistic or collectivistic nature of the cultural background. However, there is also evidence for mood- and meditation-induced intraindividual variability (with negative mood and focused-attention meditation being associated with a bias towards persistence, and positive mood and open-monitoring meditation being associated with a bias towards flexibility), suggesting that genetic and cultural factors do not determine metacontrol settings entirely. We suggest a theoretical framework that explains how genetic predisposition and cultural learning can lead to the implementation of metacontrol defaults, which however can be shifted towards persistence or flexibility by situational factors.

COGNITIVE CONTROL AND METACONTROL

Human behavior is characterized by its considerable flexibility, which in contrast to other species, and other primates, allows behavioral adjustments without extensive training and practice. The processes that are thought to be responsible for this flexibility are commonly referred to as cognitive-control processes or executive functions (e.g., Diamond, 2013). While there is no agreed-upon inventory of human cognitive control processes, a particularly popular set of functions has been suggested by Friedman, Miyake, and colleagues (Miyake et al., 2000; Friedman & Miyake, 2004). Based on latent-factor techniques, these authors originally suggested distinguishing between inhibition (e.g., to inhibit incorrect responses), updating (e.g., to keep the content of working memory up to date), and shifting (e.g., to switch between different task sets), which they showed to go beyond generic factors like perceptual speed or intelligence (Friedman et al., 2006). However, a later study suggested that at least one of these functions (inhibition) is perfectly correlated with a common factor shared by all considered functions, which might imply that inhibition is an emerging property of the interaction between different functions, rather than a separable function itself (Friedman et al., 2008).

Other approaches have used functional considerations to identify factors involved in cognitive control. Goschke (2003) has argued that humans are often facing control dilemmas that are likely to require continuous adjustments of the interplay between antagonistic control systems. He discusses three of such dilemmas: (a) the plasticity-stability dilemma (should one rely on available habits or construct a new action plan on the fly?); (b) the maintenance-switching dilemma (should one stick with one's current intention or give it up for a better opportunity?); and (c) the selection-monitoring dilemma (should one focus on relevant information only or consider irrelevant, but possibly

interesting information as well?), and points out that they all imply a fundamental dilemma between persistence and flexibility of control and behavior. While this dilemma does not map Friedman and Miyake's two or three control factors in a one-to-one fashion, it is obvious that these factors would be likely to play a key role in regulating persistence and flexibility.

A similar scenario of cognitive control as emerging from the interplay of two antagonistic systems or factors has been developed by Cools (2006, 2008; Cools & D'Esposito, 2011). According to this scenario, brain areas involved in cognitive control are fueled by two separable dopaminergic pathways: one originates in the ventral tegmental area and targets the prefrontal cortex (the mesofrontal pathway), and the other originates in the substantia nigra and targets the striatum (the nigrostriatal pathway). How well that assumption fits with the approaches of Friedman and Miyake, and of Goschke, becomes clear if one considers the known contributions of the prefrontal cortex and the striatum to cognitive control. The prefrontal cortex is known to house the key working memory functions, which are crucial for maintaining action goals and other information over time (Durstewitz, Seamans & Sejnowski, 2000), while the striatum is essential for regulating the updating of working memory content by new incoming information (Cools & D'Esposito, 2011) and for interrupting ongoing control in the case of situational changes (Frank, Samanta, Moustafa & Sherman, 2007).

Dopamine can drive cognitive processes only if and where it reaches dopaminergic receptors. The modeling-based approach of Durstewitz and Seamans (2008) focuses on these receptors and their distribution in prefrontal cortex, which according to their suggestion can assume two different control states. One state is driven by the dominance of dopaminergic receptors of the D1 family, which in turn supports cognitive maintenance, while the other state is driven by the dominance of D2 receptors,

which is assumed to support mental flexibility. Cognitive control can thus be biased towards maintenance or flexibility by making either D1 receptors or D2 receptors more dominant. It is interesting to consider that D1 receptors by far outnumber D2 receptors in the prefrontal cortex, while the opposite holds for the striatum (Beaulieu & Gainetdinov, 2011; Cams, Kelly, & Palacios, 1990). This can be taken to imply that a stronger activity of the ventral tegmental area would be likely to activate more D1 receptors while a stronger activity of the substantia nigra would activate more D2 receptors, so that the approaches of Cools and D'Esposito (2011) and of Durstewitz and Seamans (2008) can be considered very similar if not functionally equivalent.

To summarize, there are psychometric, functional, neural, and computational reasons to assume that cognitive control does not reflect the operation of a unitary function but rather emerges from the interplay of probably two antagonistic systems or components. Of particular importance for our present aims, the relationship and balance between these systems does not seem to be fixed but variable to at least some degree. This means that the control style of a given individual can differ from that of another, but also from one situation to another. In other words, there should be intraindividual and interindividual variability in control styles. More specifically, the way a given individual exerts control operations in a given situation can be biased either towards persistence (of goals, preferences, working-memory content, etc.) or towards flexibility. Hence, it might be possible to control cognitive control to some degree, an ability that Hommel (2015) referred to as *metacontrol*. We adopt this label to refer to the ability to adopt different control styles in the face of different tasks, challenges, or other kinds of impact (cf., Boureau, Sokol-Hessner & Daw, 2015). In the following, we will assume that metacontrol styles vary on one single dimension ranging from extreme persistence to extreme flexibility, but we will discuss the possible existence of other binary dimensions,

including speed-accuracy, intentional-automatic, and exploitation-exploration, at the end of this article.

The aim of the present article is to discuss whether and how metacontrol settings can be shared, that is, whether metacontrol settings can be transferred from one human to another and how this might be achieved. Given the emphasis of this special issue on instruction, the most efficient technique to share metacontrol settings would be to instruct another person to adopt a particular metacontrol policy. That this is possible in principle is suggested by research on speed-accuracy trade-offs. As we will explain at the end of this article, optimizing the speed or the accuracy of one's performance can be considered to represent a metacontrol policy, and it has been shown that such policies can be reliably induced by means of instruction (e.g., Vickers & Packer, 1982). While we argue that the speed-accuracy dimension may well be related to the persistence-flexibility dimension we will be focusing on in the following, we are not aware of any study that has attempted to instruct individuals to be persistent or flexible directly. What we therefore will do is to consider various more indirect and less immediate "instructions", that is, ways in which the social context (culture, peers, situational cues) guides individuals towards adopting particular metacontrol policies—the social transmission of metacontrol.

One reason why direct instruction may indeed be more difficult than in the speed-accuracy case relates to semantics. While instructing individuals to be as fast or as accurately as possible defines clear-cut criteria that do not leave space for interpretation, that is not applied to persistence and flexibility. The persistence of Super-Mario to reach his ultimate goal requires substantial flexibility on the way, and (as we will see in the following) being set for flexibility in the sense we are using the term is often accompanied by distractibility, a lack of inhibition, and other phenomena that are considered much less positive as the term flexibility might imply. Along the same lines, one might consider

flexibility in the Wisconsin Card Sorting task, for instance, a means to be particularly goal-persistent. Such interpretational ambiguities are unavoidable when using concepts from everyday language, and even the most comprehensive definition will not exhaust or replace the semantic overhead that such use necessarily brings with it (Hommel & Colzato, 2015). Later in this article, we will provide a mechanistic operationalization of persistence and flexibility that will help to reduce interpretational uncertainty. In the meantime, we invite the reader to tentatively interpret persistence and flexibility with respect to the impact of the current goal on selection processes in a broader sense, so that persistence stands for a strong top-down influence of the current goal on the selection of cognitive units (e.g., stimulus interpretations, response representations, tasks) while flexibility stands for a greater autonomy of the inter-unit interactions and more room for bottom-up influences.

The existence of interindividual variability in metacontrol is a necessary requirement for sharing, because without such variability sharing would be superfluous. The same is true for intraindividual variability. Even if people would differ in metacontrol settings, but the settings would be so permanent that changing them is impossible, sharing should not work. That these kinds of variability exist is not obvious, given the claim of Friedman et al. (2008) that human cognitive-control functions are almost entirely genetically determined. If that would really be the case, intraindividual variability would be exclusively explained by genetic variability, and cultural and situational factors should have no impact on the operation, efficiency, and style of cognitive control. In the following, we will first discuss evidence suggesting that intraindividual variability does exist and that it is associated with both genetic and cultural factors. We then continue to discuss intraindividual variability, with a focus on mood and meditation, the factors that have been demonstrated to affect metacontrol settings in particularly systematic ways.

Then we discussed how metacontrol might work in principle, how the demonstrated interindividual and intraindividual differences might impact the mechanism of metacontrol, and in particular how culture and situational factors might bias metacontrol towards persistence or flexibility. We conclude by relating the persistence-flexibility metacontrol dimension focused on in this article to other dimensions that have been discussed in the literature, and by pointing out open questions that call for further research.

INTERINDIVIDUAL VARIABILITY IN METACONTROL

Genetics

Evidence for interindividual variability comes from behavioral genetics studies of polymorphisms that are known to be related to dopaminergic processing in the mesofrontal and the nigrostriatal pathway. COMT Val¹⁵⁸Met affects the efficiency of frontal dopaminergic processing (Chen et al., 2004) and DRD2 C957T the level of striatal dopamine (Hirvonen et al., 2009a, 2009b). As polymorphisms of these genes seem to affect the relative efficiency of either the frontal or striatal dopaminergic pathway, or D1 or D2 receptors dominating the frontal and striatal pathway, respectively, one would expect that carriers of different polymorphisms differ with respect to their control style, especially in tasks that require persistence or flexibility. Table 1 provides an overview of the available key findings.

*** TABLE 1 ***

Indeed, carriers of different polymorphisms of the COMT Val¹⁵⁸Met gene were shown to differ in their efficiency to switch between tasks (Colzato, Waszak, Nieuwenhuis, Posthuma, & Hommel, 2010a). More specifically, carriers of a

polymorphism that can be assumed to increase the dominance of the frontal dopaminergic system (i.e., Met- carriers) were shown to have greater difficulties in task switching than carriers of other polymorphisms. In another study, the same gene was found to predict the degree to which people benefit from playing video games. In particular, carriers of a polymorphism that increases the dominance of the striatal dopaminergic system (Val/Val) showed more pronounced transfer from videogame training to task switching in a laboratory setting (Colzato, van den Wildenberg, & Hommel, 2014). In a reversal learning task, Val/Val homozygotes exhibited worse performance than Met/Met homozygotes at the acquisition stage but outperformed them at the reversal stage (Nolan, Bilder, Lachman, & Volavka, 2004), suggesting that their genetic predisposition impairs cognitive stability but enhances cognitive flexibility. Moreover, in a Stroop task with different levels of required cognitive stability and flexibility, Rosa et al. (2010) found Met/-carriers to show better performance when cognitive flexibility was required.

Genes with a stronger impact on striatal/D2 processing were also found to have an impact on relative persistence/flexibility. For instance, carriers of the T/T polymorphism of the DRD2 C957T gene perform better than carriers of other polymorphisms in a verbal working memory task (Jacobsen, Pugh, Menci, & Gelernter, 2006) and an attentional blink task (Colzato et al., 2011), but exhibit more dysfunctional impulsivity and less efficient inhibition in a stop-signal task (Colzato, van den Wildenberg, van der Does & Hommel, 2010b), and a less effective, more parallel action cascading strategy (Stock, Arning, Epplen & Beste, 2014).

Another interesting gene to highlight the striatal/D2 processing is the DRD2/ANKK1 Taq Ia polymorphism. Carriers of at least one A1 allele (A1+) have a 30% reduced striatal receptor density as compared with carriers of the homozygous A2/A2 (A1-) variant (Ritchie & Noble, 2003). Stelzel et al. (2010) reported significantly

reduced task-switching costs in carriers of the A1+ variant and, along the same line, Markett et al. (2011) found that DRD2 A1+ carriers displayed a larger backward inhibition effect (in a task that is taken to diagnose a control mechanism that contributes to cognitive flexibility by reducing proactive interference by no longer relevant task sets).

On the one hand, these behavioral genetics studies provide preliminary evidence that dopamine-related interindividual differences are related to differences in metacontrol by creating systematic biases towards more persistence or more flexibility—a proof of principle. Moreover, the outcomes of these studies fit with findings using spontaneous eyeblink rates as indicators of individual (presumably nigrostriatal) dopamine levels (see Jongkees & Colzato, 2016 for a recent review). For instance, individuals with high blink rates showed increased cognitive flexibility but decreased cognitive persistence (Dreisbach et al., 2005; Tharp & Pickering, 2011), while individuals with low blink rates showed a deeper attentional blink (Colzato, Slagter, Spapé & Hommel, 2008a).

On the other hand, however, there are at least two reasons to treat these findings with caution. First, there is increasing concern regarding replicability in genetic studies, not the least because the often very small effects would actually call for much larger samples than most behavioral genetics studies have tested. We emphasize that the cited studies differ from most other genetics studies in that they were guided by a systematic theoretical framework and relatively specific hypotheses, but it is nevertheless true that more replication studies are needed. Second, it is commonly easier to predict *that* carriers of different polymorphisms of candidate gene should differ in performance on a particular task than to predict the direction of this effect. Theoretically speaking, one might expect that polymorphisms that reduce the efficiency of the frontal or D1-based dopaminergic system should shift the balance between persistence and flexibility towards the latter, while polymorphisms that reduce the efficiency of the striatal or D2-based dopaminergic

system should have the opposite effect. Likewise, one might expect that increasing the efficiency of the frontal/D1-based system would lead to more persistence while increasing the efficiency of the striatal/D2-based system would lead to more flexibility. Unfortunately, however, the current insight into the impact of genes on neuromodulation is too limited to predict exactly which polymorphisms impair and which polymorphisms improve processing in a given system. One key problem is that there are reasons to assume that the function relating dopamine levels to efficiency is not linear but follows an inverted U-shape (Cools, 2006; Cools & D'Esposito, 2011). Hence, even if it would be possible to predict whether a given polymorphism leads to a relative increase or decrease of the individual dopamine level in a particular pathway (which given that polymorphisms can affect various factors including receptor sensitivity, binding, dopaminergic production and transport is very difficult already), it is currently impossible to determine theoretically the level or processing characteristic that allows for the most efficient handling of a particular task. This in turn makes it very hard to predict whether an increase in dopamine moves an individual towards the optimal level (and thus improves performance) or away from that level (and thus impairs performance).

A final point of interest is that genetic effects are commonly asymmetric, in the sense that a given gene may affect persistence but not flexibility, or vice versa. For instance, Rosa et al. (2010) did find a COMT-Met advantage for tasks requiring cognitive stability, but they did not find a Val advantage for tasks requiring cognitive flexibility. As we will elaborate below, this might suggest that genetic effects targeting dopaminergic pathways do not directly impact the metacontrol setting but rather the neural machinery realizing this setting. This means that an impairment to realize flexibility based on limitations of the underlying dopaminergic pathway or receptor system need not prevent a bias towards flexibility at the level of metacontrol settings.

Culture

There are plenty of studies on various aspects of how culture (a concept that we will use broadly to refer to the impact of particular groups of individuals; see Heine, 2008) affects human cognition in general, but studies focusing on the impact of culture on cognitive control processes are relatively rare. One of the reasons is that cultural studies are commonly more interested in the self-assessment of individuals (e.g., the perception of personal control: Rothbaum, Weisz & Snyder, 1982; Ji, Peng & Nisbett, 2000) than in their objective functioning and the processing underlying it. Another reason is that the conceptualization of human cognition in cultural studies tends to be less informed by mechanistic considerations than more lower-level cognitive or neuroscientific approaches, so that aspects of what might actually be considered to be related to cognitive control is often discussed as perception, attention, or thinking. However, as we will argue, some of the findings discussed under these headings do seem to relate to cognitive control styles as defined in the present article, which is why we nevertheless consider some of these studies. Table 2 provides an overview of the key factors being tested and the key findings regarding metacontrol.

**** Table 2 ****

Nationality/ethnicity

Studies in cultural psychology are often following the practice of comparing individuals from different countries that can be considered to differ in cultural background, and indeed, if the concept of culture merely refers to groups of individuals, a country can certainly be considered to represent such a group. And yet, nationality and citizenship are increasingly problematic criteria to define culture in a time of rather

extreme mobility and globalization. Moreover, the comparison of countries often confounds other factors that, as we will see in the case of religion, seem to be at least just as potent. These caveats aside, a rather well-developed research line has systematically explored the cognitive differences between US-Americans and Japanese, which are commonly taken to reflect the impact of individualism and collectivism, respectively (e.g., Masuda & Nisbett, 2001). From a societal point of view, individualism and collectivism refer to the degree to which a social system holds either the individual or all in-group members responsible for each given person, including this person's behavior and well-being. Systematic research on international differences in norms, regulations, values, and procedures have resulted in the construction of a country-specific individualism scale, that is part of Hofstede's widely accepted cultural dimensions framework (<https://geert-hofstede.com/national-culture.html>; Hofstede, Hofstede & Minkov, 2010). From an individual point of view, the individualism-collectivism dichotomy has been translated into the degree to which individuals construct their social self as either independent from others or as socially interdependent (Markus & Kitayama, 1991). Among other things, individuals with an independent self would experience their identities and consider their behavioral control independent from others and their relationships with them, while individuals with an interdependent self would more strongly rely on social relationships in defining themselves and identifying appropriate behavior.

Comparisons of US-Americans and Japanese have revealed a number of well-replicated outcome patterns that are important for our discussion. When processing visual displays, US-Americans have a stronger preference for focusing on foreground objects than Japanese have, while Japanese process more background information than US-Americans (Nisbett and Masuda, 2003). This tendency remains rather stable or even

becomes stronger over inspection time (Masuda et al., 2008) and affects retrieval as well, as shown by better recognition in Japanese, but not in US-Americans, when focal objects were presented later with the original rather than a novel background (Masuda & Nisbett, 2001). These observations fit with findings showing that Japanese participants perform more poorly than US-Americans in the Rod and Frame test, which requires the dissociation of foreground object and visual context (Kitayama, Duffy, Kawamura & Larsen, 2003). These and many related findings (for a brief overview, see Heine, 2008: Chapter 9) suggest that US-Americans focus more on the most salient, and presumably most relevant information of visual displays than Japanese participants do, and these observations have been taken to imply an analytic versus holistic processing style, respectively. With respect to control styles, this can be taken to imply that US-Americans have a stronger bias towards persistence (the control style inducing an analytic processing mode) than Japanese have and/or Japanese participants have a stronger bias towards flexibility (the control style inducing a holistic processing mode) than US-Americans have (see the section on mechanisms for a more detailed explanation how persistence/flexibility leads to specific processing modes).

These observations confirm the prediction of systematic intraindividual variability and control styles. However, the setup of the discussed studies does not allow ruling out a number of other factors, including the possibility of specific genetic differences between the average US-American and the average Japanese. Moreover, the USA cannot be considered particularly homogeneous with respect to various aspects of culture, an argument that increasingly applies to other countries as well. Even more problematic is the suggestion that comparisons between US-Americans and Japanese come down to a comparison of individualism and collectivism. While the United States are the top scorer worldwide in Hofstede's scale of country-specific individualism (<https://geert->

hofstede.com/national-culture.html), Japan is the top scorer of East Asian countries, with a score that is about three times as high as that of, say, Taiwan or Indonesia. That does not seem to make the mindsets of Japanese individuals particularly representative of collectivism. Fortunately, there is evidence that the reported Western-Eastern differences can be replicated with samples from other countries. For instance, Caucasian Australians were found to show equal performance for global and local levels of multi-level stimuli (large letters made of small letters: Navon, 1977), while both second-generation Asian Australians and Asians from Hong Kong, mainland China, Singapore, Malaysia, Indonesia, and Korea showed much better performance for global than for local levels (McKone et al., 2010). While the lack of a *global-preference effect* in the Caucasians amounts to a non-replication of the frequently reported Navon (1977) effect, this study provides at least some evidence for generalization across countries. Finally, the USA with its strong emphasis of a Protestant ethic differs systematically from Japan in terms of religion which, as we will see, has a systematic impact on metacontrol.

Religion

As do nationalities, religions show considerable differences with respect to the degree of individualism and collectivism, and the amount of individual independence versus interdependence they advocate. Dutch neo-Calvinism is an extreme example. This version of Protestantism was developed by Dutch statesman and theologian Abraham Kuyper in the late 1800s (Bratt, 1998) and soon adopted as part of the Dutch national identity, as evident from the fact that neo-Calvinism has been adopted as the official ideology of a political party, a trade union, a newspaper, a university and many schools. Importantly for our purposes, neo-Calvinism is based on the concept of sphere sovereignty, which emphasizes that each societal sphere or sector has its own responsibilities and authorities, and stands equal to other spheres. This concept has

penetrated Dutch culture and caused a considerable segregation of Dutch society (often called *pillarization*). Applied to everyday life, it has established the idea that, in a nutshell, everyone should mind his or her own business, which among other things has led to a relatively liberal policy regarding abortion, drug use, and euthanasia in the Netherlands, but also been exported by Dutch emigrants to South Africa as the ideological basis for apartheid (Boesak, 1984). Neo-Calvinism and the sphere sovereignty concept are considered a major component of economic progress in the Netherlands and the extreme degree of individualism (the country occupies the fourth rank worldwide of Hofstede's individualism scale, after the US, Australia and the UK). As another extreme, Buddhism advocates a particularly strong form of collectivism. One of its core doctrines, Anatta, denies the existence of a separate self in the sense of a permanent, integral, autonomous being within an individual existence. Key advocates of this approach, as the Dalai Lama (2007), consider what people think about their self, their personality and ego, as temporary creations, if not delusions (a claim that is surprisingly similar to the perceptual-bundle approach of David Hume, 1739). Practicing Buddhism is accordingly aimed to overcome any reminding barriers between self and other. "To forget the self", Zen Master Dogen (1976) writes, "is to be enlightened by all things, to be enlightened by all things is to remove the barriers between oneself and others". From this perspective, it is unsurprising that countries with a strong Buddhist tradition, like Taiwan, are scoring particularly low on the Hofstede individualism scale (17/120, as compared to 80/120 for the Netherlands).

If one assumes that being exposed to a particular religion create similar kinds of biases as reported for nationality/ethnicity, one would expect that religions advocating individualism should be associated with a stronger bias towards persistence (or a less pronounced bias towards flexibility) than religions advocating collectivism (Hommel &

Colzato, 2010). Indeed, Dutch neo-Calvinists showed a less pronounced global-preference effect (i.e., faster responses to the global than to the local level of multi-level stimuli; Navon, 1977) than Dutch atheists matched for race, intelligence, education, sex, and age (Colzato, van den Wildenberg & Hommel, 2008b). This observation is still consistent with Nisbett and Miyamoto's (2005) suggestion that it is the individualistic vs. collectivistic nature of the cultural background that matters (Cohen & Hill, 2007), but it suggests that it might well be religion or ideology, rather than nationality or ethnicity, that is providing that background.

A major conceptual problem of many studies on the impact of cultural factors on the processing of global and local aspects of visual information is that the tasks being tested can be interpreted as conflict tasks. For instance, multi-level stimuli, like the often used Navon letters (i.e., large letters made of small letters: Navon, 1977), are likely to create an attentional and/or decision-making conflict, as the global and the local elements commonly imply different responses. Given that attentional resources are limited, the same can be assumed for complex visual displays with a focal object and a rather rich background, as used in many intercultural studies (see Nisbett & Masuda, 2003; Nisbett & Miyamoto, 2005; Heinen, 2008, Chapter 9). Dealing with conflict is effortful (Botvinick, 2007), which may be taken to imply that more balanced performance profiles, such as more equivalent performance on global and local aspects of a display, simply reflects higher motivation (i.e., invested effort). While this may still be an interesting effect that even bears some connection to cognitive control in a wider sense, it would not necessarily be as specific as we and other researchers have suggested. This problem is particularly pressing with respect to the finding on religious orientation. There is ample evidence that religiousness as such is associated with reduced conflict between goals and increased self-monitoring and regulation (McCullough & Willoughby, 2009), suggesting

that engaging in *any* kind of religion improves performance on *any* task involving selection.

The first part of this implication was tested by comparing Dutch neo-Calvinists with matched Dutch atheists on the one hand and Italian Roman Catholics with matched Italian atheists (or seculars, as confessing atheists are difficult to find in Italy) on the other on Navon's multi-level task (Colzato et al., 2010c). Given that Roman Catholicism puts strong emphasis on collectivistic values and the social interdependence of appropriate behavior (e.g., John Paul II, 1987), the expectation was that this should lead to an increased, rather than a decreased global-precedence effect. The comparison between Dutch neo-Calvinists and Dutch atheists replicated the findings of Colzato et al. (2008b) by showing that the neo-Calvinists performed more equally in the global and the local task; in other words, they showed a less pronounced global-precedence effect than the atheists. The study also tested more liberal Calvinists and baptized atheists (i.e., individuals that were raised as conservative neo-Calvinists but no longer believed or engaged in religious practice), and it turned out that the liberal Calvinists fell in between the more conservative neo-Calvinists and the atheists, while the performance of the baptized atheists was indistinguishable from that of the neo-Calvinists. This suggests that the effect is rather sticky and does not depend on continuous religious practice. Even more importantly, the Italian Catholics showed the exact opposite effect as the neo-Calvinists, namely, a much stronger global-precedence effect than the Italian seculars. This rules out the possibility that religiousness per se is responsible for moderating the global-local effect, it rather seems to be the specific faith and, presumably, the degree of individualism or collectivism it implies. This latter assumption was reinforced by the fact that Colzato et al. (2010c) were able to replicate the increased global-precedence effect obtained for the Roman Catholics in Israeli Orthodox Jews (a population that also emphasizes

collectivistic values: Ichilov, 2005; Sagy, Orr, & Bar-On, 1999) as compared to Israeli seculars. Further support comes from another replication of the increased global-precedence effect in Taiwanese Zen Buddhists as compared to matched Taiwanese atheists (Colzato, Hommel, van den Wildenberg & Hsieh, 2010d).

All the studies on religion we have considered so far may be taken to imply that individualistic religions lead to better performance than collectivistic religions, but there is evidence speaking against that interpretation. Given that the multi-level task induces conflict, a more selective focus should be beneficial. In terms of metacontrol, this implies that greater persistence (rather than flexibility) would lead to more balanced performance and, hence, to a smaller global-precedence effect. If it is correct that individualistic ideology or religion lead to greater persistence, as we would argue, it makes sense that people with an individualistic cultural background perform better. But other tasks are conceivable, tasks in which performance benefits from less persistence and more flexibility. This was the rationale of Colzato, Hommel, and Shapiro (2010e), who compared Dutch neo-Calvinists and matched Dutch atheists in an attentional blink task. This task requires the report of two targets presented within a rapidly presented visual stimulus stream (for reviews, see Dux & Marois, 2009; Hommel et al., 2006). While the first target is commonly reported accurately, the second is often missed if it follows the first after an only short lag—the attentional blink. Of particular interest, there are reasons to assume that this effect reflects the inefficient distribution of attentional resources: most or all resources are allocated to the processing of the first target, so that too little is left for the second (Olivers & Nieuwenhuis, 2006; Shapiro et al., 2006). With respect to metacontrol, this translates into a problem of too much persistence: focusing too much on one event at a time should reduce performance in this task, while more flexibility should be helpful. If so, one would expect that neo-Calvinists show a stronger attentional blink:

as compared to atheists, their bias towards persistence should lead to a more exclusive allocation of attentional resources to the first target, which would make them more likely to miss the second. This is indeed what Colzato et al. (2010e) found. The main theoretical implication is that neither religiousness in general nor engaging in an individualistic religion necessarily improves performance. Rather, individualistic religions are associated with a stronger bias towards persistence, which can improve performance in tasks that benefit from persistence but impair performance in tasks that benefit from flexibility; collectivistic religions in turn are associated with a stronger bias towards flexibility, which can improve performance in task that benefit from flexibility but impair performance in tasks that benefit from persistence.

Let us now consider in some more detail how persistence might improve performance in persistence-heavy tasks. Conflict tasks with multi-level stimuli might benefit from persistence by increasing the selectivity of information processing. Higher persistence would thus allow to exclude irrelevant information more efficiently, which would allow to better exclude global information when responding to local stimuli and vice versa. As the global-precedence effect is mainly due to the difficulty to exclude global information when responding to local stimuli (Navon, 1977), more efficient exclusion of irrelevant information would tend to make responding to local and to global stimuli equally efficient, which in turn would tend to reduce the global-precedence effect. The same reasoning could be applied to the observation that Taiwanese Buddhists take more notice of other people's actions than matched Taiwanese atheists do (Colzato et al. 2012). But an alternative interpretation is possible. Rather than affecting the weighting and selection of relevant vs. irrelevant information, an individualistic religion may merely be associated with a smaller attentional focus. Processing the global aspects of a multi-level stimulus arguably requires a larger focus than processing a single stimulus at the

local level, and it is possible that zooming-in on local stimuli is easier for members of individualistic religions or ideologies. This may even account for the impact of religion on the attentional blink, if we only assume that attentional foci can move in both space and time: members of individualistic religions may also have a smaller temporal focus, which might impair their ability to process two consecutive events.

Testing between the selectivity and the focus account requires a task in which having a smaller spatial or temporal focus does not improve performance. These criteria apply to the Simon task, which was used by Hommel et al. (2011). The Simon task requires participants to carry out spatial responses to a non-spatial feature of a stimulus that is randomly presented on the left or right of some reference point. If the stimulus location happens to coincide with the location of the correct response, performance is better than if that is not the case (Simon & Rudell, 1967)—an outcome pattern that is referred to as the Simon effect (Hommel, 2011). As predicted by the selectivity account, but not by the focus account, the Simon effect was smaller in Dutch neo-Calvinists than in matched Dutch atheists, and larger in Italian Roman Catholics than in matched Italian seculars (Hommel et al., 2011). These findings suggest that religion is associated with a degree of selectivity to which relevant information is processed. The findings do not necessarily exclude the possibility that religion also impacts the spatial or temporal focus, but they do not require this assumption.

Another comparison provides some more insight into how interindividual differences in cognitive control may affect inhibition-related processes. On the one hand, religion was found to be systematically related to performance in a temporal discounting task (Paglieri et al., 2013). In particular, Dutch neo-Calvinists were more willing to wait for monetary rewards than both Italian Roman Catholics and Dutch atheists, and Italian Catholics were less tolerant of delay than either Dutch Calvinists or Italian seculars. To

the degree that patience in a temporal discounting task reflects the inhibition of immediate reward-consuming tendencies (Kirby & Marakovic, 1996), this pattern suggests that neo-Calvinism is associated with increased, and Catholicism with reduced inhibitory abilities. On the other hand, however, no differences between Dutch neo-Calvinists and Dutch atheists, or between Italian Roman Catholics and Italian seculars were obtained in a stop-signal task (Hommel et al., 2011). As we will argue below (see section on mechanisms), this suggests that religion does not operate on dedicated inhibitory systems but on control functions that can generate inhibition as a byproduct. Note that this implication fits well with the psychometric observation that inhibition does not seem to be a separable stand-alone factor (Friedman et al., 2008).

Sexual orientation

Both nationality and religious belief are just two indicators of interpersonal segregation and group-formation, which represent the key constituents of cultural systems (Heine, 2010). Sexual orientation is another indicator, especially for individuals with less common orientations. Interestingly, there is evidence that sexual orientation has an impact on metacontrol. It has often been suggested that homosexuals have a kind of “sixth sense” for recognizing the sexual orientation of others, especially of other homosexuals—an ability referred to as gaydar (Shelp, 2002). Scientific research confirmed the existence of this ability, at least under some circumstances. In particular, Ambady, Hallahan, and Conner (1999) observed that homosexuals are more accurate than heterosexuals in detecting the sexual orientation of unfamiliar others in pictures and brief video clips, but this benefit goes away when the video clips are longer. This suggests that it is not the knowledge about orientation-relevant perceptual cues that makes the difference, but the speed at which these cues can be extracted from brief presentations. Considering the findings on local versus global processing, and the idea that a high degree of persistence

might increase the focus on relevant information, which in turn would reduce the global-precedence effect, Colzato, van Hooijdonk, van den Wildenberg, Harinck, and Hommel (2010f) tested the possibility that homosexuals have a stronger bias towards persistence. If they would, homosexuals should exhibit a less pronounced global-precedence effect than heterosexuals. Colzato et al. tested this possibility by comparing homosexuals and heterosexuals, matched in terms of race, intelligence, sex, mood, age, personality, religious background, educational style, and socio-economic situation, in a Navon-style multi-stimulus task. As predicted, homosexuals showed a significantly smaller precedence effect, which means that they showed less difficulty than heterosexuals in processing details.

INTRAINDIVIDUAL VARIABILITY IN METACONTROL

Mood

At least two research lines have tested the possibility, and provided evidence that mood—or the functional or neural state underlying it—entertains an intimate link to metacognition. For one, positive mood is suspected to promote loose thinking and efficient brainstorming (Ashby, Isen & Turken, 1999), and many studies have indeed reported that divergent thinking benefits from positive-mood induction (Baas et al., 2008; Isen, 1999). Both neuroscientific (Ashby et al., 1999) and functional (Nijstad, De Dreu, Rietzschel & Baas, 2010) considerations suggest that positive-going mood (and the underlying increase of dopaminergic levels) creates a less focused, more flexible control state that allows for a less constrained flow of information and the consideration of information that is only vaguely associated with task-relevant objects. As typical divergent-thinking tasks, like the Alternate Uses Task that requires participants to identify as many uses of a simple object as they can think of, benefit from a lack of constraints, it makes sense that positive mood improves performance in such tasks. From a metacognition perspective, these

findings suggest that the induction of positive mood leads to a shift of the assumed balance between persistence and flexibility towards the latter, which in turn provides evidence that this balance can change within minutes, if not seconds.

For another, mood induction has been reported to have a systematic impact on attentional selectivity. For instance, Dreisbach & Goschke (2004) induced no, positive, or negative affect before having participants perform in a task-switching experiment. Positive affect enhanced cognitive flexibility and reduced perseveration, but also increased distractibility by irrelevant information, suggesting that shifted metacontrol towards flexibility. Along the same lines, Müller et al. (2007) presented participants with prospective monetary gains in a set-shifting task. Interestingly, the impact of gains on persistence and flexibility was modulated by the subjective evaluation of the reward cues: participants who reported increasing their effort in response to reward cues showed increased cognitive stability, while participants who reported a positive, relaxed attitude towards reward cues showed increased flexibility. Similarly, under dual-task conditions, performance on the primary task is less affected by information related to the secondary task after induction of negative mood (Zwosta, Hommel, Goschke & Fischer, 2013).

A related research line has considered mood as an important (Botvinick, 2007) if not necessary (Inzlicht, Bartholow & Hirsh, 2015) internal cue to trigger control adjustments. Several cognitive tasks are diagnostic with respect to the degree to which participants are able to exclude task-irrelevant information, with the Stroop task (MacLeod, 1991), the Simon task (Hommel, 2011), and the flanker task (Eriksen & Eriksen, 1974) being the most prominent among them. The effects of these tasks consistently indicate that people are not able and/or willing to exclude irrelevant information entirely, so that performance is impaired if irrelevant stimulus information suggests or promotes an incorrect response. Interestingly, however, the size of these

effects can differ from trial to trial: e.g., the effect of irrelevant flankers is more pronounced after compatible trials (i.e., trials in which the irrelevant flanker indicated the same response as the relevant target) than after incompatible trials (i.e., trials in which the flanker indicated an incorrect response; Gratton, Coles & Donchin, 1992). This result pattern, which has been replicated for other conflict tasks as well, has been taken to reflect control adjustments triggered by conflict (Botvinick, Braver, Barch, Carter & Cohen, 2001; Egner, 2007; Verguts & Notebaert, 2009). Later versions of this account have emphasized the role of affective states (Botvinick, 2007), the assumption being that conflict induces negative affect, which in turn may be the trigger to focus more on the task and the relevant information. In other words, negative affect might shift metacontrol towards more persistence, which fits with Dreisbach and Goschke's (2004) claim that positive affect shifts metacontrol towards more flexibility.

A number of findings are consistent with the idea that trial-to-trial control adjustments can be moderated by affect. For instance, these adjustments are reduced or even eliminated after trials that are followed by monetary gains (van Steenbergen, Band & Hommel, 2009, 2012a) and when the task is performed after induction of positive mood (van Steenbergen, Band & Hommel, 2010), and increased in remitted depressive patients after acute tryptophan depletion (van Steenbergen et al., 2012b). On the one hand, it is important to point out that these findings do not necessarily require the assumption that emotional experience and subjective affect play a causal role in control adjustment. In fact, establishing a subjective affective experience is arguably taking so much time that an intervening role in trial-to-trial adjustments does not seem plausible. Moreover, there is no reason to believe that concepts referring to subjective experience do not overlap in terms of their underlying neural or functional mechanisms (Hommel & Colzato, 2015), suggesting that emotion and affect may not be a factor in cognitive control but rather the

experience thereof (Hommel, Moors, Sander & Deonna, in press). On the other hand, however, the available findings strongly suggest that affective states are systematically associated with signals that trigger shifts in metacontrol towards persistence (such as negative mood) or flexibility (such as positive mood). Given the key role of dopaminergic state-changes in the processing of reward (Schultz, 2000) and the establishment of mood states (Ashby et al., 1999), as well as the key role of dopaminergic pathways in cognitive control, this should not come as a surprise but rather as converging evidence that the concept of self-control and emotion might indeed represent different sides of the same coin.

Meditation

Many meditation practices include active efforts to train cognitive abilities that obviously relate to attention and cognitive control in a wider sense. According to Lutz, Slagter, Dunne, and Davidson (2008), most techniques can be sorted into two categories: focused-attention meditations that are coaching the meditator to better focus on a single thought or event and to avoid any sort of distraction, and open-monitoring meditations that are teaching the meditator to open up and accept any possible upcoming thought. Brief consideration reveals an obvious resemblance of this pair of techniques to the two metacontrol states under discussion—persistence and flexibility, respectively. Some studies have investigated whether extensive meditation training affects control processes, and attentional control in particular (for a review, see Lippelt, Hommel & Colzato, 2014). But, more importantly for our purposes, there is also evidence that only briefly engaging in meditation has a systematic impact on metacontrol. For instance, in both practitioners and novices, brief bouts of open-monitoring meditation substantially improved divergent thinking without having impact on convergent thinking, while brief bouts of focused-attention meditation tended to have the opposite effect (Colzato, Ozturk & Hommel,

2012; Colzato, Szapora, Lippelt & Hommel, in press). This suggests that engaging in open-monitoring meditation promotes metacontrol bias that is useful for finding as many suitable solutions to a vaguely defined problem as possible (which is how divergent thinking is operationalized) while focused-attention meditation promotes a bias that is useful for finding the only possible solution to a well-defined problem (which is how convergent thinking is operationalized)—a description that clearly implies flexibility and persistence, respectively. This scenario also fits with the observation that engaging in convergent thinking increases task shielding and reduces shifting flexibility in a dual task situation (Fischer & Hommel, 2012), an outcome that parallels the findings of Dreisbach and Goschke (2004) for negative mood induction.

Along the same lines, brief bouts of open-monitoring meditation produced a significantly smaller attentional blink in meditation novices than engaging in focused-attention meditation (Colzato, Sellaro, Samara, Baas & Hommel, 2015), confirming the prediction that open-monitoring meditation promotes a less temporally-focused allocation of attentional resources. While open-monitoring meditation facilitates performance in tasks that rely on flexibility, it also impairs performance in tasks that rely on persistence. Notably, open-monitoring meditation, as compared to focused-attention meditation, reduced trial-to-trial adjustments in a Simon task (Colzato, Sellaro, Samara & Hommel, 2015).

MECHANISMS OF METACONTROL SHARING

Findings from behavioral genetics and from cultural studies have demonstrated the existence of systematic intraindividual differences with respect to indicators of metacontrol biases. The complexity of dopaminergic interactions underlying control processes is not yet sufficiently understood to allow for directed predictions under many circumstances, but there are clear proofs of principle that polymorphisms of genes

impacting frontal and striatal dopaminergic processing are associated with systematic outcome patterns in tasks tapping into metacontrol. Cultural studies suggest systematic relationships between the individualistic versus collectivistic nature of the dominant national ideology or religious orientation on the one hand and systematic biases of metacontrol towards persistence and flexibility, respectively, on the other. We note that neither behavioral genetics nor cultural studies allow for a causal interpretation of the available observations. Both research lines are correlational in nature, which makes it difficult or impossible to exclude the impact of other, merely correlated factors. It is also possible that what has been considered cultural effects are actually genetic in nature, as people with particular metacontrol tendencies might prefer some religions or subcultures over others. And, conversely, given the often very homogeneous populations investigated in genetics studies, what looks like genetic effects may actually reflect cultural impact. Nevertheless, it seems clear that cognitive control is not a uniform functional given but a system that shows systematic variability that is associated with dopaminergic functioning and cultural differences. This fits with from studies on the impact of mood, affect, and meditation on cognitive control, which provide substantial evidence that metacontrol settings are not fixed but variable to at least some degree. Importantly, this implies that the factors responsible for the interindividual variability in metacontrol settings we have discussed do not account for all individual differences, but space is left for situational and state-dependent effects. This fulfills our second criterion for the transfer of metacontrol to make sense, as it means that individuals are able to change their metacontrol biases according to external signals and communication with others.

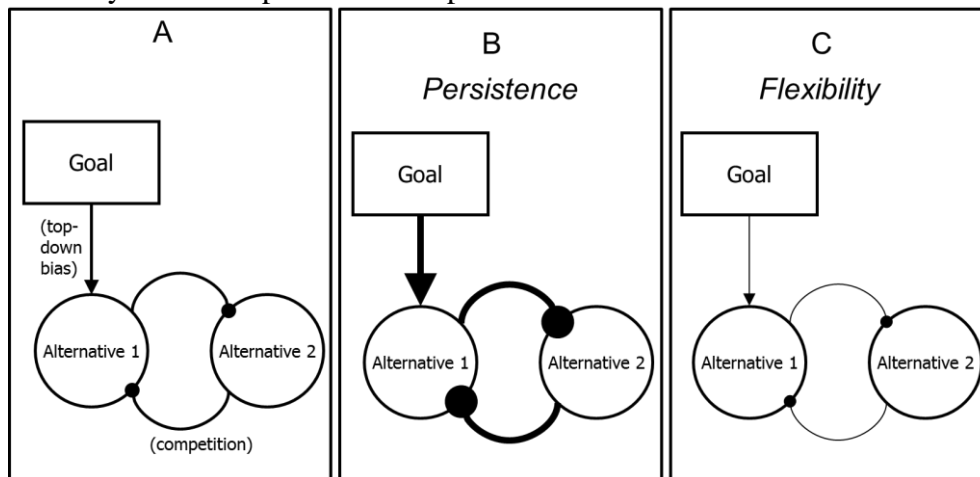
But how does metacontrol work? Given the apparent reliance of metacontrol, and the balance between persistence and flexibility in particular, on dopamine, a neuromodulator that very broadly impacts the how but not the what of control, a

mechanistic model of metacontrol must not be content- or domain-specific. Hence, metacontrol is unlikely to have a direct impact on how control operations implement and fine-tune perceptual, attentional, and action processes to carry out a particular task but it would rather be expected to moderate the processing style reflected by these processes.

As we have suggested elsewhere (Colzato et al., 2010c; Hommel, 2015), a mechanistic model would need to consider the basic architecture of human decision-making. According to the critical review of Bogacz (2007), increasing neuroscientific insights favor competitive decision-making models over passive evidence-collecting models. In particular, biologically plausible models need to assume that the evidence collected for one given alternative is related and compared to the evidence collected for other alternatives in a winner-takes-all fashion. As shown in the cartoon version of such a model in Figure 1A, competitive decision-making can be considered as the competition of representations of possible alternatives for selection. The representation of a given alternative would increase in strength as a function of the available evidence supporting it (e.g., the representation of one response increases as more evidence is available that the stimulus it is mapped on was presented), which in turn would not only increase the probability that it is finally selected (and the corresponding actions carried out) but also inhibit the representation of other alternatives (the representation of the other response, say). As compared to a passive evidence-selection model, such a competitive model would speed up decision-making, as the activation difference between given alternatives would be a function of both the available evidence for each representation and the available evidence for each alternative. While competitiveness refers to the relationship between decision-making alternatives, the second key ingredient of biologically plausible decision-making models is the fact that competition is biased by goal states (Desimone & Duncan, 1995). Accordingly, the probability of a given alternative to be selected does not

only depend on the evidence supporting it but also on the degree to which it fits with current intentions and goals of the decision-maker. In the figure, this is indicated by goal states favoring one (or more) of the available alternatives, but it is just as possible that various alternatives are supported by goal states in a more graded fashion; for instance, grasping a cup of water with the dominant and the non-dominant hand would both be supported by the goal to quench one's thirst, but the less effortful dominant-hand action might receive stronger support because it uses fewer resources (cf., Rosenbaum et al., 1995).

Figure 1: Schematic model of metacontrol. (A) Metacontrol is assumed to affect two parameters: the degree of competition between decision-making alternatives and the degree to which this competition is biased by the current goal. (B) Extreme persistence is characterized by strong competition and top-down bias. (C) Extreme flexibility is characterized by weak competition and top-down bias.



If we can thus assume that the basic architecture of human decision-making is characterized by competitiveness and top-down bias, as indicated in the figure, we need to ask how metacontrol might influence processes using such an architecture. Given that metacontrol is unlikely to operate on specific content, it is unlikely to relate to the representations of alternatives or the goals that provide top-down input. Rather, metacontrol is likely to moderate the degree to which competition and top-down bias are taking place (Hommel, 2015). An extreme degree of persistence can be assumed to strengthen the degree to which goal states bias decision-making and/or the degree of

competition between alternatives (in the absence of diagnostic evidence, we will not distinguish between these possibilities; for a broader discussion see Hommel, 2015), as sketched in Figure 1B. In contrast, an extreme degree of flexibility would strongly reduce the impact of goal states and/or the degree of competition, as sketched in Figure 1C. Following Hommel (2015), we will refer to this scenario as the Metacontrol State Model (MSM). Let us now consider how such a model would account for the outcome patterns reviewed so far, before we discuss some necessary extensions.

We have seen that interindividual variability in metacontrol biases is associated with the genetic setup and the cultural background of individuals. At first sight, this may be surprising given the evidence that what Friedman, Miyake and colleagues have identified as the three core components of cognitive control (updating, shifting, and inhibition) are almost entirely predicted by genetics (Friedman et al., 2008). It is true that the genetic effects on metacontrol are often very, very small and accounting for just a few percent of performance. However, this must be seen in light of the fact that the tasks that are used to assess cognitive control are not process-pure, which means that only a few percent of the performance are actually reflecting cognitive control. Accordingly, the small effects of genetic studies may actually capture a substantial portion of cognitive control. Moreover, many more genes than have been investigated so far may contribute to cognitive control, so that future insights into the human genome may increase the variability accounted for by genetic differences. The extraordinarily large samples needed for meaningful genetic analyses commonly prohibit the investigation of interactions between genes, it may be these interactions that account for the lion's share of control-related variability. Finally, it is certainly possible that the genetic setup and the cultural background are not independent. There may well be systematic genetic differences between different populations, be they defined by nationality, religion, sexual orientation,

or any other way. In that sense, finding systematic effects of both genetics and culture does not need to be a contradiction, even if the contribution of one of these factors is considered very high. At the same time, however, it is also true that most genetic studies, and in particular the one by Friedman et al. (2008), were conducted with very homogeneous samples. While many data referring to the cultural background are not reported, it seems very likely that the participants shared many more characteristics and environmental influences than, say, US Americans and Japanese. This implies that the available genetic studies may drastically underestimate contributions from cultural factors, including religious conviction, values, and other metacontrol-relevant aspects. For the time being, we in any case do not consider reported high percentages of genetically predicted variability and a strong impact of culture as contradictory.

Genetics

With respect to possible genetic influences, we hesitate to directly relate the functional implications of metacontrol biases to specific neural or neuromodular processes. As we have pointed out, it is difficult to say which exact level of dopamine in the frontal pathway is necessary to promote optimal performance in a persistence-heavy task, whether and how that level depends on the exact level in the nigrostriatal pathway, whether it is the tonic or the phasic level that is more important, how tonic and phasic levels interact, and so forth and so on. It also remains unclear whether and to what degree the two relevant dopaminergic pathways interact. While their activity is driven by different sources, the ventral tegmentum and the substantia nigra, these sources are notoriously difficult to segregate and delineate in humans (e.g., Chowdhury, Lambert, Dolan & Düzel, 2013). This raises the possibility that their control is synchronized to some degree or perhaps even that the two pathways are controlled by the same input or system. And yet, note that the genes we have considered, and even a number of other

factors, were shown to impact metacontrol in an asymmetric fashion. That is, an impairment of persistence does not necessarily lead to more flexibility, and vice versa, suggesting that the components that realize the balance between persistence and flexibility are not fully integrated but are autonomous to some degree.

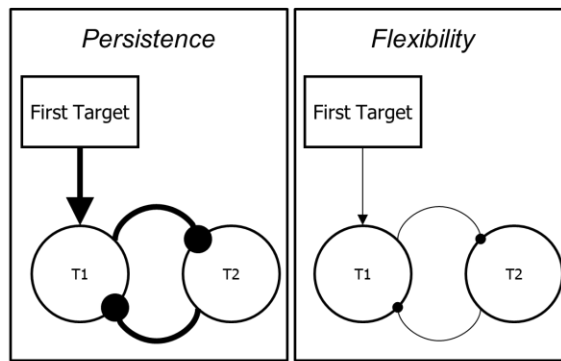
In other words, while persistence and flexibility may be considered opposite poles on a single dimension at a (meta)control level (at which a shift towards persistence necessarily implies a shift away from flexibility, and vice versa), these control settings still need to be translated into contributions from partly independent systems. It is the interaction of these systems from which the actual balance between persistence and flexibility emerges, and these emerging properties may be less binary and symmetric than the original settings. The relationship between the input and the effect of metacontrol settings can thus be considered to be similar to steering a car: while the steering wheel regulates direction on a single left-right dimension, blocking the wheels to go right does not make the car turning left. Nevertheless, the available findings suggest that particular kinds of dopaminergically-relevant genetic setups promote persistence and/or impair flexibility, while other setups have the opposite effect. In our cartoon model, this would suggest that some setups are associated with a configuration that tends more towards the extreme shown in Figure 1B while other setups are associated with a configuration that tends more towards the extreme shown in Figure 1C.

If so, this would be expected to affect performance in an attentional blink task as sketched in Figure 2. A persistence-biased metacontrol configuration would make attention rather selective. That would be true for both space and time, but it is time that matters in the attentional blink task. If the first of two targets appears (T1), it would receive strong top-down bias from the goal representation, which in this task can be considered to hold templates of possible targets. The support would lead to a strong

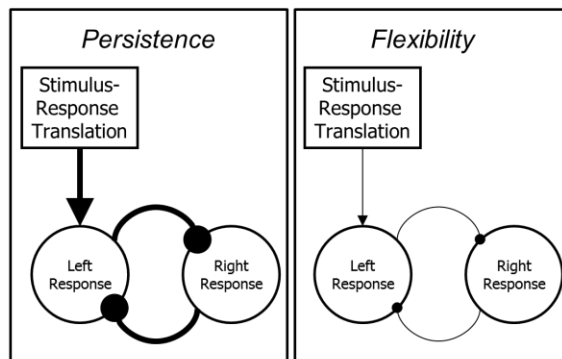
suppression of other events, which in the case of a quickly succeeding second target (T2) would lead to a strong inhibition of its representation. This would make missing the second target more likely, which in turn implies a stronger attentional blink. Stronger blinks were found indeed for carriers of polymorphisms that are assumed to be associated with a less effective striatal dopaminergic pathway (Colzato et al., 2011) and in individuals with relatively low spontaneous eyeblink rates (Colzato et al., 2008a), which is likely to reflect nigrostriatal functioning. A less extreme focus on the first target would be more efficient in this task, which is what the findings show and what the overinvestment account of the attentional blink (Olivers & Nieuwenhuis, 2006; Shapiro et al., 2006) has suggested.

The same genetic setup would be expected to have negative consequences in tasks that are more selective and less inclusive in nature, and so it is not surprising that the genetic setup that allows for better performance in the attentional blink task is also associated with a greater tendency towards dysfunctional impulsivity (Colzato et al., 2010b). It is also of interest that our account has implications that relate to inhibition without including a dedicated inhibitory mechanism (cf., Munakata, Herd, Chatham, Depue, Banich, & O'Reilly, 2011). Note that a persistence-biased configuration would have more severe consequences for the decided-against alternative than a flexibility-biased configuration, as explained in our attentional blink scenario. Inhibition would thus be a byproduct of persistence and focusing, and impulsivity a byproduct of flexibility, which would fit with the assumption of Friedman et al. (2008) that their inhibition factor might represent an emerging property of general control abilities.

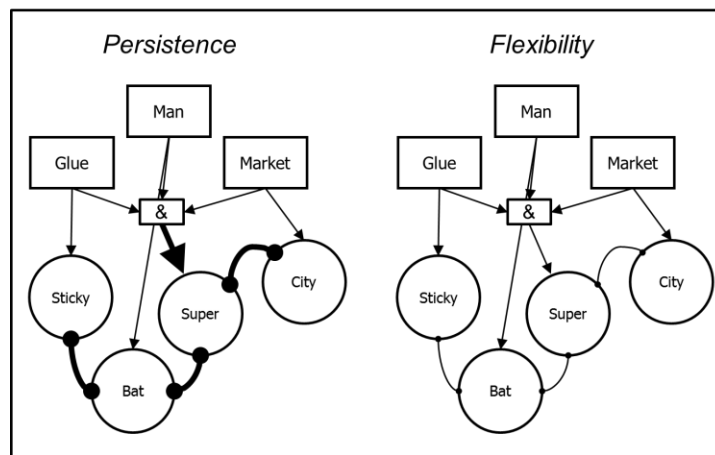
Attentional Blink Task



Simon Task



Convergent Thinking



Divergent Thinking

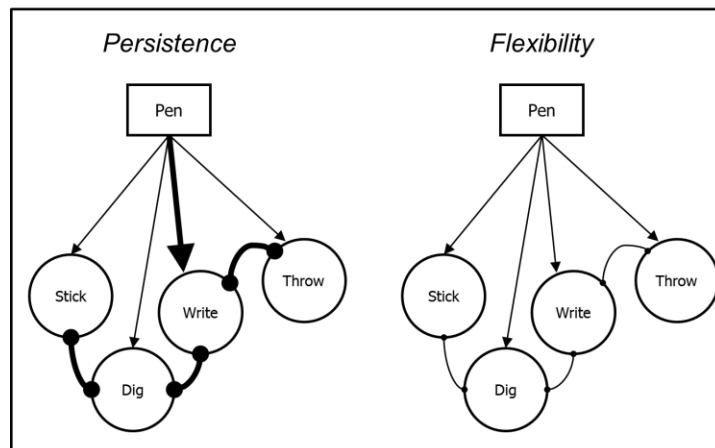


Figure 2: Scenarios illustrating how persistence or flexibility biases might affect performance in the Attentional Blink task, the Simon task, convergent thinking in the Remote Association Task, and divergent thinking in the Alternate Uses Task. Constraining goal representations are shown in rectangles and competing decision-making alternatives in circles (the two targets in the Attentional Blink task, the two response alternatives in the Simon task, or the verbal responses in the convergent and divergent thinking tasks). Note that a persistence bias is characterized by strong goal impact and strong mutual inhibition, while a flexibility bias is characterized by weak goal impact and weak mutual inhibition.

Culture

To account for the impact of culture on metacontrol, MSM applies the same reasoning as suggested for understanding the impact of genetics. Indeed, it is easy to imagine that particular kinds of cultural backgrounds are associated with particular biases. For instance, engaging in individualistic religions like neo-Calvinism may generate a bias towards persistence, while engaging in collectivistic religions like Catholicism, Judaism, or Buddhism may generate a bias towards flexibility. As a consequence, one would expect that members of individualistic religions tend to focus strongly on relevant information while members of collectivistic religions would integrate more nominally irrelevant information. This accounts for the observed attentional differences between US-Americans and Japanese, but also for the observation that neo-Calvinists show a smaller Simon effect but a larger attentional blink, while Catholics show the exact opposite pattern. As indicated in Figure 2, more persistent metacontrol would impair performance in the attentional blink task, due to an over-investment of resources into the first target, which leads to a greater neglect of the second. As also indicated, persistent metacontrol would improve performance in the Simon task, however. This task induces response conflict (in incompatible trials) by presenting stimuli at a location that corresponds to the incorrect response, which has been shown to activate this response's representation (Sommer, Leuthold & Hermanutz, 1993). As the figure indicates, this creates a conflict between the correct response, which is activated by the translation of the relevant stimulus

attribute (such as color or shape) according to the instructed stimulus-response rules, and the incorrect response activated by stimulus location. More persistent metacontrol would reduce this conflict and facilitate its resolution by increasing the impact of the relevant stimulus information and increasing the inhibition that the representation of the correct response can exert on the representation of the incorrect response. Hence, the correct response will receive less interference and be more efficient in outcompeting alternatives. This would be expected to reduce the Simon effect in members of cultures that induce a persistence bias—such as neo-Calvinists, which is indeed what the data show.

So, the eventual mechanism that is responsible for cultural effects is easy to envision but its emergence is less obvious. How is it possible that, say, neo-Calvinism creates a persistence bias? In the following, we will develop a theoretical scenario that accounts for the impact of cultural factors on metacontrol. As we will explain, this scenario relies on MSM, to which we add three assumptions (or two, as the first was implied by the first version already): (a) metacontrol states have a perceivable impact on behavior; (b) culturally appropriate behavior generates positive feedback; and (c) positive feedback reinforces both the behavior and the underlying metacontrol state, and thus makes their future occurrence more probable.

To account for any impact of cultural factors on metacontrol states, or in fact any internal state, one needs to assume that these internal states can be made visible to the social environment (as claimed by our first assumption), so that this environment can provide selective (positive or negative) feedback (as required by our second assumption). Feedback requires criteria and these criteria must not refer to unobservable internal states but to observable behavior. For metacontrol states to be affected by social feedback, they therefore must generate specific kinds of observable behavior, as sketched in Figure 3. More specifically, particular metacontrol states must generate particular kinds of behavior

that are sufficiently distinguishable from behaviors that are generated by other metacontrol states. If thus metacontrol state X generates behavior A, and metacontrol state Y generates behavior B, A and B must be sufficiently distinguishable for the social environment to react differently to them.

We are not aware of any study that has directly tackled that issue but we do not consider this assumption particularly far-fetched either. Take, for instance, the way individualistic and collectivistic cultures are characterized by Hofstede et al. (2010). Members of individualistic cultures are assumed to look after themselves and their immediate family members only, to communicate more explicitly, and to rely on personal values. Members of collectivistic cultures, in contrast, are assumed to belong to in-groups that look after them in exchange for loyalty, to communicate more implicitly, and to rely on values based on their social network (Wursten & Jacobs, 2014). Consider what that implies for day-to-day behavior. Members of individualistic cultures would need to focus on much less information, on much fewer persons, on much fewer personal cues, which in comparison to members of collectivistic cultures would allow them to concentrate much more on salient events and communication channels. Such cultural differences are likely to be related to observable behavioral differences. For instance, a conforming member of an individualistic culture would show more coherent behavior, less variability related to switching between different informational sources, rely more on talking rather than body signals, and so forth. As we have argued, efficiently engaging in such behaviors would benefit from a metacontrol bias towards persistence, while the behavior expected from a member of a collectivistic culture would show the opposite characteristics and would thus benefit from a stronger metacontrol bias towards flexibility. As people will tend to establish a metacontrol state that makes their behavior more efficient, this suggests that increasing efficiency is accompanied by an increasingly specific one-to-one mapping

between metacontrol states and particular kinds of behavior.

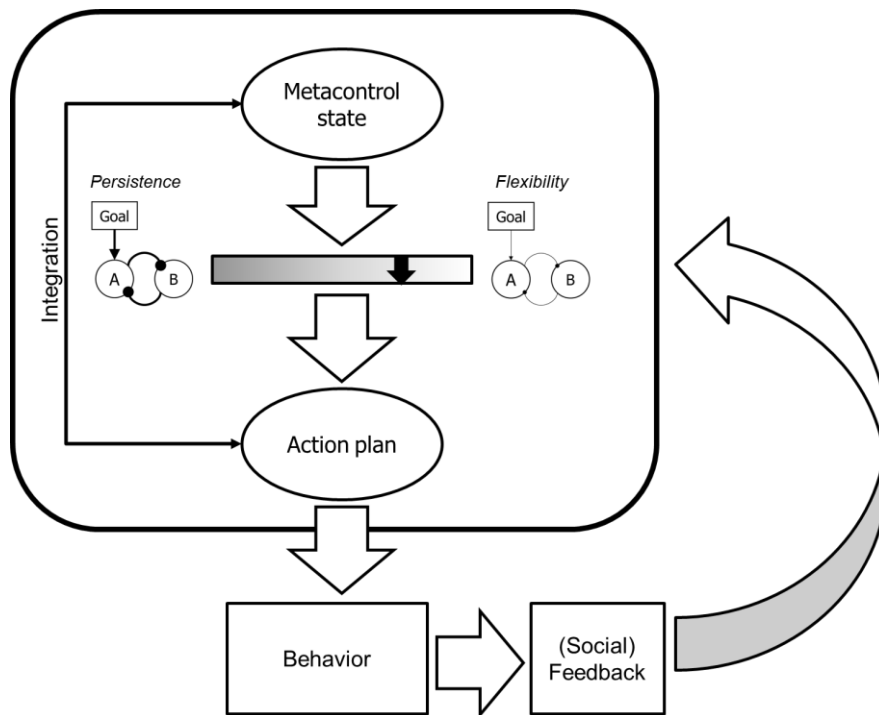


Figure 3: A mechanism of acquiring metacontrol state preferences through social feedback. The present metacontrol state is assumed to determine the current balance between persistence and flexibility, as indicated by the black arrow on the gray scale. This balance has an impact on the characteristics of action plans, which in turn translate into overt behavior that receives positive or negative feedback, including social feedback that reflects the conformity of the behavior with the cultural norms and values. Repeated sharing of positive feedback leads to the integration of metacontrol states and actions.

Establishing a one-to-one mapping between behavior and the underlying metacontrol state implies the frequent co-occurrence of behavior and state, which in turn implies that behavior and state are exposed to the same kind of social feedback. Accordingly, social approval of the behavior will often take place at a time the corresponding metacontrol state is active. Applying a simple Hebbian learning rule (what fires together wires together) would mean that social approval reinforces both behavior and metacontrol state, which can be assumed to make their future reappearance more likely (as suggested by our third assumption). The more behaviors are associated with a particular metacontrol state, the more often it will be reestablished, which implies a

particularly frequent occurrence of metacontrol states that generate culturally conforming behaviors. If our assumption that particular cultural norms and values, such as expressed by a particular religion, often imply similar or identical metacontrol states, this would mean that these particular states would be very frequent and dominant in everyday life. It makes sense to assume that this is likely to lead to the chronification of the respective state and make it the default.

Having established a default metacontrol setting may have a stabilizing function and improve subjective well-being. Not having a default creates uncertainty regarding the optimal metacontrol setting, which implies conflict between alternative options. Given that conflict is associated with negative affect and the motivation to actively reduce it (Botvinick, 2007), this means that creating a default is likely to improve well-being. Most of the laboratory tasks we have considered so far may benefit from, but do not require one specific metacontrol state, which implies that the interindividual differences we have discussed reflect people's chronified default settings.

Situational effects

As we have discussed, metacontrol states are not only related to rather long-lasting factors like genetics or cultural impact, but they also vary as a function of situational circumstances, such as mood or meditation. While these factors are likely to leave less permanent traces than genetics and culture, there is no reason why the temporary metacontrol biases they induce should impact performance in metacontrol-sensitive tasks in any other way than longer-lasting biases do. For instance, assuming that negative mood and focused-attention meditation tend to induce a persistence bias while positive mood and open-monitoring meditation tend to induce a flexibility bias, the impact of these biases on creative thinking, the best-documented effect of these factors, can be explained as shown in Figure 2. Convergent thinking, as operationalized by the Remote Association

Task (Mednick & Mednick, 1967), can be characterized as finding a highly constrained search for one single possible solution. The example uses a common item of this task (which word can go with “Glue”, “Man”, and “Market?”), for which “Super” is the correct answer. A persistence bias is likely to support this search as strong support for the alternative that fits the search criteria and a strong inhibition of alternatives that do not (e.g., other associates of the three search words) would be expected to speed up finding the right solution. A flexibility bias, however, would not be helpful, as this would not provide the needed guidance for the search process. Divergent thinking, as operationalized by the Alternate Uses Task (Guilford, 1967), can be characterized as finding a vaguely constrained search for as many solutions as possible. The example uses a common item of this task (what you can you do with a pen?), and it shows some of many possible solutions. It is obvious that a persistence bias would not be helpful in this task, as it would speed up identifying the first possible item (“Write”, in the example) but, as this would lead to a strong inhibition of all other alternatives, it would take more time to reactivate these inhibited alternatives when searching for a second item. A flexibility bias, in turn, would reduce that problem and allow to rapidly considering and reporting various possibilities.

The evidence for intraindividual variability triggered by mood manipulations and meditation suggests that the acquisition of long-lasting default settings does not prevent situational metacontrol adjustments. One possibility would be that defaults are effective only in situations where no specific metacontrol setting is required, but can be overwritten by situational factors. Another possibility is that defaults demarcate a range of preferred or dominant metacontrol states, which can be modified but act as a kind of reference point. If so, positive mood and open-monitoring meditation, say, would tend to shift metacontrol towards flexibility irrespective of the default value, but the short-term effect

in the long-term bias would operate on metacontrol in an additive fashion, so that the interindividual difference would still exist. Preliminary evidence for this possibility was provided by Akbari Chermahini and Hommel (2012), who induced positive mood in participants before they performed a divergent-thinking task. Positive-going mood increased the individual eyeblink rates (a marker of striatal dopamine), as one would expect, but only individuals with low blink rates improved in divergent thinking. Considering that medium blink rates are associated with best performance in divergent thinking (Akbari Chermahini & Hommel, 2010), this suggests that positive mood induction increases striatal dopamine levels in everyone, and probably to the same degree, but whether this is advantageous depends on the original level (i.e., on whether the increase is moving the level of this person towards or away from the optimal region). In other words, the actual performance seems to be predicted by the additive combination of long-term (tonic) in short-term (phasic) dopaminergic impact—but resolving this issue calls for more studies, ideally with pharmacological interventions.

While mood and meditation can both be considered situational factors (given the evidence that meditation novices and practitioners do not differ in metacontrol-sensitive tasks), they are likely to affect metacontrol in different ways. Given the dopaminergic implications and effects of mood changes, it seems plausible that mood does not necessarily change the metacontrol setting itself but rather moderates the resulting balance between frontal and striatal dopaminergic pathways. Meditation, in contrast, is likely to promote particular metacontrol states directly. In fact, the entire concept of meditation can be considered as a training technique developed to establish particular metacontrol states—a persistence-heavy state in the case of focused-attention meditation and a flexibility-heavy state in the case of open-monitoring meditation. Taken together, long-term and short-term effects on metacontrol can be conceptualized as reflecting the

establishment of a preferred range of metacontrol values on the persistence-flexibility scale indicated in Figure 3 and more short-term shifts towards persistence or flexibility induced by situational factors.

There is another set of findings that calls for one more assumption however. It has been shown that asking Western participants to use personal pronouns, like “I”, “me”, and “mine” (as compared to relational pronouns like “we”, “us”, “ours”), induces a local, context-insensitive processing strategy (Kühnen & Oyserman, 2002) in the speaker and reduces the degree to which he or she considers and cognitively represents other people in a given situation (Colzato, de Bruijn & Hommel, 2012). This suggests that engaging in a more individualistic versus a more collectivistic activity tends to induce a corresponding shift of metacontrol towards persistence and flexibility, respectively. Hence, not only can a particular metacontrol state affect action planning but planning and performing a particular action can change the metacontrol setting. This suggests that the frequent co-occurrence of metacontrol states and culturally appropriate actions does not only lead to their joint social approval, but this in turn leads to the integration of metacontrol state and action, as indicated in Figure 3. Note that this integration implies the emergence of a self-maintaining cultural feedback loop. For instance, we have discussed that living in an individualistic culture will more often require explicit, verbal communication to express one’s needs and intentions as compared to a collectivistic culture. Expressing one’s needs and intentions commonly requires the use of personal pronouns (except if they are relational in nature, which however is less likely in an individualistic culture), which in turn promotes a metacontrol state that has been integrated with such behaviors—a persistence-heavy metacontrol setting that is, which in turn makes other individualistic actions more likely, and so forth.

CONCLUSIONS AND OPEN QUESTIONS

We have seen that genetic disposition and culture are associated with systematic interindividual variability in relative metacontrol biases towards persistence or flexibility. This means that one precondition for interpersonal sharing of metacontrol settings is fulfilled: if people differ in metacontrol settings, it may make sense to transfer them from one to another. We also have seen that situational factors can bias metacontrol towards persistence or flexibility, with mood and meditation being our key examples. The existence of interindividual variability demonstrates that the apparently rather permanent default settings due to genetic, cultural, or other factors do not fully determine the setting but leave some space for variability and, hence, for situational adjustments and sharing. This meets the second of our two requirements for successful sharing.

We then suggested MSM, a model of metacontrol, which we extended to account for cultural learning. The model explains how genetic predisposition and cultural exposition might induce particular default values of metacontrol, and how these values might be moderated by situational factors. While the MSM serves well to integrate findings from various domains and research lines, we consider it still preliminary, as a working model that is. The reason is that a number of important questions remain unanswered so far, and it is not unlikely that answers to these questions will change aspects of the model, or at least provide more detail and add quantitative precision. In the following, we discuss some of the most pressing questions of that sort.

First, we have treated the metacontrol dimension as unidimensional and as ranging from persistence to flexibility. This decision seems to serve well for sorting most of the available findings, but more insight into the neural machinery underlying metacontrol may require more complex theorizing. We have seen some evidence that this machinery is partly independent, in the sense that genetic predisposition targeting the frontal

dopaminergic pathway may impair persistence but may leave flexibility intact, while genetic predisposition targeting the nigrostriatal dopaminergic pathway may have the opposite effect. This suggests that not all of the balance between persistence and flexibility may emerge from the direct opposition of these two pathways, which could have been one theoretical option, as this would seem to imply a more direct impact of the state of one pathway on the state of the other. We have suggested that the setting itself might be separate from the emerging balance, so that the impairment of one component of this balance (such as one dopaminergic pathway) need not change the metacontrol setting itself. However, it may well be that it is not the opposition between pathways that matters but rather relative contributions from different dopaminergic receptor systems, and it is not quite clear how that might change the interpretation of genetic effects. Moreover, the enormous efforts required for the investigation of interactions between polymorphisms of different genes will make it difficult to assess of what kind and how strong the impact of such interactions on metacontrol or its realization may be.

Second, we have discussed a number of tasks that arguably are sensitive to metacontrol settings, in the sense that some tasks can be assumed to benefit from persistence while others can be assumed to benefit from flexibility. And yet, no psychological task can be considered process-pure. For instance, we have argued that the Simon task and the Remote Association Task benefit from persistence, while the Attentional Blink task and the Alternate Uses Task benefit from flexibility. While we believe that these are reasonable arguments, it is certainly true that performing the Simon task and the Remote Association Task involves processes and operations that call for some degree of flexibility: e.g., the Simon task is known to invite trial-to-trial adjustments (Stürmer, Leuthold, Soetens, Schröter & Sommer, 2002) and the Remote Association Task does require the systematic search through memory. Along the same lines, both the

Attentional Blink task and the Alternate Uses Task does require the continuous representation of target templates—some degree of persistence that is. More precisely assessing and quantifying the reliance of a task on persistence and flexibility seems useful but difficult to manage. This need not preclude the demonstration of proofs of principles, as our review demonstrates, but it will represent a challenge for developing a more systematic psychophysics of metacontrol.

Third, we have discussed evidence that dopamine levels relate to performance in persistence- and flexibility-diagnostic tasks in an inverted U-shape fashion (Akbari Chermahini & Hommel, 2010; Cools & D'Esposito, 2011). This is not uncommon for effects related to neuromodulators or in fact for almost all neurochemical effects, but as long as there is no method to directly access and standardize dopamine levels, specific and in particular directed predictions will remain difficult to make. For instance, as long as it is impossible to objectively capture and describe the dopaminergic state that allows one given individual to show optimal performance in a particular task, it will be impossible to predict the exact effects of a given dopaminergic or dopamine-related manipulation, such as mood induction. The more systematic consideration and validation of diagnostic cues, such as spontaneous eyeblink rates, may help to tackle this problem.

Finally, it remains to be seen how the persistence-flexibility dimension we have considered in this article relates to other dimensions that have been discussed in the literature. One often-investigated dimension refers to the ability of humans to regulate the speed vis-à-vis the accuracy of their responses. The common observation is that increasing speed is often possible but associated with a loss of accuracy, while the increase of accuracy comes with the loss of speed: the speed-accuracy trade-off. Several theories have been suggested (for a review, see Bogacz, Wagenmakers, Forstmann & Nieuwenhuis, 2010), ranging from the assumption that speed emphasis leads to the

priming of cortical integrators (e.g., Furman & Wang, 2008) or the increase of striatal activity (which results in reduced inhibition)(Forstmann et al., 2008) to the cortically initiated slowdown of responding through the subthalamic nucleus (Frank, Scheres & Sherman, 2007) or the strengthening of synapses connecting cortical integrators and striatal neurons (Lo & Wang, 2006). Obviously, all these options can be considered to relate to the balance between the prefrontal and striatal mechanisms, which we assume underlie the regulation of persistence and flexibility. Indeed, it is easy to imagine that a strong bias towards flexibility, as shown in the right panels of Figure 2, allows for fast responding while a strong bias towards persistence, as shown in the left panels, slows down responses but makes them more accurate by making sure that the outcome represents the goal state. Accordingly, the metacontrol state model we propose arguably captures a substantial part of the functional and neural mechanisms underlying speed-accuracy trade-offs. Moreover, considering the possibility that the mechanism is neuromodulatory in nature, as we suggest, raises the possibility that all four of the available theoretical suggestions are correct. That is, changing the balance between the mesocortical and the nigrostriatal dopaminergic pathway may change the relative activity of both prefrontal and striatal systems, which in turn may systematically modulate subthalamic activity. That the frontal-striatal interaction becomes more effective through the strengthening of synaptic connections would also be a reasonable assumption. Hence, we consider the possibility to relate research on speed-accuracy trade-off and on the metacontrol of persistence and flexibility as a promising way to go.

A second theoretical line of reasoning is related to the contrast between will and habit, to use the original terms, between intentional and automatic control or, to use the latest disguise of this conceptual distinction, between model-based and model-free action control (e.g., Dolan & Dayan, 2013). The commonality of all these conceptual pairs is the

idea that action tendencies can be driven by goals and by stimuli, so that action control can be considered the resolution of conflict arising whenever goals and stimuli suggest different actions. A standard example is the Simon effect: when intending to respond by pressing the left or right key in response to the red or green color of a stimulus, say, responses take more time when the horizontal stimulus location does not coincide with the response location. The idea is that this increasing reaction time reflects a conflict, or the time needed to resolve the conflict, between the response implied by the color (the intentional response tendency) and the response implied by the location of the stimulus (the automatic response tendency)(e.g., Kornblum, Hasbroucq & Osman, 1990). The metacontrol state model suggests that the degree to which goals and stimuli contribute to action control is dependent on the metacontrol setting, and we have discussed evidence showing that religion indeed determines the degree of the Simon effect. Interestingly, the mentioned study comparing neo-Calvinists, atheists, and Roman Catholics on the Simon task revealed that neo-Calvinists no longer showed a significant Simon effect (Hommel et al., 2011). This suggests that the presence and size of the Simon effect depends on metacontrol settings, which in turn fits with the observation that electrophysiological evidence of stimulus-induced response tendencies in the Simon task disappear if the stimulus is presented before the stimulus-response mapping (Valle-Inclán & Redondo, 1998). This means that the instruction and, thus, the goal is the precondition for automatic tendencies to occur (Hommel, 2000). Hence, automaticity is goal-contingent (Bargh, 1989) and, thus, not really automatic. This undermines the common distinction between intentional and automatic tendencies and suggests that automaticity reflects the strategic use of environmental information for action control rather than goal-unrelated, stimulus-driven determination. Considering the role of metacontrol and its impact on the relative weight given to internally-triggered and stimulus-driven processes is likely to help

replacing the misleading distinction between intentional and automatic (or model-based and model-free) processes by a more realistic integrative model of action control.

A third line of theorizing we would like to briefly consider is related to the distinction between exploitation and exploration. The underlying idea is that many activities are associated with a control dilemma related to the question whether one should continue with the present activity or switch to an alternative option. This might relate to foraging (should one keep searching for food in a given area or explore other areas?), memory (should one keep searching for a word in the present semantic category or switch to another one?), or goals (should one keep trying to reach the given goal or give up and switch to another one?)(e.g., see Hills & Dukas, 2012). Hills (2006) has reviewed evidence that the regulation of exploitation and exploration is strongly related to dopaminergic functioning in various species, perhaps in interaction with other neuromodulators, such as norepinephrine (Cohen, McClure & Yu, 2007; Hills, Todd & Goldstone, 2010). The mechanism controlling the degree of exploitation and exploration has been characterized as a domain-general higher-level control process that is generated by a network including the prefrontal cortex. The process is assumed to determine the degree of persistence, which relies on goal representations and working memory, and inhibitory processes that propagate switching to new goals (Hills et al., 2010). Note how well this scenario fits with the one we have suggested to account for persistence-flexibility control. Also of interest, evidence for the domain-generalty of the control process has been provided by having human participants search through a visual array, in which resource spaces were arranged in either a clumpy or a dispersed fashion, before performing a Scrabble task involving a search for words that could be made from particular letter sets (Hills, Todd & Goldstone, 2008). It turned out that word-searching participants stayed longer within a given letter set before moving to the next after having

searched the clumpy array than after having searched the diffuse array. Moreover, within groups of participants, those who explored more in space also explored more across letter sets. Note that these findings parallel the observations from meditation studies: both the meditation and the search studies suggest a kind of metacontrol priming, in the sense that a metacontrol state established for one task seems to bias the metacontrol style in a succeeding task. We thus conclude that the available theorizing regarding the mechanisms underlying exploitation and exploration raises the possibility that this conceptual pair overlaps substantially or even entirely with the one we have focused on in the present article—persistence and flexibility.

Taken altogether, we conclude that the extended MSM we suggest does not only account for various findings from genetic, culture, and behavioral studies, for reported effects of mood and meditation, and for the social and cultural sharing of metacontrol states. It may also have the potential to integrate findings from investigations on related conceptual pairs, including speed and accuracy, intentional and automatic processing, and exploitation and exploration.

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