Optimizing perception

across the adult lifespan

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Abstract

While our sensors allow us to take up information on the world around us, perception is the process by which we make sense of it. Perception is one of the most essential functions of the human mind as it connects us with the world and allows us to interact with it – ensuring well-being and independence. It is intimately tied to other processes, such as motor control and memory. While perception seems trivial, the underlying processes are quite complex. The information obtained from our senses is inherently ambiguous and uncertain. Perception is understood as a probabilistic inference process that seeks to reduce uncertainty in order to provide us with a valid interpretation of our surroundings. During this process, predictions play a central role. Prior and sensory information are considered to be fused (based on their relative reliability) to infer the most probable state of the world.

Aging introduces a particular challenge to perception as it gives rise to even more uncertainty: As we grow older, internal noise in nearly all sensory systems increases while our tolerance for external noise decreases. In parallel, many cognitive abilities – such as working memory or processing speed – are subject to pronounced decline. However, one particular strength of growing older is that we gain more and more knowledge about ourselves and the world around us. This knowledge may provide a powerful resource to adapt to current challenges and could be used to improve our predictions. But in order to be beneficial, sensory and predictive signals need to be adequately balanced – in theory, predictions should become more important with age.

Across two different studies, I could show that aging increases the reliance on predictions, which has consequences for both motor control and memory processes. The first study examined how age and cognitive processes modulate tactile suppression during reaching. Tactile suppression was about three times stronger in older adults compared to younger adults, indicating greater reliance on sensorimotor predictions with age. Furthermore, increased task demands due to the introduction of an additional memory task overall led to increased tactile suppression but did not modulate the age effect. Across age groups, stronger tactile suppression effects were associated with lower cognitive control capacities.

The second study focused on the impact of prior knowledge on object memory. I investigated whether older and younger adults' memory performance for objects embedded in real-world scenes were differentially affected by object-scene inconsistencies (e.g. ketchup in the shower). Object-scene inconsistencies were beneficial for memory performance in both age groups. However, this memory advantage was attenuated in older adults. Additionally, older adults showed an enhanced

congruency-bias when asked to match recognized objects to their original context. The findings from this study highlight the role of predictive processes for memory performance and reveal slight disadvantages when predictions are violated.

While greater reliance on predictions may overall be an adaptive mechanism that helps us to improve our performance across different tasks, the decisions we make may still be wrong at times. Luckily, our decisions are usually accompanied by a subjective feeling of confidence. Confidence is an online process that monitors and controls our decisions and informs us whether we should trust or doubt them. It is highly important for successful behavior.

In two studies, I investigated how perceptual confidence is affected by age and increased task demands. In the first study, I could show that both younger and older adults can adequately distinguish between correct and incorrect perceptual decisions. Higher confidence was associated with better performance. However, on average, this ability was reduced in older adults compared to younger adults. Furthermore, individual differences in confidence efficiency and cognitive control capacities were closely related. The second study challenged metaperceptual abilities in a sample of younger adults and revealed that confidence comparisons across visual and tactile decisions are possible without any major costs in confidence efficiency or response times compared to confidence judgments made within the same modality. The study provided evidence that confidence is stored in an abstract, modality-independent format. It remains to be clarified how this ability is affected by age. In contrast to the previous study, though, confidence efficiency and cognitive control capacities were not correlated – most likely due to variance restrictions in an age-homogeneous sample.

Taken together, the four studies presented in this thesis contribute to our understanding on how different information is valued in response to individual challenges and current task demands. They further provide evidence that valuation processes are largely preserved with age and may serve as adaptive mechanisms to optimize performance in the face of pronounced sensory and cognitive changes. However, the efficiency of these mechanisms seems to rely on the availability of cognitive control resources.

Contents

1 Introduction

1.1 General introduction

Around the globe, populations are rapidly aging. For example, in Germany, about 22% of the population were age 65 or above in 2021. According to Destatis, this number is expected to increase to 31% by 2060 (Statistisches Bundesamt, 2022). The social and economic consequences of this demographic shift and how they can be properly addressed have been a matter of debate for several decades. One major concern is that the number of people living with dementia will also increase (Prince et al., 2013), placing an additional burden on healthcare systems (Wimo et al., 2017). Given this strong focus on declining abilities, disease and decreased independency with advanced age in public debates, we are surrounded by many misconceptions and negative stereotypes of aging. Specifically, older age is often depicted as a time of frailty and poor mental functioning (North & Fiske, 2015). This, in turn, may have negative effects on older adults' health and well-being (Dionigi, 2015).

However, aging is not a passive process of inevitable deterioration. Aging research is slowly starting to correct our misconceptions. While aging research was similarly biased towards general functional decline and pathological processes in its beginnings, the perspective now has changed. More recent research has shown that aging is a highly individual, dynamic and adaptive process that allows us to optimize our performance relative to our current abilities (Cabeza et al., 2018; Reuter-Lorenz & Park, 2014). The feared negative effects of aging are substantially delayed to very old age and may be brief (Gerstorf et al., 2015). In 2020, the World Health Organization (WHO) acknowledged the diversity of aging processes by declaring 2021–2030 the "United Nations Decade of Healthy Ageing" (World Health Organization, 2020b). With their novel definition of healthy aging as "[...] *the process of developing and maintaining the functional ability that enables well-being in older age* (World Health Organization, 2020a, p. 9)", they specifically promote a change in perspective: from disease-centered to function-centered.

Perception is one of the most essential functions of the mind as it allows us to actively gain a meaningful understanding of our surroundings. It is the basis for performing our daily tasks and activities – such as reading, crossing a busy street or opening a can of food for your 'starving' cat. Perception is closely tied to action and cognition, helping us to carry out our plans and pursue our goals. When getting older, our perceptual systems play an important role in ensuring

well-being and maintaining a high quality of life (Tseng et al., 2018). However, as aging research has been dominated by a strong focus on cognition and pathological changes, our understanding of perceptual aging in typical older adults is still quite limited. In particular, the mechanisms that help us to optimize our perceptual performance as we get older are not well understood. Interactions between perception, action and cognition have rarely been considered, although more and more efforts are being made to describe functional links (e.g. Maes et al., 2017; Monge and Madden, 2016).

The aim of my dissertation project is to expand our knowledge on how perception can be optimized for action and cognition in the face of pronounced sensory and cognitive changes. Studying groups of healthy older and younger adults, my goal is to not only focus on age differences but also age similarities, considering robustness as well as potential vulnerabilities. In the following introductory sections, I will provide the background information that is needed to understand my studies. In particular, I will explain some of the mechanisms that help us to optimize our perceptual decisions and provide an overview of the sensory and cognitive challenges we face as we get older. I will then outline the single experiments and summarize my main findings in separate chapters. Finally, in the closing chapter, I will discuss and integrate my key findings.

1.2 Making sense of uncertain sensory information

To most of us, perception might seem trivial. Walking on the sideway, seeing a squirrel running across the street while hearing birds chatter in the trees and experiencing the warmth of the sun on our skin – it all happens so smoothly and effortlessly, creating the impression we had direct access to the world around us. But for the most part, this is not true. Although the processes that enable us to experience our surroundings are very efficient, they are also highly complex.

It all starts with our eyes, ears, skin and other sensory organs that allow us to detect specific physical properties, such as light and sound. Each sensory organ belongs to a larger sensory system that is specialized in processing this input and transmitting it to higher processing areas in our brain. Perception is the process by which we make sense of this sensory input. However, the transition from sensation (activation of sensory organs) to perception (a meaningful, accurate and informative interpretation of our surroundings) is quite challenging. This is because the information obtained from our senses is inherently uncertain, allowing many possible interpretations. Uncertainties may arise from different factors. Sensory signals are ambiguous, meaning that different physical stimuli may cause similar activation patterns in our sensory organs. In

addition, our sensory systems are noisy since the same stimulus will not always cause the same response on repeated occasions. As we age, this internal noise even increases (e.g. Decorps et al., 2014; Morrell et al., 1996; Owsley, 2016). Finally, different environmental conditions, such as fog, haze or rain, can also lead to increased noise.

Given this noisy and ambiguous input – how can we extract meaning from it? Many elaborate models of perception understand perception as a probabilistic (Bayesian) inference process (e.g. Friston et al., 2017; Kersten et al., 2004; Knill & Pouget, 2004; Rao & Ballard, 1999). The goal of that process is to reduce uncertainty and infer the most probable state of the world (Knill & Pouget, 2004). There are different mechanisms that support this process. Here, I will focus on the role of prior knowledge and predictions as well as perceptual confidence.

1.2.1 Prior knowledge and predictions

The idea that our past experiences help us to interpret the present can be dated back to Hermann von Helmholtz' notion on "unconscious inference" at least (von Helmholtz, 1856), but it is still at the core of many theories and sophisticated models of perception today (e.g. Friston et al., 2017; Knill & Pouget, 2004; Press et al., 2020; Rao & Ballard, 1999). A compelling way to demonstrate the effect of prior knowledge on perception can be so-called *Mooney images* (Mooney & Ferguson, 1951). Mooney images are two-tone pictures of e.g. objects, faces or animals, that are very difficult to disambiguate without any prior knowledge about its content. Initially, most people will experience them as meaningless black and white "blobs". But once they have seen the corresponding source image, the two-tone images provide a coherent percept.

Mooney images are an example where very specific prior knowledge is required to aid interpretation. However, there are also more general environmental 'rules' that can be applied over a range of different scenarios. When we take a look at our sensory environment, we will notice that it is not random but full of regularities and compositional rules despite its complexity (Geisler, 2008; Girshick et al., 2011; Võ, 2021). To name a few: Light is coming from above(-left) our heads not from below (Mamassian & Goutcher, 2001). We usually see faces in an upright orientation and not inverted (Yin, 1969). Objects adhere to the laws of physics (e.g. gravity) and are typically found within a certain context (e.g. a bed belongs in the bedroom not the bathroom; Võ, 2021). Our perceptual systems have been shaped by the environments we live in and some assumptions about the environment may be innate (see e.g. Hershberger, 1970). But as we age, we gain a deeper understanding of our surroundings and the experiences we make will continuously inform our perceptual decisions.

Predictive processing

Over the last decades, *predictive processing* theories and the view of our brain as a "hypothesis-testing machine" have become increasingly popular (Kersten et al., 2004; Knill & Pouget, 2004; Rao & Ballard, 1999). At the core of these theories is the idea that our brains store and continuously update all of the "beliefs" we have about our environment and that we have gathered through experience in an "internal model of the external world". From this internal model, our brains can generate predictions for ongoing perceptual experience that enable robust percepts despite noisy and ambiguous sensory input. These predictions are considered to occur at different levels in the cortical hierarchy and are made about the input at lower levels. They are then compared to the actual representations.

Within a Bayesian framework, predictions can be formalized as "priors". Priors place constraints on the processing of sensory information and substantially reduce the number of possible interpretations. They are fused with the observed sensory input ("likelihood") to generate a percept ("posterior") that represents the most probable cause of the sensory input (Kersten et al., 2004). What we perceive is a fine balance between the prior and sensory information and is dominated by the information with the relatively higher precision. Thus, the noisier the sensory input becomes, the greater the effect of the prior on the interpretation.

As we and the world around us are subject to change, it is important that our predictions remain accurate. This is achieved through constant updating processes during which *prediction errors* play a key role (e.g. Friston, 2005; Press et al., 2020; Rao & Ballard, 1999). Prediction errors arise when there is a mismatch between the predicted and actual sensory input. To briefly illustrate this: We could imagine we're going for a walk in a park. Within this context, we would probably expect to see someone taking their dogs for a walk. Seeing someone walk their cat might be an unexpected sight. At first glance, we might not recognize the cat as a cat and take it as a fluffy dog instead. Our brain's goal is to minimize surprise and avoid further prediction errors in the future. There are two main possibilities to accomplish this goal. First, an action – such as moving our eyes to different parts of the environment – could be initiated to sample more information that is in line with our predictions. Second, learning processes to update and improve our internal model can be triggered.

Predictions about the sensory consequences of actions

Predictions can be based on different sources. They do not only concern external states but also internal ones and can help us to anticipate the consequences of our own actions. Sensorimotor predictions flexibly regulate our tactile sensitivity during movement planning and execution (Voss et al., 2008; Voudouris & Fiehler, 2017). A well-known phenomenon is *tactile suppression*, which refers to the observation that sensations on a moving limb are attenuated compared to a limb at rest (Chapman et al., 1987). Tactile suppression is thought to depend on a forward model that estimates future sensory states based on internal representations of motor commands. The predicted and actual sensory feedback are continuously compared to stabilize performance. When there is a match, the delayed and noisy afferences are suppressed and perceived as weaker. When there is a mismatch, the afferent signals are not suppressed. Tactile suppression is a way to down-regulate predictive sensory states and its magnitude reflects the strength of the predictions (Fiehler et al., 2019).

Initially, tactile suppression was considered to be a cancellation mechanism that primarily relies on an efference copy of the motor command and attenuates the associated predicted sensory signals (e.g. Bays et al., 2006; Blakemore et al., 1998). However, not only self-generated signals on a moving limb are suppressed but also external ones (Buckingham et al., 2010; Voss et al., 2008), suggesting that tactile suppression may be the result of more general predictions of sensory movement consequences. Recent evidence corroborates that those predictions are quite specific and not just an unspecific, blanket reduction in tactile sensitivity (Fuehrer et al., 2022).

The down-regulation of predicted sensory changes helps to distinguish our own movements from externally generated ones and attribute agency accordingly (Blakemore et al., 1998; Kilteni & Ehrsson, 2017). Another purpose of tactile suppression may be to free capacities for processing reach-relevant somatosensory signals (Gertz et al., 2018; Gertz et al., 2017).

Functional role of predictions

Predictive mechanisms play a central role at various processing levels, rely on many different sources and are not only important for perception but also for cognition and motor control. Sensorimotor predictions are essential for the planning and execution of goal-directed movements (Juravle et al., 2017; Voss et al., 2008) and allow us to distinguish our own movements from externally generated ones, thereby stabilizing our sense of agency (Blakemore et al., 1998; Kilteni & Ehrsson, 2017). Context-based predictions are useful to quickly search for, recognize or remember the location of objects within a scene (Bar, 2004; Henderson, 2017; Neider & Zelinsky,

2006; Wynn et al., 2020). In general, predictions are crucial for successful behavior and rapid responses to environmental changes. They enable robust and meaningful information uptake, help us to overcome sensory processing delays and efficiently interpret current sensory information. Predictive mechanisms can lead to an enhancement and suppression of expected information, ensuring that our perception is both valid and informative (Press et al., 2020). Especially when sensory noise is increased or the sensory information is incomplete, greater reliance on predictions can optimize our performance. Recent predictive processing theories particularly emphasize the role of the precision of the sensory input (Press et al., 2020; Spaak et al., 2022). High precision should increase the sensitivity towards unexpected information, whereas low precision should bias processing in line with our predictions.

1.2.2 Perceptual confidence

Being based on noisy and ambiguous sensory information, our perception is prone to errors. Thus, it is crucial to critically reflect upon our perceptual experiences to know whether we should trust or doubt them. This ensures that we interact safely with our environment and allows us to assess possible risks and costs of potentially wrong perceptual decisions. For example, if I'm not sure whether my cat has just hissed at me, I wouldn't approach him (unless we have to got to the vet – in that case, getting my cat's health checked would outweigh the negative effect of getting a scratch). Furthermore, reflecting upon our perceptual decisions may help us to update our internal model of the outside world – especially when we find that a perceptual decision was indeed wrong (Rao & Ballard, 1999).

Perceptual confidence describes our ability to judge whether a perceptual decision is correct given the available sensory evidence (Drugowitsch et al., 2014; Fleming et al., 2012; Mamassian, 2016). Although confidence judgments and stimulus characteristics are related, confidence judgments are not just an estimate of the amount of uncertainty in a stimulus (Pouget et al., 2016). Instead, confidence reflects whether we can reliably access *our own* uncertainty underlying our perceptual decisions. As confidence judgments are based on a primary decision, a so-called Type I decision, they are often referred to as Type II judgments. Accordingly, they have been established as a subtype of *meta*perception or, more generally, *meta*cognition (Metcalfe, Shimamura, et al., 1994; E. Norman et al., 2019).

Metaperception comprises two main functions, namely, self-monitoring and self-controlling our own perception (Mamassian, 2020; see also the framework proposed for metamemory, Nelson & Narens, 1990). Both functions are closely connected. Monitoring is the process that makes the

outcome of a perceptual decision available for further (re)evaluations. Taken by itself, monitoring would be useless if it cannot be used for control purposes. Control is enabled through monitoring and means that metaperceptual information can change the information used at the perceptual level, e.g. through the initiation, continuation or termination of an action. For example, it has been shown that confidence is an online process that controls how much sensory information is needed to commit to a perceptual decision (Balsdon et al., 2020).

Objective task performance and subjective confidence

As confidence is a reevaluation of our perceptual performance, it should be in line with our actual performance in order to elicit meaningful subsequent responses. Indeed, there is robust evidence that subjective confidence and objective task performance are closely related. Typically, confidence will be higher when our perceptual decision was objectively correct and lower when it was objectively incorrect (Pollack & Decker, 1958; Yeung & Summerfield, 2012). This relationship has been demonstrated in different modalities, including e.g. the visual (Barthelmé & Mamassian, 2010), tactile (Peirce & Jastrow, 1884) and auditory modality (Emmerich et al., 1972). Furthermore, additional information that was not used to make the perceptual decision, such as decision times, can inform our confidence judgments. Specifically, faster decisions indicate higher confidence (de Gardelle & Mamassian, 2014; Kiani et al., 2014).

However, objective task performance and confidence can also diverge. For example, when viewing visual illusions, we have a strong impression that our percept is correct when it is objectively incorrect. According to the classical confidence definition, we would be "overconfident" in these cases. Thus, recent research suggests that confidence might be better understood as an estimate of self-consistency rather than correctness (Caziot & Mamassian, 2021; Mamassian, 2020; Mamassian & de Gardelle, 2021). Self-consistency reflects the stability or reproducibility of our perceptual decision. If we repeatedly faced the same stimulus under the same conditions and made repeated perceptual decisions about it, our confidence would be high if we have the impression that we're making the same perceptual decision over and over again. Conversely, if our decisions feel random, confidence should be low. This updated confidence definition has the advantage that it relates to one's perceptual sensitivity and takes prior beliefs or perceptual biases into account. For simplicity reasons, I will use the classical definition within this thesis. Correctness and self-consistency can be considered to be the same in the absence of sensory biases and when stimulus categories are well defined (Mamassian & de Gardelle, 2021).

Measuring confidence

How can confidence be measured experimentally? Influenced by the seminal work by Peirce and Jastrow (1884), perceptual confidence is commonly measured in retrospective (although prospective judgments are also possible, see e.g. Fleming et al., 2016) using rating scales. This method requires participants to first complete a perceptual task, e.g. they have to decide whether a stimulus is tilted to the left or right. Afterwards, they indicate on a rating scale how confident they are that their perceptual decision was correct (see Figure 1a). Applying a modified Signal Detection Theory (SDT) framework (Green & Swets, 1966; Maniscalco & Lau, 2012), two main metaperceptual aspects can then be estimated – *confidence sensitivity* and *confidence bias*. Confidence sensitivity reflects how well an observer can distinguish between correct and incorrect perceptual decisions. Confidence bias describes an average level of confidence irrespective of accuracy. While rating scales have the advantage that they appear quite intuitive to use, large individual differences on how these scales are actually used can occur when participants are not properly trained. Some people may exhibit pronounced confidence biases because they only use the upper or the lower endpoints instead of exploiting the whole scale. This should particularly be avoided when younger and older adults are tested as older adults may show increased overconfidence (see e.g. Hansson et al., 2008).

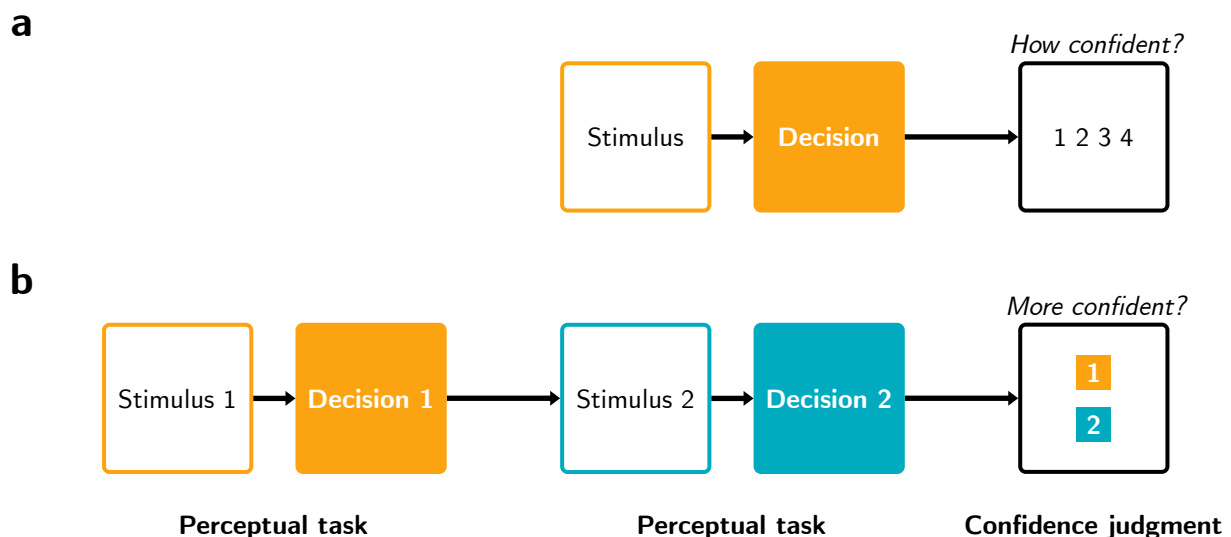**Figure 1.** Methods to measure confidence. (a) Confidence ratings: Participants first complete a perceptual task and indicate on a rating scale how confident they are that their perceptual decision was correct. (b) Confidence forced-choice: Participants complete two perceptual tasks in succession and then indicate which of their two perceptual decisions is more likely to be correct. Figure adapted from Mamassian (2020).

The confidence forced-choice paradigm (Barthelmé & Mamassian, 2009; Mamassian, 2020) offers an elegant solution to this problem by controlling confidence bias experimentally through relative confidence judgments. In this paradigm, participants complete two perceptual tasks after one another. After the second task, they are asked to choose whether they think their first perceptual decision or their second one is more likely to be correct (see Figure 1a). Confidence sensitivity can be analyzed by estimating and comparing the slope of two psychometric functions: One that is based on the trials that were chosen as confident and one based on the complete, i.e. unsorted, trial set.

If an observer has good confidence sensitivity, they should be able to select those trials that let to a better performance. Accordingly, the "chosen" psychometric function should be steeper than the "unsorted" psychometric function. Conversely, if an observer has poor confidence sensitivity, both psychometric functions would be almost identical. Figure 2 illustrates this idea and simulates the psychometric functions for an observer with good and poor confidence sensitivity, respectively.
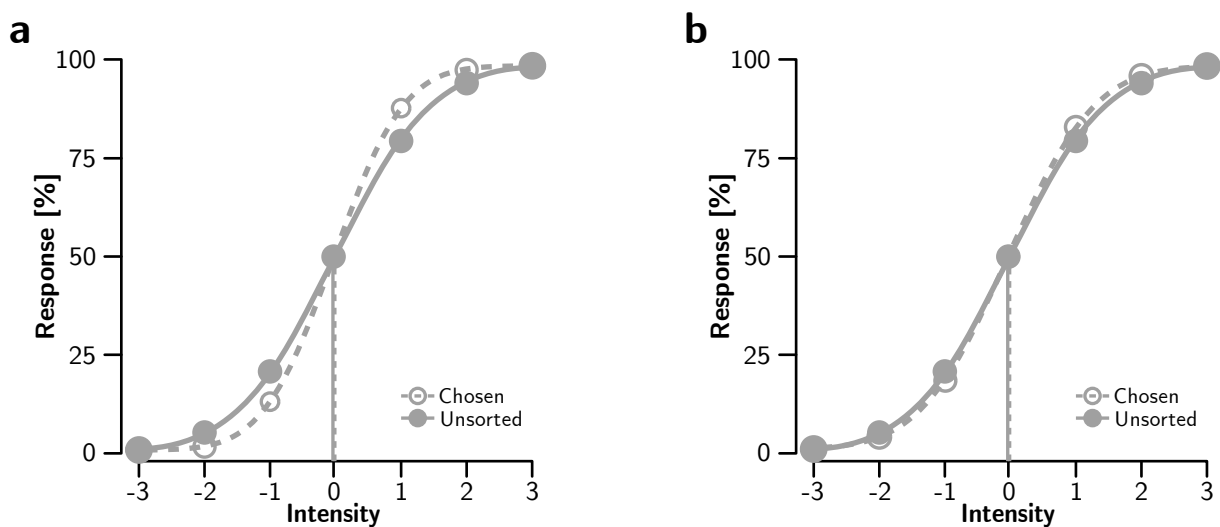

Figure 2. Confidence sensitivity in the confidence forced-choice paradigm. The difference in slope for the "chosen" (open circles, dashed line) psychometric function and "unsorted" (filled circles, solid line) psychometric function is an indicator for confidence sensitivity. Confidence sensitivity increases with the difference in slopes. Thus, (a) is an example of good confidence sensitivity and (b) is an example of poor confidence sensitivity.

Neural correlates of confidence

How confidence is encoded in the human brain is still debated. A central question is whether it relies on the recruitment of domain-specific or domain-general resources that enables confidence judgments across tasks (de Gardelle & Mamassian, 2014), modalities (de Gardelle et al., 2016) and even domains, such as perception and cognition (Mazancieux et al., 2020). A domain-specific

account suggests that there are specific metacognitive mechanisms for different tasks, whereas a domain-general account proposes that a common resource helps to monitor our performance across different tasks. There is an agreement that different subregions of the prefrontal cortex (PFC) and parietal cortex are crucial for a variety of metacognitive tasks (for a review, see Grimaldi et al., 2015; Rouault, McWilliams, et al., 2018).

However, the involvement of some regions also appears to be task-dependent. It has been shown that prospective and retrospective confidence judgments engage distinct subregions of the PFC (Fleming & Dolan, 2012). While the medial PFC (mPFC) encodes prospective confidence judgments, both the anterior PFC (aPFC) and dorsolateral PFC (DLPFC) are involved in retrospective judgments. Furthermore, confidence in perceptual tasks and memory tasks have been found to rely on both shared and distinct neural substrates (Rouault, McWilliams, et al., 2018). For example, gray matter volume of the precuneus, a subregion within the parietal cortex, correlated positively with confidence sensitivity in a memory task but not a perceptual task (McCurdy et al., 2013). Similarly, increased connectivity between precuneus and medial aPFC was associated with better metamemory and it was suggested that the medial and lateral part of the aPFC contribute differentially to the monitoring of mnemonic and perceptual information, respectively (Baird et al., 2013). Regarding the precuneus, though, there is also evidence that it may not be exclusively involved in memory tasks. Morales et al. (2018) found that it is also engaged in confidence for perceptual tasks and may be a domain-general component of metacognition along with other regions as part of a frontoparietal network (Morales et al., 2018).

When it comes to perceptual tasks, there is robust evidence that the aPFC and DLPFC are essential to generate confidence judgments. Gray matter volume in the aPFC correlated positively with confidence sensitivity (Fleming et al., 2010; McCurdy et al., 2013) and lesions to the aPFC (Fleming et al., 2014) as well as TMS (Rahnev et al., 2016) affected metaperceptual performance. Activity in the DLPFC could be linked to visual confidence (Lau & Passingham, 2006) and depressing DLPFC activity through transcranial magnetic stimulation (TMS) led to decreased confidence sensitivity (Rounis et al., 2010). Recently, Shekhar and Rahnev (2018) tried to disentangle the distinct functions of aPFC and DLPFC for metaperception. They suggested that the DLPFC reads out the strength of the sensory signal and passes this information to the aPFC. The aPFC then combines this information with additional information to generate a confidence judgment.

Apart from the PFC, other regions – such as the ventral striatum (Hebart et al., 2016) and anterior cingulate cortex (Baird et al., 2013) – are also engaged in perceptual confidence judgments and could enable confidence comparisons across domains. The involvement of the ventral striatum is particularly interesting as it encodes expected value (Knutson et al., 2005) and may suggest that confidence is valuable or rewarding, underpinning the role of confidence for learning.

1.2.3 Interim summary

Perception is an inference process that is not only shaped by the incoming sensory information but also by predictions and confidence. Predictions help us to anticipate the states of both the environment and ourselves and adequately respond to environmental changes. When sensory noise is increased, predictions become particularly relevant. By biasing perceptual processing towards predictions, the impact of noisy sensory input can be reduced and our perception optimized. However, perception still remains prone to errors. Perceptual confidence is a way to acknowledge perceptual uncertainty. It informs us whether we should trust or doubt our perceptual decisions, helps us to assess potential risks and adjust our behavior accordingly. Apart from perception, predictions and confidence are also essential for cognition and motor control.

1.3 Age-related changes and challenges

1.3.1 Sensory and perceptual decline

Be it vision (Owsley, 2016), audition (Morrell et al., 1996), touch (Decorps et al., 2014), smell or taste (Boyce & Shone, 2006) - it is a normal part of getting older that our senses gradually start to decline. This decline starts at different ages for different modalities and progresses at different rates (Gadkaree et al., 2016). While sensory decline in vision, touch and audition becomes particularly noticeable in our mid-40s and 50s, taste and smell only start to deteriorate between the age of 60 and 70 (Boyce & Shone, 2006; Corso, 1971). However, large individual differences exist. Sensory decline seems to occur independently in each sensory system and impairments in one sensory modality do not generalize across other modalities (Cavazzana et al., 2018; Gadkaree et al., 2016).

Age-related changes to our sensory systems occur at different levels. If we take a look at the visual system, optics as well as sensory processing (retina to early visual cortex) and perceptual processing (mid and high level visual cortex) are affected by decline (for a review,

see e.g., Andersen, 2012; Lin et al., 2016; Owsley, 2016; Spear, 1993). At the optical level, healthy aging goes along with various changes to the crystalline lens. As we get older, the crystalline lens becomes yellowish and less transparent (Artigas et al., 2012; Said & Weale, 1959). Together with an age-related decrease in pupil size (Winn et al., 1994), this may result in reduced retinal illumination. Furthermore, the crystalline lens becomes less elastic, impairing our ability to accommodate, which is known as presbyopia or age-related farsightedness (Glasser & Campbell, 1998). In early visual areas, it is well documented that aging affects different basic visual functions, such as visual acuity (Gittings & Fozard, 1986), spatial contrast sensitivity (Owsley et al., 1983) and motion processing (Bennett et al., 2007; Billino et al., 2008; J. F. Norman et al., 2003). For example, under photopic conditions, older adults show a decline in contrast sensitivity specifically at intermediate and high spatial frequencies but not at low spatial spatial frequencies. And, of course, age effects can also be found at higher perceptual levels, affecting e.g. our ability to identify faces in different views (Habak et al., 2008) or recognize objects in unusual contexts (Rémy et al., 2013).

Visual abilities age quite differently and vulnerabilities are very specific. Performance across different visual tasks is not correlated, indicating that there is no single common factor that drives age-related perceptual changes (Shaqiri et al., 2019). While optical age-related changes diminish the quality and quantity of the sensory input that is transmitted to higher processing areas, they cannot sufficiently explain the observed declines in sensory and perceptual processing (Andersen, 2012; Elliott, 1987). Similarly, age-related changes in early sensory processing cannot account for the reported changes at higher perceptual processing levels. There is consensus, however, that a large part of visual decline can be attributed to functional, rather than structural, changes in central visual areas. One particular problem that leads to performance differences is that our visual system becomes more susceptible to internal and external noise (Andersen, 2012; Pilz et al., 2010; Yang et al., 2009).

1.3.2 Cognitive decline

It is well-documented that aging has an impact on our cognitive abilities. Although we might not be aware of it, cognitive decline already starts in our 20s and 30s, but it becomes most noticeable in our 60s (Hartshorne & Germine, 2015; Salthouse, 2009). Different cognitive functions are affected by decline, e.g. memory, processing speed, reasoning and executive function (Hertzog et al., 2003; Lacreuse et al., 2020; Park & Reuter-Lorenz, 2009; Park et al., 1996; Salthouse, 1985; West, 1996). Within an individual, this decline seems to occur simultaneously for different

cognitive functions, i.e. it underlies a common factor (Ghisletta et al., 2012; Kiely, Anstey, et al., 2015). Across individuals, however, the rate of cognitive change differs greatly (Wilson et al., 2002). While some people may experience rapid decline in their cognitive abilities, other people may experience slow decline, stability or even slight improvement. The differentiation between 'normal' aging and disease processes can be challenging, e.g. due to differences in prior intelligence (Deary et al., 2009), and changes may occur gradually (Gauthier et al., 2006).

In structural imaging studies, age-related decline may present e.g. as volumetric shrinkage or decreased white matter integrity (Giorgio et al., 2010; Head et al., 2004; Raz et al., 2005; Walhovd et al., 2011). Primarily affected by these structural changes are the hippocampus, cerebellum and prefrontal cortex. The visual cortex, in contrast, appears to be mostly spared (Allen et al., 2005; Raz et al., 2005; but see also Salat et al., 2004), which might explain why visual abilities do not decline simultaneously (Shaqiri et al., 2019). Although loss of structure does not necessarily imply loss of function, there is some evidence that age-related structural brain changes are linked to performance decline in cognitive tasks. For instance, hippocampal volume could be linked to memory performance (Rosen et al., 2003; but this relationship is absent when controlling for age, Tisserand et al., 2000) and white matter integrity in the frontal lobe was associated with better performance on cognitive control tasks (Ziegler et al., 2010).

Executive functions

In the next paragraphs, I will focus more on one very prominent aspect of cognitive aging: age-related decline in executive function (EF; Lacreuse et al., 2020). EF is an umbrella term for a set of cognitive control processes that are essential to flexibly and voluntarily – as opposed to automatically – guide and adapt our behavior (Diamond, 2013). It is considered to be one of the main functions of the prefrontal cortex (PFC; Miller & Cohen, 2001; Yuan & Raz, 2014). EF and metacognition are conceptually closely related and even rely on shared neural correlates (Fernandez-Duque et al., 2000; Roebers, 2017).

Three core EFs can be distinguished, namely *inhibition*, *shifting*, and *updating* (Miyake et al., 2000). Latent variable analyses have shown that these three core EFs are moderately (inter)correlated but can still be separated (although inhibition may be part of a "Common EF" variable; see e.g. Friedman & Miyake, 2017; Miyake & Friedman, 2012). Together, they build the basis for higher-order EFs – such as logical reasoning and problem solving (Collins & Koechlin, 2012; Diamond, 2013).

Inhibition describes the ability to suppress prepotent responses, habits and distractions (Friedman & Miyake, 2004; Hasher et al., 1999). A classical example is the Stroop effect (Stroop, 1935). When asked to indicate the ink color of a color word (e.g. "red", "green", "blue"), response times and error rates are usually increased when there is a mismatch between the color name and its inking (e.g. "red" printed in green). Stroop interference effects have been shown to increase with advanced age (Cohn et al., 1984; Comalli Jr. et al., 1962; Nicosia & Balota, 2020; but see also Rey-Mermet & Gade, 2018). Another task that taps inhibition ability is the antisaccade task (Hallett, 1978; Munoz & Everling, 2004; R. J. Roberts et al., 1994). The antisaccade task requires participants to make a voluntary saccade into the opposite direction of a peripherally presented visual stimulus, suppressing the urge to directly look at it. Older adults tend to have more difficulties to suppress a reflexive saccade towards that stimulus. This is e.g. shown by increased directional errors or increased saccadic latencies for correct antisaccades (Butler et al., 1999; Munoz et al., 1998; Peltsch et al., 2011).

Shifting refers to the ability to flexibly switch back and forth between different tasks or mental sets (Miyake et al., 2000). Typical tasks measuring shifting abilities are the Trail Making Test (TMT; Reitan & Wolfson, 1985), specifically part B, and the Wisconsin Card Sorting Test (WCST; Grant & Berg, 1948). The TMT is an easy connect-the-dots task and consists of two parts. During part A, participants are required to sequentially connect 25 numbered dots in ascending order as fast and accurately as possible. Part B is similar except that participants now have to switch between numbers and letters (e.g., 1-A, 2-B, 3-C, etc.). Older adults usually show longer execution times on both parts of the Trail Making Test, but also have more pronounced 'switching' costs in part B (Tombaugh, 2004). The WCST (WCST; Grant & Berg, 1948) is a complex task that requires participants to sort cards based on a rule (e.g. number, shape, color) that they need to figure out through feedback. After a number of correct sorts, the rule changes and participants must infer the new sorting rule. Older adults tend to make more perseverative errors on the WCST, i.e. they stick longer to the old rule instead of the new rule (Ashendorf & McCaffrey, 2008; Rhodes, 2004).

Updating is defined as the ability to dynamically monitor, maintain and actively manipulate working memory contents (Miyake et al., 2000). A common task to measure updating ability is the *n*-back task (Kirchner, 1958). In the *n*-back task, participants are presented with a sequence of stimuli (e.g. letters) and have to indicate whether the current stimulus and the stimulus shown *n* positions earlier are the same. As *n* increases, participants make more errors and respond slower. Different studies have shown that older adults make more omission errors and are more

susceptible to lures than younger adults (Bopp & Verhaeghen, 2018; Kirchner, 1958; McCabe & Hartman, 2008). Another test that involves updating abilities is the Digit Symbol Substitution Test (DSST), a subtest of the Wechsler Adult Intelligence Scale (Wechsler, 2008). The DSST is a paper-pencil test where participants are presented with a table containing nine digits that are paired with different symbols each. The task is to copy as many symbols as possible within 90 seconds into empty spaces below a row of numbers. Performance on the DSST decreases with age, but this may partially be due to age-related differences in motor speed (Hoyer et al., 2004; Jaeger, 2018; Salthouse, 1992).

1.3.3 Linking sensory and cognitive decline

In a first attempt to understand age-related changes in perception and cognition comprehensively, researchers were particularly interested in finding links between age-related sensory decline and cognitive decline. Does sensory decline lead to cognitive decline or vice versa? Could there be a third factor affecting them both? Different but not mutually exclusive theories have been proposed, such as the *common-cause hypothesis*, the *sensory deprivation hypothesis*, the *information degradation hypothesis*, and the *cognitive-load-on perception hypothesis* (for a review, see e.g., Ebaid & Crewther, 2020; K. L. Roberts & Allen, 2016; Schneider & Pichora-Fuller, 2000).

Briefly, the common cause hypothesis (Baltes & Lindenberger, 1997; Lindenberger & Baltes, 1994; Lindenberger & Ghisletta, 2009) suggests that a common biological factor negatively affects sensory processing and cognitive function with advanced age. Such a common factor could be e.g. altered dopaminergic functioning in older adults (S.-C. Li & Lindenberger, 1999). The sensory deprivation hypothesis (Lindenberger & Baltes, 1994; Oster, 1976) proposes that low sensory stimulation over time (Sekuler & Blake, 1987) speeds up degenerative processes and leads to cognitive impairments. The information degradation hypothesis (Monge & Madden, 2016; Schneider & Pichora-Fuller, 2000) states that poor (*degraded*) sensory input (either due to biological aging or experimental manipulation) compromises perceptual processing, which, in turn, may also impair cognitive processing. Finally, the cognitive-load-on perception hypothesis (Baltes & Lindenberger, 1995; Sweller, 1994) suggests that cognitive decline places a cognitive load on perception, which is then compromised.

So far, evidence for either of these hypotheses remains ambiguous (see e.g. Lindenberger & Ghisletta, 2009; Monge & Madden, 2016). Most studies investigating the link between sensory and cognitive decline have used correlational analyses and only took very basic perceptual abilities, such as visual acuity, into account. As perceptual abilities age quite differently (Shaqiri et al.,

2019), it might be better to take a look at the contributions of specific cognitive functions in specific perceptual tasks. The *Inhibitory Theory* (Hasher & Zacks, 1988; Hasher et al., 1999) and *Processing-Speed Theory* (Salthouse, 1996) are cognitive aging theories that focused on age-related differences in specific cognitive functions and tried to explain how they contribute to performance differences on other tasks. In the following, I will briefly describe both theories.

The Inhibitory Theory

The *Inhibitory Theory* (Hasher & Zacks, 1988; Hasher et al., 1999) proposes that individual differences in task performance can largely be attributed to an individual's ability to suppress or ignore ongoing goal-irrelevant information and actions. According to Hasher and Zacks (1988), less efficient inhibitory mechanisms in older adults may explain age-related performance differences in various tasks, such as episodic memory, visual search and reaction time tasks (e.g. Kausler, 1991; Madden, 1983; J. H. Mueller et al., 1980). Goal-irrelevant information is assumed to occupy more resources than it normally would, leading to a competition between relevant and non-relevant information in working memory. This may affect the quality of initial encodings and could impair retrieval processes. Behaviorally, this is reflected in greater distractibility, forgetting information and producing incorrect responses or slower correct responses. However, recent evidence also suggests that decreased inhibitory control is not only associated with costs but may also have benefits, such as gaining more information about one's environment, better memory for previously irrelevant information and finding creative solutions to problems (Amer et al., 2016).

The Processing-Speed Theory

The *Processing-Speed Theory* (Salthouse, 1996) is based on the observation that processing efficiency is reduced in older adults compared to younger adults. Age-related slowing seems to be a global phenomenon as it has been observed for different measures of processing speed that are also highly correlated (e.g. Salthouse, 1985, 1993, 1994). The theory suggests that age-related slowing negatively affects cognition due to two mechanisms at play, namely a *limited time mechanism* and a *simultaneity mechanism*. The limited time mechanism suggests that cognition is impaired since processing operations cannot be completed in the limited time available when they are executed slowly. The simultaneity mechanisms suggests that slower processing leads to losing previously processed information, which impairs the integration of different information at later stages.

1.3.4 Beyond decline

However, not all of our abilities decline with advanced age. There's evidence from both behavioral and functional neuroimaging studies that promotes a more nuanced view on age-related changes and challenges the idea of general biological deterioration as the standard explanation for age-related differences.

With regard to behavioral findings, it has been shown that different cognitive abilities peak at different ages (Hartshorne & Germine, 2015). For example, while our abilities to retell stories and remember word pairs peak in early adulthood, we perform best on vocabulary knowledge tasks and arithmetic problems in our late 40s. One particular advantage of getting older is that we gain more and more knowledge about ourselves and the world around us. Not surprisingly, it has been found that world knowledge remains preserved with advanced age and may even improve up until the age of 70 years (Park et al., 2002; Park & Reuter-Lorenz, 2009). Intact prior knowledge provides a powerful resource to adapt to age-related challenges and may aid other cognitive functions. It has been suggested that it is a key factor in understanding older adults' memory decisions (Umanath & Marsh, 2014).

Findings from functional neuroimaging have helped to establish three mechanisms, namely *reserve*, *maintenance* and *compensation*, that are useful to better characterize age-related changes and understand individual differences in performance (Cabeza et al., 2018). *Reserve* refers to the life-long accumulation of neural resources that diminish the effects of age- or disease-related neural decline (Barulli & Stern, 2013; Stern, 2009). Genetic but also environmental factors, such as physical activity or education, can affect reserve. *Maintenance* describes recovery and repair processes that promote the preservation of neural resources (Nyberg et al., 2012). *Compensation* denotes the recruitment of additional neural resources to improve performance in the face of increased cognitive demands. In order to count as compensatory activity, it is important that the observed age-related differences in neural activity are indeed linked to better performance. Otherwise, it may be a sign of inefficiency or dedifferentiation (S.-C. Li & Lindenberger, 1999; Lindenberger & Baltes, 1994). Cabeza et al. (2018) summarize these three mechanisms as follows: *"Reserve is about how much you have, maintenance is about how well you keep it, and compensation is about when and how you use it."*

Compensation through prefrontal recruitment

In the human brain, the PFC seems to play a critical role in compensatory mechanisms. Even though prefrontal regions are susceptible to age-related atrophy (Raz et al., 2005) and have

been suggested to account for several age-related deficits (West, 1996), numerous studies found increased overactivation of prefrontal regions with advanced age (e.g. Eyler et al., 2011; Gutchess et al., 2005; Heuninckx et al., 2008; but see also Nyberg et al., 2010). Critically, prefrontal overactivation was associated with improved task performance across different tasks, including perceptual and memory tasks but also more complex motor tasks (e.g. Bergerbest et al., 2009; Gutchess et al., 2005; Heuninckx et al., 2008; Reuter-Lorenz et al., 2000). As some studies also reported decreased activation in more posterior regions (e.g. visual cortex) along with increased prefrontal activation, these findings are collectively referred to as "posterior-anterior shift" (Davis et al., 2008) and support the idea that prefrontal overactivation compensates for processing deficits in other regions.

The Scaffolding Theory of Aging and Cognition

From HAROLD (Hemispheric Asymmetry Reduction in Older Adults; Cabeza, 2002) to CRUNCH (Compensation-Related Utilization of Neural Circuits Hypothesis; Reuter-Lorenz & Cappell, 2008), different theories of cognitive aging have been proposed that try to explain decreased, stable and improved (cognitive) performance with age. But the Scaffolding Theory of Aging and Cognition (STAC/STAC-r; Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Park, 2014) provides the most integrative framework as it combines the findings from behavioral as well as structural and functional neuroimaging studies (for a recent review, see Oosterhuis et al., 2022). Aging leads to changes both in brain structure, e.g. atrophies (Raz et al., 2005) and dopamine receptor depletion (K. Z. H. Li et al., 2001; Wong et al., 1997), as well as brain function, e.g. alterations in the "default-mode" network (Damoiseaux et al., 2008; Persson et al., 2007), that influence one another. Because these age-related changes negatively affect an individual's overall cognitive abilities and the rate of cognitive decline over time, the STAC model proposes that our brain needs to find ways to adapt to them. This is realized through compensatory "scaffolding" mechanisms, such as increased frontal activity or bilateral recruitment (Cabeza, 2002; Davis et al., 2008; Reuter-Lorenz & Cappell, 2008). While these scaffolding processes may not be as efficient as the fine-tuned networks in young adulthood, they do allow to maintain a high level of cognitive function as we get older. Critically, scaffolding is seen as a lifelong and continuously adaptive process but it becomes particularly important in older age. It is shaped by our past experiences and current challenges and may be improved through interventions, e.g. cognitive trainings, learning and social engagement.

1.3.5 Interim summary

Healthy aging goes along with pronounced changes to our sensory and cognitive abilities. But not all of our abilities decline with age. Over the last years, it has become more and more evident that aging is a highly individual and dynamic process that includes deterioration but also stability and improvement (Hartshorne & Germine, 2015; Park & Reuter-Lorenz, 2009). The aging brain is remarkably adaptive (Park & McDonough, 2013). However, characterizing age-related changes, functional limitations and resources comprehensively remains challenging. A useful approach may be to consider the interplay of sensory, perceptual, cognitive and motor processes (see e.g. Billino & Pilz, 2019). When interpreting behavioral performance differences between younger and older adults, both the negative effects of age-related decline and compensatory mechanisms need to be taken into account.

1.4 Outline

The overarching theme of my dissertation project is to investigate how older and younger adults dynamically value different information in response to individual challenges (e.g. increased sensory noise with advanced age) and current task demands to optimize their performance. I conducted four different experiments that can be divided into two key areas and thus, will be presented in two separate chapters. Chapter 2 focuses on the adaptive balancing of sensory and predictive signals and consideres the role of expected (study 1a) and unexpected information (study 1b). Chapter 3 changes the perspective from a more perceptual level to the metaperceptual level and examines how well we can monitor our perceptual decisions with advanced age (study 2a) and when task demands are increased (study 2b).

As previously described, one challenge that our perceptual systems face with advanced age is that the information obtained from our senses becomes less reliable (e.g. Decorps et al., 2014; Owsley, 2016). At the same time, we gain more and more knowledge about ourselves and the world around us (Park & Reuter-Lorenz, 2009), which helps us to improve our predictions. Predictive processing theories propose that perception is a fine balance between prior and sensory information and is dominated by the information with the relatively higher precision (e.g. Kersten et al., 2004; Press et al., 2020). Thus, the first aspect should decrease the influence of sensory information and the latter aspect should increase the influence of predictions. Together, they should work in the same direction: An increased reliance on predictions with age. Study 1a and study 1b tested this idea in two different close to real-world scenarios in which predictions were

based on different sources (i.e. ourselves or the external environment). While increased reliance on predictions might overall be a beneficial mechanism – especially when our predictions are accurate – interferences can be imagined, e.g. when our predictions are violated. This idea is explored in study 1b. Even though increased reliance on predictions can improve our performance when sensory noise is increased, it does not prevent us from making errors. Perceptual confidence is way to acknowledge the uncertainty underlying our perceptual decisions and can be considered as an internal performance feedback (Mamassian, 2016). Thus, especially in the absence of external feedback, it is an important signal that informs us whether we should trust our perceptual experiences, whether we should adjust our behavior to acquire more information or whether our knowledge should be updated. Study 2a investigated how confidence is maintained later in life. Study 2b examined whether confidence judgments across different senses are as efficient as confidence judgments made within the same modality.

Study 1a (Klever et al., 2019) was concerned with sensorimotor predictions. Studying 26 older adults and 23 younger adults, we investigated age effects on tactile suppression during reaching. Tactile suppression describes the phenomenon that sensory signals on a moving limb are attenuated compared to a limb at rest (Juravle et al., 2017). Since tactile suppression is considered to be more pronounced when sensorimotor predictions are more reliable (Voudouris et al., 2019), we expected to find stronger sensory attenuation in older compared to younger adults (see e.g. Wolpe et al., 2016). Apart from age-related changes in the reliability of sensory and predictive signals, respectively, cognitive processes may additionally contribute to altered tactile suppression effects (Park & Reuter-Lorenz, 2009; van Hulle et al., 2013). Thus, we introduced an additional memory task to examine how increased cognitive task demands modulate tactile sensitivity in younger and adults. Furthermore, using correlational analyses, we explored whether pronounced age-related differences in cognitive control capacities (Miyake & Friedman, 2012; Park & Reuter-Lorenz, 2009) as well as movement times (Salthouse, 1996) can explain individual differences in tactile suppression.

Study 1b (Klever, Islam, et al., 2023) addressed the question how expectations about scene context affect older and younger adults' memory for objects that are either congruent or incongruent with the context they are embedded in. Since reliance on predictions might be increased with advanced age (Chan et al., 2021; Klever et al., 2019) and increased sensory noise could weaken the effects of surprise (Press et al., 2020), the benefit of object-scene inconsistencies for memory performance (Greve et al., 2019) might be attenuated in older adults. Studying 23 older and 23 younger adults, we investigated this potential side effect. Participants freely

viewed photographs of real-world scenes (Öhlschläger & Võ, 2017) that contained semantically incongruent target objects (e.g. a ketchup bottle in a shower) half of the time. After a delay, we presented participants with the target objects and additional distractor objects and asked them whether they were old or new, i.e. previously presented in one of the scenes or not. Memory performance for congruent and incongruent objects, respectively, provides insights on what information – expected or unexpected – is valued. To examine potential congruency biases (Brod & Shing, 2019), we further asked participants to indicate in which scene objects indicated as "old" were previously presented.

Study 2a (Klever et al., 2022) was concerned with age effects on visual confidence. Applying a confidence forced-choice paradigm (Mamassian, 2020), we tested 29 older and 30 younger adults on their ability to distinguish correct from incorrect perceptual decisions. The confidence forced-choice paradigm allows to derive a bias-free estimate of confidence efficiency and avoids confounds that might arise from overconfidence (Hansson et al., 2008) and the application of rating scales. Since sensory and cognitive decline as well as increased noise in neural representations might compromise the evaluation of uncertainty, confidence efficiency might be reduced in older adults (see e.g. Palmer et al., 2014). As previous evidence did not allow to draw conclusions about the factors that might lead to differential metaperceptual abilities in younger and older adults (Palmer et al., 2014), we additionally considered the contributions of individual cognitive control capacities (Miyake & Friedman, 2012) and processing dynamics (Kiani et al., 2014; Salthouse, 1996) to efficient confidence judgments.

Study 2b (Klever, Beyvers, et al., 2023) introduced a challenge to younger adults' judgments confidence and explored the possibility that confidence judgments made across different senses diminish confidence efficiency. Similarly to study 2a, we applied a confidence-forced choice paradigm. But this time, we asked 54 younger participants to not only compare their confidence across two perceptual tasks that involve the same modality but also across different modalities (here: visual and tactile discrimination tasks). Previous research suggested that confidence serves as a common currency across different visual tasks (de Gardelle & Mamassian, 2014) as well as across visual and auditive tasks (de Gardelle et al., 2016). However, increased overconfidence in the tactile sense might challenge this ability (Deroy & Fairhurst, 2019; Fairhurst et al., 2018). We reasoned that confidence efficiency should not be affected by whether confidence judgments were made about two perceptual tasks involving the same or different modalities if confidence was stored in an abstract, modality-independent format. If it was modality-specific, however, we would expect greater confidence efficiency for confidence judgments that were made within the

same modality. Furthermore, using correlational analyses, we aimed to elaborate on the results of study 2a and explored whether individual cognitive control capacities contribute to efficient confidence judgments in younger adults.

Taken together, these four studies have expanded our knowledge on how valuation processes, i.e. the balancing of sensory and predictive signals as well as perceptual confidence, contribute to stabilize perception, cognition and action control across the adult lifespan. They also provided insights on potential vulnerabilities and interferences. The following two chapters (i.e. chapter 2 and chapter 3) are written as brief summaries of the four studies and describe their background, design and key findings. Since the studies are either already published in scientific journals (study 1a, study 2a), are accepted for publication (study 2b) or are currently under review (study 1b), more detailed descriptions of each study can be found under A Publications. In the closing chapter, I integrate and discuss those findings and describe possible directions for future research.

2 Reliance on predictions

2.1 Age effects on tactile suppression

Age effects on sensorimotor predictions: What drives increased tactile suppression during reaching? (Klever et al., 2019) – published in *Journal of Vision*

2.1.1 Background

Study 1a was concerned with sensorimotor predictions and investigated age effects on tactile suppression during reaching. Tactile suppression refers to the phenomenon that sensations on a moving limb are attenuated compared to rest (Chapman et al., 1987; Juravle et al., 2017). It is thought to rely on an internal forward model that predicts the sensory consequences of an action and suppresses the associated predicted sensory feedback (Bays et al., 2006; Wolpert & Flanagan, 2001). As sensory signals become more noisy with age (Decorps et al., 2014) while increased life experience increases the reliability of predictive signals, the weighting of sensorimotor predictions should be amplified, resulting in stronger tactile suppression effects with age (in accordance with Bayesian integration principles; Körding & Wolpert, 2004; Wolpe et al., 2016). But also factors such as age-related movement slowing (Buckles, 1993) and pronounced structural changes to the cerebellum (Raz et al., 2005; Walhovd et al., 2011) – a key neural correlate of the forward model (Shadmehr & Krakauer, 2008) – may affect forward model function and could contribute to altered suppression effects.

The goal of study 1a (Klever et al., 2019) was to test whether aging increases the reliance on sensorimotor predictions by measuring tactile suppression effects during reaching in 26 older adults (59–78 years) and 23 younger adults (18–27 years). A second aim was to examine how additional cognitive task demands modulate suppression effects and explore the relationship between movement time characteristics and suppression effects as well as the contribution of available cognitive control resources to suppression effects.

2.1.2 Methods

Participants completed three different *Yes-No* tactile detection tasks (baseline, reaching, reaching+) during which they received vibrotactile stimulations on their right index finger. In the baseline task, participants simply rested their right hand on the table and indicated whether they

had noticed a tactile simulation or not. In both reaching conditions, participants had to touch four out of nine squares on a touchscreen in a predefined sequence. The spatial arrangements of those squares corresponded to the layout of the Corsi Block-Tapping Task (Berch et al., 1998). After movement completion, participants indicated whether they had noticed a tactile simulation or not. In the reaching condition, the target squares were white and numbered from one to four. In the reaching+ condition, the four target squares turned white after one another (for 1000 ms each) and participants now had to memorize the correct order, inducing additional cognitive load. The order of both reaching conditions was balanced across participants.

We determined 50% detection thresholds for all three experimental conditions (baseline, reaching, reaching+). To analyze the effect of reaching on tactile perception, we substracted each participant's baseline detection threshold from the thresholds determined in both reaching conditions, respectively – as successfully done in previous studies (see e.g. Gertz et al., 2018; Voudouris & Fiehler, 2017). Values greater than zero indicate tactile suppression.

In addition to the three tactile detection tasks, we characterized individual cognitive control capacities for each participant using three established tasks that capture key facets of <u>executive function</u> (Miyake & Friedman, 2012), namely: *inhibition* as measured with a computerized version of the Victoria Stroop Test color naming (VST-C; Stroop, 1935) included in the Psychology Experiment Building Language (PEBL) Test Battery (S. T. Mueller & Piper, 2014), *shifting* as assessed with the Trail Making Test Part B (TMT-B; Reitan and Wolfson, 1985), and *updating* as measured with the Digit Symbol Substitution Test (DSST), a subtest of the Wechsler Adult Intelligence Scale (Wechsler, 2008). To better evaluate individual task demands, we further determined the maximal block span for each participant (Härting et al., 2000).

2.1.3 Results

We observed stronger tactile suppression in older adults compared to younger adults in both reaching conditions (see Figure 3a), arguing for increased reliance on predictive signals with age (Wolpe et al., 2016) and preserved forward model function (Vandevoorde & de Xivry, 2019). Furthermore, we found that higher task demands due to an increased memory load led to stronger suppression effects in both age groups but did not specifically modulate the age effect. Secondary task demands may affect forward model function by withdrawing processing resources from sensory input, but they do not significantly contributed to the observed age effect.

Reaction and movement times were overall slower in older compared to younger adults, confirming age-related slowing (Buckles, 1993; Salthouse, 1996). Reaction times were defined as the

time difference between the onset of the four numbered squares and start button release (reaching condition) or the extinction of the last target square and start button release (reaching+ condition). Movement times captured the time difference between start button release and first screen contact. The modulation of reaction and movement times due to the different conditions was similar in both age groups. Reaction times were faster in the reaching+ condition compared to the reaching condition. Movement execution, however, was longer in the reaching+ condition than the reaching condition. These patterns are likely to reflect the procedure differences in both conditions. Critically, there was no interaction, indicating similar strategy use in both age groups. Overall speed in the reaching tasks did not scale with tactile suppression effects.
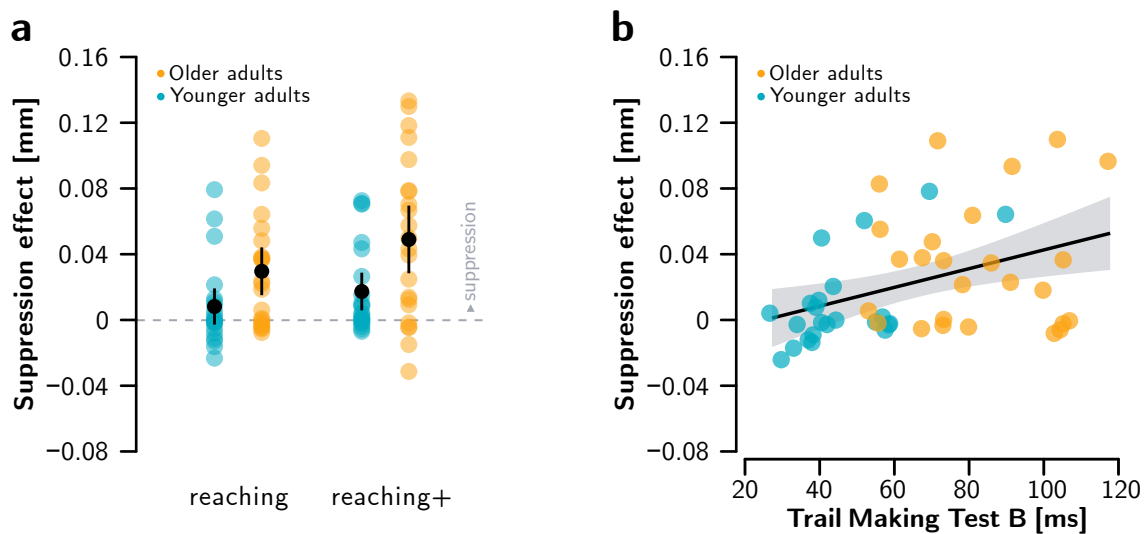

Figure 3. (a) Tactile suppression effects in $n = 22$ older adults (orange) and $n = 21$ younger adults (blue) for both reaching conditions. Tactile suppression effects were calculated by subtracting each participant's baseline detection threshold from the respective detection thresholds determined in both reaching conditions. Each participant is represented by a single colored dot. Black dots show the mean across participants with error bars indicating 95% confidence intervals. (b) Tactile suppression effects in the reaching condition scale with shifting ability as measured by the TMT-B. Please note that this figure contains data from the complete sample, i.e., $n = 26$ older adults and $n = 23$ younger adults. The shaded area represents the 95% confidence interval around the regression line.

Across age groups, we found that stronger tactile suppression in both reaching conditions was associated with lower cognitive control capacities as measured with the VST-C, TMT-B and DSST (except for performance in VST-C and tactile suppression in the reaching plus memory condition). Taking the TMT-B as an example, we found that performance could explain 16% and 24% of the variation in tactile suppression effects in the reaching and reaching plus memory condition, respectively. Figure 3b shows the correlation between performance in the TMT-B and tactile suppression in the reaching condition. These findings add to previous evidence linking stronger tactile suppression to reduced connectivity in frontostriatal circuits (Wolpe et al., 2016).

2.2 Age effects on the memory advantage for unexpected objects

Aging attenuates the memory advantage for unexpected objects in real-world scenes (Klever, Islam, et al., 2023) – manuscript under review at *Heliyon*

2.2.1 Background

Study 1b was concerned with context-based predictions and addressed the question how expectations about scene context affects older and younger adults' memory for objects that are either congruent or incongruent with the context they are embedded in.

Our visual environment is predictable most of the time. Growing up, we will learn that objects are typically found within a certain context (Võ, 2021). For example, a bottle of shampoo is usually found in the shower. We can use this knowledge to make predictions about similar environments, which e.g. helps us to identify or search for objects in novel environments (Bar, 2004; Henderson, 2017; Neider & Zelinsky, 2006). However, there might also be situations that violate our expectations – e.g. when we discover a bottle of shampoo in the fridge. Situations that violate our expectations are particularly relevant because they signal us that our knowledge needs to be updated or that our behavior needs to be adjusted (Press et al., 2020). As we get older, prior knowledge plays a crucial role for memory (Umanath & Marsh, 2014). Increased reliance on predictions may be overall helpful to optimize memory performance. But it might become disadvantageous when predictions are violated as it might attenuate the memory advantage for unexpected information (Greve et al., 2019; Press et al., 2020).

The goal of study 1b (Klever, Islam, et al., 2023) was to investigate how prior knowledge of scene structure and violations of expectations affect object memory in a group of 23 older adults (52 – 81 years) and 23 younger adults (18–38 years). In contrast to previous studies, the target objects were naturally embedded in the scenes and we refrained from informing participants about potential object-scene inconsistencies (see e.g. Brod & Shing, 2019; Chen et al., 2022) to minimize age-related vulnerabilities due to increased associative demands or strategic processes (Naveh-Benjamin, 2000; West, 1996). Furthermore, we used a simple free-viewing paradigm without an additional (search) task (see e.g. Wynn et al., 2020) since additional tasks affect how scene information is processed and might lead to pronounced age-related differences (Draschkow et al., 2014; Neider & Kramer, 2011).

2.2.2 Methods

The experiment was conducted online via Testable and consisted of two main parts. During part one, participants viewed 60 photographs of real-world scenes taken from the SCEGRAM database (Öhlschläger & Võ, 2017) for 3000 ms each. The photographs contained target objects of which half were incongruent with the surrounding context (e.g. a ketchup bottle in the shower). Participants were not aware of the existence of those target objects as they were instructed to memorize the scene as a whole with no emphasis on specific objects. After viewing the 60 scenes, a short break followed during which participants filled out unrelated questionnaires regarding their perceptual experiences. Then, the second part started. Here, participants saw images of the 60 target objects plus additional 60 distractor objects without any contextual information. For each object, they indicated whether it was "old" or "new", i.e. presented in the first part of the experiment or not. In case they responded that the object was "old", they had to select one out of three possible scenes during which the object was previously presented. Of these three scenes, one scene always provided contextual information congruent with the object, the other two scenes provided incongruent contextual information.

2.2.3 Results

We found that both younger and older adults remembered objects encoded in an incongruent context better than congruent ones. However, this benefit was less pronounced in older adults (see Figure 4a).

Regarding memory for the encoding context, we found that younger and older adults performed equally well if the objects were previously presented in a congruent context. If the objects were previously presented in an incongruent context, though, both younger and older adults made considerably more errors when matching them to their original context. However, error rates were higher for older adults (see Figure 4b). Further inspections of those errors revealed that older adults' memory representations were biased more towards prior knowledge. While younger adults mistakenly chose a congruent scene for an object that was originally presented in an incongruent context in 37% of the time, older adults favored congruent scenes in 72% of the time.

Analyzing response times for old/new decisions, we corroborated age-related slowing (Buckles, 1993; Salthouse, 1996). But overall, retrieval processes were similarly shaped in older and younger adults. Responses were faster for distractors compared to congruent or incongruent objects. There were no differences in response times for congruent and incongruent objects.
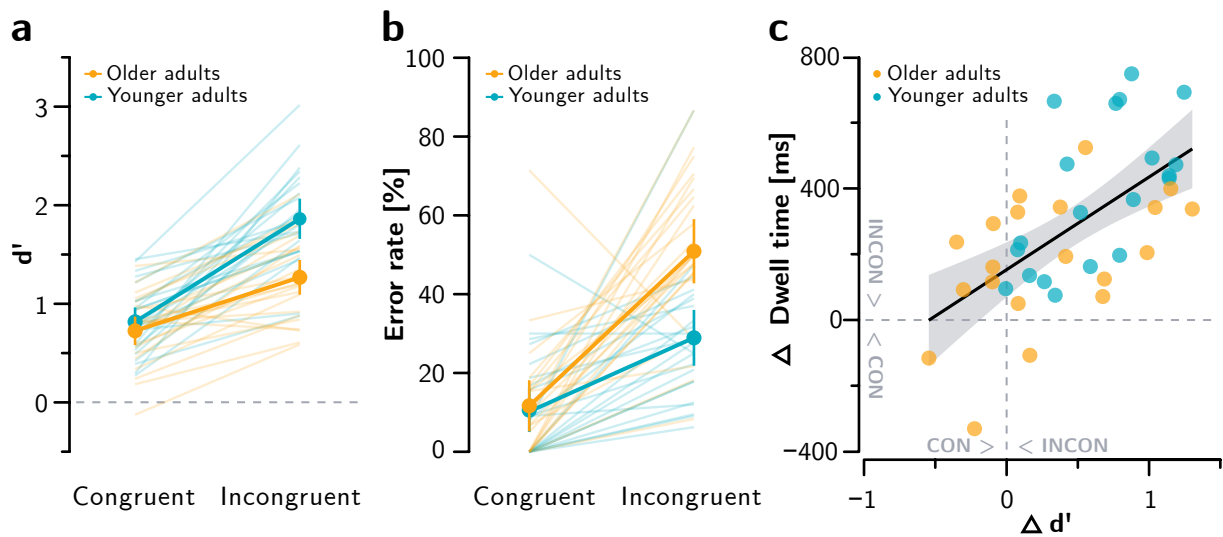
Figure 4. Effects of encoding context (congruent vs. incongruent) on object recognition performance (a) and error rates during scene selection (b) in $n = 23$ older adults (orange) and $n = 23$ younger adults (blue). Colored semi-transparent lines provide individual data. Filled dots and solid lines show the mean across participants. Error bars provide 95% confidence intervals. (c) Relationship between dwell times on target objects during encoding and object recognition performance in an ongoing project with data from different groups of $n = 20$ older and $n = 20$ younger adults. Each participant is represented by a single colored dot. The shaded area represents the 95% confidence interval around the regression line.

Since this study was conducted online, it remains to be clarified at what memory stages (i.e. encoding or retrieval) age-related differences emerge. In an ongoing study, we investigate contributions of different eye movement behavior during encoding. Preliminary results show that older adults overall spend less time looking at incongruent objects compared to congruent objects. While first fixations on incongruent objects were equally long in younger and older adults and lasted longer than first fixations on congruent target objects, younger adults refixated the incongruent objects more often than older adults – resulting in the observed overall dwell times differences between age groups. Differences in dwell times scaled with the memory advantage for incongruent objects (see Figure 4c), supporting a critical role of active vision for memory performance (Ryan & Shen, 2020).

3 Monitoring perceptual decisions

3.1 Age effects on visual confidence

Age-related differences in visual confidence are driven by individual differences in cognitive control capacities (Klever et al., 2022) – published in *Scientific Reports*

3.1.1 Background

Study 2a shifted the perspective to the metaperceptual level and was concerned with age effects on visual confidence. Over the last decade, perceptual confidence has been extensively studied in younger adults and elaborate methods to measure and model confidence judgments have been developed (e.g. Mamassian & de Gardelle, 2021; Maniscalco & Lau, 2012). It has been shown that younger adults are able to adequately monitor their perceptual performance. This is e.g. reflected in a correlation between subjective confidence ratings and objective performance. Usually, confidence ratings will be lower for incorrect decisions and higher for correct decisions (Pollack & Decker, 1958; Yeung & Summerfield, 2012).

Confidence is an important signal that helps us to optimize our perceptual performance and subsequent behaviors. So far, some developmental aspects have been characterized in children (e.g. Baer et al., 2018; Baer & Odic, 2020; Filippi et al., 2020), but only few studies have addressed how confidence is maintained later in life (e.g. Filippi et al., 2020; Palmer et al., 2014). Sensory decline as well as pronounced age-related changes to the prefrontal cortex – a critical neural correlate of perceptual confidence (Grimaldi et al., 2015; Rouault, McWilliams, et al., 2018) – may compromise the quality of confidence judgments later in life.

The goal of study 2a (Klever et al., 2022) was to investigate whether visual confidence is subject to age-related changes studying 29 older adults (60–78 years) and 30 younger adults (19–38 years). A second aim was to elaborate on the factors that may influence the efficiency of confidence judgments as previous studies did not allow to draw sufficient conclusions (Filippi et al., 2020; Palmer et al., 2014). In particular, we focused on the role of age-related changes in processing dynamics (Salthouse, 1996) as well as cognitive control capacities (Park & Reuter-Lorenz, 2009) for efficient confidence judgments.

3.1.2 Methods

Using a confidence forced-choice paradigm (Mamassian, 2020; Mamassian & de Gardelle, 2021), we compared groups of older and younger adults on their ability to judge the quality of their perceptual decisions. The confidence forced-choice paradigm avoids the influence of confidence bias and focuses on confidence sensitivity instead, which is quite critical when testing older and younger adults (see e.g. Hansson et al., 2008). It further allows to consider differences in response times that might affect confidence calibration (Baranski & Petrusic, 1994; Kiani et al., 2014). Participants completed two contrast discrimination tasks in succession and subsequently provided a confidence judgment, i.e. they chose the perceptual decision they thought was more likely to be correct. If a participant can reliably track their uncertainty underlying these perceptual decisions, they should be able to select the perceptual decisions that led to a better performance. This, in turn, is then reflected in higher contrast sensitivity for those trials that were chosen as relatively more confident compared to contrast sensitivity estimated for the complete, i.e. unsorted, trial set. Conversely, if a participant has poor insight into their perceptual performance, the gain in contrast sensitivity for the chosen trials would be minimal. To analyze confidence efficiency, we calculated a confidence modulation index (CMI) for each participant. The CMI – as defined in Equation 1 – reflects the gain in contrast sensitivity from the unsorted trial set to the chosen trial set, standardized by the sensitivity derived from the unsorted trial set. Higher values indicate higher confidence efficiency.

$$CMI = 100 \times \frac{Sensitivity_{chosen} - Sensitivity_{unsorted}}{Sensitivity_{unsorted}} \tag{1}$$

We further assessed individual cognitive control capacities for each participant. Critical tests were again VST-C (S. T. Mueller & Piper, 2014; Stroop, 1935), TMT-B (Reitan & Wolfson, 1985) and DSST (Wechsler, 2008), but we additionally included subtest 3 of the LPS-2 (Kreuzpointner et al., 2013) as a measure for nonverbal logical reasoning. We have refined our approach to prepare our cognitive control measures for further analyses. Instead of analyzing single measures as we did in study 1a (Klever et al., 2019), we now obtained a *global* EF score for each participant by averaging the *z*-scores for each measure. This approach has the advantage of emphasizing the common variance of those measures, increases reliability (Rushton et al., 1983) and allows to characterize the key facets of executive function (Miyake & Friedman, 2012) comprehensively.

3.1.3 Results

We found that both younger and older adults can adequately judge their own uncertainty underlying their perceptual decisions. Confidence judgments were linked to perceptual performance in both age groups. However, confidence efficiency was – on average – lower in older adults compared to younger adults (see Figure 5a).

Although decision times were overall lengthened in older adults (Buckles, 1993; Salthouse, 1996), they were similarly shaped by confidence in both age groups, i.e. higher confidence was associated with faster responses (de Gardelle & Mamassian, 2014). This effect even remained when considering stimulus difficulty as a possible confound (see Figure 5b). As this benefit in response times did not scale with confidence efficiency, individual differences in processing speed dynamics cannot account for individual differences in confidence efficiency. Cognitive control capacities, on the other hand, were closely related to confidence efficiency, explaining 16% of its variance – even when controlling for age (see Figure 5c).
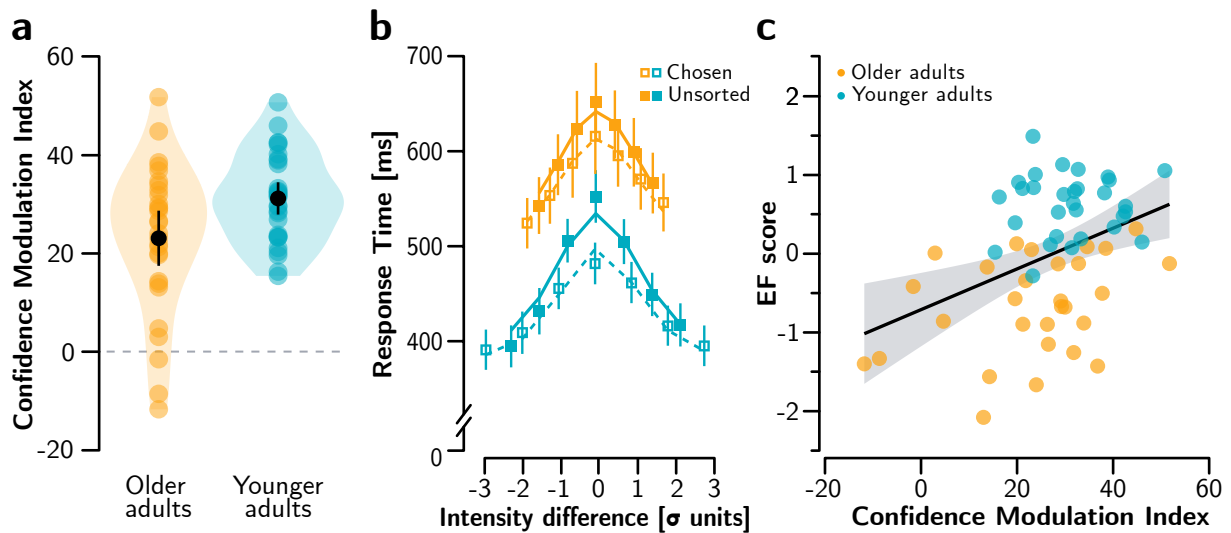

Figure 5. Metaperception in $n = 29$ older (orange) and $n = 29$ younger adults (blue). (a) Confidence Modulation Index (CMI) for participants in both age groups. Each participant is represented by a single colored dot, shaded areas visualize 95% of the data distribution smoothed by a kernel density function. Black dots show the mean across participants with error pars indicating 95% confidence intervals. (b) Response times as a function of age group and confidence set (chosen vs. unsorted) when taking stimulus difficulty into account. Stimulus difficulty here refers to the contrast difference between the test and standard stimulus (given in standard deviation units of the psychometric function) and is divided into seven equidistant bins. Open squares (chosen trial set) and filled squares (unsorted trial set) show the average group data with error bars indicating 95% confidence intervals. Dashed lines (chosen trial set) and solid lines (unsorted trial set) depict the average fitted data. (c) Correlation between CMIs and EF scores. EF scores provide a global measure for individual cognitive control capacities and are obtained by averaging z-scores from four cognitive tasks, i.e., VST-C, TMT-B, DSST and LPS-3. The shaded area represents the 95% confidence interval around the regression line.

3.2 Cross-modal confidence judgments

Cross-modal metacognition: Visual and tactile confidence share a common scale (Klever, Beyvers, et al., 2023) – accepted for publication in *Journal of Vision*

3.2.1 Background

Study 2b (Klever, Beyvers, et al., 2023) was not concerned with age effects but tested whether increased task demands due to cross-modal confidence judgments affect confidence efficiency in younger adults. Previously, it has been suggested that confidence can be computed on an abstract scale and may serve as a "common currency" across different visual decisions (de Gardelle & Mamassian, 2014) as well as across visual and auditory decisions (de Gardelle et al., 2016). So far, evidence is scarce on whether direct confidence judgments across visual and tactile decisions are possible without any costs in confidence efficiency (see e.g. Faivre et al., 2018). Overconfidence in the tactile sense might compromise cross-modal confidence judgments (Deroy & Fairhurst, 2019; Fairhurst et al., 2018).

The goal of study 2b was to challenge metaperceptual abilities in 54 younger adults and investigate whether confidence judgments are compromised when they had to be made across visual and tactile decisions. If confidence was modality-specific, confidence judgments should be easier when the perceptual decisions were made within the same modality rather than across modalities. Conversely, if confidence was modality-independent and stored in an abstract format, cross-modal confidence judgments should not compromise confidence efficiency. Furthermore, we aimed to elaborate on the results of study 2a (Klever et al., 2022) and tested whether individual differences in cognitive control capacities are associated with confidence in a sample of younger adults. Such a correlation may reflect the involvement of domain-general processes in metacognitive judgments (Rouault et al., 2023; Rouault, McWilliams, et al., 2018).

3.2.2 Methods

We again applied a confidence forced-choice paradigm (Mamassian, 2020; Mamassian & de Gardelle, 2021). But this time, we included two different perceptual tasks, i.e. a visual contrast discrimination task and a vibrotactile discrimination task. To avoid possible confounds due to differences in Type I task performance, perceptual performance was controlled by a staircase procedure. Confidence judgments were made about the correctness of two perceptual decisions involving either the same modality (i.e. visual–visual, tactile–tactile) or different modalities (i.e.

visual–tactile, tactile–visual). To minimize task-switching costs, the experiment was divided into four different blocks and the order of perceptual tasks was kept constant within each block. Similarly to study 2a, we calculated CMIs for each participant and all four conditions (i.e. visual unimodal, visual cross-modal, tactile unimodal, tactile cross-modal). Additionally, we obtained individual EF scores for each participant using the same approach as in study 2a.

3.2.3 Results

Our findings show that confidence judgments were robustly related to perceptual performance in both modalities. Importantly, confidence efficiency was not affected by whether confidence judgments were made about visual and tactile decisions or two perceptual decisions involving the same modality (see Figure 6). This finding is in line with the idea that confidence is stored in a modality-independent format (de Gardelle et al., 2016). Interestingly, we observed a slight bias (53.7%) to indicate tactile decisions as more confident when confidence judgments were made across modalities. However, on average, this bias was minor and did not substantially compromise confidence efficiency.

Analyses of response times indicated that confidence formation processes might be slightly altered between unimodal and cross-modal confidence judgments. We found that perceptual response times were slightly lengthened in the cross-modal-blocks compared to the unimodal blocks. However, confidence judgments were made faster across modalities than within, compensating for this time increase. In contrast to study 2a, we were not able to link individual cognitive control capacities and confidence efficiency – presumably due to variance restrictions in an age-homogeneous sample.
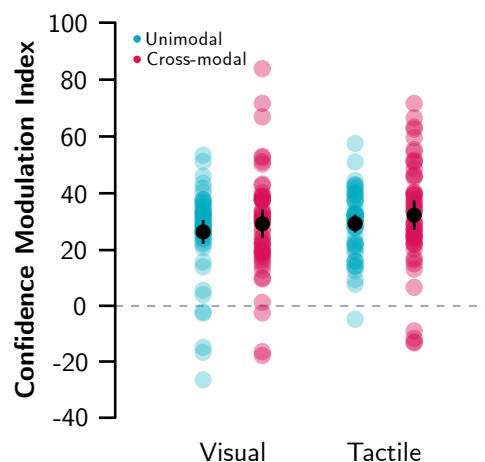

Figure 6. Confidence Modulation Index (CMI) as a function of modality (visual vs. tactile) and comparison type (unimodal in blue vs. cross-modal in red) in a group of $n = 54$ younger adults. Each participant is represented by a single colored dot. Black dots show the mean across observers. Error bars indicate 95% confidence intervals.

4 General discussion

In this dissertation, I examined how older and younger adults value different information in response to individual challenges (e.g. increased sensory noise) and current task demands to optimize and stabilize their performance. Study 1a and study 1b investigated the balancing of predictive and sensory signals. Specifically, greater reliance on predictions could be an adaptive response to minimize the influence of noise sensory information. This idea and potential side effects were tested in two different close to real-world scenarios, in which predictions were based on different sources. Study 2a and study 2b addressed the question whether we can acknowledge the uncertainty that underlies our perceptual decisions – an aspect of metaperception (Mamassian, 2016). Since both response times (Buckles, 1993; Salthouse, 1996) and cognitive control capacities (Hasher & Zacks, 1988; West, 1996) are subject to pronounced age-related changes, we examined their contributions to efficient performance.

Reliance on predictions

Study 1a and study 1b provide evidence for an enhanced impact of predictions with age. In study 1a, we found that older adults relied more strongly on somatosensory predictions than sensory feedback, which is reflected in greater tactile suppression effects compared to younger adults. Tactile suppression was, on average, about three times stronger in older adults. We thereby extend previous work demonstrating increased sensory attenuation with age in a force-matching task (Wolpe et al., 2016) and show that this age effect is robust across different paradigms. Since proprioceptive signals become more noisy with advance age (Goble et al., 2009), we suggest that increased reliance on sensorimotor predictions might be an adaptive mechanism to reduce the influence of noisy sensory information in accordance with Bayesian integration principles (Körding & Wolpert, 2004). Our findings further argue for preserved recalibration of the internal model of motor control with advanced age (compare also Vandevoorde & de Xivry, 2019). Furthermore, we found that increasing task demands by introducing an additional memory task during reaching led to increased suppression effects in both age groups. Interestingly, the magnitude of this increase was similarly pronounced in older and younger adults. We would have expected this effect to be more pronounced in the group of older adults if tactile suppression was primarily driven by task demands. Thus, we propose that cognitive demands overall modulate internal model function. Aging, however, specifically changes the balance between sensory and predictive signals.

Interesting questions for future research are to explore both the advantages and disadvantages of an overreliance on sensorimotor predictions with advanced age. While increased reliance on sensorimotor predictions may help to distinguish between self- and externally generated sensations and could stabilize our sense of agency (David et al., 2008; Kilteni & Ehrsson, 2017), it could also reduce internal model updating and thereby impair motor learning (Trewartha et al., 2014).

Increased reliance on predictions does not only concern motor control but also cognition. Prior knowledge and predictions have been suggested to be a key factor in understanding older adults' memory performance (Umanath & Marsh, 2014). In study 1b, we investigated potential side effects for memory performance that might stem from an overreliance on expected information with advanced age. Object-scene inconsistencies (e.g. a bottle of ketchup in the shower) violate our expectations and thus, provide informational gain, which is relevant for knowledge updating and could aid memory (Greve et al., 2019). We found that older adults' memory performance for objects embedded in real-world scenes overall profited from violated expectations (Wynn et al., 2020). However, this benefit was attenuated in comparison to younger adults. We suggest that the embedding of target objects helped to automatically process object-scene inconsistencies (Cornelissen & Võ, 2017; Evans & Wolfe, 2022) and minimized associative demands that are particularly susceptible to aging (Naveh-Benjamin, 2000). This – together with refraining from providing explicit instructions about object-scene inconsistencies – might be the reason why we were able to observe overall similar effects in younger and older adults and, in particular, robust memory advantages for objects encoded in an incongruent context (c.f. Brod & Shing, 2019; Chen et al., 2022). However, we also found that older adults' memory representations were biased more towards congruent information. When asked to select the scene in which recognized target objects were presented, older adults exhibited a greater congruency bias, i.e. they selected those scenes that provide a congruent context for the target object. The findings from study 1b highlight that increased reliance on predictions might also have disadvantages. In particular, the effects of unexpected information may be attenuated, which might affect our ability to update our knowledge accordingly and could limit adaptability to changing environments and affordances (Press et al., 2020). It remains to be clarified at what memory stages age-related differences occur, i.e. during encoding and/ or retrieval. Preliminary data suggest that they are already present during encoding. In an ongoing study, we found that older adults spent overall less time fixating incongruent objects than younger adults. Differences in dwell times scaled with differences in memory performance, i.e. longer dwell times were associated with better memory. Thus, active vision seems to be critical for memory performance (Ryan & Shen, 2020).

Monitoring perceptual decisions

Increasing the reliance on predictive signals is one possibility to optimize performance in the face of increased sensory noise with age (although it may also come along with disadvantages – see study 1b). However, greater weighting of predictive signals does not prevent us from making errors. Perceptual confidence is essential for many aspects of everyday life and informs us whether we should trust or doubt our perceptual experiences. Especially low confidence in the correctness of our perceptual decisions is a crucial signal that tells us whether we should adjust our behavior. In principal, it is similar to detecting an error (Boldt & Yeung, 2015). In the absence of external feedback, confidence helps us to improve learning (Hainguerlot et al., 2018).

In study 2a we demonstrate that both younger and older adults can adequately judge the quality of their perceptual decisions. Confidence judgments reliably tracked the correctness of perceptual decisions. But on average, we found that confidence efficiency was reduced in older adults compared to younger adults. Previous studies have reported a similar decline in confidence efficiency with advanced age (Palmer et al., 2014) or a trend toward it (Filippi et al., 2020). As those studies measured confidence with the help of rating scales, the evaluation of confidence efficiency might have been compromised by confidence biases (Hansson et al., 2008; Mamassian, 2016). Our findings substantiate this previous evidence and rule out possible confounds due to pronounced biases.

However, there are also studies that report no age-related changes in confidence efficiency in a visual dot-discrimination task (Rouault, Seow, et al., 2018) and a gamified version of it (McWilliams et al., 2023). There are several possible explanations for these discrepancies. The studies finding no age differences were conducted online, whereas the studies finding significant age effects took place in laboratory settings. As online studies rely on self-selection recruitment, they might attract more computer literate older adults. Moreover, it is possible that a gamification approach increased motivation and impelled participants to do their best. And lastly, differences in the first-order task may contribute to different effects on confidence efficiency.

The factors that contribute to age-related differences in confidence efficiency need further clarification. Age-related slowing (Buckles, 1993; Salthouse, 1996) and reduced cognitive control capacities with advanced age (Hasher & Zacks, 1988; West, 1996) might interfere with efficient confidence judgments. These two possibilities are discussed under the corresponding sections below. Another interesting question for future research would be whether aging leads to increased confidence noise, which, in turn, affects confidence efficiency. Tackling this question, though, would probably require large data sets (Mamassian & de Gardelle, 2021).

In study 2b, we challenged metaperceptual abilities in a sample of younger adults by introducing a second perceptual task that involved another modality. Participants now had to make confidence judgments about two perceptual decisions that either involved the same or different modalities. We found that increased task demands due to the introduction of a second modality did not compromise confidence judgments. Cross-modal confidence judgments were as efficient as unimodal ones, although response times were slightly altered (i.e. perceptual decision times were increased, but this time cost was compensated through faster confidence judgments). Additionally, we observed a slight bias to indicate tactile decisions as more confident (53.7%) when confidence judgments were made across senses. Tactile overconfidence seems congruent with previous research suggesting higher confidence in tactile rather than visual information when faced with ambiguous evidence (Fairhurst et al., 2018) and may be attributed to the belief that touch provides more directness and certainty (Deroy & Fairhurst, 2019). However, this bias did not lead to substantial costs in confidence efficiency. Overall, these findings are in line with the idea that confidence is stored in an abstract format and can be estimated using a "common currency" across different perceptual decisions (de Gardelle et al., 2016; de Gardelle & Mamassian, 2014). A common currency supports behavioral control as it facilitates the combination of different information and may be useful to optimize choices. For example, it may help to prioritize different tasks (Aguilar-Lleyda et al., 2020).

From developmental studies we know that confidence is already stored in an abstract format by the age of 6 years (Baer et al., 2018; Baer & Odic, 2020). An interesting question for future research is how aging affects our ability to make confidence judgements across different tasks, modalities or even domains and whether they remain as efficient later in life. It may be possible that biases to favor information from one modality over the other are more pronounced in older adults. As we know, our sensory systems are subject to decline that starts at different ages for different modalities and progresses at different rates (e.g. Gadkaree et al., 2016). While remediation devices, such as glasses and hearing aids, constantly remind us that our visual and auditory abilities are subject to decline, we might be less aware of sensory deficits in the tactile sense (Cavazzana et al., 2018). Thus, the "fact-checking" function and the associated overreliance on the tactile sense might be more pronounced in older adults (Deroy & Fairhurst, 2019) and could compromise confidence comparisons across the visual and tactile sense to an extent where they become less efficient.

Contributions of processing dynamics

The reduction of processing speed is one of the most pronounced functional age differences (Buckles, 1993; Salthouse, 1996). Across our studies, we consistently confirmed age-related slowing. It might be possible that slowing leads to compromises in task performance. When inspecting response (and movement) times in our studies, we found that the overall patterns were strikingly similar in younger and older adults. For example, in study 2a, we found that – irrespective of age – responses were faster for the perceptual decisions that participants chose as relatively more confident (even when controlling for the effect of stimulus difficulty). We thereby extended previous research showing that response times vary with confidence in younger adults to older age (e.g. de Gardelle & Mamassian, 2014; Kiani et al., 2014). Critically, in none of our studies, differences in response times could explain the performance differences we observed between younger and older adults. They were neither related to age-related differences in tactile suppression (study 1a), object memory (study 1b) nor visual confidence (study 2a).

Contributions of cognitive control capacities

Another prominent facet of healthy aging concerns cognitive decline that is particularly pronounced for executive functions (EF; Hasher & Zacks, 1988; Miyake & Friedman, 2012; West, 1996). In study 1a and study 2a, we corroborated reduced cognitive control capacities with advanced age (Park & Reuter-Lorenz, 2009; West, 1996). We were able to link individual differences in cognitive control capacities with individual differences in tactile suppression (study 1a) and confidence efficiency (study 2a).

In study 1a, we found that lower cognitive control capacities were associated with stronger tactile suppression across both age groups (and in both reaching conditions), suggesting that cognitive control resources affect how sensory and predictive information are balanced. More specifically, limited control resources might contribute to an overreliance on predictive signals during movement control (compare also Monge & Madden, 2016; Vandevoorde & de Xivry, 2019). Since the prefrontal cortex is the primary neural correlate of EFs (Miller & Cohen, 2001; Yuan & Raz, 2014), this finding adds to previous research showing increased reliance on sensorimotor predictions with age was associated with functional connectivity in frontostriatal circuits (Wolpe et al., 2016).

In study 2a, we observed substantial variability in confidence efficiency (especially within the group of older adults). We were able to show that 16% of the variance in confidence efficiency can be explained by individual differences in cognitive control capacities. Specifically, higher cognitive

control capacities were associated with higher confidence efficiency. This finding underlines the conceptual and functional overlap between metacognition and EF (Fernandez-Duque et al., 2000; Roebers, 2017). However, it is also in contradiction to previous studies that were unable to provide a link between confidence and cognitive control capacities (Filippi et al., 2020; Palmer et al., 2014). In these studies, the functional link might be attenuated since the focus lay on very specific aspects of the concept and was only assessed with a single measure, namely performance on the Trail Making Test (Palmer et al., 2014), or two very complex EF tasks, i.e. the Simon task and Tower of London task (Filippi et al., 2020). Furthermore, samples that are too homogeneous in terms of age and education might restrict the range of individual differences in cognitive control capacities. This might explain why the link between cognitive control capacities and confidence efficiency was attenuated in study 2b despite using a similar paradigm and the same EF battery. Indeed, when we performed an exploratory analysis pooling the data sets from study 2a and 2b, we were able to determine a significant moderate correlation between both measures.

4.1 Conclusions

The four studies presented in this dissertation have shown that valuation processes are crucial to optimize and stabilize performance in the face of age-related sensory and cognitive changes as well as increased task demands. Despite pronounced age-related slowing and cognitive decline with age that was consistently confirmed in my studies, the valuation processes that I have investigated here seem to be largely preserved with age (although slight differences in comparison to younger adults exist). In particular, our brains seem to harness the power of prior knowledge and predictions to stabilize motor control and improve memory decisions. Overall, increased reliance on predictions may provide a beneficial, adaptive mechanism but interferences can emerge when our predictions are violated. Confidence judgments remain mostly reliable with age and continuously inform us about the correctness of our perceptual decisions, providing a crucial resource for behavioral control. However, my findings also suggest that the efficiency of these valuation processes is influenced by the availability of cognitive control resources.

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A Publications

Study 1a

Age effects on sensorimotor predictions: What drives increased tactile suppression during reaching?

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Age effects on sensorimotor predictions: What drives increased tactile suppression during reaching?

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Tactile suppression refers to the phenomenon that tactile signals are attenuated during movement planning and execution when presented on a moving limb compared to rest. It is usually explained in the context of the forward model of movement control that predicts the sensory consequences of an action. Recent research suggests that aging increases reliance on sensorimotor predictions resulting in stronger somatosensory suppression. However, the mechanisms contributing to this age effect remain to be clarified. We measured age-related differences in tactile suppression during reaching and investigated the modulation by cognitive processes. A total of 23 younger (18–27 years) and 26 older (59–78 years) adults participated in our study. We found robust suppression of tactile signals when executing reaching movements. Age group differences corroborated stronger suppression in old age. Cognitive task demands during reaching, although overall boosting suppression effects, did not modulate the age effect. Across age groups, stronger suppression was associated with lower individual executive capacities. There was no evidence that baseline sensitivity had a prominent impact on the magnitude of suppression. We conclude that aging alters the weighting of sensory signals and sensorimotor predictions during movement control. Our findings suggest that individual differences in tactile suppression are critically driven by executive functions.

Introduction

Developmental changes across the adult life span provide a critical source of functional differences between individuals. Although the demographic shift toward older populations in many societies has provided a strong impetus to investigate decline and stability of functional resources during aging, our understanding of behavioral age effects so far is mostly limited to defined domains and falls short of sufficiently considering the complexity of aging processes (see, e.g., Cabeza, Nyberg, & Park, 2005; van den Bos & Eppinger, 2016). Age-related changes are well documented for sensory capacities, motor performance, and in particular cognition (for reviews, see Owsley, 2011; Park & Reuter-Lorenz, 2009; Seidler et al., 2010). However, interactions between age effects on percep-

tion, action, and cognition are often neglected. Only recently endeavors to understand those functional links and how they shape age-specific capacities have begun to increase (Maes, Gooijers, Orban de Xivry, Swinnen, & Boisgontier, 2017; Monge & Madden, 2016).

Sensorimotor suppression can be considered as a well-suited opportunity to investigate complex mechanisms of functional aging. It involves efficient interactions between motor, sensory, and predictive processes. The phenomenon is based on dynamic gating of sensory information during movement preparation and execution. The crucial link between motor actions and perception of sensory stimulations is provided by the forward model of motor control (Shadmehr & Krakauer, 2008; Wolpert, Diedrichsen, & Flanagan, 2011; Wolpert & Flanagan, 2001). The model proposes that movement control relies on internal representations of motor commands and predicted sensory consequences of the corresponding movement. Performance is stabilized by a continuous comparison between sensory information from the environment and predicted movement consequences. In this framework, efficient regulation of performance can be achieved by enhancement and suppression of sensory signals that are relevant and irrelevant for movement control, respectively.

Tactile suppression, in particular, refers to the attenuation of tactile signals during movement planning and execution when presented on a moving limb compared to rest (for review, see Juravle, Binsted, & Spence, 2017). Originally, tactile suppression was primarily considered as a cancellation of specific afferences that are predicted based on the efference copy of the motor commands (e.g., Bays, Flanagan, & Wolpert, 2006; but see Chapman & Beauchamp, 2006). For instance, self-applied forces (Bays, Wolpert, & Flanagan, 2005; Shergill, Bays, Frith, & Wolpert, 2003) or self-tickling sensations (Blakemore, Frith, & Wolpert, 1999; Blakemore, Wolpert, & Frith, 1998) are perceived less intensely than when triggered externally. However, there has been cumulating evidence that not only self-generated, but also externally generated tactile signals are suppressed when applied to a moving limb (e.g., Buckingham, Carey, Colino, de Grosbois, & Binsted, 2010; Fraser & Fiehler, 2018; Voss, Ingram, Wolpert, & Haggard, 2008). Thus, tactile suppression during movements is not limited to afferences predicted from specific efference copies of motor commands, but can emerge from general predictions of sensory movement consequences, e.g., tactile signals from the moving limb. Accordingly, reduced neuronal activity in secondary somatosensory areas related to tactile signals has been observed for self-generated (Blakemore et al., 1998; Shergill et al., 2013) as well as for externally triggered stimulations (Jackson, Parkinson, Pears, & Nam,

2011; Parkinson et al., 2011) during movement. Therefore, it has been suggested that tactile suppression reflects a general gating mechanism fueled by the forward model. Sensory information irrelevant for movement execution is attenuated and thereby putatively capacities for optimizing voluntary movements are freed (Brown, Adams, Parees, Edwards, & Friston, 2013; Gertz, Voudouris, & Fiehler, 2017; Haggard & Whitford, 2004). Consistently, a lack of suppression or even enhancement has been observed when tactile information is relevant to action performance (Colino, Buckingham, Cheng, van Donkelaar, & Binsted, 2014; Juravle, Colino, Meleqi, Binsted, & Farnè, 2018; Voudouris & Fiehler, 2017a, 2017b).

Given pronounced sensory and motor changes during aging, functional effects on somatosensory suppression can be expected. Integration of sensory and motor signals might be challenged by increased somatosensory noise (e.g., Decorps, Saumet, Sommer, Sigaudo-Roussel, & Fromy, 2014), greater movement variability (e.g., Contreras-Vidal, Teulings, & Stelmach, 1998; Darling, Cooke, & Brown, 1989), or general movement slowing (e.g., Buckles, 1993). However, behavioral evidence is sparse. Age effects on somatosensory suppression have been considered only recently in a study by Wolpe et al. (2016). They measured the perception of forces applied to the index finger in a well-established matching task (see Bays et al., 2005; Shergill et al., 2003). Forces were generally felt less intensely when they were self-produced than when they were externally produced. Data supported that this effect increased with age, providing first evidence for stronger tactile suppression in older adults. Stronger suppression argues for a greater reliance on predictive signals while weighting sensory input less. This altered balance might be attributed to the basic principles of Bayesian integration (Körding & Wolpert, 2004) and could represent an adaptive mechanism during aging. Accumulating experience across the life span makes predictive signals more reliable, but sensory signals become increasingly noisy. Thus, the weighting of sensorimotor predictions is amplified, which contributes to a greater attenuation of the sensory action consequences.

Although age-related reliability changes in sensory and predictive signals provide a plausible account for increased somatosensory suppression, also cognitive processes are likely to play a critical role that has not been considered so far. Cognitive resources are subject to massive decline during aging (Hasher & Zacks, 1988; Park & Reuter-Lorenz, 2009; West, 1996), and numerous studies have provided evidence for close interactions between age effects on cognition and sensorimotor control, respectively. Older adults have been consistently found to show higher dual task costs when they have to share attentional resources between

a motor task and secondary cognitive demands (Doumas, Rapp, & Krampe, 2009; Huxhold, Li, Schmiedek, & Lindenberger, 2006; Lee, Wishart, & Murdoch, 2002; Lövdén, Schaefer, Pohlmeyer, & Lindenberger, 2008; Overvliet, Wagemans, & Krampe, 2013). Age-related changes in motor learning processes have been linked to memory resources (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2010; Trewartha, Garcia, Wolpert, & Flanagan, 2014) and also to executive functions (Heuer & Hegele, 2014; Heuer, Hegele, & Sülzenbrück, 2011; Huang, Gegenfurtner, Schütz, & Billino, 2017; Huang, Hegele, & Billino, 2018). These findings suggest that cognitive resources represent a major modulator of sensorimotor control in old age. Thus, it is to be clarified how cognitive processes contribute to increased somatosensory suppression in older adults. There is indeed evidence that auditory (Cao & Gross, 2015) as well as tactile (van Hulle, Juravle, Spence, Crombez, & van Damme, 2013) suppression can be modulated by attentional mechanisms in younger adults, suggesting a critical functional role in predictive processes (compare also Brown et al., 2013).

We aimed to investigate whether cognitive processes contribute to increased tactile suppression during aging. We assessed the attenuation of tactile perception during reaching movements compared to rest, using a paradigm that has yielded reliable suppression effects in younger adults (Buckingham et al., 2010; Fraser & Fiehler, 2018; Gertz, Fiehler, & Voudouris, 2018; Gertz et al., 2017). It has been consistently shown that externally generated, unpredictable tactile signals are attenuated when applied to the reaching limb. Being irrelevant for movement execution, they are assumed to be suppressed due to general predictions of sensory movement consequences. In addition, these suppression effects are specifically bound to the reaching limb and are not explained by secondary demands involved in the reaching movement (cf. Gertz et al., 2018). We manipulated cognitive task demands during reaching by introducing an additional memory task. In addition, we assessed individual executive resources in our participants. Cognitive decline during aging is most pronounced for executive functions (Hasher & Zacks, 1988; West, 1996), and they might crucially modulate the balancing of sensorimotor signals. We expected to corroborate stronger tactile suppression effects in older adults indicating an increased reliance on sensorimotor predictions. We further hypothesized that age effects are modulated by cognitive task demands and individual executive resources. More specifically, higher cognitive task demands as well as limited individual availability of cognitive resources might contribute to increased suppression.

Methods

Participants

A total number of 49 participants, of which 23 were younger adults (11 females), ranging in age from 18 to 27 years ($M = 22.6$, $SD = 2.6$), and 26 older adults (13 females), ranging in age from 59 to 78 years ($M = 69.3$, $SD = 5.2$) took part in this study. Participants had normal or corrected-to-normal vision. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971), yielding ambidexterity in three participants, i.e., laterality indexes 18, 10, and zero, respectively, and right-handedness in all other participants, i.e., laterality indexes ≥ 50. Using a detailed interview protocol, we further screened out any history of ophthalmologic, neurologic, or psychiatric disorders as well as medications presumed to interfere with visuomotor capacities. In addition, all participants were screened for mild cognitive impairment using a cutoff score of ≥ 26 on the Montreal Cognitive Assessment scale (Nasreddine et al., 2005). Participants received financial compensation or course credits. Methods and procedures agreed with the Declaration of Helsinki (World Medical Association, 2013) and were approved by the local ethics committee of the Faculty of Psychology and Sports Science, Justus Liebig University Giessen. Informed consent was obtained by all participants, and protection of data privacy was provided.

Assessment of executive functions

Individual executive capacities were characterized by performance in three established measures known to be highly sensitive to aging (compare with Park & Reuter-Lorenz, 2009). The Victoria Stroop Test (VST) uses different colored naming tasks to provide a measure of inhibitory control (Strauss, Sherman, & Spreen, 2006; Stroop, 1935). We ran a computerized version of this test included in the Psychology Experiment Building Language (PEBL) Test Battery (Mueller & Piper, 2014). In particular, the response latency when naming the color of ink of written color words giving an incongruent color indicates the difficulty of inhibiting a dominant response, classically called Stroop interference. The Trail Making Test, specifically part B (TMT-B), captures cognitive flexibility and task-switching ability (Kortte, Horner, & Windham, 2002; Reitan & Wolfson, 1985). The task requires continuous switching between the numerical system and the alphabetical system. The Digit Symbol Substitution Test (DSST), a subtask of the Wechsler Adult Intelligence Scale (Wechsler, 2008), taps working memory and set
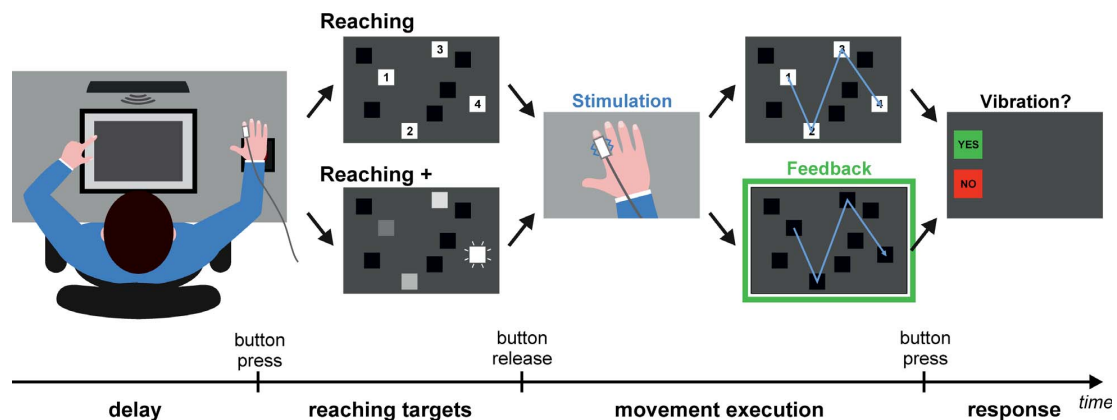
Figure 1. Schematic top view of the setup and trial procedure. Participants sat in front of a table, which was equipped with a touchscreen, a start button, and a speaker. In the baseline condition (not shown in detail), participants performed the detection task while the stimulated right hand was at rest. In the reaching condition, four out of the nine black squares turned white simultaneously and permanently. A fixed order was given by consecutive numbers. In the reaching plus memory condition, four squares turned white after one another, each for 1,000 ms, and participants had to remember their temporal order. In both reaching conditions, tactile stimulation was applied with a variable onset after release of the start button. After finishing the reaching movement in the reaching plus memory condition, participants were provided with performance feedback (green/red frame). At the end of each trial, participants indicated whether they had felt a vibration or not via the respective response squares.

shifting. A series of symbols has to be correctly coded within a time limit.

Experimental setup and stimuli

Figure 1 illustrates the setup and summarizes the procedure of the experimental task. Participants sat in front of a 21-in. ELO touchscreen (ELO TouchSystems ET2125C, resolution of $1,280 \times 960$ pixel, refresh rate of 100 Hz) at a distance of approximately 25 cm. The touchscreen was horizontally placed and tilted by 15° toward the participants in order to allow for comfortable viewing of and reaching toward the display. A custom-made input device was positioned 16 cm to the right of the touchscreen's center. It was composed of a start button embedded in a hand-rest cup so that it could be handled comfortably by the heel of the right hand.

Targets for reaching movements were provided on the touchscreen using an arrangement of nine black squares (2.5×2.5 cm each) on a gray background. The spatial arrangement corresponded to the outline of the Corsi Block Tapping Task (Berch, Krikorian, & Huha, 1998) that is typically used to assess spatial working memory (see Figure 1).

Vibrotactile stimulation was applied by a custom-made tactile stimulator (Engineering Acoustics Inc., Casselberry, FL) that was attached to the dorsal part of participants' right index finger. Position of the stimulator was chosen not to interfere with touching the

screen when reaching with the finger. Stimuli were presented for 35 ms and at a frequency of 100 Hz. In order to mask any auditory cues emerging from the tactile stimulators, we presented white noise via an external loudspeaker hidden behind the touchscreen.

The presentation of tactile stimuli and reaching targets was controlled by MATLAB (MathWorks, Natick, MA) using the Psychophysics Toolbox (Brainard, 1997; Kleiner, 2010).

Procedure

Our experimental procedure started with a short introduction to our setup in order to allow all participants to get acquainted with our equipment. This introduction included the demonstration of vibrotactile stimulations as well as the use of the touchscreen as input device. We particularly took care that those older adults who reported to have only minor experience with technical devices felt comfortable with our setup.

Tactile detection was then measured under three different conditions, i.e., baseline, reaching, and reaching plus memory (see Figure 1). We investigated perceptual performance based on psychometric functions that were determined from a *Yes–No* detection task. This method of single stimuli is known to be well accepted by participants naïve to psychophysical measurements and allows efficient threshold estimations from a limited number of trials (Jäkel & Wichmann, 2006; Leek, Dubno, He, & Ahlstrom, 2000;

Yeshurun, Carrasco, & Maloney, 2008). However, because psychometric functions derived from *Yes–No* tasks are prone to response biases, careful consideration of individual decision criteria is indicated during data analysis. Participants performed a tactile detection task in which signal intensity was varied by 12 constant levels defined by peak-to-peak displacements. Because age-related differences in tactile sensitivity are well documented (A. K. Goble, Collins, & Cholewiak, 1996), we chose for each adult group an appropriate intensity range that was supposed to comprise just detectable to reliably detectable intensities. Intensities, defined as peak-to-peak displacements, ranged from 0.007 mm to 0.085 mm for younger adults and from 0.009 mm to 0.169 mm for older adults. Each of the 12 intensity levels was presented eight times, giving overall 96 stimulation trials. In addition, we included 24 catch trials without tactile stimulation in order to impose uncertainty about the presence of a stimulus. For each condition, we, thus, presented a total of 120 trials.

All participants first performed the detection task under the baseline condition in which the stimulated right hand was at rest. Participants were informed that a tactile stimulation would be present or absent in each trial, but the proportion of trials with and without stimulation was not specified. The start of each trial was indicated by a black circle displayed on a gray background for 700 ms. After the circle was extinguished, a tactile stimulation followed in the respective trials. In order to prevent participants anticipating the moment of stimulation, onset varied between 10 ms and 100 ms in steps of 10 ms. This range of delays was assumed to be sufficient to introduce reliable ambiguity about the timing of the tactile stimulus because it matches documented duration discrimination thresholds (Grondin, 2010; Rammsayer, 1990). There is no evidence for pronounced age effects on temporal discrimination (Rammsayer, Lima, & Vogel, 1993). In addition, catch trials contributed to further ambiguity about the stimulus onset. Onsets were randomized and balanced across trials. Two vertically arranged squares, a green one labeled "yes" and a red one labeled "no," appeared on the left side of the display 700 ms after the disappearance of the black start circle. Participants responded whether they felt a stimulation or not by touching the respective square with their left index finger. The vertical arrangement of the two response squares was randomized across participants but was kept constant for each individual participant. After the response, no feedback was given, and the next trial started.

The baseline condition was followed by the reaching condition and reaching plus memory condition. The order of these two conditions was randomized across participants. The procedure of the tactile detection task in both reaching conditions was equivalent to the baseline condition but was embedded in reaching tasks. Required reaching movements were comparable across both reaching conditions. They comprised a sequence of taps on four target squares and the sequence was defined completely before movement onset. Each trial started with the participants pressing the start button with the heel of the right hand. After a delay of 2,000 ms, the targets for the reaching movements were presented.

In the reaching condition, four out of the nine black squares turned white simultaneously and permanently. A fixed order was given by consecutive numbers. Participants had to touch the white squares in their ascending order with the right index finger to which the stimulator was attached. Reaching movements were instructed to be executed immediately after onset of the white squares and as naturally as possible. The onset of the tactile stimulations was locked to the release of the start button so that detection performance was measured during movement execution. Timing of the tactile stimulations was subject to the delay jitter described above. Ambiguity about stimulus onset was important in order to prevent strategic changes in movement execution, e.g., slowing at the moment of stimulation. When the reaching movement was completed, participants returned the right hand to the start button. The response squares were then displayed, and participants indicated whether they had noticed a tactile stimulation and the next trial started.

In the reaching plus memory condition, four out of the nine black squares turned white after one another, each for 1,000 ms. Participants were instructed to remember the sequence of squares. After the last square turned back to black, they had to touch the remembered squares in the correct order with their right index finger. Again, reaching movements were instructed to be executed immediately after extinction of the last white square and as naturally as possible. The onset of the tactile stimulations was locked to the release of the start button so that detection performance was measured during movement execution. Timing of the tactile stimulations was again subject to the given delay jitter in order to keep the stimulus onset sufficiently ambiguous. When the hand returned to the start button, feedback on the memory performance was provided for 200 ms. If the sequence of squares was touched in the correct order, a green frame was displayed around the arrangement of black squares, otherwise a red frame was given. Afterward, participants indicated whether they had noticed a tactile stimulation and the next trial started.

Executive functions were assessed after completion of the tactile detection tasks in the three different conditions. In addition to the executive tests, we determined the maximal block span of each participant using the respective subtest of the Wechsler Memory

Scale (Härting et al., 2000). We chose a constant block sequence length of four blocks in the reaching plus memory condition in order to keep the task procedure comparable across participants. The block span measure allowed the evaluation of individual memory task demands. Overall, the procedure took about 60–90 min so that the duration was still appropriate for the older participants.

Data analysis

Tactile detection performance under the three experimental conditions was analyzed by fitting cumulative Gaussian functions to the detection rates for the different intensity levels. We used the psignifit 4 toolbox in MATLAB, which provides an accurate Bayesian estimation of psychometric functions and has been shown to be robust to overdispersion in measured data. In particular, the toolbox has been evaluated for data from *Yes–No* paradigms as used in our procedure, and extensive numerical simulations support accuracy of derived estimates (Schütt, Harmeling, Macke, & Wichmann, 2016). From the fitted psychometric functions, we determined 50% detection thresholds. Due to inconsistent detection data, psychometric functions could not be fitted for six participants in the reaching plus memory condition (two younger and four older adults). For all other functions, goodness of fit was evaluated by comparing the measure of deviance with the critical chi-square value for 13 comparisons, $\chi^2_{13, \ 95\%} = 22.36$ (Wichmann & Hill, 2001). Deviance is defined as the log-likelihood ratio between the saturated model, i.e., no residual error between empirical data and model predictions, and the best-fitting model. Smaller deviance values indicate better fits. Out of all 141 estimated functions, 99.29% met this criterion. In order to consider possible response biases that could impose a critical confound when interpreting psychometric estimates, we analyzed the lower asymptotes, γ, of the psychometric functions. The lower asymptotes indicate individual decision criteria, i.e., participants' inclination to report the presence of a stimulus. We particularly aimed to clarify whether response biases systematically varied across the different measurement conditions and, thus, could contribute to threshold differences. Running a mixed ANOVA with the within-subject factor *measurement condition* (baseline, reaching, reaching +) and the between-subject factor *age group* (younger adults vs. older adults), we found no evidence for a critical confound. The lower asymptotes were affected neither by *measurement condition,* $F(2, 82) = 1.76$, $p = 0.179$, $\eta_p^2 = 0.04$, nor by an interaction between *measurement condition* and *age group,* $F(2, 82) = 1.11$, $p = 0.334$, $\eta_p^2 = 0.03$. We indeed determined a significant main effect of *age group,* $F(1, 41) = 4.59$, $p =$

0.038, $\eta_p^2 = 0.10$, indicating higher guess rates in older adults. Although this might contribute to an overall underestimation of detection thresholds in older adults and, thus, an underestimation of the age effect on detection thresholds (compare with Morgan, Dillenburger, Raphael, & Solomon, 2012), tactile suppression effects can be considered as undistorted because they were evaluated within individual participants.

Tactile suppression effects were assessed by subtracting each participant's baseline detection threshold from their thresholds determined in the reaching condition and the reaching plus memory condition, respectively (compare, e.g., Gertz et al., 2017; Voudouris & Fiehler, 2017a). The resulting difference values represent the strength of tactile suppression. Positive values indicate suppression during movement execution. Note that, due to the missing detection thresholds for the abovementioned six participants in the reaching plus memory condition, we calculated tactile suppression effects only for 43 participants in this particular condition.

For the reaching and the reaching plus memory conditions, we collected reaction times and movement times. For the former condition, reaction time was defined as the time between the onset of the numbered squares and the release of the start button. For the latter condition, it was defined as the time difference between the extinction of the last white square and the release of the start button. Movement time was given by the difference between the release of the start button and the first screen contact. For statistical analyses, time measures were averaged across trials for each participant.

Accuracy of reaching movements was assessed by the proportion of correctly reproduced reaching sequences. Accuracy in the reaching plus memory condition provides a measure of individual task demand. Please note that, in the reaching condition, accuracy was expected to deviate only minimally from 100% as participants just had to follow the order of the four numbers correctly. However, the touch sequence was sometimes not registered appropriately because participants touched the screen too weakly or in an unfavorable angle. Thus, accuracy in the reaching condition can be considered as a technically determined upper limit.

Basic age effects on tactile perception were explored by contrasting detection thresholds in younger and older adults using separate *t* tests for each measurement condition, i.e., baseline, reaching, and reaching plus memory conditions. Tactile suppression effects were analyzed using a mixed ANOVA with the within-subject factor *reaching condition* (reaching vs. reaching +) and the between-subject factor *age group* (younger adults vs. older adults). The link between cognitive measures and tactile suppression was explored by linear

regression analyses. In order to back up our results against violations of assumptions underlying these parametric statistical methods, we complemented our analyses by bootstrapping methods (Efron & Tibshirani, 1993). For group comparisons and regression analyses, we computed 95% percentile confidence intervals using 2,000 bootstrap samples. Given evidence from extensive simulations studies, we assumed relative robustness of ANOVAs (Berkovits, Hancock, & Nevitt, 2000; Wilcox, 2012). A significance level of $\alpha = 0.05$ was applied for all statistical analyses. If not stated otherwise, descriptive values are given as means $\pm$ *SEM*s.

Results

In order to explore basic perceptual performance in both age groups, we first contrasted tactile detection thresholds in younger and older adults. Figure 2 illustrates the thresholds we derived for each age group in the three different measurement conditions. We observed robust age effects on tactile perception. Older adults consistently showed higher detection thresholds than younger adults in the baseline condition, 0.040 ± 0.004 mm versus 0.014 ± 0.002 mm, $t(47) = 5.91$, $p < 0.001$, $d = 1.73$, 95% CI [0.017, 0.034]; the reaching condition, 0.075 ± 0.008 mm versus 0.026 ± 0.006 mm, $t(47) = 4.84$, $p < 0.001$, $d = 1.40$, 95% CI [0.027, 0.067]; and the reaching plus memory condition, 0.090 ± 0.011 mm versus 0.032 ± 0.006 mm, $t(41) = 4.69$, $p < 0.001$, $d = 1.44$, 95% CI [0.035, 0.082]. In all conditions, older adults needed approximately three times higher intensity levels than younger adults for detecting the tactile stimulation on their right index finger. Cohen's d values indicate pronounced age effects on tactile perception. Please note that these effects might indeed be subject to an underestimation because the lower asymptotes of psychometric functions suggested that older adults were more inclined to report the presence of a stimulus, possibly reducing the age effect (compare with the section *Data analysis*).

Tactile suppression effects during reaching were quantified using threshold difference measures. Baseline thresholds were subtracted from thresholds in the reaching and the reaching plus memory condition, respectively. Figure 3A provides exemplary psychometric functions for the three measurement conditions derived for a typical younger and a typical older participant. Functions for both reaching conditions are shifted to the right on the stimulus intensity axis, indicating higher detection thresholds. Suppression effects in each age group are summarized in Figure 3B.

In the reaching condition, we were not able to observe tactile suppression consistently. We determined
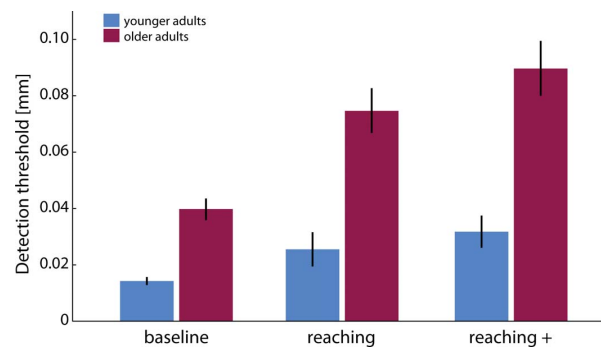

Figure 2. Detection thresholds in younger and older adults for all three conditions, i.e., baseline, reaching, and reaching plus memory condition. Stimulus intensity is defined as peak-to-peak displacement in millimeters. Error bars indicate ± 1 *SEM*.
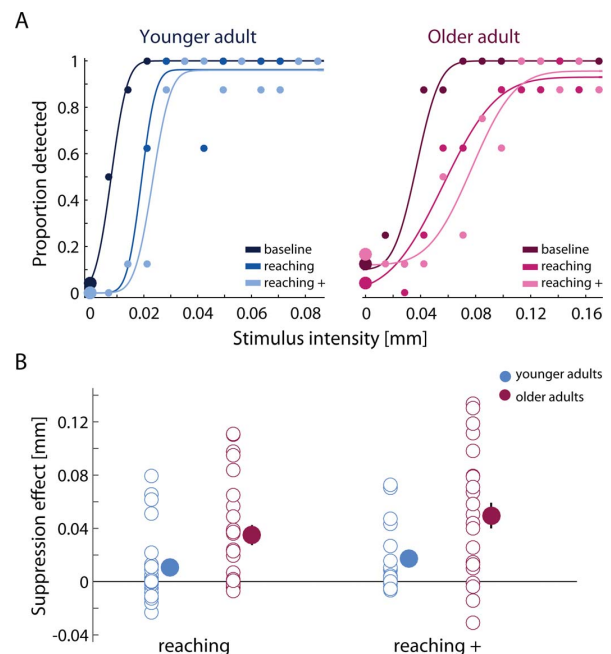

Figure 3. Tactile suppression effects in younger and older adults. (A) Psychometric functions in the three conditions, i.e., baseline, reaching, and reaching plus memory, for an exemplary younger and an exemplary older adult; stimulus intensity is defined as peak-to-peak displacement in millimeters; please note that the scale of stimulus intensity on the *x*-axis varies between age groups; data points for each intensity level are based on eight trials each except for the zero-intensity level that comprised 24 catch trials without tactile stimulation. (B) Tactile suppression effects given by the detection threshold differences between the baseline condition and the respective reaching condition; open symbols illustrate individual data, filled symbols average data in each age group; error bars indicate ± 1 *SEM*.

suppression effects >0 in 47.83% of the younger and 71.43% of the older adults. On average, younger adults showed tactile suppression of 0.011 ± 0.006 mm, but this effect failed to differ significantly from zero, $t(22) = 1.83$, $p = 0.081$, $d = 0.38$, 95% CI [−0.001, 0.020]. In contrast, older adults showed an average suppression effect of 0.035 ± 0.008 mm, yielding a significant difference from zero, $t(25) = 4.64$, $p < 0.001$, $d = 0.91$, 95% CI [0.017, 0.046]. In the reaching plus memory condition, the majority of participants in both age groups showed tactile suppression, i.e., 73.08% and 77.27% in younger and older participants, respectively. On the group level, suppression effects were pronounced and differed significantly from zero for younger adults, 0.018 ± 0.006 mm, $t(22) = 3.00$, $p = 0.007$, $d = 0.65$, 95% CI [−0.067, 0.030], and for older adults, 0.050 ± 0.011 mm, $t(25) = 4.64$, $p < 0.001$, $d = 1.01$, 95% CI [0.030, 0.070].

We were particularly interested in determining whether tactile suppression effects vary systematically between age groups and between reaching conditions that involve differential task demands. To this end, we ran a 2 × 2 mixed ANOVA on the suppression effects with the between-subject factor *age group* and the within-subject factor *condition*. The analysis yielded significant main effects for *age group*, $F(1, 41) = 7.98$, $p = 0.007$, $\eta_p^2 = 0.16$, and *condition*, $F(1, 41) = 7.53$, $p = 0.009$, $\eta_p^2 = 0.16$. There was no significant interaction effect between *age group* and *condition*, $F(1, 41) = 0.97$, $p = 0.330$, $\eta_p^2 = 0.02$, so that main effects could be interpreted directly. In both reaching conditions, older adults consistently showed larger tactile suppression effects in comparison to younger adults. In addition, independent of age group, suppression effects were more pronounced when task demands were enhanced by memory load, i.e., suppression was more pronounced in the reaching plus memory condition than in the reaching condition.

We scrutinized the described main effects by exploring their link to individual perceptual capacities and individual task demands. First, we considered the possibility that the age-related increase in tactile suppression was driven by the overall higher detection thresholds in older adults. We used baseline detection thresholds as a reference for tactile perception and found no evidence for a significant correlation with the magnitude of suppression during reaching, neither in the reaching condition, $r(49) = 0.17$, $p = 0.245$, 95% CI [−0.04, 0.37], nor in the reaching plus memory condition, $r(43) = 0.16$, $p = 0.319$, 95% CI [−0.10, 0.45]. Note that, because baseline thresholds enter these analyses twice, i.e., with a positive sign for perceptual capacity and with a negative sign for suppression effects, a systematic negative bias is inherent to these correlations. Thus, we indeed cannot rule out an impact of perceptual capacities on the magnitude of suppres-

sion effects. However, given the observed weak positive correlations that did not significantly deviate from zero, it appears rather unlikely that individual threshold differences are the main driving factor for the variability in suppression effects.

In addition, we aimed to clarify how task demands might modulate tactile suppression. In the reaching plus memory condition, the task required memory resources. The extent of task demands consequently depended on individually available resources. More pronounced suppression effects in older adults in comparison to younger adults could be triggered by age-related differences in memory capacities and, thus, differences in task demands. Indeed, our two age groups varied substantially in their memory capacities, and it can be plausibly assumed that task demands in the reaching plus memory condition were more challenging for older adults. We determined significant age-related differences in the maximal block span measure we obtained for each participant, $t(47) = −5.87$, $p < 0.001$, $d = −1.67$, 95% CI [−1.69, −0.82]. Older adults reached, on average, a maximal memory span of 5.0 ± 0.1 blocks, and younger adults accomplished a sequence of 6.3 ± 0.2 blocks. Congruently, older adults showed lower accuracy in our block span task in the reaching plus memory condition than younger adults, 76.89 ± 3.29% versus 91.51 ± 1.42%, $t(41) = −4.02$, $p < 0.001$, $d = −1.24$, 95% CI [−22.17, −8.02]. Please note that, in the reaching condition, when accuracy was supposed to exclusively rely on putative difficulties in touchscreen handling, older and younger adults showed comparable accuracy rates, 89.52 ± 2.23% versus 91.45 ± 1.65%, $t(47) = −0.68$, $p = 0.500$, $d = −0.20$, 95% CI [−8.45, 3.67]. However, the extent of individual demands was not significantly linked to suppression effects. Correlations between maximal block span measures as well as accuracy and suppression effects did not reach significance, $r(43) = −0.27$, $p = 0.075$, 95% CI [−0.51, 0.01], and $r(43) = −0.12$, $p = 0.464$, 95% CI [−0.47, 0.18], respectively.

Because different strategies in accomplishing the additional memory task might obscure effects of individual task demands, we investigated time measures of the reaching movements that could indicate systematic differences between age groups. Reaction times and movement times in each reaching condition are illustrated in Figure 4.

We submitted both time measures to 2 × 2 mixed ANOVAs with the between-subject factor *age group* and the within-subject factor *condition*. Analyses yielded significant main effects of *age group* for reaction time $F(1, 41) = 34.69$, $p < 0.001$, $\eta_p^2 = 0.46$, and for movement time $F(1, 41) = 28.74$, $p < 0.001$, $\eta_p^2 = 0.41$. These main effects consistently support typical age-related slowing in our sample. In addition, timing of reaching movements was modulated by *condition*.
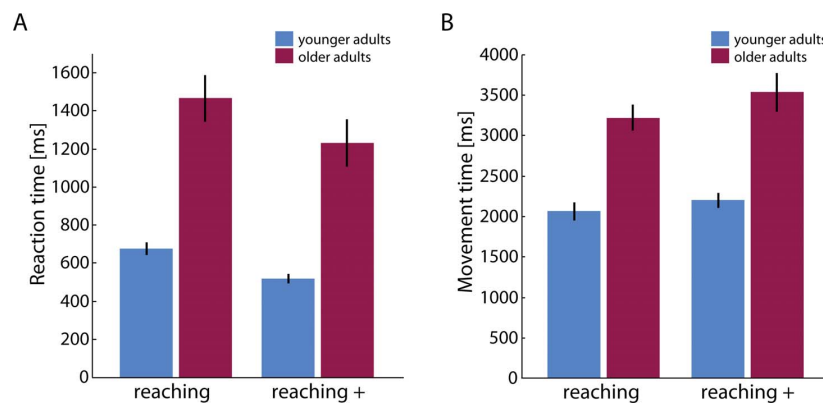
Figure 4. Time measures in the reaching condition and the reaching plus memory condition for younger and older adults. (A) Average reaction times. (B) Average movement times. Error bars indicate ± 1 *SEM*.

Reaction times tended to be shorter in the reaching plus memory condition, $F(1, 41) = 3.74$, $p = 0.060$, $\eta_p^2 = 0.08$, whereas movement times were significantly slower $F(1, 41) = 5.82$, $p = 0.020$, $\eta_p^2 = 0.12$. This pattern most likely emerges from the specific procedure in each condition. In the reaching condition, the start of the reaching movement is preceded by locating the first reaching target on the display. Movement execution then is directly guided by the visible target numbers. In contrast, in the reaching plus memory condition, the start of the reaching movement can be already prepared during successive presentation of the targets. Movement execution is slowed by repeated decisions on where to reach next. Most importantly, we found no evidence for interactions effects between *age group* and *condition* on time measures: for reaction time: $F(1, 41) = 0.33$, $p = 0.567$, $\eta_p^2 = 0.01$; for movement time: $F(1, 41) = 1.83$, $p = 0.183$, $\eta_p^2 = 0.04$. Thus, participants in both age groups can be assumed to have applied similar strategies to accomplish the reaching tasks.

Finally, we investigated whether individual executive capacities contribute to differences in tactile suppression. We assessed individual executive functions with established measures, i.e., the VST, the TMT-B, and the DSST. Age groups differed significantly in all measures, all ps < 0.001. We aimed to test whether suppression effects can be predicted by executive functions. We found consistent correlations between our measures and tactile suppression in both reaching conditions across all participants, indicating that more pronounced suppression effects were linked to lower performance in the executive tests. All correlations, except for the correlation between the VST and the suppression effect in the reaching plus memory condition, $r(43) = 0.18$, $p = 0.261$, 95% CI [−0.17, 0.53], reached significance, rs ranging between 0.31 and 0.49, ps ≤ 0.031. Because all tests tap the same functional domain, intercorrelations accordingly were high, rs >

0.59, ps < 0.001. For a simple linear regression analysis, we chose the TMT-B, capturing primarily cognitive flexibility because it was most robustly linked to suppression in the reaching, $r(49) = 0.40$, $p = 0.005$, 95% CI [0.14, 0.62], as well as in the reaching plus memory condition, $r(43) = 0.49$, $p = 0.001$, 95% CI [0.15, 0.73]. Figure 5 illustrates the correlations for both conditions. Higher time measures in the TMT-B indicate lower cognitive flexibility. Depiction of group membership for each data point suggests that the reported correlations are not merely driven by group differences but can actually be observed across the whole sample. Please note that our data supports a specific link between executive functions and tactile suppression because neither tactile thresholds in the baseline condition nor overall speed in the reaching tasks, both measures highly age-sensitive, correlated with suppression effects.

Using performance in the TMT-B as predictor explained 16% and 24% of the variance in the tactile suppression effect in the reaching condition, $F(1, 48) = 8.74$, $p = 0.005$, $R^2 = 0.16$, and the reaching plus memory condition, $F(1, 42) = 12.82$, $p = 0.001$, $R^2 = 0.24$, respectively. Overall, the regression analysis supported that executive resources critically contribute to individual differences in the magnitude of tactile suppression during reaching, independent of task demands.

Discussion

This study was concerned with age effects on tactile suppression and the specific contributions of cognitive processes. Recent evidence indicates stronger suppression in older adults, putatively due to an increased reliance on sensorimotor predictions (Wolpe et al.,
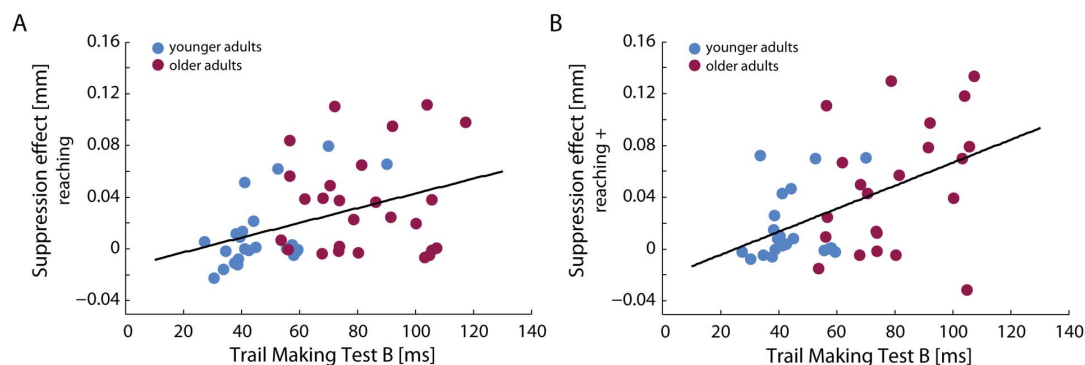
Figure 5. Correlations across all participants, i.e., younger and older adults, between cognitive flexibility as measured by the TMT-B and tactile suppression effects as given by detection threshold differences. (A) Data in the reaching condition. (B) Data in the reaching plus memory condition.

2016). We investigated tactile suppression during reaching in an established paradigm that is known to reliably induce an attenuation of tactile signals on the moving limb (Fraser & Fiehler, 2018; Gertz et al., 2018; Gertz et al., 2017; Voudouris & Fiehler, 2017a). Furthermore, we explored how the magnitude of suppression was modulated by cognitive task demands and individual executive resources, respectively. Task demands were manipulated by introducing a secondary memory task linked to the primary reaching task. Comparison between tactile suppression in conditions with and without additional memory load allowed us to evaluate the impact of cognitive task demands. Moreover, we tested whether tactile suppression is associated with available individual executive resources.

Our main aim was to examine whether the reliance on sensorimotor predictions reduces tactile sensitivity and whether this effect is modulated by age. We succeeded in triggering tactile suppression during reaching in both younger and older adults. The magnitude of suppression in young adults was overall consistent with findings from previous studies that used a comparable paradigm (Fraser & Fiehler, 2018; Gertz et al., 2018; but see Gertz et al., 2017) but, indeed, just failed to reach significance in the reaching condition without additional memory load. We speculate that our adaptation of the reaching task might have induced an attenuation of suppression effects. While typically only single reach targets have been used, we presented a sequence of reach targets. Thus, in our task, movement execution can be supposed to overlap with movement planning. This might result in attenuated suppression in comparison to straight execution because sensory attenuation has been found to be less pronounced during movement planning (Voss et al., 2008). Most importantly, our results support stronger tactile suppression with increasing age. On average, older adults

showed approximately more than three times stronger suppression than younger adults. This finding extends recent evidence for an age-related increase of somatosensory suppression in a force-matching task (Wolpe et al., 2016), confirming that the age effect is reliable across paradigms.

Because we derived tactile suppression effects by subtracting baseline thresholds from thresholds during reaching, a possible confound with secondary attentional demands inherent to the movement task has to be considered. Whereas in the baseline condition, attention can be exclusively focused on a possible tactile stimulation, in the reaching condition, also movement execution requires attention. Divided attention per se might contribute to an attenuation of sensory signals. However, it appears rather unlikely that suppression effects are primarily driven by attentional demands. There is converging evidence that suppression effects observed in our paradigm are not explained by general attentional differences. Gertz et al. (2018) showed that a secondary visual discrimination task does not modulate suppression effects. Furthermore, suppression effects occur on the hand involved in the reaching movement but not on the static hand (e.g., Voss et al., 2008; Voudouris & Fiehler, 2017a, 2017b). Similarly, it has been reported that tactile suppression occurs even when the movement is just planned but not executed (e.g., Buckingham et al., 2010; Voss et al., 2008), indicating that suppression effects are not exclusively bound to specific attentional demands. These findings, overall, suggest that observed suppression effects predominantly originate from planning and execution of the movement itself.

Somatosensory suppression has been discussed in the context of a forward model predicting the sensory consequences of movements (Shadmehr & Krakauer, 2008; Wolpert et al., 2011; Wolpert & Flanagan, 2001). Indeed, it has been previously claimed that this internal

model of motor control is prone to age-related decline. This claim is supported by several findings showing that sensorimotor adaptation is reduced in old age (Bock, 2005; Buch, Young, & Contreras-Vidal, 2003; Heuer & Hegele, 2008; Seidler, 2006). Because adaptation substantially relies on the evaluation of prediction errors, age effects have been interpreted as indicating a vulnerability of the forward model. In addition, the cerebellum, which is considered as a critical neural substrate of the forward model (Shadmehr & Krakauer, 2008), is subject to massive structural changes during aging (Raz et al., 2005; Sowell et al., 2003; Walhovd et al., 2011). Several studies have linked cerebellar decline to age-related changes in internal models (Bernard & Seidler, 2014; Boisgontier, 2015; Boisgontier & Nougier, 2013; Seidler, 2006). We propose that increased tactile suppression qualifies the general notion of age-related decline in the forward model.

Consistent with the study by Wolpe et al. (2016), our results support an increased reliance on sensorimotor predictions. Given that proprioceptive signals during movements become increasingly noisy with age (D. J. Goble, Coxon, Wenderoth, van Impe, & Swinnen, 2009), the altered balance of signals might indicate a beneficial adaptive mechanism that agrees with Bayesian integration principles (Körding & Wolpert, 2004). Increased weighting of sensorimotor predictions and reduced weighting of sensory signals, for example, could stabilize the sense of agency in old age, i.e., the experience to control one's own actions and their consequences (David, Newen, & Vogeley, 2008). It critically relies on the evaluation of congruency between predicted action consequences and actual sensory outcome. Increased sensory noise putatively could compromise the reliability of this evaluation so that reduced weighting of these afferent signals might be favorable. We conclude that aging is linked to a shift in weighting of sensory signals and sensorimotor predictions during movement control, respectively, suggesting preserved recalibration of the forward model across the adult life span (compare also Vandevoorde & Orban de Xivry, 2018). However, please note that our results did not indicate that tactile suppression directly scales with tactile sensitivity, i.e., no pronounced positive correlations between baseline tactile detection thresholds and the magnitude of suppression effects were observed. Thus, although differential signal noise can be discussed as a plausible account for shifted weighting of predictions and sensory signals, additional functional mechanisms need to be considered.

A prominent functional age difference concerns processing speed. General slowing and, in particular, slowing of movements are well documented (Buckles, 1993; Salthouse, 1996). Congruently, we observed

typical age-related slowing of reaction and movement times in our reaching tasks. Slowing, however, is unlikely to explain the observed age effects on tactile suppression as tactile suppression has been shown to be generally stronger with faster movements (Cybulska-Klosowicz, Meftah, Raby, Lemieux, & Chapman, 2011; Gertz et al., 2017; but see Fraser & Fiehler, 2018). Thus, if movement speed modulated tactile suppression, we might have rather underestimated the age differences. However, we speculate that such modulation might be calibrated to the individual range of movement speed. Therefore, we propose that age-related slowing does not bias our results. Moreover, time measures might be considered as indicative for task demands because previous evidence suggests that movement initiation is faster in easier tasks (Hesse, de Grave, Franz, Brenner, & Smeets, 2008). Due to the overall differences in processing speed, a comparison between our conditions only seems feasible within each age group. Indeed, for both groups, reaction times were consistently shorter in the reaching plus memory condition, seemingly in conflict with the intended boost in task demands. We, though, suggest that the link between movement initiation and task demands does not apply to our specific paradigm. Time measures in both reaching conditions cannot be directly compared because the differential contributions of reaction and movement times to overall reaching time vary systematically due to the different task procedures. The extended preparation phase in the reaching condition systematically speeds up reaction times, whereas repeated decisions based on memory enhance movement times. In contrast, in the reaching condition movement initiation takes longer, but execution directly guided by visual cues is faster. This pattern did not differ between age groups. Hence, we conclude that our main findings are not qualified by differential time measures in both age groups.

Our second main aim of this study was to scrutinize the contribution of cognitive processes to age effects on tactile suppression. We manipulated cognitive demands during reaching by introducing an additional memory task. This load substantially boosted the magnitude of tactile suppression across both age groups. We propose that the additional task increased the weighting of predictive signals by withdrawing processing resources from sensory input. Our results add to previous evidence that tactile suppression is reduced when attention is directed to the stimulus location (van Hulle et al., 2013). Notably, age effects were not modulated by the additional cognitive load. This finding appears in conflict with the well-documented increase in dual task costs in older adults (Huxhold et al., 2006; Li & Lindenberger, 2002; Lindenberger, Marsiske, & Baltes, 2000). It appears rather unlikely that the absence of more pronounced dual task costs was due to insuffi-

cient task demands. Accuracy rates as well as individual maximal span measures suggested that the additional memory task was challenging for the older adults. We speculate that enhanced task demands overall magnify tactile suppression effects, but they do not specifically drive the age-related increase in suppression. If tactile suppression was merely a function of task demands, then age effects should have been more pronounced when the load was enhanced. A similar pattern has been reported for the impact of aging and memory resources on motor adaptation (Trewartha et al., 2014). While memory resources can be linked to performance in motor learning tasks, age effects are independent of the age-related memory decline. Thus, forward model function seems to be overall modulated by memory load, but aging specifically alters the balance between predictive and sensory signals.

The most pronounced age-related changes in cognition concern executive functions (Hasher & Zacks, 1988; West, 1996). Indeed, they might be crucial for the efficient balancing of predictive and sensory signals in the forward model. Some core resources include cognitive flexibility, task-switching abilities, allocation and shifting of attention, and inhibitory capacities. Our findings provide evidence for a strong link between executive resources, in particular, cognitive flexibility and task-switching ability, and the magnitude of tactile suppression. Lower performance in executive tasks was associated with more pronounced suppression across both age groups. Limited executive resources might contribute to an over-reliance on predictive signals. Given the pronounced age-related decline in executive functions, we suggest that they qualify as a plausible candidate resource that drives age effects on tactile suppression.

Neural changes during aging have been extensively studied, and it can be speculated how they relate to increased somatosensory suppression. Although the functional correlates of suppression are not completely understood, some key regions have been identified. They comprise subcortical regions, in particular, the cerebellum (Blakemore et al., 1998; Shadmehr & Krakauer, 2008; Synofzik, Lindner, & Thier, 2008) as well as cortical regions, including somatosensory areas of the parietal lobe (Parkinson et al., 2011; Shergill et al., 2013; Wolpert, Goodbody, & Husain, 1998), the supplementary motor area, the medial frontal cortex, and the prefrontal cortex (Haggard & Whitford, 2004). Aging is associated with widespread structural brain changes; however, volume loss is most pronounced in frontal areas (Raz et al., 2005; Sowell et al., 2003). These areas not only represent the main neural correlates of executive functions (Aron, 2008; Rushworth, Hadland, Paus, & Sipila, 2002), but also are a prominent part of the functional network for somatosensory suppression. In addition to regional gray matter changes, forward model function might be most critically challenged by connectivity changes during aging (Gunning-Dixon, Brickman, Cheng, & Alexopoulos, 2009; McWhinney, Tremblay, Chevalier, Lim, & Newman, 2016; Sala-Llonch, Bartrés-Faz, & Junqué, 2015; Sullivan & Pfefferbaum, 2006). Age-related decrease in connectivity shows a posterior–anterior gradient with the prefrontal white matter being particularly vulnerable to age-related functional decline. Indeed, Wolpe et al. (2016) provided evidence that the age-related increase in somatosensory suppression is associated with reduced connectivity in frontostriatal circuits. In addition, frontostriatal connectivity is crucially modulated by dopaminergic transmission (Jahanshahi et al., 2010), which is subject to age-specific decline (Kaasinen, 2000; Rinne, Lönnberg, & Marjamäki, 1990). These age-related changes in the dopamine system have not only been associated with impaired motor function, but also with cognitive deficits, specifically with declined executive functions, which are grounded in frontal brain regions (Bäckman et al., 2000; Klostermann, Braskie, Landau, O'Neil, & Jagust, 2012; Volkow et al., 1998). In summary, evidence suggests that age-related differences in tactile suppression are linked to frontal connectivity changes and that dopamine plays a major role in regulating the integration of sensorimotor predictions and sensory signals (compare also Wolpe et al., 2018).

Conclusions

Our findings provide evidence for age-related changes in forward model function and expand our understanding of individual differences in movement control. We corroborated stronger tactile suppression in older adults, indicating an increased reliance on sensorimotor predictions that can be observed across different perceptual paradigms. We were particularly interested in how cognitive processes, which are known to deteriorate during aging, modulate suppression effects. Although dual task demands overall triggered an increase in tactile suppression, they did not significantly contribute to the observed age effect. Thus, secondary cognitive task demands increase the weighting of predictive signals putatively by withdrawing processing resources from sensory input but do not specifically drive age-related changes. In contrast, we determined a strong association of suppression effects with individual executive functions so that they qualify for driving age differences in tactile suppression. Our findings highlight the role of executive functions for weighting predictive and sensory information during movement control (compare also Chang, Shibata, Andersen, Sasaki, & Watanabe, 2014;

Monge & Madden, 2016) and elaborate complex interactions between cognition and action. We conclude that the fine tuning of forward model function is subject to significant age effects that are linked to declining executive resources (compare with Vandevoorde & Orban de Xivry, 2018). It remains to be clarified whether increased reliance on predictions provides a beneficial adaptive mechanism, i.e., compensation for declining sensory capacities, or can also be detrimental to behavioral control because over-reliance on predictions might hamper plasticity.

Keywords: healthy aging, individual differences, sensory attenuation, movement control, executive functions

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Study 1b

Aging attenuates the memory advantage for unexpected objects in real-world scenes (under review)

Klever, L., Islam, J., Võ, M. L.-H., & Billino, J. (2023). Aging attenuates the memory advantage for unexpected objects in real-world scenes. *Heliyon (under review)*.

1 **Aging attenuates the memory advantage for unexpected objects in real-world scenes**

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1

17 **Abstract**

18 Across the adult lifespan memory processes are subject to pronounced changes. Prior

19 knowledge and expectations might critically shape functional differences; however,

20 corresponding findings have remained ambiguous so far. Here, we chose a tailored approach

21 to scrutinize how schema (in-)congruencies affect older and younger adults' memory for

22 objects embedded in real-world scenes, a scenario close to everyday life memory demands. A

23 sample of 23 older (18 – 38 years) and 23 younger adults (52 – 81 years) freely viewed 60

24 photographs of scenes in which target objects were included that were either congruent or

25 incongruent with the given context information. After a delay, recognition performance for

26 those objects was determined. In addition, recognized objects had to be matched to the scene

27 context in which they were previously presented. While we found schema violations

28 beneficial for object recognition across age groups, the advantage was significantly less

29 pronounced in older adults. We moreover observed an age-related congruency bias for

30 matching objects to their original scene context. Our findings support a critical role of

31 predictive processes for age-related memory differences and indicate enhanced weighting of

32 predictions with age. We suggest that recent predictive processing theories provide a

33 particularly useful framework to elaborate on age-related functional vulnerabilities as well as

34 stability.

35

36 **Keywords:** aging, prior knowledge, schema violations, object memory, scene perception

2

Introduction

We continuously accumulate knowledge about the world. From repeated experiences we learn that our environment follows compositional rules. For instance, objects underlie physical constraints (a toothbrush does not float in space) and are usually found within a certain context (a toothbrush belongs in the bathroom). By abstracting and storing these regularities as schemata, our brains can predict future encounters with similar environments and objects (Võ, 2021). This prior knowledge of scene structure is particularly useful for object identification, when searching for specific objects or guiding attention towards goal-relevant information (Bar, 2004; Henderson, 2017; Neider & Zelinsky, 2006). Schemata do not only support perception, but are also key for memory processes (Gilboa & Marlatte, 2017; Tse et al., 2007; van Kesteren et al., 2012). Given pronounced age-related changes in memory capacities, the functional role of schemata for age effects on object memory might be critical. However, so far studies have rarely addressed how prior knowledge and expectations affect older adults' memory for context-embedded objects.

While many cognitive functions, such as processing speed, memory capacities, and inhibitory control are subject to age-related decline, world knowledge remains stable or even improves (for review, Park & Reuter-Lorenz, 2009). An amplified impact of prior knowledge has been suggested to contribute to older adult's decline and stability in memory performance (Umanath & Marsh, 2014). Increased reliance on predictions could serve as a compensatory mechanism to optimize memory decisions. However, this advantage might fail and even turn to a disadvantage when predictions are violated and an overreliance on them becomes detrimental. Although our environment is generally predictable, deviations from expectations are essential for knowledge updating and adjusting behaviour appropriately (Press et al., 2020). A specific disadvantage for processing unexpected information would critically limit adaptivity to changing environments and affordances.

Corresponding studies have provided heterogenous findings. A memory advantage for objects that are congruent with schema-based expectations about a given scene has been shown when explicit instructions about the possible (in)congruency of objects were provided (Brod & Shing, 2019; Chen et al., 2022; Webb & Dennis, 2020). Overall similar object recognition performance was found across age groups, but the memory advantages for schema-congruent objects were more pronounced in older adults. The age-related benefit was observed in absolute recognition performance as well as in memory for object details.

69 Findings suggest an enhanced schema bias in older adults. While boosting recognition
70 performance, the overreliance on prior knowledge induces increased false alarm rates,
71 qualifying a putative age-specific advantage. In contrast to prioritized processing of schema-
72 congruent object information, memory studies that refrained from giving explicit instructions
73 about (in-)congruency yielded contrary results. Here, memory advantages for objects
74 incongruent with scene context were observed (Hess & Slaughter, 1990; Mäntylä &
75 Bäckman, 1992; Prull, 2015; Wynn et al., 2020). Overall object recognition performance was
76 consistently equivalent across age groups. However, age effects on the incongruency
77 advantage have remained ambiguous. While Hess and Slaughter (1990) reported a more
78 pronounced advantage in older adults using schematic line drawings of scenes, no age effects
79 (Qin et al., 2014) or even an opposite trend (Mäntylä & Bäckman, 1992; Prull, 2015; Wynn et
80 al., 2020) was suggested by studies focusing on objects embedded in real-world scenes.
81 Although the latter studies reported robust recognition advantages for incongruent objects,
82 older adults showed less elaborated memory representations of incongruent objects.

83 We here aimed to specifically focus on naturalistic scenarios in which memory for objects
84 might be required in everyday life. We particularly considered three criteria for the memory
85 task to be close to real-world affordances. First, we presented objects naturally embedded in
86 real-world scenes (cf., Brod & Shing, 2019; Chen et al., 2022; Hess & Slaughter, 1990; Webb
87 & Dennis, 2020). Photographs were supposed to ensure a standardized and controlled
88 presentation of scenes (cf., Mäntylä & Bäckman, 1992; Prull, 2015; Qin et al., 2014). Second,
89 we presented the scenes in a free-viewing paradigm without additional task, e.g., a search
90 task or an explicit object memory task (cf., Hess & Slaughter, 1990; Webb & Dennis, 2020;
91 Wynn et al., 2020). Tasks per se affect how context information in scenes is processed (see
92 Draschkow et al., 2014; Neider & Zelinsky, 2006) and might confound age effects (see
93 Neider & Kramer, 2011; Smith et al., 2021). Finally, we refrained from providing explicit
94 instructions on scene inconsistencies (cf., Brod & Shing, 2019; Chen et al., 2022; Webb &
95 Dennis, 2020), avoiding strategic processes that are especially vulnerable during ageing
96 (West, 1996). This tailored approach allows us to scrutinize how prior knowledge and
97 expectations shape age effects on object memory in real-world scenes.

4

98 **Methods**

99 *Participants*

100 A total of 23 older (11 males, age [years]: $M = 69.3$, $SD = 8.0$) and 23 younger adults (11

101 males, age [years]: $M = 26.8$, $SD = 6.1$) participated in this study. Older adults were part of

102 our local database and screened for cognitive impairment using the MoCA (Nasreddine et al.,

103 2005). Younger adults were recruited by calls for participation and matched in terms of

104 educational background and reported gender. Neurologic or psychiatric disorders were

105 screened out by self-report. Procedures and methods conformed to the Declaration of

106 Helsinki (World Medical Association, 2013) and the local ethics guidelines of the German

107 Association of Psychology that do not require a specific approval for behavioural studies.

108 *Setup*

109 Data was collected via an online platform (https://www.testable.org/). Participants carried out

110 the experiment using their own stationary computers. General instructions ensured

111 undisturbed, quite conditions and a fixed viewing distance from the screen. Stimulus size was

112 standardized by a calibration procedure.

113 *Stimuli*

114 We used indoor scenes photographs taken from the SCEGRAM database (Öhlschläger & Võ,

115 2017). They gave context information by six different room types (e.g., kitchen, bathroom).

116 Target objects were naturally embedded in these scenes and were either congruent or

117 incongruent with the given context (see Figure 1A for examples). Target objects without

118 scene context and distractor objects, taken from another database (Blechert et al., 2014), were

119 used for recognition. In addition, scenes without target objects were presented for matching

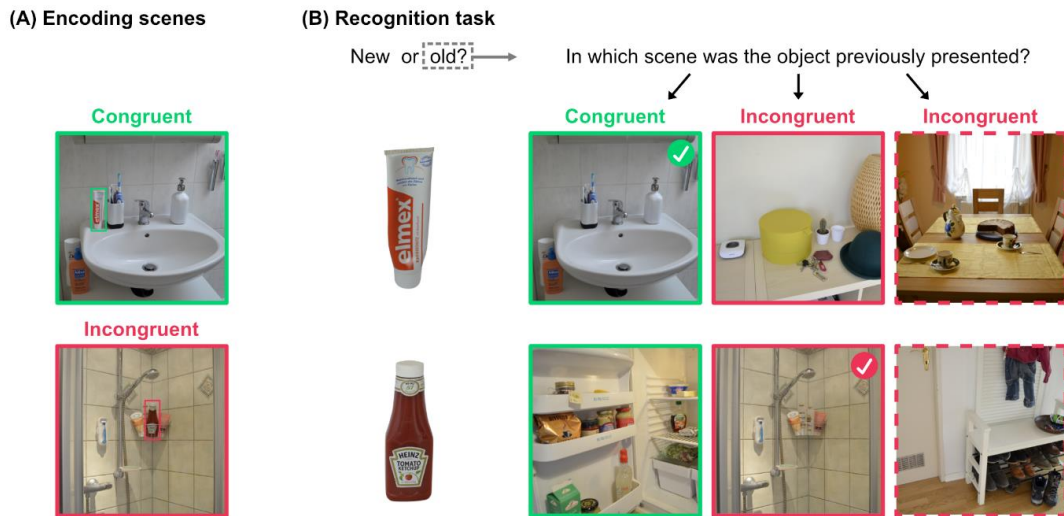120 recognized objects to their remembered context.

5

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Figure 1. Illustration of encoding and recognition procedures. (A) Scenes for encoding contained naturally embedded objects that were either congruent or incongruent with the given context. (B) Recognition procedure for a congruent target (upper row) and an incongruent target object (lower row). *Note*: Coloured frames and labels are here used for illustration and were not used in the actual procedures.

Procedure

Participants first freely viewed 60 scenes, of which half contained target objects congruent or incongruent with the context, respectively. Instructions called for memorizing the scenes in general and did not point to objects. The scenes were presented in randomized order, 3000 ms each with an ISI of 800 ms. Subsequently, participants filled out some unrelated questionnaires, introducing a delay of $M = 14 \pm 1$ min. Finally, participants were presented with the 60 target and 60 distractor objects after one another in randomized order. They had to label each object as *old* or *new*, i.e. whether they have seen it in the scenes or not. If labelled as *old*, objects had to be matched to the scene presented in previously. Three alternative scenes were offered, one scene giving a congruent, two scenes giving an incongruent context (see Figure 1B). Responses were entered via the keyboard. All participants were familiarized with the procedure by two preceding demonstration trials based on additional scenes and objects, not included in the main experiment.

Data analyses

Recognition performance was assessed in terms of the sensitivity d prime index (d'). To evaluate how well participants remembered the scene context of objects, we calculated the

6

143 proportion of scene selection errors relative to the overall number of correct decisions. Data

144 were analysed using mixed ANOVAs with the between-subject factor *age group* (older vs.

145 younger) and the within-subject factor *context* (congruent vs. incongruent). We assessed the

146 congruency bias during scene selection by the proportion of congruent selections relative to

147 the overall number of selection errors for incongruent target objects. Response times for *old*

148 and *new* decisions were explored using median values. Data were submitted to a two-factorial

149 ANOVA with the between-subject factor *age group* (older vs. younger) and the within-

150 subject factor *object type* (distractor, congruent, incongruent). If appropriate, main analyses

151 were followed by post hoc paired comparisons with Bonferroni-Holm correction.

152 Significance level was set to $\alpha = .05$ in all statistical analyses. If not stated otherwise,

153 descriptive values are given as means ± SEMs.

Results

Object memory

156 We first determined whether object memory systematically varies between the two context

157 conditions and two age groups (Figure 2). We submitted d' values to a two-factorial ANOVA

158 with *age group* as between-subjects factor and repeated measures on the factor *context*. The

159 analysis yielded significant main effects of *age group*, $F(1, 44) = 11.47$, $p = .001$, $\eta_p^2 = .21$,

160 and *context*, $F(1, 44) = 134.11$, $p < .001$, $\eta_p^2 = .75$. However, these main effects were

161 qualified by a significant interaction effect, $F(1, 44) = 13.43$, $p < .001$, $\eta_p^2 = .23$. Follow-up *t*-

162 tests showed that memory for objects encoded in an incongruent context was better than those

163 encoded in a congruent context both in older, $t(22) = 7.57$, $p < .01$, $d = 1.58$, and younger

164 adults ($t(22) = 7.57$, $p < .01$, $d = 1.58$, and $t(22) = 8.94$, $p < .01$, $d = 1.87$, respectively).

165 Notably, this memory advantage was less pronounced in older adults: While object memory

166 was comparable between both age groups in the congruent context condition, $t(44) = 0.87$, p

167 $= .388$, $d = 0.25$, older adults' memory performance was lower in the incongruent context

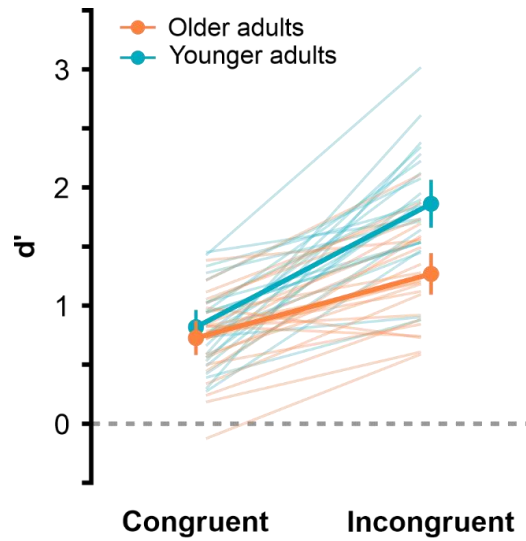168 condition, $t(44) = 4.32$, $p < .01$, $d = 1.28$.

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Figure 2. Effects of age group and encoding context, i.e., congruent and incongruent, on object

memory. Filled dots show the mean across observers and semi-transparent lines provide individual

data. Older adults are plotted in orange, younger adults in blue. Error bars give 95% confidence

intervals.

Scene memory

Participants' ability to remember the correct scene context of target objects was evaluated by

the error rates in matching correctly recognized objects to corresponding scenes (Figure 3).

We ran a two-factorial ANOVA with *age group* as between-subject factor and repeated

measures on the factor *context*. The main effects for *age group*, $F(1, 44) = 10.48$, $p = .002$,

$\eta_p^2 = .19$, and *context*, $F(1, 44) = 69.24$, $p < .001$, $\eta_p^2 = .61$, reached significance, but were

qualified by a significant interaction effect, $F(1, 44) = 9.12$, $p = .004$, $\eta_p^2 = .17$. Follow-up *t*-

tests indicated that older and younger adults made considerably more errors assigning

incongruent than congruent objects to the correct scenes ($t(22) = 6.95$, $p < .01$, $d = 1.45$, and

$t(22) = 4.59$, $p < .01$, $d = 0.96$, respectively). However, the increase in error rates was more

pronounced in older adults. Whereas error rates of both age groups did not differ for

congruent target objects, $t(44) = 0.25$, $p = .804$, $d = 0.07$, older adults were especially prone

to errors when assigning incongruent objects to their corresponding scenes, $t(44) = 3.99$, p
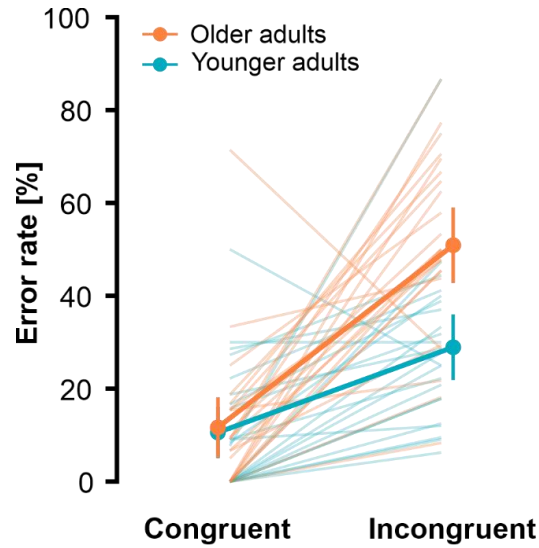
$< .01$, $d = 1.18$.

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188

189   *Figure 3*. Effects of age group and encoding context, i.e., congruent and incongruent, on error rates

190   during scene selection. Filled dots show the mean across observers and semi-transparent lines provide

191   individual data. Older adults are plotted in orange, younger adults in blue. Error bars give 95%

192   confidence intervals.

193   Exploration of scene selections for incongruent objects showed that older adults erroneously

194   favoured the congruent scene in 72% of the time, whereas younger adults showed a rate of

195   37%. These rates support a more pronounced congruency bias in older adults.

196   *Response times*

197   We analysed how response times in the object recognition task varied across age groups and

198   object types, i.e., distractor, congruent, and incongruent objects. Median response times were

199   submitted to a mixed ANOVA with the between-subject factor *age group* and the within-

200   subject factor *object type* (Figure 4). We determined a significant main effect for *age group*,

201   indicating age-related slowing, $F(1, 44) = 25.99$, $p < .001$, $\eta_p^2 = .37$. The main effect for

202   *object type* was also significant, $F(2, 88) = 10.45$, $p < .001$, $\eta_p^2 = .19$. There was no

203   interaction between both main effects, $F(2, 88) = 0.50$, $p = .607$, $\eta_p^2 = .01$, suggesting that

204   response times were similarly affected across age groups. The main effect of *object type* was

205   followed up by paired comparisons. Responses were faster for distractors than for congruent

206   objects, $t(45) = 4.54$, $p < .01$, $d = 0.67$, and incongruent objects, $t(45) = 3.50$, $p < .01$, $d =$

207   0.52), target objects. Response times for congruent and incongruent target objects did not

208   differ, $t(45) = 0.67$, $p = .502$, $d = 0.10$.

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Figure 4. Mean response times as a function of age group and object type, i.e., distractor, congruent, incongruent. Error bars correspond to 95% confidence intervals.
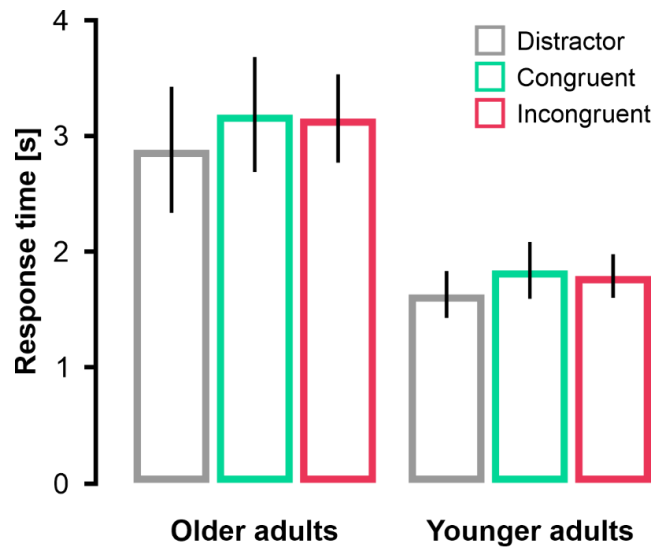
210 *Figure 4*. Mean response times as a function of age group and object type, i.e., distractor, congruent,

211 incongruent. Error bars correspond to 95% confidence intervals.

212 **Discussion**

213 Prior knowledge has been suggested to be a key factor in understanding older adults' memory

214 performance (Umanath & Marsh, 2014). However, it is not well understood how violations of

215 expectations affect memory for context-embedded objects – especially under naturalistic

216 viewing conditions. Object-scene inconsistencies challenge prior knowledge and provide

217 substantial informational gain which could aid memory (Greve et al., 2019). This benefit

218 might be attenuated in older adults. Using well-controlled photographs of real-world indoor

219 scenes containing object-scene (in)consistencies, we addressed the question whether

220 violations of scene context expectations affect memory for embedded objects differentially in

221 older and younger adults.

222 We found that schema violations are overall beneficial for object memory in older and

223 younger adults. As target objects were embedded in a rich, natural environment, we suggest

224 that object-scene relationships were automatically processed (Cornelissen & Võ, 2017; Evans

225 & Wolfe, 2022). This might have facilitated to observe robust memory benefits in older

226 adults. Associative demands, being especially challenging in old age (Naveh-Benjamin,

227 2000), were minimized. However, the incongruency advantage was less pronounced in the

228 older age group. Older adults' memory representations were substantially biased towards

229 congruent information. This was reflected in a greater number of schema-congruent errors

230 (see also Brod & Shing, 2019; Chen et al., 2022). A congruent congruency bias has been

231   observed for memory of object locations in scenes (Wynn et al., 2020), but here we showed

232   that it is of even broader relevance, affecting memory for the whole scene context. Analysis

233   of response times overall corroborated age-related slowing. Retrieval processes, though, were

234   similarly shaped in both age groups – with faster responses for distractors and no difference

235   for objects encoded in a congruent or incongruent context.

236   Our findings are consistent with recent models on how prior knowledge shapes perception

237   (Press et al., 2020). Information processing is supposed to be first biased towards prior

238   knowledge. But when an event is greatly unexpected, it elicits surprise, which, in turn, could

239   signal the necessity to update existing knowledge, leading to enhanced processing. Although

240   rooted in perception, this model may be applied to memory and is in principle compatible

241   with previous accounts (Greve et al., 2019; van Kesteren et al., 2012). Our data indicate that

242   older and younger adults weigh unexpected information differently, but we can only

243   speculate at which memory stages, i.e., encoding or retrieval, age-related differences emerge.

244   Given the crucial role of active vision for memory (Ryan & Shen, 2020), age-related

245   differences in encoding could explain why the memory advantage for incongruent objects is

246   attenuated in older adults. It is well documented that younger adults fixate incongruent

247   objects earlier, longer, and more frequently (e.g., Bonitz & Gordon, 2008; Loftus &

248   Mackworth, 1978), while processing of congruent objects is reduced (Spaak et al., 2022). We

249   suppose that this fixation pattern also holds for older adults, leading to an overall augmented

250   encoding of incongruent information. However, it might be less pronounced due to greater

251   viewing of congruent regions (Wynn et al., 2020) and possibly a reduced motivation for

252   exploring novel information (Düzel et al., 2010). Alternatively, retrieval processes might be

253   biased towards congruent information due to age-related vulnerabilities in critical functional

254   neural networks involving in particular the ventromedial prefrontal cortex and the medial

255   temporal lobes (Gilboa & Marlatte, 2017; van Kesteren et al., 2012).

256   Our findings provide novel insights into the role of expectations for object memory in

257   naturalistic scenarios and age-related vulnerabilities. We have shown that incongruent

258   context efficiently boosts object memory across the adult lifespan and that the principle

259   mechanisms are quite similar in older and younger adults. Schema violations can be

260   beneficial for stabilizing memory performance in older age. However, the advantage is

261   significantly attenuated and qualified by an overall congruency bias in older adults. We

262   suggest that our memory data reflects critical age-related changes that can be related to recent

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263 predictive processing theories (compare Press et al., 2020; Spaak et al., 2022). These have put

264 forward that functional efficiency of predictions crucially depends on the precision of the

265 information input. While high precision is supposed to go along with a particularly high

266 sensitivity to unexpected information, low precision is supposed to bias processing towards

267 predictions. Given reduced sensory precision with increasing age, it appears consistent that,

268 although violations of expectations remain a powerful way to enhance information

269 processing, this mechanism is weakened. At the same time, an increased bias towards

270 predictions, e.g., a more pronounced congruency bias, can be expected. To conclude,

271 predictive processing theories seem well suited to contribute to our understanding of age-

272 related functional changes and allow to consider vulnerabilities as well as stability within a

273 coherent framework.

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Study 2a:

Age-related differences in visual confidence are driven by individual differences in cognitive control capacities

Klever, L., Mamassian, P., & Billino, J. (2022). Age-related differences in visual confidence are driven by individual differences in cognitive control capacities. *Scientific Reports*, *12*(1), 1–13. https://doi.org/10.1038/s41598-022-09939-7.

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Age-related differences in visual confidence are driven by individual differences in cognitive control capacities

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Visual perception is not only shaped by sensitivity but also by confidence, i.e., the ability to estimate the accuracy of a visual decision. Younger observers have been reported to have access to a reliable measure of their own uncertainty when making visual decisions. This metacognitive ability might be challenged during ageing due to increasing sensory noise and decreasing cognitive control resources. We investigated age effects on visual confidence using a visual contrast discrimination task and a confidence forced-choice paradigm. Younger adults (19–38 years) showed significantly lower discrimination thresholds than older adults (60–78 years). To focus on confidence sensitivity above and beyond differences in discrimination performance, we estimated confidence efficiency that reflects the ability to distinguish good from bad perceptual decisions. Confidence efficiency was estimated by comparing thresholds obtained from all trials and trials that were judged with relatively higher confidence, respectively. In both age groups, high confidence judgments were associated with better visual performance, but confidence efficiency was reduced in older adults. However, we observed substantial variability across all participants. Controlling for age group, confidence effciency was closely linked to individual differences in cognitive control capacities. Our findings provide evidence for age-related differences in confidence efficiency that present a specific challenge to perceptual performance in old age. We propose that these differences are driven by cognitive control capacities, supporting their crucial role for metacognitive efficiency.

Human behaviour and its underlying neural mechanisms are mostly studied with a specific focus on a particular functional domain, e.g., perception, cognition, motivation, or motor functions. Although this approach has allowed detailed models and theories, complexity of behaviour can only be captured comprehensively when interactions across domains are also considered[1–3]. A particularly influential, well-investigated higher-level concept that shapes behaviour is metacognition. It refers to the ability to evaluate the quality and consequences of one's own thoughts and behaviours[4,5]. Metacognition has been widely studied in psychology during the last decade (for review, see[6]). There is consensus that it is key for optimizing performance by balancing actual outcome and subjective estimates of its quality. However, a better understanding of individual differences in metacognitive resources and their impact on behavioural performance is just beginning to emerge.

Individual differences are particularly pronounced in the ageing population, offering a unique window to possible variability in metacognitive efficiency. Ageing, from a behavioural perspective, can be understood as an umbrella term that incorporates gradually changing resources in all functional domains and at the same time adaptive mechanisms that can stabilize performance. Although the view of ageing as a process of deterioration and decline might still be prominent, understanding of age-related differences has gradually shifted towards a more complex characterization, including stability, decline, and compensation[7–9]. Metacognition could crucially contribute to optimizing performance in the face of age-related resource decline[10–13]. However, evidence so far has remained equivocal.

Since the prefrontal cortex has been consistently identified as a critical neural functional correlate of metacognition[14–16], vulnerabilities during ageing have been assumed. Prefrontal areas are subject to the most pronounced age-related volume loss[17,18]. In addition, consistent with the involvement of the prefrontal cortex,

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91

metacognition is considered to be closely related to higher-order cognitive processes, i.e., executive function[19,20]. Executive function is not unitary but involves a number of components that have been vividly debated over time[21,22]. There is however consensus on three functional core components, namely updating, shifting, and inhibition[23,24], that crucially fuel adaptive information processing and thereby efficient behavioral control. Age-related decline in executive function, indeed, is the most prominent facet of cognitive ageing[25–27]. Thus, clear predictions about age-related effects on metacognition can be derived, though it still seems a matter of debate how sensitive this functional capacity is to age.

The majority of studies that have investigated age-related differences in metacognition so far has focused on memory performance, so called metamemory[28]. Metamemory is typically assessed by subjective measures of how confident an individual feels about the quality of their own memory performance, e.g., by giving a prospective or retrospective judgement on a rating scale. Several studies have reported an increased mismatch between actual performance and the judgements on one's own abilities in older adults[29–36]. They tend to be overconfident about the quality of their memory performance. On the other hand, there are almost as many studies that have found only minor or even no age effects on the accuracy of metamemory[28,37–39]. Metacognition in other functional domains, e.g., problem solving, linguistics, perception, even seems to elude any age effects[28,40,41]. Heterogenous results might be due to the use of rating scales for assessing confidence. Ratings could confound individual biases to distribute judgements across the scale, so evaluation of metacognition sensitivity from ratings is challenging[42,43]. Moreover, confidence judgements in commonly used cognitive tasks are made on rather complex decisions involving multiple criteria that might generate additional biases hard to control.

Given these issues, the investigation of metacognition in perceptual tasks has attracted increasing consideration, establishing the term metaperception as a subtype of metacognition (for review, see[42]). Perceptual tasks qualify for a well-structured assessment of metacognition since they typically are characterized by simple decisions based on some sensory evidence, e.g., contrast or orientation discrimination. Metacognition in a perceptual task describes an observer's ability to monitor, evaluate, and control their own perception. Perceptual confidence provides a prototypical example for this ability. Perceptual decisions are accompanied by a subjective sense of (un)certainty, depending on the strength of sensory signals. Having access to a reliable measure of one's own uncertainty is a crucial aspect of perceptual confidence. Confidence about one's own decisions is fundamentally related to the accuracy of decisions (e.g.,[44], see also[45]). Observers will report high confidence when their perceptual decision is objectively correct, and low confidence when it is objectively incorrect. During ageing the quality of confidence judgements in perceptual tasks, i.e., how well they map the correctness of decisions, might be particularly challenged by pronounced age-related sensory decline due to peripheral vulnerabilities and increasing noise in neural representations[10,46–48] that hamper the evaluation of (un)certainty.

Only a single study so far has considered age effects on metacognition in a perceptual task. Palmer and colleagues[28] assessed metacognition in the memory as well as in the visual domain, studying a sample that covered the adult age range from early to late adulthood. Though providing first insights into age-related decline in metacognitive efficiency across functional domains, some conclusions appear unsettled because of several ambiguities in the results. Metacognitive efficiency did not decline consistently across perception and memory. While metacognition in the perceptual task decreased with age, only minor differences were found in the memory task. Given that evidence for domain-general versus domain-specific metacognitive systems remains controversial[49–52], the result might point to critical confounds inherent to the chosen tasks. In addition, the reported dissociation between metacognitive efficiency and executive function awaits scrutiny since the latter was assessed rather rudimentarily by a single measure, putatively not capturing capacities comprehensively.

We aimed to investigate how age affects metacognitive abilities in visual perception using a confidence forced-choice paradigm[42,53]. In this paradigm, observers are asked for two perceptual decisions sequentially, e.g., in our study on two contrast discrimination tasks, and then have to indicate about which of the two decisions the feel more confident. This method allows to assess perceptual performance precisely and to derive a bias-free measure of confidence, avoiding confounds that could emerge from confidence rating scales. Confidence measures in this paradigm are not affected by possible idiosyncratic confidence biases that have been reported in older adults[29,32]. It allows analyses based on the signal detection theory framework, controlling for differences in perceptual task performance. The procedure also provides the opportunity to analyse response times that change significantly during ageing and could affect the calibration of confidence judgements in perceptual tasks[54,55]. Furthermore, we considered executive function as a cognitive key capacity that might play a critical role for confidence efficiency. We hypothesized that older adults show decreased metacognitive abilities in perceptual tasks and that these age effects are crucially driven by individual differences in cognitive control capacities, i.e., executive function.

Methods

Participants. A total of 30 younger adults (18 females) and 30 older adults (17 females) participated in this study. The participants' age ranged from 19 to 38 years with a mean of 24.6 years ($SD = 4.4$) in the younger group and from 60 to 78 years with a mean of 68.8 years ($SD = 4.7$) in the older group. Recruitment of participants was managed by calls for participation at the University of Giessen and in local newspapers. Older adults reported slightly fewer years of school education than younger adults, 12.1 years ($SD = 1.5$) and 12.9 years ($SD = 0.5$), respectively. Higher academic degrees were completed by 66.7% of older adults. All younger adults either were currently enrolled in an academic program or had already completed a degree (43.3%). Our sample thereby is characterized by a bias towards higher educational levels when compared with the basic population. Higher educational attainment has been discussed to slow down age-related changes so that an underestimation of age-related differences in our given sample might be considered ([56], but see[57]). However, most importantly, educational background is comparable across both age groups, avoiding a potential confound with regard to the planned comparisons. Any history of ophthalmologic, neurologic, or psychiatric disorders as well as medica-

	Older adults ($n = 30$)		Younger adults ($n = 30$)	
	M (SD)	**Range**	**M (SD)**	**Range**
Age (years)	68.8 (4.7)	60–78	24.6 (4.4)	19–38
School education (years)	12.1 (1.5)	9–13	12.9 (0.5)	10–13
MoCA (raw score)	27.7 (1.6)	24–30	*n.a.*	*n.a.*
DSST (raw score)	60.2 (11.3)	42–99	82.3 (11.8)	59–106
TMT-B (s)	77.4 (23.0)	39.3–133.2	43.5 (13.2)	24.2–89.4
VST-C (s)	69.1 (42.2)	21.9–193.9	25.5 (5.4)	15.5–36.0
LPS-3 (raw score)	16.9 (3.4)	8–22	22.1 (3.5)	16–31
Digit span (max. backwards)	4.4 (0.9)	3–7	5.0 (1.0)	4–7

Table 1. Characteristics of participants and cognitive results. *MoCA* Montreal Cognitive Assessment, *DSST* Digit Symbol Substitution Test, WAIS-IV; *TMT-B*, Trail Making Test, part B, *VST-C* Victoria Stroop Test colour naming, *LPS-3* LPS intelligence scale, subtest 3, logical reasoning; *M*: mean; *SD*: standard deviation; *n.a.* not assessed; where applicable, comparisons between older and younger adults using *t*-tests yielded significant differences in the reported measures, all *p*'s ≤ 0.01.

tions presumed to interfere with visual functioning were screened out by a detailed interview protocol. Older adults were further screened with regard to visual acuity and mild cognitive impairment. We measured visual acuity binocularly using the Freiburg Visual Acuity Test[58] and confirmed normal or corrected-to-normal acuity, i.e., decimal acuity > 0.7. In addition, we applied the Montreal Cognitive Assessment Scale using a cut-off score of ≥ 23, excluding pathological cognitive decline[59–61]. Table 1 gives an overview of the main characteristics of participants. Methods and procedures were approved by the local ethics committee at Justus Liebig University Giessen and adhered to the principles of the Declaration of Helsinki[62]. All participants provided informed written consent prior to the experiment. Participants were compensated with course credits or money.

Assessment of individual differences in cognitive abilities. We characterized cognitive abilities of our participants using a battery of established measures that particularly allowed for evaluation of executive function (EF). Table 1 summarizes participants' performance in the different cognitive tasks. We aimed to assess EF comprehensively, considering key facets of cognitive control processes[23]. It is important to note that so far metacognition has not been linked to a specific candidate EF facet[19,20]. Thus, our assessment was tailored for covering the EF concept broadly and deriving a composite measure that provides a robust indicator of cognitive control capacities that are supposed to support efficient information processing. Critical single measures included: the Digit Symbol Substitution Test (DSST)[63], measuring updating ability; the Trail Making Test part B (TMT-B)[64], measuring shifting ability; the Victoria Stroop Test colour naming (VST-C)[65,66], measuring inhibition ability; the LPS-3[67], a subtest of a major German intelligence test battery, measuring nonverbal reasoning ability. In order to combine the single measures, we consistently scaled them so that higher scores indicated better cognitive control capacities. Then, for each participant a global EF score was derived by averaging the *z*-scores obtained for the individual measures. In addition, we assessed the maximal backward digit span[68] in order to evaluate short-term memory capacity that qualified as a possible confounding issue given the procedural details of our task procedures.

Setup and stimuli. Visual stimuli were presented on a calibrated 32-inch Display++ LCD monitor (Cambridge Research Systems, Rochester, UK) with a spatial resolution of 1920 × 1080 pixels and a refresh rate of 120 Hz noninterlaced. The setup was placed in a darkened room and participants were seated at a distance of 100 cm in front of the monitor, resulting in a display size of 41° × 23°. White and black pixels had a luminance of 112.7 and 0.1 cd/m^2, respectively, measured with a CS-2000 Spectroradiometer (Konica Minolta). Stimulus presentation was controlled by MATLAB using the Psychophysics toolbox[69,70]. A standard gamepad was used as input device (Microsoft SideWinder).

Stimuli were vertical Gabor patches displayed on an average grey background. Sinusoidal gratings had a spatial frequency of 0.8 cyc/° with randomized phase and the standard deviation of the Gaussian envelope was 1°. The contrast of the Gabor patches was sampled from seven different levels ranging from 13 to 31% in steps of 3%. The stimulus configuration consisted of two Gabor patches presented to the left and right of a central fixation dot at 4.2° eccentricity along the horizontal meridian. The fixation dot was black and had a diameter of 0.2°. One Gabor patch, i.e., the standard patch, had a fixed contrast of 22%, whereas the contrast of the other Gabor patch, i.e., the test patch, varied. Laterality of standard and test patches, respectively, was randomized.

Procedure. We assessed metacognitive abilities in visual perception using a confidence forced-choice paradigm[53,71,72]. Figure 1 depicts a typical trial.

Each trial consisted of two consecutive perceptual tasks, specifically contrast discrimination tasks, and a final confidence task. A fixation dot was shown for 500 ms, which was followed by two Gabor patches presented simultaneously for 180 ms. Then the display turned grey and participants decided whether the left or right patch appeared higher in contrast (first perceptual decision). Responses were entered with the respective index fingers using the trigger buttons on the back of the gamepad. Then, an equivalent second task followed, using different
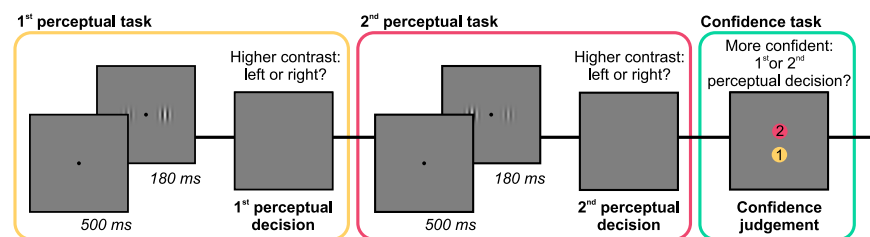
Figure 1. Trial procedure of the confidence forced-choice paradigm. Participants were presented with two consecutive perceptual tasks in which they had to decide which of two simultaneously presented Gabor patches appeared higher in contrast. After the second perceptual decision, they were asked for a confidence judgement, i.e. they had to indicate which of the two perceptual decisions they felt more confident about. Please note that colour is here used to illustrate the consecutive steps in each trial and was not used in the actual procedure.

patches and another contrast decision was made (second perceptual decision). Afterwards, participants indicated which of the two perceptual decisions they felt more confident about (confidence judgement). The response was given with the right thumb using two vertically aligned buttons on the top side of the gamepad. The buttons were mapped to the first or second perceptual decision, respectively. The mapping was visualized on the display and balanced across participants.

Before data collection, a detailed instruction protocol and sufficient practice trials secured that participants were familiar with the stimulus configuration, could comfortably follow the trial procedure, and handled the gamepad effortlessly. Subsequently, participants completed a total of 420 trials, subdivided into 6 blocks with 70 trials each. The number of trials was determined as a compromise between a sufficiently large number to properly estimate confidence and a session duration sufficiently short to reduce fatigue. Contrast levels of the test patches in the two consecutive contrast discrimination tasks were independently varied according to the method of constant stimuli, i.e., each of the 7 contrast levels was presented in 60 trials for the first and second contrast discrimination task, respectively.

Data analyses. Based on participants' confidence judgements, we divided perceptual decisions into two confidence sets: The first set included perceptual decisions that were chosen in the confidence task, i.e., they were associated with a relatively higher confidence, and this set was therefore labelled as *chosen*. The second set considered the ensemble of all perceptual decisions and was labelled as *unsorted*. We analysed perceptual performance for both sets by fitting cumulative Gaussian functions to the percentage of responses in which observers reported the contrast of the test patch as higher than the standard patch. The inverse standard deviation of these functions is a measure of contrast sensitivity. We used the psignifit 4 toolbox in Matlab that provides an accurate Bayesian estimation of psychometric functions and has been shown to be robust to overdispersion in measured data[73]. Goodness of fit of the psychometric functions was assessed with the measure of deviance D which supported good fits between the model and the data. Both sets showed similar Goodness of fit measures ($t(58) = 1.82$, $p = 0.074$, 95% CI [-0.117, 2.506], $d = 0.26$).

We quantified metacognitive efficiency, i.e., the relative sensitivity gain driven by confidence, calculating a confidence modulation index (CMI) according to Eq. (1). The CMI gives the sensitivity increase for the set of decisions chosen as confident relative to the set of unsorted decisions as a percentage of the sensitivity derived from the unsorted decisions.

$$CMI = 100 \times \frac{Sensitivity_{chosen} - Sensitivity_{unsorted}}{Sensitivity_{unsorted}} \tag{1}$$

An individual observer who derives their confidence judgements completely dissociated from their perceptual decisions will show a CMI close to zero. However, the closer the confidence judgement is linked to the actual accuracy of the perceptual decision, the higher the CMI will be, indicating better metacognitive sensitivity. Given that the CMI provides a proportional measure, values were arcsine-square-root transformed before they were submitted to statistical procedures. Inspecting the distribution of CMIs in our sample, we identified outlier data for one older participant. Their CMI deviated more than 1.5 times the interquartile range from the range borders of the complete sample. In order to enhance validity of our data and reduce unsystematic noise, we discarded this participant from our analyses.

Processing time measures for perceptual decisions were explored using median response times (RT). Response times below 100 ms and larger than 3000 ms were discarded because they were considered as anticipatory or delayed, respectively. The exclusion rate was less than 1% for each participant. Since perceptual decision times vary with stimulus intensity and confidence in a given task[54,55], we disentangled both parameters by using a model introduced in previous studies[74,75]. The model separates the effects of stimulus intensity and confidence on response times, allowing for a specific evaluation of both factors. We first normalized stimulus values for each individual considering their psychometric functions. We calculated the signed distances S between the 7 used stimulus intensities and the point of subjective equality in standard deviation units of the psychometric function. Chosen and unsorted confidence sets were considered separately. We then fitted an exponential model

94

with three free parameters to the median RTs for each of the 7 stimulus intensity levels. The model is defined by Eq. (2). $RT(S)$ gives the fitted RT for a normalized stimulus intensity level S. C gives the corresponding mean confidence across all included perceptual decisions. We encoded confidence with 1 for perceptual decisions that were selected in the confidence choice task and with 0 for perceptual decisions that were not chosen.

$$RT(S) = \alpha - \beta e^{-\frac{1}{2}S^2} - \gamma C \qquad (2)$$

The model yields three parameters, i.e., α, giving the generic RT, β, capturing the exponential change in RT due to differences in stimulus intensity, and γ, capturing the linear change in RT due to confidence.

Sensitivity and RT data were analysed by mixed ANOVAs with the within-subject factor *confidence set* (chosen vs. unsorted) and the between subject factor *age group* (older adults vs. younger adults). *T*-tests were used for age group comparisons of the CMI, cognitive measures, and RT parameters. If Levene's test indicated unequal variances, degrees of freedom were adjusted appropriately. Associations between CMI and critical parameters were investigated by correlational analyses. For group comparisons and correlational analyses, we computed 95% percentile confidence intervals using 2000 bootstrap samples. A significance level of α = 0.05 was applied for all statistical analyses and tests were two-sided. If not stated otherwise, descriptive values are given as means ± 1 SEM.

Results

We initially explored the overall response patterns of older and younger adults in the confidence forced-choice paradigm. Age effects on visual confidence were then analysed in detail by exploiting contrast sensitivity functions derived from the chosen und unsorted confidence sets, respectively. Differences in metacognitive efficiency were scrutinized considering the role of processing speed and executive functions.

Overview of response patterns.   Figure 2 illustrates confidence judgements for perceptual decisions at different task difficulty levels, i.e., different contrast differences between the standard and test Gabor patches. The separation of data for correct and incorrect decisions provides a rough overview of visual confidence in our paradigm.

In general, participants more often felt confident about their perceptual decisions when these were objectively correct than incorrect, indicating that they evaluated their performance appropriately. This difference in average confidence judgements for correct and incorrect decisions increased when task difficulty decreased. The data patterns hence support that our paradigm captured metacognitive abilities in visual perception in both age groups. However, Fig. 2 also suggests age-related differences since the separation of data for correct and incorrect decisions is clearly less pronounced in older adults.

A more detailed description of the confidence judgement patterns in older and younger adults is given in Fig. 3, showing all pairs of stimulus difficulties that were subjected to a confidence choice. For comparison, the figure also shows a simulated idealized observer that makes its confidence judgments as well as one would predict from the sensory noise that controls perceptual performance. Here, sensory noise was chosen as the average for the older adults. The probabilities of choosing the first perceptual task as more confident are shown separately for each task difficulty and each combination of perceptual decisions, respectively. The panel in the last column is an aggregate of all four possible pairs of perceptual decisions. Metacognitive abilities are reflected in each map by a pattern of probabilities that varies in two dimensions. Probabilities of choosing the first perceptual task should gradually increase with contrast difference values in the first perceptual decision. In parallel, they should gradually decrease with contrast difference values in the second perceptual decision. The simulated idealized observer pattern demonstrates that sensory noise in older adults and the chosen stimulus difficulties are suitable to expect an appropriate range of confidence judgements. It also provides a critical reference for evaluating the empirical patterns. Confidence probability maps for both age groups reflect metacognitive abilities in the perceptual task. However, the expected patterns are prominent in younger adults, whereas in older adults the gradient of probabilities is substantially blurred. Importantly, the aggregated patterns appear symmetric, anchored at minimal stimulus strengths, ruling out critical response biases due to task order.

In summary, the exploration of response patterns in the confidence forced-choice paradigm suggests that in both age groups participants appropriately derived confidence judgements on their perceptual decisions and thus demonstrated metacognitive abilities. However, evidence for age-related differences emerges and is followed up by quantifying how close confidence judgements are linked to perceptual decisions.

Psychometric analyses.   We were initially interested in determining whether contrast sensitivity varies between the two confidence sets, i.e., chosen and unsorted sets, and between the groups of older and younger adults. We consistently observed higher contrast sensitivity for the chosen confidence set than for the unsorted confidence set, a signature of metacognitive sensitivity. Figure 4 shows example psychometric functions of contrast discrimination for a representative older (a) and younger (b) adult, respectively. The functions derived from the two confidence sets differ in slope, indicating higher contrast sensitivity for the chosen confidence set. Points of subjective equality lie close to each other.

Analysis of pooled sensitivity data corroborated inspection of the example psychometric functions. Figure 5a illustrates contrast sensitivity we determined for each confidence set in both age groups. We submitted sensitivity data to a two-factorial ANOVA with *age group* as between-subjects factor and repeated measures on the factor *confidence set*. The analysis yielded significant main effects of *age group*, $F(1, 57) = 30.30$, $p < 0.001$, $\eta_p^2 = 0.35$, and *confidence set*, $F(1, 57) = 114.79$, $p < 0.001$, $\eta_p^2 = 0.67$. However, these main effects were qualified by a significant interaction between both factors, $F(1, 57) = 14.67$, $p < 0.001$, $\eta_p^2 = 0.21$. The interaction effect was followed up by
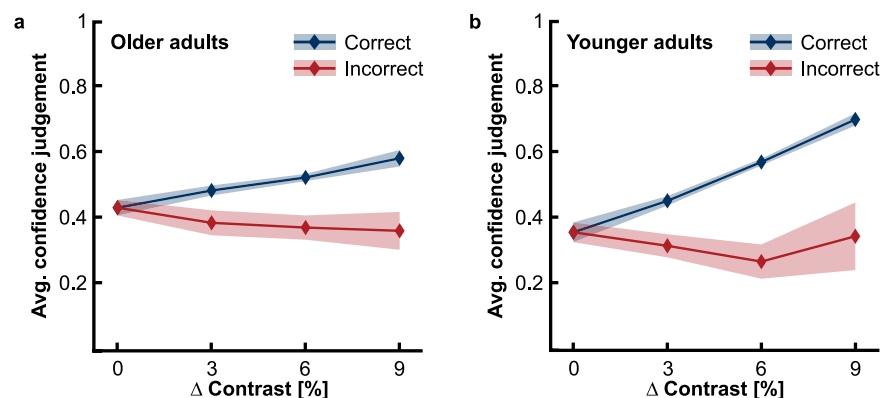
Figure 2. Average confidence judgements for perceptual decisions at different task difficulty levels, plotted separately for correct and incorrect decisions. (**a**) Data for older adults. (**b**) Data for younger adults. Task difficulty level is given as absolute contrast difference between the standard and test patches; task difficulty decreases with difference. Confidence judgements were coded as 1 for chosen and as 0 for not chosen. Please note that confidence judgements were made between two perceptual tasks in a trial. The probability of choosing a decision as confident depends on the difficulty of the other task. We collapsed confidence judgements across the different difficulties. The correctness label for perceptual decisions on patch pairs with zero contrast difference is arbitrary. Shaded areas give 95% confidence intervals.

t-tests. They corroborated lower sensitivities in older adults for both confidence sets (both p's < 0.001). Effect sizes were similar, i.e., $d = 1.39$ for the chosen and $d = 1.44$ for the unsorted confidence set. The sensitivity advantage for the chosen confidence set was significant for both age groups (both p's < 0.001); however, the difference was less pronounced in older adults, i.e., $d = 0.42$ vs. $d = 0.55$, respectively.

Figure 5b highlights these findings by giving a scatterplot of sensitivities for the unsorted confidence set against sensitivities for the chosen confidence set. Data for older and younger adults are illustrated in different colours. Whereas individual data points for younger adults lie exclusively above the diagonal identity line, those for older adults overall lie closer to and sometimes even marginally below it. Average values show not only lower sensitivities but also a smaller shift from the identity line in older adults. Confidence intervals suggest similar data precision in both age groups.

We further inspected whether the points of subjective equality (PSE) differ between the chosen and unsorted confidence sets. PSEs should logically lie close to zero, i.e., standard and test patches should be indistinguishable when there is no contrast difference. A shift of PSEs for the chosen confidence set could indicate that confidence judgements rely on a biased criterion and thus metacognitive efficiency is inherently limited. Comparisons of PSEs for the chosen and unsorted confidence sets yielded consistent results. For older as well as for younger adults the PSEs for the chosen and unsorted confidence sets did not deviate from each other (older adults: $t(28) = 0.06$, $p = 0.953$, $d < 0.01$; younger adults: $t(29) = -0.05$, $p = 0.960$, $d < 0.01$).

Confidence efficiency. In order to investigate individual differences in metacognitive efficiency, we analysed the sensitivity increase for the set of perceptual decisions chosen as confident relative to the set of unsorted decisions as a percentage of the sensitivity derived from the unsorted decisions, i.e., the CMI (see "Methods"). Figure 5c gives these confidence efficiencies. We initially used one-sample t-tests to evaluate whether CMIs differed from zero. Results supported positive CMIs in older adults, $t(28) = 8.21$, $p < 0.001$, $d = 1.52$, as well as in younger adults, $t(29) = 18.99$, $p < 0.001$, $d = 3.47$. Both age groups thus showed some ability to judge the validity of their perceptual decisions. However, on average, metacognitive sensitivity was significantly lower in older compared to younger adults, $t(45.34) = -2.51$, $p = 0.016$, $d = -0.66$. Whereas the link between confidence judgements and objective accuracy of perceptual decisions triggers a relative sensitivity benefit of over 30% in younger adults, $M = 31.21 \pm 1.64$, the benefit is limited to less than 25% in older adults, $M = 23.04 \pm 2.81$. Please note that we observed substantial variability of CMIs in our sample, especially pronounced in the group of older adults (Levene's test: $F = 4.87$, $p = 0.031$). We next aimed to scrutinize which functional capacities drive the described age effect.

We were particularly interested in the role of cognitive control capacities since their decline essentially characterizes cognitive ageing. We captured them by an EF score covering key facets. Figure 6a gives EF scores in both age groups. On average, older adults showed less cognitive control capacities than younger adults, $t(46.88) = -9.37$, $p < 0.001$, $d = -2.44$.

We investigated the link between confidence efficiency and cognitive control capacities considering our complete sample in order to comprehensively exploit interindividual variability. Figure 6b illustrates the link between the CMI and the EF score. We determined a robust correlation of $r(59) = 0.40$, $p = 0.001$, 95% CI [0.17, 0.57]. EF scores explained 16% of the variance in confidence efficiency. Depiction of age group membership for each data point suggests that this correlation is not merely driven by group differences but actually describes a general link. Consistently, a partial correlation analysis controlling for the factor age group, though attenuating the correlation,
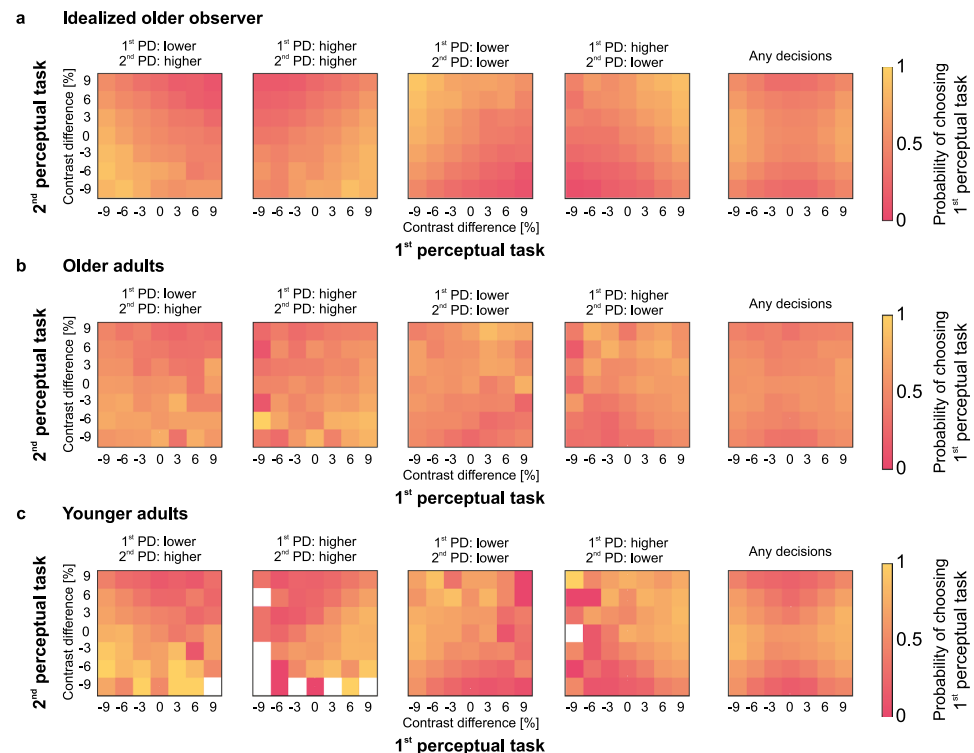
Figure 3. Descriptive illustration of metacognitive abilities in visual perception giving (**a**) an idealized older observer simulated to have a sensory noise equal to the average of the older adults, (**b**) older adults, and (**c**) younger adults. The first four plots in each panel show the probability of choosing the 1st perceptual decision (PD) as the most likely to be correct in the confidence judgement, i.e., associating it with relatively higher confidence, for each of the four possible combinations of perceptual decisions in the two consecutive contrast discrimination tasks. Decisions here apply to the test patches, i.e., code whether the test patches were indicated as lower or higher in contrast than the standard. The last plots on the right show the probability across all trials. The *x*- and *y*-axes give the contrast difference between the test patches and the standard patch in the first and second perceptual tasks, respectively. Metacognitive ability is indicated in these plots by a pattern of probabilities that dynamically depends on task difficulty, i.e., absolute contrast difference, and correctness of the perceptual decisions in both consecutive tasks. White cells in these plots represent the specific combination of consecutive perceptual decisions and stimulus strengths that did not occur in our data set.

yielded corresponding results, $r(56) = 0.26$, $p = 0.045$. 95% CI [− 0.01, 0.50]. Our findings thus indicate that age-related differences in metacognitive efficiency are crucially driven by cognitive control capacities.

Short-term memory capacity represents another resource that is subject to prominent age-related changes. Considering that the procedure of our paradigm putatively necessitates relevant memory resources, we wanted to check whether the age effect on confidence efficiency can be explained by a confound inherent to the task demands. The digit span measure we used to assess short-term memory capacity indicated significantly lower capacities in our older adult group, $t(57) = − 2.82$, $p = 0.007$, $d = − 0.58$. However, we found no evidence that the CMI is linked to individual differences in memory capacity, $r(59) = 0.12$, $p = 0.363$, 95% CI [− 0.17, 0.41]. Given this result, we consider it as rather unlikely that confidence efficiency had been compromised by task demands that might be more challenging for older adults with lower memory resources.

We finally explored whether age-related slowing could contribute to differences in metacognitive efficiency. Since confidence scales with response times, i.e., higher confidence is linked to faster responses, lower confidence to slower responses, the calibration of confidence judgements might critically rely on timing dynamics. Increased processing time might be detrimental to metacognitive efficiency. First, we analysed median RTs by a two-factorial ANOVA with *age group* as between-subjects factor and repeated measures on the factor *confidence set*. Figure 7a shows average RTs as a function of age group and confidence set.

We observed a significant main effect for *age group*, $F(1, 57) = 13.38$, $p = 0.001$, $\eta_p^2 = 0.19$, indicating slower RTs for older adults (chosen: $M = 561 \pm 30$ ms; unsorted: $M = 595 \pm 33$ ms) as opposed to younger adults (chosen: $M = 419 \pm 21$ ms; unsorted: $M = 457 \pm 23$ ms). In addition, a significant main effect of *confidence set* supported faster RTs for the chosen confidence set, $F(1, 57) = 88.17$, $p < 0.001$, $\eta_p^2 = 0.61$. There was no interaction between
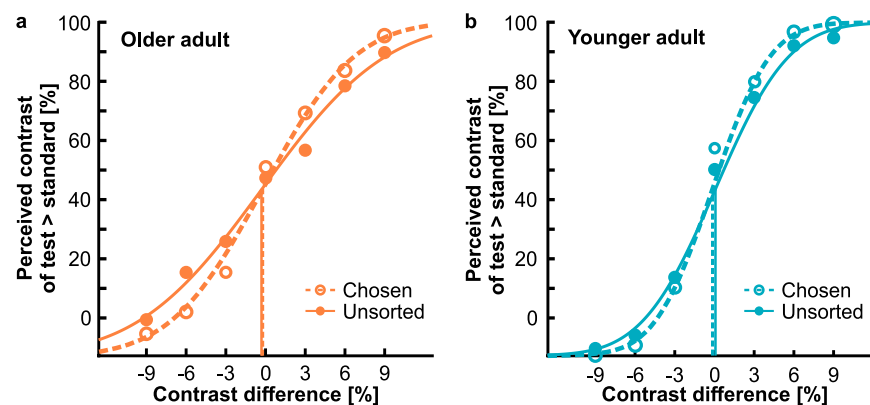
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Figure 4. Psychometric functions of contrast discrimination for (**a**) an example older adult and (**b**) an example younger adult. Proportion of decisions indicating higher contrast of the test patch compared to the standard patch is plotted as function of stimulus intensity given as the contrast difference between the test patch and the standard patch. Dashed lines and open dots represent data from the chosen confidence set, solid lines and closed dots represent data from the unsorted confidence set.
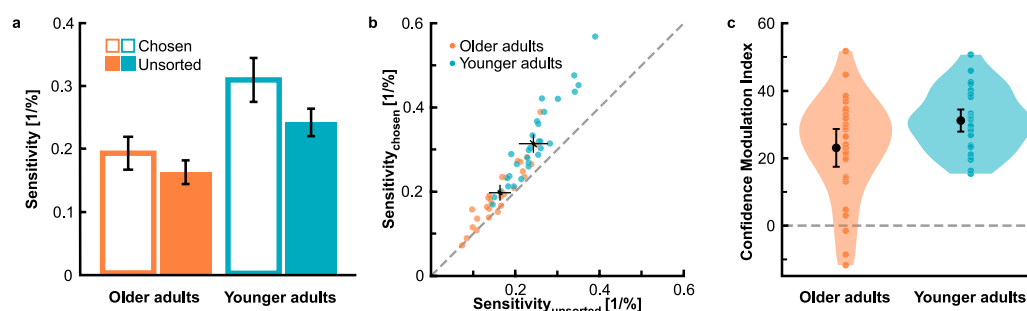

Figure 5. Contrast sensitivity and confidence. (**a**) Average contrast sensitivity as a function of age group and confidence set; open bars illustrate data from the chosen confidence set, closed bars represent data from the unsorted confidence set. (**b**) Contrast sensitivity for the chosen confidence set plotted against contrast sensitivity for the unsorted confidence set; each dot represents data from an individual participant, data for older and younger adults are plotted in different colours; dashed line marks the identity line; black closed dots give average sensitivities in each age group. (**c**) Confidence Modulation Index (CMI) as a function of age group; CMIs give the percental sensitivity increase from the set of unsorted trials to the set of chosen trials; coloured dots illustrate individual data and black dots represent the mean; shaded areas display 95% of the data distribution smoothed by a kernel density function. Error bars give 95% confidence intervals.

both main effects, $F(1, 57) = 0.32$, $p = 0.572$, $\eta_p^2 < 0.01$. The relationship between RTs and confidence was similar in both age groups.

Since RTs are not only affected by confidence but also by stimulus difficulty, we further clarified potential age-specific contributions. We disentangled both factors by modelling the RTs in each age group with three free parameters (see "Methods"). Fitting results are illustrated in Fig. 7b. Consistent with the previous analysis, the first parameter α, giving the generic RT, significantly differed between the two age groups (older adults: $M = 524 \pm 31$ ms; younger adults: $M = 438 \pm 25$), corroborating age-related slowing, $t(57) = 2.23$, $p = 0.030$, $d = 0.58$. For both parameters β and γ, giving the influence of stimulus intensity and confidence on RTs, respectively, we determined values that consistently differed from zero for older and younger adults (all p's < 0.001). RTs became slower with decreasing stimulus intensity, i.e., increasing difficulty, and faster with confidence. Most importantly, neither the parameter β nor the parameter γ differed between age groups (β: $t(33.17) = -0.43$, $p = 0.672$, $d = -0.11$; γ: $t(57) = -0.71$, $p = 0.483$, $d = -0.18$). These results corroborate that perceptual decision times underlie similar mechanisms in older and younger adults. Concluding, we directly tested whether the RT differences in the chosen relative to the unsorted confidence set were linked to confidence efficiency. Figure 7c gives the RT differences as a function of the CMI. Both parameters were not significantly correlated, $r(59) = 0.10$, $p = 0.450$, 95% CI [−0.18, 0.44]. Overall, RT analyses suggest that individual differences in metacognitive efficiency do not emerge from processing speed dynamics.
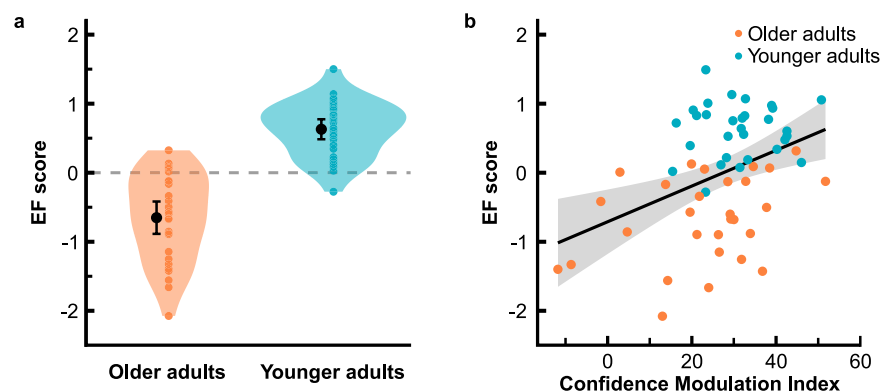
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Figure 6. Cognitive control capacities and metacognitive sensitivity. (**a**) EF score as a function of age group; EF scores provide a combined measure for cognitive control capacities averaging *z*-scores from DSST, TMT-B, VST-C, and LPS-3; coloured dots illustrate individual data and black dots represent the mean; shaded areas display 95% of the data distribution smoothed by a kernel density function. Error bars give 95% confidence intervals. (**b**) EF scores as a function of CMIs; data for older and younger adults are plotted in different colours; shaded area gives 95% confidence interval.
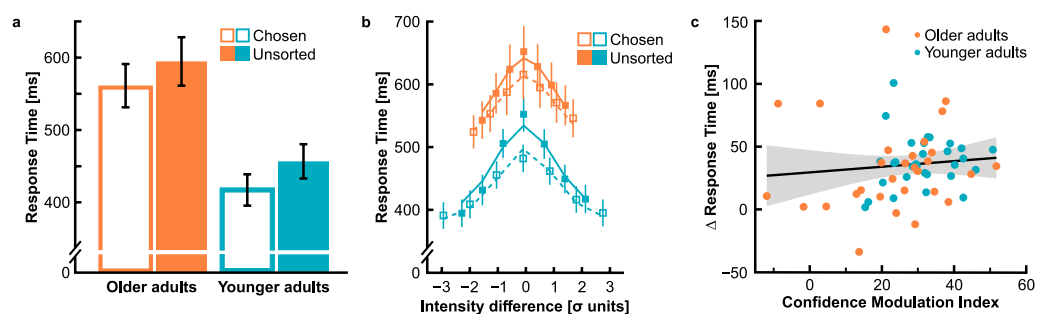

Figure 7. Response times (RT). (**a**) Average RTs as a function of age group and confidence set; open bars illustrate data from the chosen confidence set, closed bars represent data from the unsorted confidence set. (**b**) RTs for bins of stimulus intensities, i.e., contrast difference between test and standard patches, given in standard deviation units of the psychometric function (see "Methods"); symbols represent average group data, lines represent the average fitted data; dashed lines and open symbols represent data from the chosen trial set, solid lines and closed symbols represent data from the unsorted trial set; colour code for age groups corresponds to (**a**). (**c**) RT differences between the unsorted and the chosen confidence sets as a function of CMIs; data for older and younger adults are plotted in different colours. Error bars and shaded areas give 95% confidence intervals.

Discussion

Our perception relies on decisions about sensory evidence and the subjective confidence in the accuracy of these decisions. Visual perception is subject to pronounced age-related changes, however, the complexity of processes that contribute to these changes is still not well understood[7]. In this study, we were interested in age effects on visual confidence, i.e., the ability to evaluate the quality of one's own perceptual decisions. Given age-related vulnerabilities in neural and cognitive resources that have been shown to be critical for metacognition, we hypothesized that confidence efficiency decreases with age.

We investigated visual confidence in a sample of healthy older and younger adults with an established confidence forced-choice paradigm that avoids idiosyncratic judgement biases[71,72]. We characterized participants' executive function capacities using a comprehensive executive function (EF) score that covers the key facets of cognitive control. We were thus able to examine the role of individual differences in cognitive control resources for confidence efficiency. Our results show that older adults do have access to a reliable measure of their uncertainty underlying perceptual decisions. Confidence judgements were consistently linked to the accuracy of perceptual decisions in both age groups. However, the efficiency of this link significantly decreases with age. While confidence judgements explained a sensitivity benefit of over 30% in younger adults, this benefit was limited to less than 25% in older adults. Across our participants we observed substantial individual differences in confidence efficiency. We determined that 16% of the variance in confidence efficiency can be explained by individual cognitive control resources. Importantly, the critical impact of executive function was not exclusively

defined by age-related differences, but showed as a general functional link that drives individual differences in metacognition.

Our findings provide critical evidence for age-related differences in metacognition across the adult lifespan and expand our understanding on how it impacts visual perception. In the confidence forced-choice paradigm, we observed that older adults could selectively choose the interval that led to a higher performance in some cases. This indicates that they can evaluate the quality of their percepts. When compared to younger adults, though, this ability is reduced on average. Since our paradigm was tailored to minimize the impact of response and confidence biases that have been shown to vary with age[29,32], our results support original age effects on metacognition in a visual task. Congruently, the only previous study concerned with such effects reported reduced performance introspection with increasing age[28]. However, those findings remained ambiguous. Older adults showed lower awareness of their perceptual performance, but confidence was assessed by ratings scales which might make the evaluation of confidence sensitivity prone to confounding biases[42,43]. In addition, inconsistent results across different functional domains that emerged in the study await further clarification[49–52].

Our findings might be complicated by several factors that require careful consideration. Task difficulty might affect quality of confidence judgements. For our contrast discrimination task, we chose sinusoidal gratings with a spatial frequency of 0.8 cyc/° for which age differences in contrast sensitivity were expected to be negligible[76]. We yet found clear age effects on contrast discrimination thresholds, putatively triggered by relatively short presentation times[77,78]. Older adults showed higher thresholds and given that we used the method of constant stimuli for threshold measurement, higher task difficulty is implied for our group of older adults. Differences in task difficulty could, in turn, compromise confidence decisions[79]. Whereas rather difficult tasks compromise identification of high confidence trials, rather easy tasks compromise identification of low confidence trials. However, the fit of the psychometric functions suggested that the applied intensity range was well-suited to capture performance across age groups. There was no difference between the quality of fits in both age groups. Thus, we consider it as rather unlikely that probably unavoidable differences in task difficulty can explain the systematic age effects on the accuracy of confidence judgements. Furthermore, we ruled out that differential task difficulties emerging from short-term memory affordances explain age-related differences in visual confidence. Older and younger adults differed significantly in short-term memory resources, but we could not determine a relevant impact of this parameter on the efficiency measure derived from our paradigm.

It might be also speculated that differences in processing speed can contribute to age effects on visual confidence. The reduction of processing speed is probably the most pronounced and robust functional age difference[11,80]. Higher confidence in perceptual decisions is found to be associated with faster response times[74,75]. This link could basically rely on two mechanisms. First, observers might consider response times when forming their confidence judgements, deriving a higher confidence judgement from shorter response times. Although we assume that confidence judgements were primarily based on an appraisal of accuracy, response times were likely integrated to some degree. Secondly, the implicit experience of confidence at the time of the perceptual decisions might speed up responses. Since the detailed timing of processes that contribute to forming a confidence judgement eludes examination, both processes are difficult to distinguish. However, age-related slowing might critically interfere with both mechanisms and thus could be detrimental to metacognitive efficiency in older adults. As expected, we determined significantly prolonged response times in older adults compared to younger adults. However, and importantly, response times were similarly modulated by confidence in both age groups. We found that, independent of age, responses were speeded up for perceptual decisions that are judged with higher confidence. In sum, we thus corroborate previous results showing differences in response times as a function of confidence in younger adults[74,75] and extend these findings to older age. Individual differences in processing speed do not interfere with efficient confidence judgements. In contrast, response times are consistently shaped by the confidence in the accuracy of perceptual decisions.

A main focus of our study was on the link between executive function and visual confidence. Given the substantial conceptual overlap between metacognition, i.e., monitoring of decision quality, and executive function, i.e., cognitive control, a functional relationship suggests itself[4,23,44]. Both concepts have been shown to rely on shared neural resources, in particular in the prefrontal cortex[14–16,81,82]. Recent studies suggest that this functional overlap might specifically represent the signature of domain-general processes that characterize metacognition[82,83]. Ageing offers a powerful proxy to individual differences in executive function[11,18,25–27]. For example, critical age-related differences in error monitoring have been described, a capacity that can be plausibly linked to confidence judgements[84,85]. We captured individual cognitive control resources in a comprehensive score of executive function that was supposed to cover facets of the concept broadly[23]. Older adults on average showed lower EF scores than younger adults, consistent with established findings of age effects on executive function[11]. Thus, cognitive control resources could be identified as a plausible candidate driver of age-related differences in metacognitive efficiency. Most importantly, we were able to exploit the variability in EF scores across our older and younger participants to reveal a general functional link between cognitive control resources and visual confidence. Please note that the measures that contribute to our EF score exclusively rely on visual information processing. Although we cannot exclude that this congruency with our perceptual task might contribute to the reported link to some degree, we suggest that a significant impact is rather unlikely. Indeed, almost all established measures of executive function rely on visual information and are considered as indicative for cognitive control capacities across heterogenous tasks[24]. Our finding is in line with previous evidence suggesting that metacognition basically relies on cognitive control resources[33,86,87]. We are aware of conflicting results indicating that metacognition and cognitive control might be better understood as independent capacities[28,40]. However, we suggest that in some studies the functional links might be attenuated by executive function measures covering only specific facets of the concept. In addition, restriction of the range of individual differences in cognitive control resources due to very homogenous samples with regard to age and education can be assumed to obscure functional links.

100

Our study was dedicated to visual confidence; thus, we can only speculate whether our findings also hold for confidence in other perceptual domains and even more generally for other functional domains, in particular metamemory. Although behavioural evidence suggests some domain-specific contributions to metacognition[82], overall general, domain-independent mechanisms are proposed and supported by neuroimaging[50,82,83,87,88]. For confidence in perceptual tasks, findings consistently suggest similar mechanisms across different tasks and modalities[74,75,82]. Heterogeneity of results with regard to age effects on metamemory hampers systematic evaluations[31,33,35,38]. Inconsistent results might emerge in part from specific biases due to applied methods of measuring metacognitive parameters. In summary, we propose that our findings on age effects and the pivotal impact of cognitive control resources hold not only for visual confidence but also for confidence in other perceptual domains and more generally for other decision tasks.

To conclude, we showed that older adults have access to a reliable measure of their own uncertainty when making visual decisions. Metacognitive capacities are key for behavioural control. For instance, a reduced performance introspection could result in not being able to identify relevant aspects of a task and inefficient allocation of resources[89]. However, we found clear age-related differences in metacognition. Our results suggest reduced confidence efficiency in older adults. In principle, these age effects could be due to compromised reliability of judgements but also due to declining cognitive control resources[90]. Exploiting individual differences across our complete sample, we corroborated the crucial functional role of cognitive control resources for metacognition. We propose that age effects on visual confidence are primarily mediated by this functional link. This finding is in line with converging evidence that age-related changes in perception and sensorimotor control are critically driven by executive contributions to efficient resource control[91–94].

Data availability
Data are publicly available at the https://doi.org/10.5281/zenodo.5257748.

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101

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102

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Author contributions

All authors designed research; L.K. performed research; all authors analysed and interpreted data; all authors wrote the manuscript.

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Competing interests

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Additional information

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103

Study 2b:

Cross-modal metacognition: Visual and tactile confidence share a common scale (accepted)

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1 **Cross-modal metacognition: Visual and tactile confidence share a common scale**

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1

Abstract

Humans can judge the quality of their perceptual decisions – an ability known as perceptual confidence. Previous work suggested that confidence can be evaluated on an abstract scale that can be sensory modality-independent or even domain-general. However, evidence is still scarce on whether confidence judgments can be directly made across visual and tactile decisions. Here, we investigated in a sample of 56 adults whether visual and tactile confidence share a common scale by measuring visual contrast and vibrotactile discrimination thresholds in a confidence-forced choice paradigm. Confidence judgments were made about the correctness of the perceptual decision between two trials involving either the same or different modalities. To estimate confidence efficiency, we compared discrimination thresholds obtained from all trials to those from trials judged to be relatively more confident. We found evidence for metaperception since higher confidence was associated with better perceptual performance in both modalities. Importantly, participants were able to judge their confidence across modalities without any costs in metaperceptual sensitivity and only minor changes in response times compared to unimodal confidence judgments. In addition, we were able to predict cross-modal confidence well from unimodal judgments. In conclusion, our findings show that perceptual confidence is computed on an abstract scale and that it can assess the quality of our decisions across sensory modalities.

2

106

Introduction

We explore the world with multiple senses. What we perceive is the result of committing to
perceptual decisions that are derived from uncertain sensory information. Along with these
perceptual decisions usually comes a subjective, probabilistic estimate of how confident we
are that this decision is correct (Fleming, Dolan, & Frith, 2012) or self-consistent (Caziot &
Mamassian, 2021). Perceptual confidence refers to an observer's ability to evaluate, monitor
and control their own perception and has been established as one type of "metacognition"
(Fleming, Dolan, & Frith, 2012; Fleming & Lau, 2014; Mamassian, 2016). Typically,
subjective confidence judgments and objective perceptual performance are correlated –
irrespective of whether confidence judgments were made within the visual (Barthelmé &
Mamassian, 2010), tactile (Pierce & Jastrow, 1884), or auditory modality (Emmerich et al.,
1972). Perceptual confidence has been shown to be essential for behavioral decision making
(Desender et al., 2018), setting decision criteria (van den Berg et al., 2016), as well as
allocating appropriate resources (Aguilar-Lleyda et al., 2020). These functions become even
more relevant in noisy environments, in which it would be helpful to rely on cues from
different modalities. For instance, in everyday life, we could imagine that we want to cross a
road on a rainy and foggy day. But before actually doing it, we might rather look twice, check
whether we hear an engine or feel the ground vibrating. Considering our confidence in each of
these perceptual decisions may help us decide whether it is safe to cross the road or not.
However, this would require that confidence can be efficiently compared across modalities.

Over the last years, the question how confidence can be compared across perceptual tasks,
including different modalities, or even across functional domains, such as perception and
cognition, has gained increasing attention. In particular, the question whether one common
metacognitive mechanism monitors performance across different tasks or whether specific
mechanisms monitor individual tasks has been vividly debated (Mazancieux et al., 2020;
Morales et al., 2018; Rouault et al., 2018). Typically, both possibilities have been explored
using a correlational approach (Faivre et al., 2018; Mazancieux et al., 2020; Song et al.,
2011). Specific tasks are completed separately, followed by confidence judgments on a rating
scale. Generality and specificity of metacognitive mechanisms, respectively, is then evaluated
based on the shared variance in metacognitive performance, i.e., the capacity to estimate the
accuracy of task performance, that is observed across tasks. Only few studies have addressed
the question more directly by comparing confidence judgments not only within tasks but also
across tasks (e.g., Baer & Odic, 2020, de Gardelle et al., 2016, de Gardelle & Mamassian,
2014). Despite these different approaches, findings mainly point towards a common

68   metacognitive mechanism – at least within the perceptual domain. Studies investigating the

69   link between confidence judgments in cognitive and perceptual tasks have provided mixed

70   results (for a review, see Rouault et al., 2018).

71   Within the perceptual domain, it has been shown that observers can directly compare their

72   confidence across two different visual tasks (de Gardelle & Mamassian, 2014) as well as

73   across a visual and an auditive task (de Gardelle et al., 2016). As cross-modal confidence

74   judgments were possible without any costs in metacognitive sensitivity and only minor costs

75   in response times compared to unimodal confidence judgments, confidence seems to be

76   represented in an abstract, modality-independent format. In other words, confidence can be

77   estimated using a "common currency" across different perceptual decisions. This

78   interpretation is also supported by evidence from correlational approaches showing similar

79   metacognitive performance across visual, tactile, and auditory tasks (Faivre et al., 2018; Song

80   et al., 2011; Ais et al., 2016). Furthermore, a general representation of confidence has been

81   described already early in development, at least by the age of 6 years (Baer & Odic, 2020),

82   highlighting the need for a mechanism that enables the integration and comparison of

83   perceptual decisions.

84   At the neural level, metacognitive processes across tasks involve shared and distinct brain

85   regions, depending on the task at hand (Morales et al., 2018; Rouault et al., 2018), with

86   domain-general components relying on a network encompassing the prefrontal and cingulate

87   cortex (Fleming & Dolan, 2012; Fleming, Huijgen, & Dolan, 2012; Morales et al., 2018).

88   Given the involvement of the prefrontal cortex, metacognitive processes are thought to be

89   closely related to cognitive control operations (Fernandez-Duque et al., 2000; Fuster, 2000;

90   Klever et al., 2022; Roebers, 2017), supporting general mechanisms in metacognition (see

91   Rouault et al., 2022).

92   A common currency between the visual and tactile senses appears particularly useful as both

93   senses are closely tied to each other when performing actions. Although tactile confidence

94   was first investigated over 100 years ago (Pierce & Jastrow, 1884), our understanding of it –

95   especially in multisensory situations – still lags behind (Faivre et al., 2017). So far, a common

96   currency between the visual and tactile senses is only supported by one study finding a

97   moderate correlation between metacognitive ability in a vibrotactile and a contrast

98   discrimination task (Faivre et al., 2018). As these two perceptual tasks were performed

99   separately, potential effects of cross-modal interactions might be obscured. When asking

100   participants to directly compare their confidence across tasks, their ability to adequately judge

4

their confidence could be affected by favoring one modality over the other. Recently, it has been proposed that the tactile sense might provide higher subjective certainty than vision when faced with ambiguous evidence in an illusory setting – even when tactile decisions were less accurate (Fairhurst et al., 2018). In contrast, confidence was higher in vision than touch in unambiguous cases and seemed to optimally track objective accuracy. This selective overconfidence in the tactile sense could arise from an observer's belief that touch provides more directness (Deroy & Fairhurst, 2019). Both the visual and tactile senses are actively used to sample information on our surroundings (Findlay et al., 2003; Gibson, 1962). Given the direct proximity to the target, information obtained from the tactile sense could provide greater reassurance as it might make us feel we sampled this information more actively rather than passively (Deroy & Fairhurst, 2019). Critically, overconfidence in the tactile sense could challenge the idea of a common currency between visual and tactile senses. However, given its specificity to perceptual ambiguity, the findings by Fairhurst et al. (2018) might simply highlight the notion that confidence is best understood as a measure of self-consistency rather than correctness (Caziot & Mamassian, 2021). In other words, both visual and tactile perceptions might be inaccurate, but the tactile bias might be more consistent across repeated estimates. Interestingly, when Fairhurst et al. (2018) used a measure of subjective accuracy, i.e. an observer's internal response consistency, instead of objective accuracy, confidence seemed to optimally track subjective accuracy in both modalities.

Here, we investigated whether confidence serves as a common currency between the visual and tactile sense – two senses that closely interact and are especially relevant for the planning and execution of actions. Given this close interaction, we wanted to directly examine how well observers can compare their confidence across a visual and a tactile task. To this end, we applied the confidence forced-choice paradigm (Mamassian, 2020; Mamassian & de Gardelle, 2021), where participants performed two perceptual tasks in succession and then selected the perceptual decision that they think is more likely to be correct. If confidence was modality-specific, we would expect that confidence judgments across perceptual modalities are harder than within the same modality. Conversely, if it was modality-independent, confidence judgments should not be affected by whether the perceptual tasks involved the same or different modalities. As cross-modal confidence judgments might be costly in terms of processing time, we additionally considered potential differences in response times. Furthermore, we explored whether individual differences in cognitive control capacities are linked to confidence, which could point towards the involvement of further similar, i.e. domain-general, processes (Klever et al., 2022; Rouault et al., 2018).

Methods

Participants

A total of 56 participants (13 males) with a mean age of 24.1 years (*SD* = 5.8 years) took part in this study. Sample size was determined on the basis of previous studies using similar experimental procedures for measuring perceptual confidence across different tasks (cf., de Gardelle et al., 2016; de Gardelle & Mamassian, 2014). The experimental design required a minimum of 24 participants for counterbalancing the 4 different trial configurations (see Figure 1). A power calculation done with G*Power toolbox (Faul et al., 2007) indicated that a sample size of 48 participants allowed detection of moderate effects between different experimental conditions with a power of 92% and an α-level of .05. Since we expected, based on previous studies using similar perceptual measurements, that quality of some data sets might not allow for the planned analyses, our final sample comprised few additional participants.

All participants had normal or corrected-to-normal vision and no history of ophthalmologic, neurologic, or psychiatric disorders. We characterized individual cognitive control abilities for each participant using a battery of established tasks that covers key facets of executive functions (Diamond, 2013). These functions include *updating ability*, as measured with the Digit Symbol Substitution Test (Wechsler, 2008), *shifting ability*, as measured with Part B of the Trail Making Test (Kortte et al., 2002; Reitan & Wolfson, 1985), *inhibition ability*, as measured with the Victoria Stroop Test color naming (Mueller & Piper, 2014; Stroop, 1935), and *nonverbal reasoning ability*, as measured with subtest 3 of the LPS-2 (Kreuzpointner et al., 2013). To obtain a robust, composite measure of cognitive control capacities, we z-standardized the scores for each task and then averaged them for each participant. Given the nature of our metacognitive task, we additionally assessed the maximal backward digit span (Härting et al., 2000) to evaluate short-term memory capacity that could present a confounding issue.

Methods and procedures were approved by the local ethics committee of the Faculty of Psychology and Sports Science, Justus Liebig University Giessen, and were carried out in accordance with the guidelines of the Declaration of Helsinki (World Medical Association, 2013). Participants provided written informed consent prior to the experiment and were compensated with course credits or money.

6

Setup

Visual stimuli were presented on a calibrated 32″ Display++ LCD monitor (Cambridge

Research Systems, Rochester, UK) with a spatial resolution of 1920 x 1080 pixels and a

refresh rate of 120 Hz (non-interlaced) using the Psychophysics Toolbox (Brainard, 1997;

Kleiner, 2010) in Matlab (The Mathworks, Inc., Natick, MA, USA). The background was

average grey. Participants sat at a table in a darkened room with their head stabilized on a

chin rest. The eye-monitor distance was 100 cm, leading to a display size of $41° \times 23°$.

Luminance of white and black pixels was 112.7 and 0.1 cd/m², respectively, as measured with

a CS-2000 Spectroradiometer (Konica Minolta). Tactile stimuli were applied by custom-made

vibrotactile devices (Engineering Acoustics Inc., Casselberry, FL, USA). They were attached

on the tip of both index fingers using silicone finger sleeves. Participants comfortably rested

their hands shoulder-width apart on foam pads in front of them. Due to the setup for tactile

stimulation, manual response input was excluded. Thus, we used gaze positions as response

input. Eye positions were recorded using an SR Research Eyelink 1000 Desktop Mount

system (SR Research Ltd., Mississauga, Ontario, Canada).

Stimuli and procedure

Metacognitive performance was assessed in an established confidence forced-choice

paradigm (Mamassian, 2020; Mamassian & de Gardelle, 2021). The paradigm has been

proposed to derive a bias-free measure of confidence and avoids some confounds emerging

from confidence rating scales. The approach focuses on metacognitive sensitivity, i.e. an

observer's ability to adequately judge the quality of their perceptual decisions, rather than

confidence bias (Mamassian & de Gardelle, 2021). Figure 1A summarizes the configuration

of an individual trial. Each trial comprised two consecutive perceptual decision tasks and a

confidence task. The consecutive perceptual decision tasks could either tap the same

modality, i.e. visual-visual or tactile-tactile, or different modalities, i.e. visual-tactile or

tactile-visual. After accomplishing the perceptual tasks, participants indicated which of the

two perceptual decisions they felt more confident about. Two types of confidence judgments

can be distinguished: unimodal judgments, i.e., within the visual or tactile modality, and

cross-modal judgments, i.e. across the visual and tactile modalities. Based on the four possible

trial configurations, the experiment was divided into four separate blocks with 112 trials each,

resulting in a total of 448 trials. To minimize task switching costs, the trial configuration was

kept constant within each block. Block order was counterbalanced across participants. Prior to

each block, participants completed 14 training trials to familiarize themselves with the

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199   respective trial configuration. After each block, they had the opportunity to take a break.

200   Before data collection, we provided an introduction to our procedure. In particular,

201   participants practiced the single perceptual tasks and became acquainted with providing

202   responses via gaze. The visual and tactile tasks are described in the following.
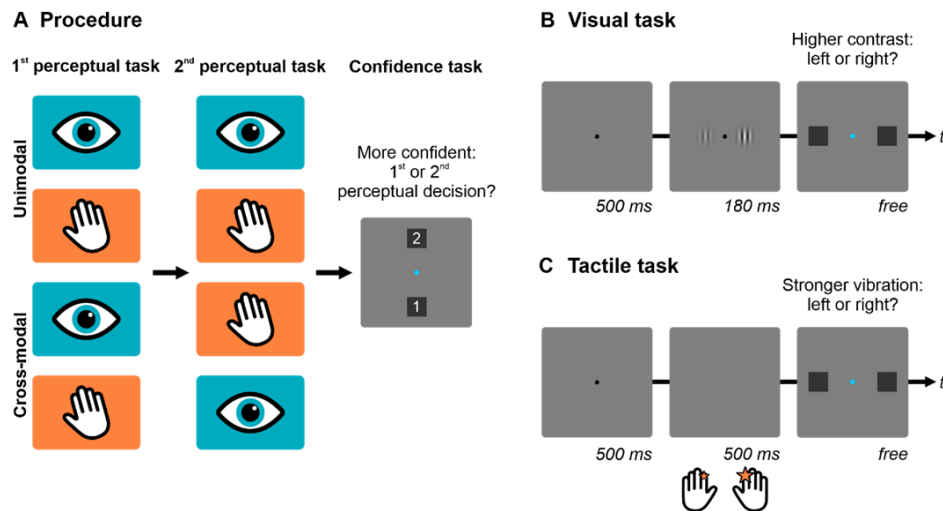
203   *Figure 1*. Procedure and subtasks of the confidence forced-choice paradigm. (A) Schematic
204   illustration of the overall trial procedure and the four different trial configurations.
205   Participants completed two perceptual tasks in succession (either visual-visual, tactile-tactile,
206   visual-tactile or tactile-visual) and then provided a forced-choice confidence judgment, i.e.
207   they indicated which of the two perceptual decisions (first or second) they felt more confident
208   being correct. (B) Visual task. Participants first saw a fixation dot, which was followed by the
209   simultaneous presentation of two Gabor patches. Then, they decided which of the two Gabor
210   patches appeared higher in contrast. (C) Tactile task. First, participants were presented with a
211   fixation dot. Then, they received two simultaneous vibrations on both index fingers and
212   decided afterwards on which finger the vibration felt stronger.

213   The visual task (Figure 1B) started with a 500 ms presentation of a central black fixation dot

214   that subtended 0.2°. Then, two vertical Gabor patches were simultaneously shown for 180 ms

215   on the left and right of the fixation dot at 4.2° eccentricity. All Gabor patches had a spatial

216   frequency of 0.8 cyc/°. The standard deviation of the Gaussian envelope was 1° and the phase

217   was randomized. Of these two Gabor patches, one always had a fixed contrast at 22%

218   (standard Gabor patch), while the contrast of the other Gabor patch was adapted throughout

219   the experiment (test Gabor patch). Laterality of standard and test Gabor patch was

220   randomized. Next, the fixation dot turned blue and two dark-grey response squares were

221   shown at 6.8° eccentricity left and right from the fixation dot. Participants' task was to decide

222   whether the left or right Gabor patch appeared higher in contrast by looking at the respective

8

223 response square. When a square was selected, it turned darker. Based on participants'

224 decision, the contrast for the test Gabor patch of the next trial was adapted by one of two

225 randomly interleaved 3-down/1-up staircases in steps of 3%: One staircase had a starting

226 value of 31% and aimed at responses favoring the test stimulus ~80% of the time; the other

227 had a starting value of 13% and aimed at responses favoring the standard stimulus ~80% of

228 the time. This procedure was based on the methods used in the visual-auditory confidence

229 study of de Gardelle and colleagues (2016). The interleaved double-staircase method allowed

230 for an overall stable performance level across the different task conditions and for minimizing

231 response biases (see also Cornsweet, 1962). In particular, with the interleaved procedure we

232 aimed to avoid systematic biases in confidence judgments due to unidirectional stimulus

233 intensity changes.

234 The tactile task (Figure 1C) began with the same fixation dot configuration as the visual task.

235 Then, participants received two simultaneous vibrations for 500 ms on both index fingers at a

236 frequency of 200 Hz. Of these two vibrations, one had a fixed intensity, defined as peak-to-

237 peak displacement, of 0.13 mm (standard vibration). The intensity of the other vibration (test

238 vibration) was adapted throughout the experiment. Again, laterality of standard and test

239 stimuli was randomized. When the horizontal response squares were shown, participants had

240 to decide whether the vibration on the left or right index finger felt stronger by looking at the

241 according square. Using similar staircases to the visual task with starting values of 0.08 mm

242 and 0.18 mm, respectively, the intensity for the test vibration of the next trial was adapted in

243 steps of 0.02 mm.

244 After the completion of two perceptual tasks, the confidence judgments were also given by

245 gaze. A blue central fixation dot and two dark-grey response squares were shown at 6.8°

246 eccentricity below and above the fixation dot. The response squares were numbered and

247 associated with the first or second perceptual decision. The mapping was visualized on the

248 screen and balanced across participants. By looking at one of the two squares, participants

249 indicated which perceptual decision (first or second) they felt more confident being correct.

250 *Data analyses*

251 Perceptual decisions were separated according to modality (visual or tactile) and comparison

252 type of the confidence judgment (unimodal or cross-modal), resulting in four conditions:

253 visual unimodal, visual cross-modal, tactile unimodal and tactile cross-modal. Based on

254 participants' confidence judgments, we divided perceptual decisions in each condition into

255 two confidence sets: The first set included perceptual decisions that were chosen in the

9

256   confidence task, i.e., they were associated with a relatively higher confidence. Accordingly,

257   we labelled this set as *chosen*. The second set comprised all perceptual decisions and was

258   labelled as *unsorted*. Please note that due to the design of the confidence forced-choice

259   paradigm the number of perceptual decisions chosen as confident is equal in both unimodal

260   conditions, i.e. visual and the tactile conditions. For the cross-modal conditions, the number

261   of chosen decisions for each modality can vary due to possible biases towards either the visual

262   or tactile modality, respectively. On average, we observed a marginal bias towards choosing

263   tactile decisions as more confident, favoring them in 53.7% of the judgments. Though

264   statistically significant, $t(55) = 2.30$, $p = .025$, $d = 0.31$, we considered the absolute imbalance

265   as minor, most importantly not complicating our further psychometric analyses.

266   We evaluated perceptual performance separately for each confidence set and condition by

267   fitting cumulative Gaussian functions to the percentage of responses in which observers

268   favored the test stimulus over the standard stimulus. The inverse standard deviation of the

269   fitted psychometric functions provides a measure of sensitivity. We used the Psignifit 4

270   toolbox in Matlab for the fitting process, as it yields an accurate estimation of psychometric

271   functions in a Bayesian framework even if the measured data is overdispersed (Schütt et al.,

272   2016). Goodness of fit of the psychometric functions was assessed with the measure of

273   deviance *D*, which supported good fits between the model and the data. By inspecting

274   boxplots for the derived sensitivity measures, we identified two participants who showed

275   visual or tactile sensitivities that deviated more than 1.5 times the interquartile range from the

276   range borders. We considered these measures as outlier data and discarded the participants

277   from further analyses to reduce unsystematic noise in our data.

278   To analyze metacognitive efficiency, i.e., the relative sensitivity gain driven by confidence,

279   we calculated a confidence modulation index (CMI) according to Equation 1. The CMI

280   quantifies metacognitive ability as the gain in sensitivity from the set of unsorted trials to the

281   set of chosen trials standardized by the sensitivity derived from the unsorted trials. Thus,

282   CMIs will increase with better metacognitive sensitivity. If an individual observer shows low

283   metacognitive sensitivity, CMIs will be close to zero. Importantly, as a unit-free proportional

284   measure, the CMI allows us to compare metacognitive sensitivity across both modalities.

285   CMIs were arcsine-square-root transformed for variance stabilization.

$$CMI = 100 \times \frac{Sensitivity_{chosen} - Sensitivity_{unsorted}}{Sensitivity_{unsorted}}$$

286   (1)

287 Processing measures for perceptual decisions as well as confidence judgments were explored

288 using median response times (RT). We excluded RTs below 150 ms and larger than 3000 ms

289 because they were considered as anticipatory or delayed, respectively. Please note that

290 perceptual and confidence response times were not measured equivalently, as perceptual

291 decisions were made via horizontal saccades and confidence judgments via vertical saccades.

292 Although reaction times for horizontal and vertical saccades, respectively, are generally found

293 similar, different underlying mechanisms might trigger systematic differences (Becker &

294 Jürgens, 1990, but see Dafoe et al., 2007). As perceptual decision times are influenced by

295 stimuli intensity and confidence (Baranski & Petrusic, 1994; Kiani et al., 2014), we separated

296 the effects of both parameters using a model that was successfully applied in previous studies

297 (de Gardelle et al., 2016; Klever et al., 2022). First, we normalized stimulus values for each

298 participant, confidence set, modality and comparison type. This was realized by calculating

299 the signed distances S between the stimulus intensities and the respective point of subjective

300 equality in standard deviation units of the psychometric function. Next, we divided the

301 normalized stimulus values into 5 bins and calculated the median response time as well as the

302 average confidence judgment C (encoded as 0 for unchosen and 1 for chosen perceptual

303 decisions) for each bin. Then, we fitted an exponential model with three free parameters (as

304 defined by Equation 2) to the median RTs, separately for each condition. The estimated

305 parameters are the following: α provides the baseline RT, β reflects the exponential change in

306 RT due to stimulus difficulty, and γ captures the linear decrease in RT due to confidence.

$$RT(S) = \alpha - \beta \times e^{-\frac{1}{2}S^2} - \gamma \times C$$

307 (2)

308 Perceptual sensitivities and RT were analyzed separately for each modality using repeated

309 measures ANOVAs with the within-subject factor *confidence set* (chosen vs. unsorted) and

310 the within-subject factor *comparison* (unimodal vs. cross-modal). To compare metacognitive

311 sensitivity across modalities, we submitted CMIs to a repeated measures ANOVA with the

312 within-subject factor *modality* (visual vs. tactile) and *comparison* (unimodal vs. cross-modal).

313 Two-sided *t*-tests were used to further analyze CMIs and RT parameters. In case of unequal

314 variances as indicated by Levene's test, degrees of freedom were adjusted. Associations

315 between CMIs and cognitive measures were scrutinized by correlational analyses. For all

316 statistical analyses, a significance level of α = .05 was applied. Descriptive values are reported

317 as means ± 1 SEM, unless stated otherwise.

11

Results

319   We initially explored response patterns across all combinations of modality (visual vs. tactile)

320   and comparison (unimodal vs. cross-modal). Then, we analyzed for each modality and

321   comparison how perceptual sensitivity functions were shaped by whether they were derived

322   from chosen or unsorted confidence sets, respectively. In a next step, we combined these data

323   in a confidence modulation index (CMI) and compared metacognitive efficiency across

324   modalities. Finally, we considered contributions of processing speed and cognitive resources

325   in the formation of confidence.

326   *Overview of response patterns*

327   A rough indicator of metacognition is given by differences in confidence with regard to

328   correct and incorrect trials. Typically, participants should report higher confidence when their

329   perceptual decision was objectively correct and lower confidence when their decision was

330   objectively incorrect. Figure 2 illustrates average confidence judgments for correct and

331   incorrect perceptual decisions at different normalized stimulus intensity levels.
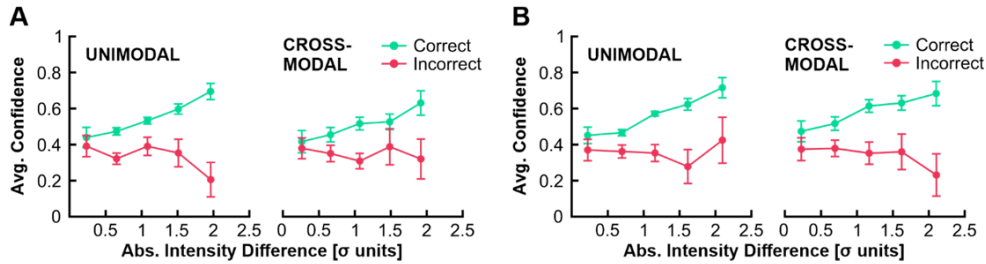
332   *Figure 2*. Average confidence judgments for correct (green) and incorrect (red) perceptual
333   decisions at different intensity levels in the visual task (A) and tactile task (B), separately for
334   the type of the comparison for the confidence judgments (unimodal vs. cross-modal).
335   Intensity levels are given as the absolute difference between stimulus intensities and each
336   participant's point of subjective equality in standard deviation units of the psychometric
337   function. They were then divided into five equi-distant bins of varying stimulus difficulty
338   with higher values indicating lower stimulus difficulty. Confidence judgments were coded as
339   1 for chosen and 0 for unchosen perceptual decisions. Please note that confidence judgments
340   were made between two perceptual decisions in a trial. The probability of choosing a decision
341   as confident depends on the difficulty of the decision in the other interval. We collapsed
342   confidence judgments across the different difficulties. Error bars provide 95% confidence
343   intervals.

344   The overall response patterns suggest that participants evaluated their perceptual performance

345   appropriately in all conditions. There were no prominent differences between unimodal and

346   cross-modal comparison conditions: Average confidence judgments were consistently higher

347   for correct than incorrect trials. Additionally, the difference in average confidence judgments

348   between correct and incorrect trials became more evident with decreasing stimulus difficulty.

349   *Psychometric analyses*

350   We were interested in determining whether sensitivities vary systematically between the

351   chosen and unsorted trial sets, as well as unimodal and cross-modal judgments. Figure 3

352   shows example psychometric functions for contrast discrimination (A) and vibrotactile

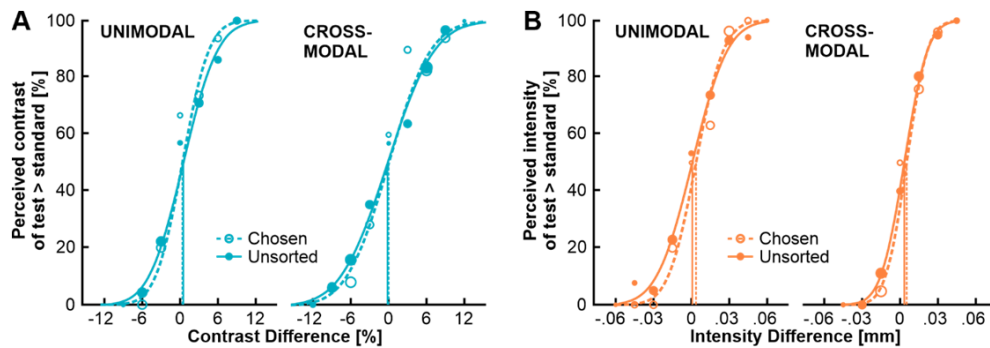353   intensity discrimination (B) for one representative participant.

354   *Figure 3.* Representative psychometric functions of contrast discrimination (A) and
355   vibrotactile intensity discrimination (B) for both unimodal and cross-modal comparison types.
356   The proportion of choosing the test stimulus over the standard stimulus is plotted as a function
357   of stimulus intensity. Stimulus intensity is given as the difference between the test and
358   standard stimulus, which is reported in percent for the visual task and peak-to-peak
359   displacement in millimetres for the tactile task. Dashed lines and open dots depict data from
360   the confident chosen trial set, solid lines and filled dots represent data from the unsorted trial
361   set.

362   As sensitivities cannot be compared across modalities, we submitted sensitivity data

363   separately for each modality to repeated measures ANOVAs with the within-subject factors

364   *confidence set* (unsorted vs. chosen) and *comparison* (unimodal vs. cross-modal). The

365   analysis yielded a strong main effect of *confidence set* for the visual task, $F(1,53) = 109.42$, p

366     $< .001$, $\eta_p^2 = .67$, as well as the tactile task, $F(1,53) = 172.25$, $p < .001$, $\eta_p^2 = .77$. Sensitivities

367   were consistently higher for the chosen confidence set in comparison to the unsorted

368   confidence set, indicating that participants were able to select the perceptual decision that is

369   more likely to be correct. Furthermore, there was a main effect of *comparison* for the visual

370   task, $F(1,53) = 4.65$, $p = .036$, $\eta_p^2 = .08$, but not for the tactile task, $F(1,53) = 0.03$, $p = .857$,

371     $\eta_p^2 < .01$. Visual sensitivity was overall higher when derived from perceptual decisions in the

372   unimodal as compared to the cross-modal condition, suggesting that contrast discrimination

13

373   was better when the task remained the same during one condition. The interaction between

374   *confidence set* and *comparison* did not reach significance in either modality, visual: $F(1,53) =$

375   0.01, $p = .947$, $\eta_p^2 < .01$, tactile: $F(1,53) = 1.20$, $p = .394$, $\eta_p^2 = .02$. The absence of an

376   interaction is particularly interesting as it suggests that participant's ability to select the

377   perceptual decision that is more likely to be correct was unaffected by whether they had to

378   choose between perceptual decisions from the same or different modalities. Figure 4

379   illustrates the effects of confidence set and comparison type on sensitivities separately for the

380   visual task (A) and tactile task (B).
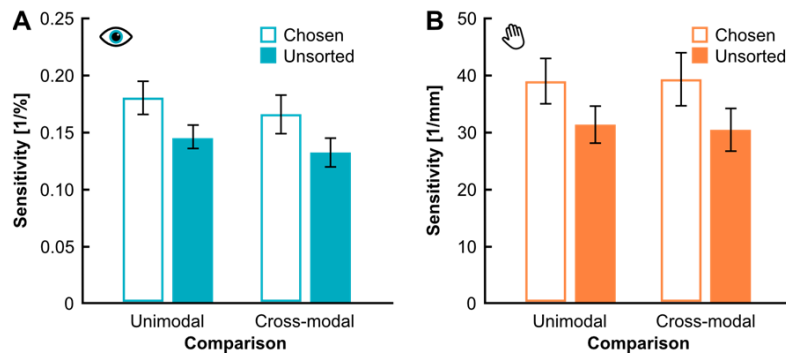
381 *Figure 4.* Average perceptual sensitivity as a function of confidence set and comparison type,
382 separately for the visual task (A) and tactile task (B). Open bars represent mean sensitivities
383 from the as confident chosen trial set, filled bars show mean sensitivities from the unsorted
384 trial set. Hatched bars represent the cross-modal conditions. Error bars indicate 95%
385 confidence intervals.

386 *Confidence efficiency*

387   As the measures of sensitivity do not allow for a direct comparison between the visual and

388   tactile tasks, we further analyzed effects of modality and comparison on confidence efficiency

389   with the help of a Confidence Modulation Index (CMI; see Methods). For the visual task, the

390   average CMI was 26.03 ± 2.11 in the unimodal condition and 28.90 ± 2.50 in the cross-modal

391   condition. For the tactile task, the average CMI was 28.96 ± 1.57 in the unimodal condition

392   and 31.90 ± 2.57 in the cross-modal condition. *T*-tests confirmed that CMIs were consistently

393   greater than zero in all conditions (all p's $< .001$). Figure 5 displays average CMIs for both

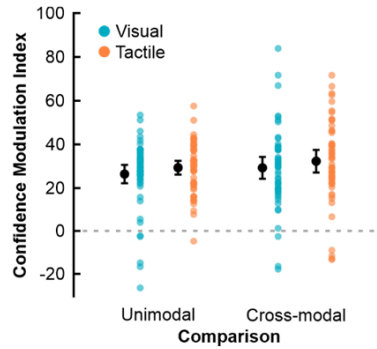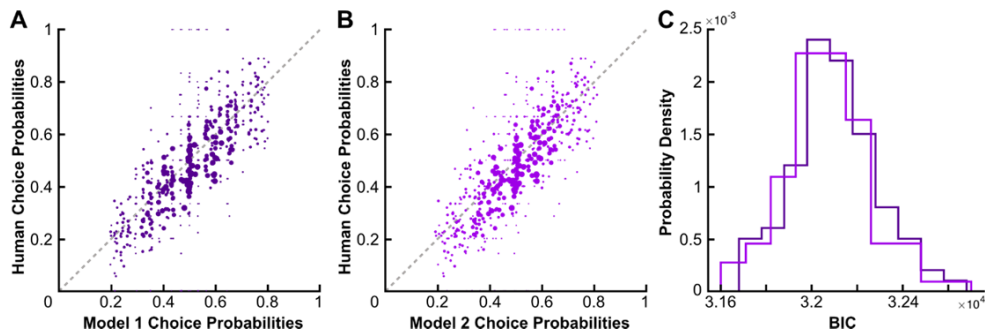394   modalities and types of comparison.

14

395 *Figure 5.* Confidence Modulation Index (CMI) as a function of modality (visual in blue vs.
396 tactile in orange) and comparison (unimodal vs. cross-modal). The CMI is a proportional
397 measure reflecting the change in sensitivity from the set of unsorted trials to the chosen trials
398 relative to the unsorted trials. Higher CMIs reflect higher metacognitive sensitivity. Colored
399 dots represent individual data points; black dots display the mean across observers with error
400 bars indicating 95% confidence intervals.

401 We submitted CMIs to a repeated measures ANOVA with the within-subject factors *modality*

402 (visual vs. tactile) and *comparison* (unimodal vs. cross-modal). There was no significant main

403 effect of *modality*, $F(1,53) = 2.28$, $p = .137$, $\eta_p^2 = .04$, or *comparison*, $F(1,53) = 2.50$, p

404 $= .120$, $\eta_p^2 = .05$, and no interaction between *modality* and *comparison*, $F(1,53) < 0.01$, p

405 $= .986$, $\eta_p^2 < .01$. Since the absence of any effects would be expected from the hypothesis that

406 confidence is stored in a modality-independent format, we calculated the corresponding Bayes

407 Factors (BF) to back up these results. Analyses of BF provided evidence that neither *modality*,

408 $BF_{10} = 0.42$, nor *comparison*, $BF_{10} = 0.41$, in isolation, nor their interaction, $BF_{10} = 0.19$, have

409 an effect on metacognitive efficiency.

410 The previous analysis used the CMI that is based on the global psychometric function (see

411 again Figure 3) where each stimulus strength presented in one interval is compared to all the

412 other stimulus strengths in the other intervals. We can also perform a finer analysis by trying

413 to fit the confidence choice probabilities between each stimulus strength across the two

414 intervals. The problem with this analysis is that it requires a large number of trials

415 (Mamassian & de Gardelle, 2021), so we decided to pool the trials across all participants after

416 transforming their perceptual data into standard scores (substracting the perceptual bias and

417 dividing by the sensory noise). The data were then grouped into 6 equal-sized bins and

418 submitted to a model of confidence forced-choice to fit the 576 confidence choice

419 probabilities (i.e. $(6_{visual} + 6_{tactile})\char`^2_{intervals} \times 4_{type1\text{-}responses}$) using the Matlab code package

420 provided in Mamassian & de Gardelle (2021).

Figure 6. Goodness of fits of two models of confidence choice probabilities. (A) Model 1 was
only fitted to the unimodal confidence comparisons but nonetheless predicted very well both
unimodal and cross-modal comparisons. There are 576 dots in this plot corresponding to all
the combinations of stimulus strengths in both intervals and all four possible perceptual
response categories. Dot size is proportional to the number of trials in the combination. (B)
Model 2 was fitted to both unimodal and cross-modal comparisons, and it also predicted very
well human data. (C) A comparison of the distributions of Bayesian Information Criteria
(BIC) for models 1 and 2 (in dark and light purple, respectively) obtained from 100 bootstraps
indicates that the two models did not differ in the quality of the fits.

We considered two models. In model 1, we only fitted the confidence choice probabilities for

the unimodal comparisons (visual-visual and tactile-tactile), but applied this model to all the

confidence choice probabilities (Figure 6A). In model 2, we fitted the confidence choice

probabilities for both unimodal and cross-modal comparisons (Figure 6B). Replicating the

previous analysis, we did not find any significant difference between metacognitive abilities

across the two tasks, namely confidence efficiency was 0.376 for the visual task (95% CI =

[0.309, 0.463], obtained from 100 bootstraps) and 0.365 for the tactile task (95% CI = [0.294,

0.427]). Importantly, there was no difference in the goodness of fits between models 1 and 2

as estimated by the BIC (Bayesian Information Criterion) measure (Figure 6C). A

Kolmogorov-Smirnov test indicates that the two models did not differ significantly in the

quality of the fits, $D(100) = .140$, $p = .261$. In other words, the cross-modal confidence

comparisons could be predicted very well from the unimodal comparisons, consistent with the

hypothesis that confidence is computed in a modality-independent format.

16

Response times

444 We were further interested in potential differences between the unimodal and cross-modal

445 conditions in terms of processing time and how they might contribute to the calibration of

446 confidence.

447 Perceptual response times were faster for visual decisions, $M = 586.36 \pm 21.20$, in comparison

448 to tactile decisions, $M = 702.18 \pm 19.67$, $t(53) = 6.29$, $p < .001$, $d = 0.86$. To analyze whether

449 perceptual response times vary systematically between the two confidence sets and the types

450 of confidence comparison, we submitted them separately for each modality to a repeated

451 measures ANOVA with the within-subject factors *confidence set* (unsorted vs. chosen) and

452 *comparison* (unimodal vs. cross-modal). We found a main effect of *confidence set* in the

453 visual task, $F(1,53) = 29.87$, $p < .001$, $\eta_p^2 = .36$, as well as the tactile task, $F(1,53) = 43.01$, p

454 $< .001$, $\eta_p^2 = .45$, indicating faster responses with higher confidence. Additionally, there was a

455 main effect of *comparison* in both modalities; visual: $F(1,53) = 74.79$, $p < .001$, $\eta_p^2 = .59$,

456 tactile: $F(1,53) = 6.71$, $p = .012$, $\eta_p^2 = .11$. However, the direction of the effect differed

457 between both modalities: In the visual task, responses were faster in the unimodal condition

458 relative to the cross-modal condition. Whereas in the tactile task, responses were slightly

459 faster in the cross-modal condition compared to the unimodal condition. There was no

460 interaction between *confidence set* and *comparison* in the visual task, $F(1,53) = 0.09$, p

461 $= .768$, $\eta_p^2 < .01$, or tactile task, $F(1,53) = 0.23$, $p = .633$, $\eta_p^2 < .01$. Figure 7 illustrates effects

462 of confidence set and comparison on median response times separately for each modality.
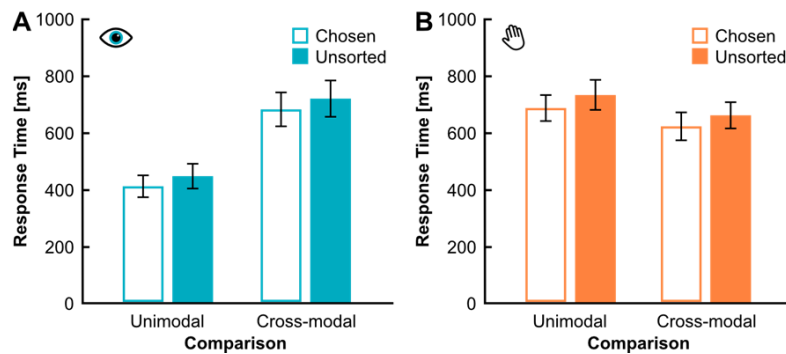
463 *Figure 7.* Median response times as a function of confidence set (chosen vs. unsorted) and
464 comparison (unimodal vs. cross-modal) for the visual task (A) and tactile task (B). Bars show
465 the mean across observers in each condition with open bars representing the chosen trial set
466 and filled bars the unsorted trial set. Hatched bars represent the cross-modal conditions. Error
467 bars indicate 95% confidence intervals.

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468 However, as response times are not only affected by confidence but vary critically with

469 stimulus difficulty, we modeled the relationship between stimulus difficulty, confidence and

470 response times (see Methods for details). Figure 8 illustrates the fitting results for each

471 modality and type of comparison. The control analysis yielded three parameters, but only α

472 (the generic RT) and γ (the confidence effect) are of primary interest. Both parameters were

473 analyzed using repeated measures ANOVAs and t-tests. In line with the previous analysis, the

474 parameter α exhibited a significant main effect of modality, $F(1,53) = 62.04$, $p < .001$, $\eta_p^2 =$

475 .54, corroborating that responses were faster for visual decisions compared to tactile

476 decisions. Interestingly, there was also a significant main effect of *comparison*, $F(1,53) =$

477 9.34, $p = .004$, $\eta_p^2 = .15$, indicating slower responses in cross-modal blocks compared to

478 unimodal blocks, and no interaction, $F(1,53) = 0.01$, $p = .929$, $\eta_p^2 < .01$. In contrast to the

479 previous analysis, γ (confidence effect) did not differ significantly from zero in all conditions

480 (all p's > .289, all d's < 0.15), except for the visual cross-modal condition, $t(53) = 2.30$, $p =$

481 .025, $d = 0.31$. However, an ANOVA suggests that γ was unaffected by *modality*, $F(1,53) =$

482 0.22, $p = .644$, $\eta_p^2 < .01$, *comparison*, $F(1,53) = 0.61$, $p = .438$, $\eta_p^2 = .01$, or their interaction,

483 $F(1,53) = 0.97$, $p = .330$, $\eta_p^2 = .02$. Thus, the speed-up of RTs with confidence found in the
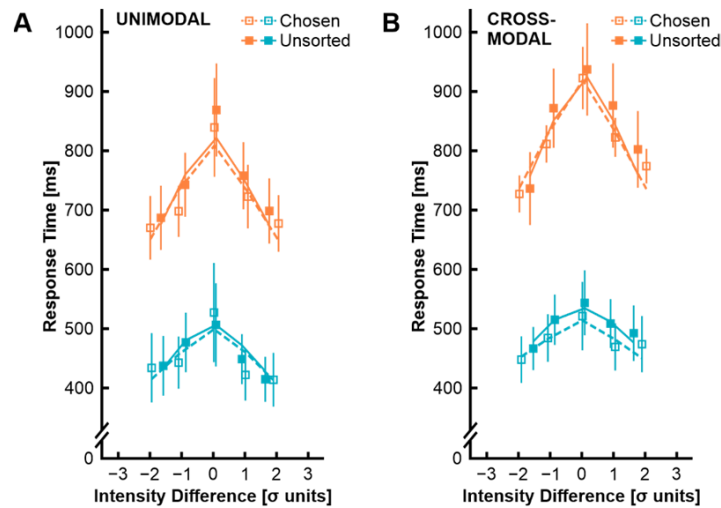
484 previous analysis can be attributed to variations in stimulus difficulty.

485 *Figure 8.* Additional analysis controlling for the effect of stimulus difficulty on response
486 times. Median response times for five equal-distant bins of stimulus intensities (in standard
487 deviation units of the psychometric function) separately for the unimodal (A) and cross-modal
488 (B) condition. Data from the tactile task is shown in orange, the visual task in blue. Open
489 squares (chosen trial set) and filled squares (unsorted trial set) depict mean response times
490 across observers with error bars showing 95% confidence intervals. Dashed lines (chosen trial

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491 set) and solid lines (unsorted trial set) show the average response time in each bin as predicted
492 by our RT model.

493 Response times for the confidence judgments were slightly faster in the cross-modal

494 conditions, $M = 527.91 \pm 66.02$ ms, as compared to the unimodal conditions, $M = 594.63 \pm$

495 68.39 ms, $t(53) = 2.24$, $p = .03$, $d = 0.30$.

496 *Cognitive resources and confidence efficiency*

497 Since we observed substantial variability in confidence efficiency – especially in the cross-

498 modal conditions (see Fig. 5) – we were interested in exploring the role of individual

499 differences in cognitive control resources that could drive this variability. Correlational

500 analyses yielded no evidence for a link between CMIs and EF scores in our data, irrespective

501 of modality and comparison condition (all p's > .19).

502 Given that the procedure of the confidence forced-choice paradigm might draw on memory

503 resources, we additionally aimed to rule out that CMIs were compromised by these task

504 demands. We explored the association between individual differences in short-term memory

505 capacity and CMIs, but we found consistently across both modalities and comparison

506 conditions no significant correlations (all p's > .36).

507 **Discussion**

508 In this study, we investigated whether confidence serves as a common currency across the

509 visual and tactile senses. A common currency would suggest that confidence for different

510 perceptual decisions is stored in an abstract, modality-independent format, allowing for quick

511 and efficient confidence judgments across different tasks (de Gardelle et al., 2016; de

512 Gardelle & Mamassian, 2014). Findings from a correlational study suggested that visual and

513 tactile confidence underlie a common mechanism (Faivre et al., 2018). However, this idea has

514 not been directly tested, yet. When visual and tactile information compete, an observer's

515 belief that the tactile sense provides more certainty and directness could compromise cross-

516 modal confidence judgments (Deroy & Fairhurst, 2019; Fairhurst et al., 2018). Using the

517 established confidence forced-choice paradigm (Mamassian, 2020; Mamassian & de Gardelle,

518 2021), we investigated visual and tactile confidence within and across modalities.

519 Additionally, we characterized participants' individual cognitive control capacities by a

520 comprehensive score that captures key facets of executive function (Miyake & Friedman,

521 2012). We considered differences in processing dynamics (Baranski & Petrusic, 1994; Kiani

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522 et al., 2014) as well as cognitive control capacities (Klever et al., 2022) that might contribute
523 to metacognitive performance.

524 Our findings provide evidence for a common currency between the visual and tactile senses.
525 We found that participants were able to evaluate the quality of their perceptual decisions
526 within and across modalities appropriately, i.e. subjective confidence judgments and objective
527 perceptual performance were related. Confidence was lower when perceptual decisions were
528 incorrect and higher when they were correct. The efficiency of this link was comparable
529 across modalities and, importantly, not compromised when confidence comparisons were
530 made across modalities. We thereby extend previous research showing that observers can
531 judge their confidence across different visual tasks (de Gardelle & Mamassian, 2014) as well
532 as visual and auditory tasks (de Gardelle et al., 2016) without any loss in metacognitive ability
533 relative to judgments within the same task. While previous research found that auditory
534 confidence was lower than visual confidence (de Gardelle et al., 2016), our results indicate
535 that visual and tactile confidence are comparable. Visual and tactile confidence might lie
536 closer together since both senses are actively used to sample information on our surroundings
537 (Findlay et al., 2003; Gibson, 1962), making them relatively more important in everyday life.
538 As confidence and behavior are tightly connected (Desender et al., 2018), good confidence
539 calibration for visual and tactile decisions might be particularly relevant for action control. In
540 line with this action-based account would also be the involvement of higher-level action-
541 specific components in confidence representation (Fleming et al., 2015).

542 We observed a small, but significant bias towards the tactile modality when participants were
543 asked to provide their confidence judgments in the cross-modal blocks (53.7%). This finding
544 seems congruent with previous reports of an overconfidence in the tactile sense (cf. Fairhurst
545 et al., 2018). Tactile overconfidence could be attributed to the belief that touch provides more
546 directness and certainty (Deroy & Fairhurst, 2019). In an informal survey after completion of
547 the experiment, most of our participants (48%) indicated that they had overall felt more
548 confident about their tactile decisions, even though performance had been controlled by a
549 staircase procedure. In contrast, higher confidence about visual decisions or no confidence
550 differences at all were each reported by only 14 participants (26%). Interestingly, an overall
551 tactile confidence bias, i.e., whether a participant reported a higher confidence about tactile
552 decisions or not, was significantly linked to the observed tactile bias in confidence judgments
553 in the cross-modal blocks ($r(54) = .377$, $p < .01$). It remains ambiguous whether participants
554 just provided a valid summary of their confidence judgments during the experiment or
555 whether a general confidence bias towards the tactile sense fueled confidence judgments in

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556 the cross-modal blocks. However, most critically, the bias did not affect participants' ability

557 to adequately compare their confidence across modalities (all p's > .33).

558 Our findings show that observers can adequately evaluate their uncertainty underlying visual

559 and tactile decisions on an abstract, modality-independent scale. Overall, cross-modal

560 confidence judgments seem to be made with ease and are as efficient as unimodal confidence

561 judgments. Even though given our study was only behavioral and so we can only speculate

562 about underlying neural mechanisms, our results suggest that confidence processes rely on

563 shared brain regions. These regions may be the ventromedial prefrontal cortex, dorsal anterior

564 cingulate cortex/pre-supplementary motor area, and parietal cortex (Levy & Glimcher, 2012;

565 Morales et al., 2018; Rouault et al., 2018).

566 To evaluate whether cross-modal confidence judgments are costly in terms of processing

567 time, we considered differences in perceptual as well as confidence response times between

568 the unimodal and cross-modal blocks. We found that response times for the perceptual

569 decisions were slightly increased in the cross-modal blocks. This effect has also been

570 observed in previous studies applying the same paradigm to two visual tasks (de Gardelle &

571 Mamassian, 2014) as well as a visual and an auditory task (de Gardelle et al., 2016). In

572 general, unimodal blocks have the advantage that the perceptual task remains constant,

573 requiring in particular no change of perceptual filters. Unimodal visual decisions in our setup

574 had the additional advantage that attention was always directed at the screen. This might have

575 led to even faster responses and could also explain why contrast sensitivity was higher for

576 visual decisions within compared to across tasks (Spence, 2002). It is likely that lengthened

577 perceptual response times in cross-modal blocks reflect task-switching costs (Kiesel et al.,

578 2010) that are related to perceptual processes and can even occur when the switch is

579 predictable (Rogers & Monsell, 1995). However, they could also indicate that confidence

580 formation processes were altered in the cross-modal blocks. In support of this interpretation is

581 the observation that confidence judgments were made faster across modalities than within.

582 Given that perceptual response times are less informative in cross-modal blocks, i.e. less

583 comparable between tasks, it might be possible that participants formed their confidence

584 judgments earlier during cross-modal blocks. However, the exact timing of processes that

585 contribute to the formation of confidence eludes examination. We suggest that confidence

586 formation processes are altered in cross-modal blocks but are overall as efficient as within the

587 same modality.

588   Previous research suggested a conceptual and functional overlap between cognitive control
589   and metacognition (Fernandez-Duque et al., 2000; Klever et al., 2022; Roebers, 2017; Rouault
590   et al., 2022). Both concepts comprise aspects of monitoring and controlling one's decisions,
591   as well as flexibly adapting behavior, making them particularly relevant in complex and
592   challenging situations (Klever et al., 2019; Miyake et al., 2000; Roebers, 2017). They are
593   thought to rely on shared brain regions in the prefrontal cortex, which have been proposed to
594   enable domain-general metacognitive processes (Rouault et al., 2022). In contrast to this
595   rationale, we did not find a significant link between individual cognitive control resources and
596   confidence efficiency in our present study. The absence of a correlation might indicate the
597   ease of confidence judgments that do not draw substantial resources. However, given the
598   previous evidence, we speculate that in our sample the variance in cognitive control resources
599   might not have been sufficient to reveal an association. Indeed, our sample size was
600   determined focusing on statistical power for detecting differences between unimodal and
601   cross-modal confidence efficiency. In order to detect a correlation between cognitive control
602   resources and confidence efficiency larger sample sizes might be needed to achieve
603   appropriate statistical power. A power calculation shows that a sample size of 84 participants
604   was needed to detect a moderate correlation with a power of 80% and an α-level of .05. Thus,
605   we might have failed to find a link due to a lack of statistical power. These considerations are
606   anecdotally supported by an exploratory analysis we ran by pooling the current data set with
607   data from our previous study on perceptual confidence using similar methods (Klever et al.,
608   2022). Given a resulting sample size of 113 participants, we determined a significant
609   moderate correlation between cognitive control resources and confidence efficiency (r(113)
610   = .273, p < .01). In sum, we propose that a putative correlation between cognitive control
611   resources and confidence efficiency awaits further clarification by appropriately powered
612   studies for testing this hypothesis. Our current data does not allow for an appropriate
613   conclusion.

614   The existence of a common currency between the visual and tactile senses supports behavioral
615   control in complex environments by using multisensory information efficiently. Especially in
616   situations where no external feedback is available, it might be useful to distinguish relevant
617   from irrelevant information and determine the tasks that should be prioritized (Aguilar-Lleyda
618   et al., 2020; Desender et al., 2018). Furthermore, it might be helpful when judging the same
619   attribute of an object (e.g. its size) using different senses. However, so far, the role of
620   confidence has been mainly considered about unimodal perceptual decisions. How confidence
621   shapes multisensory decisions remains to be explored (Deroy et al., 2016).

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622   In everyday life, we usually do not make single perceptual decisions but rather multiple

623   perceptual decisions with multiple confidence judgments over multiple stimuli. It has been

624   shown that confidence in previous decisions 'leaks' into our confidence estimates of a

625   following task (Rahnev et al., 2015). This, in turn, allows us to make global confidence

626   judgments that are helpful to predict our future performance (Lee et al., 2021). An open

627   question for future research is whether confidence leak also occurs across modalities and

628   whether global confidence judgments are possible for perceptual decisions involving different

629   senses. A common currency across modalities could facilitate these processes.

630   **Conclusions**

631   We conclude that visual and tactile confidence share a common scale. Observers can

632   adequately distinguish good from bad perceptual decisions, no matter whether confidence

633   judgments were made within the same modality or across modalities. Overall, cross-modal

634   confidence judgments are as efficient as unimodal confidence judgments and can be made

635   with ease, although the timing of confidence formation processes might be slightly altered

636   between unimodal and cross-modal confidence judgments. Open questions for future research

637   are how confidence contributes to multisensory decisions and whether global confidence

638   judgments can be made across senses.

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B Appendix

B.1 List of publications

Klever, L., Beyvers, M., Fiehler, K., Mamassian, P., & Billino, J. (2023). Cross-modal metacognition: Visual and tactile confidence share a common scale. *Journal of Vision (accepted)*. https://doi.org/10.1101/2021.07.07.451428.

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Klever, L., Voudouris, D., Fiehler, K., & Billino, J. (2019). Age effects on sensorimotor predictions: What drives increased tactile suppression during reaching? *Journal of Vision*, *19*(9), 1–17. https://doi.org/10.1167/19.9.9.

B.2 Statement regarding good scientific practice

I hereby declare that I have prepared the thesis at hand independently and without undue aid or the use of any resources other than indicated within the thesis. All parts of my thesis taken either verbatim or analogously from the published or unpublished works of or based on oral communications with others are indicated as such. Regarding all aspects of my scientific enquiries as they appear in my thesis, I have upheld the tenets of good scientific practice as laid out in the "Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis" and complied with the precept of ethics, data protection and animal welfare. I declare that I have neither directly nor indirectly given monetary or any other valuable considerations to others in connection with the thesis at hand. I declare that I have not presented the thesis at hand, either in an identical or similar form, to an examination office or agency in Germany or any other country as part of any examination or degree. All materials from other sources as well as all works performed by others used or directly referenced within the thesis at hand have been indicated as such. In particular, all persons involved directly or indirectly in the development of the thesis at hand have been named. I agree with the screening of my thesis for plagiarism via offline or online detection-software.

Gießen, 13th April 2023   Lena Cathrin Klever