Age-related differences in visuomotor integration as measured by object affordance effects - a combined behavioural and neurophysiological investigation

Elisabeth Linnet

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Age-related differences in visuomotor integration as measured by object affordance effects – a combined behavioural and neurophysiological investigation

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A thesis submitted to Plymouth University
in partial fulfilment for the degree of

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Abstract

Age-related differences in visuomotor integration as measured by object affordance effects – a combined behavioural and neurophysiological investigation.

Elisabeth Linnet

Visuomotor behaviour – from handling simple objects to operating complex devices – is of fundamental importance in our everyday lives, yet there is relatively little evidence as to how healthy ageing affects these processes. A central role is played by the human capacity for reaching and grasping. Grasping an object requires complex visuomotor transformations, including processing of the object’s extrinsic features (it’s spatial location) and intrinsic features (such as size and shape). It has been documented that action relevant intrinsic object properties automatically facilitate specific motor actions despite being task-irrelevant, the so-called object affordance effect. These effects have been demonstrated for (1) grasp type (precision and power grips being facilitated by small and large objects) and (2) object-orientation (whereby right and left handed grasps are facilitated by object-orientation), and might underlie the effortlessness with which humans can interact with objects. Yet, these paradigms have not previously been employed in the study of healthy ageing, and little is known concerning how these processes change over the life span. Elucidating these changes is of particular importance as age-related degeneration of white matter integrity is well documented. Consequently, if successful visuomotor behaviour relies on white matter integrity, age-related reductions in affordance effects should be observed. This prediction was tested in a series of experiments.

Experiment 1 investigated age-differences in object-size compatibility effects, and results corroborated our prediction of age-related reductions in object-size effects.
Experiment 2 investigated age-differences in (1) spatial compatibility effects versus object-orientation effects, and (2) the locus of the effects (facilitation versus interference effects). Results revealed (1) some evidence of larger affordance than spatial effects in both age-groups, and (2) interference effects in the younger group and both facilitation and interference effects in the older group, showing a potential change in processing modes or strategies.

Experiments 3 and 4 addressed the main competing account, the attention-directing hypothesis (according to which attentional shifts are responsible for the generation of automatic response codes, rather than the affects arising from afforded actions), by using a novel stimulus set in which such attentional differences can be ruled out. Results provided strong evidence in favour of the object-size affordance hypothesis.

A final neuroimaging experiment investigated age-differences in the object-size effect and its neural correlates by combining behavioural, functional MRI and diffusion tensor imaging (DTI) data. Results revealed evidence of age-differences, both on the behavioural and functional level. For the DTI data, we investigated all four diffusion metrics (something which is not frequently reported in the healthy ageing literature), and found widespread age-related differences in white matter integrity.

The empirical findings presented in this thesis offer a significant contribution to ageing research, by further elucidating the relationship between age-related neurophysiological changes and visuomotor behaviour. The overall picture which emerged from this series of experiments was consistent with our prediction of age-related reductions in affordance effects. Furthermore, it is likely that these age-differences may have, at least in part, a neurophysiological basis.
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Chapter 1.
The ageing human in an ageing world

1.1 An ageing world.

The effect of an increasing proportion of older individuals has been apparent for several decades, and is becoming yet more important for society at large in terms of providing adequate and sufficient healthcare systems to ensure a healthy senescence for as many people as possible. The world’s population is increasing as is the proportion of older adults. According to the United Nations Population Division (www.un.org/esa/population), it is expected that the 0-4 age-group will decline for the first time in history between 2015 and 2020. In contrast, the 65+ year group is predicted to exceed the 0-4 year group in the same time period, rising from 601 million people in 2015 to 714 million in 2020. By the year 2050, it is estimated that the total number of people aged 65+ will reach 1.5 billion. Consequently, ageing research is now the focus of thousands of laboratories worldwide, spanning a wide field of genetics, biology, biochemistry and neuroscience.

Parkinson’s disease, for example, is the second most common age-related neurodegenerative disease (after Alzheimer’s disease and other dementias) and affects approximately 1 percent of people over the age of 60 (Reeve, Simcox, & Turnbull, 2014). Furthermore, based upon United Nations Population projections worldwide and a systematic review of over 150 studies worldwide,
Alzheimer’s Disease International (ADI) expected the number of people living with dementia to reach 66 million by 2030 and 115 million by 2050 (Prince, Guerchet, & Prina, 2013). As ageing is the greatest risk factor of Alzheimer’s and Parkinson’s disease, the number of people affected will continue to rise with the longevity of the population (Gaugler, James, Johnson, Scholz, & Weuve, 2015; Reeve et al., 2014). The staggering amount of people expected to be affected by these neurodegenerative diseases alone will increase the economic impact on social and healthcare sectors and highlights the importance of continuing to advance our knowledge of age-related diseases, their causes, potential prevention and evidence-based treatment and care.

However, in order to achieve this, it is necessary to attempt to understand the processes of healthy aging. Normal, healthy ageing is accompanied by a number of biological, physiological and psychological processes which may nevertheless involve a progressive and inevitable loss of function, and although many theories have been put forward to explain this decline, none have been able to encompass all the dynamic and complex changes that happen as we age (National Institute on Aging, NIH, 2015).

1.2 The ageing human

1.2.1 The embodied human

As human beings, our sensorimotor capabilities are of fundamental importance in interactions with the world that we live in. Rather than the disembodied perspectives of the mind (such as cognitivism, which has dominated the
cognitive sciences since its formation), the human experience of ageing has been suggested to be best understood in terms of the concept of embodiment (Clarke, & Korotchencko, 2011). Based, amongst others, upon work of 20th and 19th century philosophers such as Merleau-Ponty (1962) and William James (1890), embodiment has been defined as follows: “There is an obvious and prominent fact about human beings. They have bodies and they are bodies. More lucidly, human beings are embodied, just as they are enselved” (Turner, 1984, p1, as cited in Clarke, & Korotchencko, 2011). This view entails, that “cognition depends upon the kinds of experience that come from having a body with various sensorimotor capacities, and that these individual sensorimotor capacities are themselves embedded in a more encompassing biological, psychological, and cultural context” (Varela, Thompson, & Rosch, 1993, p. 173). Consequently, our bodily capabilities and possibilities will be in an ever changing state throughout life.

Healthy ageing is inevitably accompanied by a number of inevitable biological and physiological changes and processes, and whereas some deficits or declines may be mitigated by for example exercise/training interventions and a healthy diet, others are more out of our control, such as genetic predispositions / hereditary diseases. An extensive review of age-related changes in the human body is beyond the scope of this thesis, but some of the factors which are believed to be of central importance to sensorimotor integration is necessary.
1.2.2 Muscular system and vision

Age-related declines or deficits in motor performance cannot be attributed to one single factor; rather changes which occur throughout the peripheral and central nervous systems as well as in the neuromuscular system are important (Seidler et al., 2010). The loss of muscle mass is thought to be a major determinant when it comes to loss of strength with age (Galban, Maderwald, Stock, & Ladd, 2006). There is some disagreement when it comes to the onset of skeletal muscle atrophy (muscle fibre loss), but several investigations have demonstrated that by the age of 80 up to 50 percent of muscle fibres have been lost (Faulkner, Larkin, Claflin, & Books, 2007). Some authors have suggested that the age-related decline in strength is more pronounced than that which can be explained by muscle atrophy alone, suggesting that it is also characterised by a decline in muscle quality (Goodpaster et al., 2006). However, the degree of atrophy is largely dependent on the level of physical activity, so muscle weakness can be slowed although not avoided (Faulkner et al., 2007; Vincent, Raiser, & Vincent, 2012).

Most people will be faced with some level of changes to their visual system as they age, the most common being the change in near vision (presbyopia), which is caused by a change in the eye’s ability to focus, thus necessitating reading glasses. If age-related diseases in vision are discounted (such as age-related macular degeneration, glaucoma etc.), other common changes include needing more light, having problems with glare and some older adults also experience changes in colour perception due to cataract (which can be ameliorated through
surgery). The visual cortex, however, seems to be less affected by ageing than other brain regions, both on the volumetric and microstructural level (this will be discussed further in section 1.2.3).

1.2.3 Cerebral changes

1.2.3.1 Grey matter

Advances in neuroimaging techniques have advanced our understanding of age-related neurophysiological changes, but the focus of this research has been centred primarily on how these changes affect higher order cognitive functions, whilst lower level perceptual and motor components have been studied much less extensively (Seidler, et al., 2010). There is ample evidence suggesting that normal ageing is accompanied by a number of neurophysiological changes, including volumetric decline, changes on the macrostructural (e.g. coherence of fibre orientation) and microstructural level (e.g. degree of myelination), as well as a change in functional activation patterns with activity becoming more widespread and less lateralised (Bennett, Madden, Vaidya, Howard, & Howard, 2010; Degardin, et al., 2011; Park, & Reuter-Lorenz, 2009; Salat et al., 2009).

Conventional magnetic resonance imaging (MRI) allows assessment of brain structural and volumetric information. The total grey matter volume of the human cortex is approximately 2000 cubic millimetres (Van Essen, 2005). The cortical thickness varies quite substantially by region (ranging from 1-4.5 mm) and has an overall average of approximately 2.5 mm (Fischl, & Dale, 2000; Shepard, 2001). As each cubic millimetre contains in the range of 50,000
neurons, if one assumes an average cortical thickness of 2.5 millimetres, the cerebral cortex contain in the region of 25 billion neurons (Fischl, & Dale, 2000; Wandell, Dumoulin, & Brewer, 2007). It is well established that the human brain shows age-related atrophy; this has been documented by almost every study which has examined the question. It has been documented that the onset of grey matter volumetric decline starts very early, around 20 years of age, and continues in a linear fashion (e.g. Ge et al., 2002). The detailed regional specificity of these changes is not entirely clear, partly due to the regional variation in cortical thickness. The reduction in grey matter volume is usually present along with increases in ventricular and cerebrospinal fluid (CSF) volume. These changes in fluid volume may be a result of the loss of grey matter in that it simply fills out the space from the loss of grey matter, rather than it being an independent age-related change (Seidler, et al., 2010). A voxel-based morphometry study (which allows for a detailed voxel-by-voxel analysis of regional variations in both grey and white matter) involving over 120 aged individuals, documented that the overall grey matter volumetric decline was in the region of 2.4 cubic centimetre a year and the simultaneous increase in CSF was 2.5 cubic centimetre (Smith, Chebrolu, Wekstein, Schmitt, & Markesbery, 2007). Very similar findings have been documented elsewhere (Tisserand, Visser, Boxtel, & Jolles, 2000), including another large-scale study including 330 participants (Coffey, Saxton, Ratcliff, Bryan, & Lucke, 1999).

Numerous studies, including large-scale ones (see e.g. Good et al., 2001), have found evidence that the prefrontal cortex (PFC) appears to be particularly vulnerable to grey matter atrophy, and the parietal cortex has been shown to
exhibit a greater volumetric decline than temporal regions, whilst occipital regions generally show minimal changes (Good et al., 2001; Raz et al., 2005; Resnick, Pham, Kraut, Zonderman, & Davatzikos, 2003). Considering that the most prominent grey matter volumetric changes occur in prefrontal and parietal cortices, this may be particularly relevant to age-related deficits in motor performance as older individuals appear to be more reliant on these structures for motor control than do younger individuals (Seidler et al., 2010) (discussed further below). Furthermore, a question of particular relevance would be whether the primary motor cortex, premotor cortex and supplementary motor areas show an as extensive degeneration as the rest of the prefrontal cortex, but the findings are equivocal; some studies have shown minimal age effects (Raz et al., 1997) whilst others have found widespread age-related grey matter volumetric reductions in the pre- and postcentral gyri (Good et al., 2001). A study which specifically investigated age-differences in cortical thickness found significant age-related reductions in both the primary motor cortex and somatosensory cortex, in fact, the largest reductions occurred in the primary motor cortex (Salat et al., 2004).

As for subcortical changes in grey matter volume, structures involved in movement and action also show volumetric decline, particularly the cerebellum and basal ganglia, both of which have substantial connections to premotor and parietal areas involved in sensorimotor transformations (Raz et al., 2005; Smith, et al., 2007). Furthermore, in a sample of 85 healthy adults aged 22-80 years, the volume of the caudate nucleus (which is part of the basal ganglia) has been
shown to be positively correlated with skill acquisition during motor learning (Kennedy, & Raz, 2005).

Yet, impairment might not only be due to grey matter loss in the cortical region itself. The cortical networks mediating cognitive function are connected by white matter tracts projecting between different cortical regions; association tracts (connecting cortical regions within the same hemisphere), projection tracts (cortical- to subcortical connectivity) and commisures (interhemispheric connectivity). Consequently, changes in the functional integration of cortical networks may result from changes in white matter integrity. This phenomenon, first suggested by Geschwind (1965), has been termed the “cortical disconnection” hypothesis and has been suggested to be a general mechanism underlying age-related changes in cognitive function (O'Sullivan, et al., 2001).

### 1.2.3.2. White matter

White matter volumetric decline also contributes to overall cerebral atrophy, but does not follow the same patterns of decline as grey matter. White matter maturation has been observed to continue into mid-life (Courchesne, et al., 2000). White matter volumetric decline, on the other hand, seems to begin later in life (than grey matter volumetric decline) but once started, usually around 40-50 years of age, it appears to be consistent and fast and sometimes even continue at an accelerated rate (Courchesne, et al., 2000, Ge at al., 2002). These combined changes in grey and white matter volumetric reduction may explain why overall cerebral volume appears to remain stable until mid-life. There is an increasing amount of research which has demonstrated that it is not only the
quantity, but also the quality of white matter that changes with ageing. Diffusion tensor imaging (DTI) is a recent magnetic resonance imaging (MRI) technique that allows investigation of the microstructural integrity of white matter (for an overview of the principles of DTI, see e.g. Chanraud, Zahr, Sullivan, & Pfefferbaum, 2010; Schulte, Sullivan, Muller-Oehring, Adalsteinsson, & Pfefferbaum, 2005; Soares, Marques, Alves, & Sousa, 2013).

The application of DTI is evolving rapidly as it is highly sensitive to changes at the microstructural level and is thus a valuable tool in assessing changes caused by a wide range of factors and conditions, including brain maturation/development, ageing, neurodegenerative diseases, neurological conditions, traumatic brain injury, stroke and psychiatric conditions (Alexander, Lee, Lazar, & Field, 2007; Chanraud et al., 2010). A further strong point of DTI is that it can be acquired in a short amount of time (~ 10 minutes), so a substantial amount of information can be obtained with little additional financial cost and little inconvenience for participants/patients.

There are four different DTI indices, each of which is believed to be sensitive to different physiological properties; axial diffusivity (AD), radial diffusivity (RD), mean diffusivity (MD) and fractional anisotropy (FA). These indices and how they may provide information regarding age-related changes in microstructural integrity will be discussed in further detail in chapter 8, hence only a brief recap will be presented here. Axial diffusivity is thought to reflect axonal integrity and radial diffusivity myelin integrity. The vast majority of DTI studies to date have focussed on the global measures of integrity, namely fractional anisotropy and mean diffusivity. Mean diffusivity is a measure of overall water diffusion and is
thus sensitive to necrosis. Fractional anisotropy is arguably the most reported measure as it gives a good overall measure of microstructural integrity – the downside being that it is less specific as to the type of microstructural changes. Although it is well established that healthy ageing is associated with age-related degeneration of white matter integrity (which would manifest as declines in fractional anisotropy and increases in diffusivity measures), the underlying characteristics and patterns of neural changes are far from clear as there is an extremely limited number of studies which have included all four metrics. As a matter of fact, Bennett and colleagues noted that only a total of nine other DTI studies of healthy ageing had also included axial and radial diffusivity measures (Bennett, Madden, Vaidya, Howard, & Howard, 2010).

Although there is a substantial amount of studies which have demonstrated age-related decreases in fractional anisotropy and age-related increases in mean diffusivity, whether these age-related changes are also characterised by anterior-posterior and/or superior-inferior gradients of higher-to-lower vulnerability remains controversial (Salat, 2011; Sexton, et al., 2014). It has frequently been proposed that the frontal lobe is particularly susceptible to age-related degeneration which may have fuelled the anterior-posterior gradient hypothesis as being a global phenomenon. However, it has been noted that the majority of studies which have suggested the presence of an anterior-posterior gradient, have been based on studies of the corpus callosum (Sullivan et al., 2010). In addition, based on the findings that the anterior-posterior gradient is only present in superior clusters (Benett et al., 2010) and within tracts traversing frontal and parietal cortices but not the temporal cortex (Davis, et al.,
2009), has led other to propose that the anterior-posterior gradient theory may be anatomically specific and secondary to the superior-inferior gradient (Sexton et al., 2014). Furthermore these authors (Sexton et al., 2014), who conducted one of only a handful of longitudinal DTI studies, noted that although their findings supported age-related degeneration of the frontal lobe, significant degenerations of white matter integrity were also observed in wide parts of the parietal lobe, whereas the temporal and occipital lobe were less affected. These anatomical patterns of age-related degeneration of white matter microstructural integrity thus seem to parallel those of grey matter volumetric decline described above.

The superior longitudinal fasciculus (SLF), the major white matter tract subserving fronto-parietal integration, has also shown age-related degeneration in microstructural integrity. A number of studies of motor control and action, including grasping, have demonstrated an involvement of a predominantly left-hemispheric fronto-parietal network (this will be discussed further below). Hence, the connectivity of intrahemispheric association tracts may be of particular importance to visuomotor integration. There is, however, very limited research to date on the role of white matter integrity on visuomotor functions (Schulte, Muller-Oehring, Rohlfing, Pfefferbaum, & Sullivan, 2010).

**1.2.3.3. Changes in functional activation patterns**

Despite the evidence of age-related decreases in white matter integrity, ample neuroimaging studies have demonstrated that the functional activation patterns become more widespread and less lateralised in older adults for a wide range of
cognitive tasks, including a number of motor tasks (Heuninckx, Wenderoth, & Swinnen, 2008; Seidler et al., 2010). This frequently also includes an increase in the magnitude of activation, and increasing the task complexity in motor tasks have been found to lead to an increase in the recruitment of additional brain areas, particularly the ipsilateral M1 (for reviews, see e.g. Cabeza, 2002; Park, & Reuter-Lorenz, 2009). Certain specialised functions are lateralised to each hemisphere; the left hemisphere is preferentially involved in motor control whereas the right hemisphere is preferentially involved in spatial cognition/visuospatial attention (De Schotten et al., 2011; Fling, Peltier, Bo, Welsh, & Seidler, 2011; Ivry & Robertson, 1998; Serrien, Ivry, & Swinnen, 2006).

Interhemispheric interaction and inhibition occurs via the corpus callosum and consists of complex interactions between excitatory and inhibitory processes to ensure coherent behaviour (Fling et al, 2011). Interhemispheric inhibition, (IHI) is required for some motor behaviours in order to prevent interference. For example, during hand grip the contralateral primary motor cortex (M1) inhibits the ipsilateral motor cortex via callosal connections. Transcranial magnetic stimulation (TMS) is well suited for investigating such cortico-cortical inhibitory processes, both those occurring across hemispheres (IHI), as well as inhibitory processes occurring within the ipsilateral motor cortex (Daskalakis, Christensen, Fitzgerald, Roshan, & Chen, 2002). For example, in the case of interhemispheric inhibition, a conditioning stimulus is applied to the motor cortex which inhibits the size of the motor evoked potential (MEP) produced by the test stimulus of the opposite cortex (Daskalakis et al., 2002). Studies using TMS have demonstrated that this inhibitory function diminishes with age,
which suggests that there is a decline in callosal function in the areas connecting motor cortices (Talleli, Ewas, Waddingham, Rothwell, & Ward, 2008a; Talleli, Ewas, Waddingham, Rothwell, & Ward, 2008b). Thus, reduced callosal white matter integrity may reduce inhibition from the contralateral M1 which in return could manifest as greater ipsilateral M1 activation (Langan, Peltier, Bo, Fling, Welsh, & Seidler, 2010). In a simple reaction time (RT) task, Mattay et al. (2002) found that older adults recruited more both cortical and subcortical areas than did younger adults, and that participants with fast RTs exhibited increased motor recruitment, whereas in low-performing older adults the activation patterns did not differ from those of the younger adults. In contrast, others have found that older adults with greater ipsilateral primary motor cortex (M1) activations had slower RTs (Langan et al., 2010).

Whilst the majority of research investigating increased bilateral activations in older adults have been related to prefrontal activation and cognitive tasks, and suggests that over-recruitment may be compensatory in nature, it remains unclear whether increased recruitment (particularly of the M1) for motor tasks aids or counteracts performance (Langan et al., 2010).

### 1.3 Healthy ageing and visuomotor integration

Despite the substantial amount of research which have documented age-related neurophysiological changes, perceptual and motor components have not received much attention despite visuomotor integration being of such fundamental importance in interactions with the world we live in. In our
everyday lives, we move our bodies around in, and engage with our environment. We continually interact with objects; we reach, grasp, and manipulate them - seemingly effortlessly. Yet, these behaviours require complex visuomotor transformations; the extraction of visuospatial information (the spatial location of the object relative to the person performing the action) and processing of the object’s intrinsic features which are relevant for grasping, such as the object’s size and shape. Despite its central importance, there is a paucity of evidence and surprisingly little research devoted to/engaged with elucidating the underlying mechanisms of how normal, healthy aging impacts on visuomotor behaviour.

There is evidence to suggest that with advancing age, people become increasingly reliant on information in the environment to support behaviour. This notion has been documented extensively in the domain of memory since the observations made by Craik (1983). For instance, it has been observed that older adults are more likely to be guided by external cues (e.g. hints and reminders) than younger adults who tend to rely more on self-generated cues/active control processes, possibly due to an age-related decline in attentional resources (Craik, 1983; Wang et al., 2011). It has since been documented that these findings can be extended to other domains, including perceptual processing and goal-directed action (discussed further below) (Lindenberger & Mayr, 2014). Similar findings come from Parkinson’s patients, where it has been demonstrated that external cues may either facilitate or hinder movement. For example, their attention to external stimuli may be grabbed more strongly (Poliakoff et al, 2003) and in addition, they have been
found to have difficulties in inhibiting responses to irrelevant stimuli (Wylie, Stout, & Bashore, 2005). However, appropriate sensory cues (for example floor markers), can also aid movement, for example facilitate gait impairments (Rubinstein, Giladi, & Hausdorff, 2002) or reaching movements (Majsak, Kaminski, Gentile, & Flanagan, 1998). There is little evidence, though, regarding how Parkinson’s patients respond to action-relevant stimuli (Poliakoff, Galpin, Dick, Moore, & Tipper, 2007) and the same is true for healthy older adults. There is, however, increasing evidence to suggest that healthy older adults also, albeit perhaps to a lesser extent, become more reliant on external information across several modalities, including the domains of perception and action, thus marking a gradual shift from self-initiated processes to relying more on environmental support with advancing age (Lindenberger & Mayr, 2014). In the visual domain, it has been demonstrated that older adults have difficulties in resisting entrainment by distractors and/or distracting information in a similar manner as to that observed in Parkinson’s patients (see e.g. Gazzaley, 2013). In the action domain, self-initiated, goal-directed action is typically attributed to abstract representations of a current task set which can be modified in ‘real time’ depending on current demands (Ardid, Wang, & Compte, 2007). The efficacy of this ‘real time’ updating mechanism appears to diminish with age. For instance, task-switching costs/interference effects (an increase in reaction times when switching from one task to another as well as a decrease in accuracy) have been found to be larger in older than in younger adults (Kray, & Lindenberger, 2000).
The fade-out paradigm, a variant of the task-switching paradigm, employed by Spieler and colleagues (Spieler, Mayr, & LaGrone, 2006), provides a good example of the costs associated with relying on the environment to support action. In that paradigm, participants are required to make a trial by trial selection between two tasks, indicated by a visual cue. Participants are instructed that at some point in the experiment, one of the tasks is faded out, meaning that that trial type is no longer relevant for the remaining part of the experiment. The visual cue for that task type is crossed out (but remains visible). Younger adults quickly move from the task-switching trials to the single-task trials, but older adults continue to be influenced by the cue (as demonstrated by RT costs) throughout the experiment although it is no longer relevant. Eye movement tracking suggested that in the fade-out phase, the older adults continued to fixate on the task cue (which was no longer relevant) in over 80 percent of trials whereas it was about 15-20 percent of trials for the younger group. When the irrelevant visual cue was removed in the single-task fade-out phase, the older adults showed much reduced fade-out costs (Spieler et al., 2006). Consequently, these findings seem to suggest that older adults have difficulties in moving from an initial level of high internal control in which task switching is required, to one where no selection is necessary. Furthermore, it seems to suggest that cues in the environment do not work in an either-or fashion; the type of information available and its relevance for current behavioural goals may either facilitate or counteract performance.

The anatomical configuration of the human visual system permits investigations of the separate contributions of each hemisphere for the integration of parallel
visuomotor processes (Schulte, et al., 2010). One paradigm allowing such an investigation is that of the ‘redundant target effect’, RTE, in which single or paired targets are compared. We have previously investigated age-related differences in interhemispheric visuomotor integration using the RTE paradigm (Linnet, & Roser, 2012). More specifically, participants were required to make speeded uni-manual responses to visual stimuli appearing either unilaterally, i.e. either left or right visual hemifield (restricting input to the contralateral hemisphere) or bilateral visual stimuli (allowing input to both hemispheres simultaneously). The presentation of bilateral visual stimuli usually results in faster reaction times than does unilateral visual stimuli, and it is this effect which is known as the redundant target effect. Paradoxically, this speeding of responses to bilateral stimuli is enhanced in people with disruption to the corpus callosum (the major white matter tract subserving interhemispheric integration), such as those that have had partial or complete callosotomies (split brain patients) (Iacoboni & Zaidel, 2003; Roser & Corballis, 2002; 2003).

The hemispheric coactivation hypothesis (Miller, 2004) accounts for this paradox by positing that bihemispheric processing occurs both to unilateral and bilateral stimuli in the normal brain, but only with bilateral stimuli in the disconnected brain. Basically, the assumption of the model is that in neurologically intact individuals a laterised stimulus activates the visual area in the contralateral hemisphere, which in turn activates the motor areas of both hemispheres. The activation of each motor area then combines to produce a response when a criterion is reached. When bilateral stimuli are presented, each visual area activates both motor areas. In people with callosal disconnection, a unilateral stimulus does only activate the contralateral
hemisphere. Hence, the unstimulated hemisphere does not contribute to response activation (or is as a minimum substantially delayed). Bilateral stimuli, on the other hand, activate both hemispheres simultaneously. Under this schema, neurologically intact individuals would only show a small reaction time advantage for bilateral stimuli contrary to those with callosal disconnection, which results in a greater advantage for bilateral stimuli presentations, and consequently a greater redundant target effect. Based on this theory and previous findings in both neurologically intact individuals and callosotomy patients as well as the substantial amount of research which has documented age-related degeneration of white matter integrity (particular relating to the corpus callosum), we had hypothesised that the older group would show significantly larger redundant target effects than the younger group. We found this to be true for both our simple and choice reaction time experiments. Our results were therefore congruent with the hemispheric coactivation hypothesis in which callosal disconnection (or disruption) is associated with larger redundant target effects.

In sum, there is a substantial amount of evidence which has documented age-related neurophysiological changes on both the volumetric, macro- and microstructural level. There is, however, limited evidence regarding the extent to which these changes impact on visuomotor integration. Consequently, the experiments presented in this thesis will combine behavioural, functional MRI and DTI measures in order to further our understanding of the relationship between age-related changes in microstructural integrity and their potential effects on visuomotor behaviour.
Chapter 2.
Visuomotor integration: behavioural and neurophysiological evidence.

2.1 Behavioural evidence for the integration of vision and action

2.1.1 Stimulus-response compatibility paradigm and the spatial-compatibility effect

It is well established that the spatial location of an object influences reaction times. In spatial stimulus-response compatibility (spatial SRC) tasks, performance is generally faster with a compatible mapping (e.g. when participants are asked to respond with a right key press to a stimulus appearing on the right) than an incompatible mapping (right key press to a stimulus appearing on the left). In these stimulus-response compatibility proper experiments, stimulus location is relevant to the task. A similar spatial correspondence effect is obtained in the Simon task in which stimulus location is irrelevant to the task (e.g. Simon 1969). For example, in a typical variant of the Simon task, participants are presented with stimuli appearing on the right or the left side of the screen, and they are required to press, say, the right key for a green stimulus and left key for a blue stimulus. Although stimulus location is irrelevant to the explicit task, participants generally respond faster when there is a correspondence between stimulus location and hand of response (e.g. a green stimulus appearing on the right) than when there is a conflict (e.g. a
green stimulus appearing on the left), an effect named the ‘Simon effect’, or spatial compatibility effect.

Despite the vast amount of research into the spatial compatibility effect in younger adults, there are only a handful of studies on age-related differences in the spatial compatibility effect (Proctor, Pick, Vu, & Anderson, 2005, see Proctor, Vu, & Pick, 2005 for a review). These studies suggest that older adults may be more affected by, and have greater difficulty in suppressing the irrelevant spatial information (both when the irrelevant stimulus dimension is visual or auditory), which results in larger spatial compatibility effects (Pick, & Proctor, 1999; Proctor et al., 2005; Van der Lubbe, & Verleger, 2002). These age-related increases have been found to be particularly pronounced when both the relevant and irrelevant stimulus dimensions are presented within the same modality (as is the case in one of our experiments) (Proctor et al., 2005). Thus, for visual choice tasks, the age-related increase in the magnitude of the spatial compatibility effect has been shown to be up to 1.5 – 2 times that of younger individuals (Proctor et al., 2005).

In younger individuals, it is well established that the magnitude of the spatial compatibility effect decreases with increasing reaction times (De Jong, Liang, & Lauber, 1994; Hommel, 1993; Van der Lubbe, & Verleger 2002). One study suggests that perhaps this is not the case in older individuals (Juncos-Rabadan, Pereiro, & Facal, 2008). This study, which investigated the effect in four age groups using a variant of the usual Simon task, found that the effect of the irrelevant stimulus dimension decreased with increasing reaction times in the
younger group but increased with reaction times in the oldest group, which suggests that selective suppression declines in old age.

Although there is limited evidence of how ageing affects response times in visual spatial compatibility tasks, the studies that have reported age-related increases in the magnitude of spatial compatibility effects are consistent with the literature which have demonstrated that older adults have difficulties in resisting entrainment by (visual) distractors as discussed earlier (e.g. Gazzaley, 2013). Furthermore, the age-related increase in the magnitude of the effect has been shown to increase even further (up to 3 times that of younger individuals) when employing task-switching trials – again, this would be consistent with the previously reviewed literature that older adults may be more reliant on external stimuli to guide behaviour (e.g. Lindenberger & Mayr, 2014). It should be noted though, that these effects are not necessarily ‘fixed’ as it has been shown that spatial compatibility effects can be reduced with perceptual-motor training, both for younger and older adults. In one such study of older adults, compatibility effects were reduced to about half the size after training (and importantly, their overall reaction times were similar before and after training), (Castiello, Bompani, Nonis, & Umilta, 1990). This reduced effect is similar as to that obtained with younger adults after perceptual-motor training (Umilta, & Nicoletti, 1985). These findings suggest that, in the case that particular aspects of external stimuli interfere with optimal/efficient visuomotor behaviour, it may be possible to ameliorate such consequences by the use of training interventions.
2.1.2. Affordances, object-orientation and object-size studies

As the Simon task demonstrates that the task-irrelevant stimulus property (location) facilitates compatible actions, this paradigm has frequently been employed in collecting behavioural evidence for visuomotor integration. In addition to object location, reaction times to visual stimuli have also been shown to be affected by the action relevant features contained within the object: the so-called ‘affordance’ effect. The notion of affordances, that certain objects afford or potentiate certain actions, was originally conceived by Gibson (1979). In a series of experiments Tucker and Ellis (e.g. Tucker, & Ellis, 1998, 2001; Ellis, & Tucker, 2000) investigated whether intrinsic object features would automatically potentiate associated actions.

In the first object-orientation study (Tucker, & Ellis, 1998), participants were required to categorise images of objects as being either upright or inverted by making left- or right-hand key presses. The objects presented were non-lateralised (unlike the Simon task) and were compatible with either a left- or right-handed grasp, and whilst participants were not required to attend to the horizontal orientation of the objects, this implicit horizontal orientation affected the responses; participants made faster and more accurate responses when the hand of response was compatible with the optimal hand for grasping the object (Tucker, & Ellis, 1998).

Ellis and Tucker (2000) argued that not only do objects afford grasping, they also afford a particular kind of grasp. The study of human prehension was advanced greatly by Napier's (1956; 1965) seminal work in which he divided handgrips into precision grips and power grips from a functional and
phylogenetic perspective (Ehrsson, Fagergren, Jonsson, Westling, Johansson, & Forssberg, 2000). Precision grips are pinch-grips between index finger and thumb and are used in the manipulation of small objects which require fine control. Power grips are whole-hand grips which provide high stability. Ellis and Tucker (2000) brought these grip types into the lab by using grip devices mimicking precision and power grips. They investigated whether object size would facilitate these components of grasping actions, in a similar manner as handle location affected selection of the response hand. Participants were required to categorise images of objects as being organic or manufactured by making either precision or power grip responses. The presented objects were compatible with either a power-grip or precision grip. Although object-size was irrelevant to the explicit task, participants made faster and more accurate responses in compatible conditions (e.g. a power grip to a large object) than in incompatible conditions (e.g. a power grip to a small object). Together these results suggest that visually perceived objects afford, or potentiate, action properties associated with that object even in the absence of any possibility to physically handle the objects and in absence of the intention to interact with the object. Numerous other behavioural studies have documented similar findings that the visual perception of objects potentiates associated actions (e.g. Girardi, Lindemann, & Bekkering, 2010; Goslin, Dixon, Fischer, Cangelosi, & Ellis, 2012; Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003).

### 2.1.3 Competing accounts

Alternative accounts to the object affordance view have been proposed, the main being the ‘attentional-orienting’ hypothesis (Anderson, Yamagashi, &
Karavia, 2002). Anderson and colleagues pointed out that the vast majority of affordance studies have used asymmetrical stimuli (e.g. a frying pan). Hence, in accordance with theories of attention which suppose a strong link between visual attention and motor programmes (e.g. Schneider, & Deubel, 1995), it was suggested that this asymmetry is likely to induce attentional bias to the side of the handle and furthermore, that the most visually salient part of the object has often been the most behaviourally relevant part of the object (e.g. a handle). Consequently, they argued that attentional shifts may be responsible for the generation of automatic response codes, rather than the effects arising from the actions that the object affords.

To test this idea, Anderson and colleagues (2002) presented participants with 2D line drawings of objects and non-objects, and the task was to judge if the objects were rotated clockwise or anticlockwise from their normal orientation. They documented facilitation of responses that were spatially compatible with the object’s visually salient feature, even when not action relevant (for example the hands of an analogue clock). However, it has been noted that participants may have used this visually most salient feature in order to judge the object’s orientation – in contrast, a noteworthy aspect of object-orientation and object-size studies, including those described above, has been the task-irrelevancy of object orientation (Symes, Ellis, & Tucker, 2007). More specifically, the object-orientation and object-size studies have employed categorisations tasks (i.e. participants were required to respond according to whether the objects were upright / inverted or organic / manufactured) and hence orientation and size, respectively, have always been irrelevant to the explicit task.
2.2 Neurophysiology of visuomotor integration

As discussed previously, our visuomotor abilities are crucial in our everyday lives. It could be argued that in some instances, its importance may actually increase as we get older if we are to maintain functional independence. Successful visuomotor behaviour involves an interplay between numerous domains and factors which ultimately ensure coherent behaviour and allows us to safely navigate and interact with our environment. Due to this complexity, there has been a tendency for many neurophysiological studies to focus on separate modalities (e.g. visual or motor), whilst largely ignoring large-scale cross-modal integration (e.g. Ledberg, Bressler, Ding, Coppola, & Nakamura, 2007). For example, in the case of vision, although our perception of the visual scene in front of us appears unified and coherent, the visual components can be divided into for example shape-, colour-, form-, texture-, depth-, and movement-perception – each of which can be further divided into additional sub-categories. Similarly, visuospatial abilities have been divided into distinct sub-categories, e.g. spatial visualisation, spatial perception, and mental rotation (see e.g. Bruin, Bryant, MacLean, & Gonzales, 2016). The motor domain is equally multifaceted. Thus, when also taking into account the numerous age-related neurophysiological changes, which occur on each of those levels, the complexity of investigating age-related changes in human visuomotor integration in a large-scale, cross-modal fashion becomes evident. A key visuomotor function is the human capacity for reaching and grasping objects – actions that are performed repeatedly every day, seemingly effortlessly. Even so, grasping an object requires complex visuomotor transformations which include processing
of the object’s extrinsic features (its spatial location) as well as its intrinsic features (predominantly its size and shape), (Arbib, 1981). Kinematic investigations have documented that varying object distance affects the velocity of the reaching limb whereas varying object size affects the dynamics of preshaping of the hand to match the target object (Jeannerod, 1984). These findings coupled with single-cell studies in the macaque and neuroimaging data from human participants, have led to the proposal that reaching and grasping is controlled by two distinct, but interacting visuomotor channels (Begliomini et al., 2014; Castiello, & Begliomini, 2008; Grol et al., 2007; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). These channels appear to have a physiological counterpart (Grol et al., 2007), by two anatomically segregated fronto-parietal pathways; a dorsomedial fronto-parietal reaching circuit (which includes the anterior occipito-parietal sulcus and posterior dorsal premotor cortex), and a dorsolateral fronto-parietal grasping circuit which includes the anterior intra-parietal (AIP) and ventral premotor cortex (Begliomini et al., 2014; Castiello, 2005; Castiello, Culham, & Valyear, 2006; Grol et al., 2007; Olivier, Davare, Andres, & Fadiga, 2007). A recent fMRI study (Begliomini et al., 2014) investigated reaching and reach-to-grasp movements towards small or large objects. Results largely supported previous findings in that although neural activity in the reaching and grasping networks did overlap, it was predominantly associated with either one or the other action. Others have used dynamic causal modelling to examine fMRI data to assess how fronto-parietal connectivity is modulated by planning and executing prehension movements towards small or large objects (Grol et al., 2007). Grasping small objects increased connectivity of the dorsolateral circuit whereas grasping large objects
increased interregional couplings of the dorsomedial circuit. Consequently, the authors concluded that these findings argued against dedicated cerebral circuits for reaching and grasping, and instead it was suggested that the relative contributions of these circuits may depend on the degree of online control required by the movement (Grol et al., 2007).

A number of studies of motor control and action have demonstrated the involvement of a predominantly left-hemispheric fronto-parietal network, as discussed earlier. The left-hemispheric dominance for actions performed with either hand is well documented (Rushworth, Nixon, Wade, Renowden, & Passingham, 1998). For example, such dominance is evidenced by transcranial magnetic stimulation (TMS) studies showing that TMS over the right primary motor cortex (M1) impacts on the performance of the left hand but not the right, whereas TMS over the left M1 impacts on the performance of both hands (Schluter, Krams, Rushworth, & Passingham, 2001). In addition, a PET study investigated brain activations during simple reaction time (using one hand) and choice reaction time (using two hands) (Schluter et al., 2001). When analysing which areas where more active for the choice versus the simple reaction time task, activations were restricted to the left-hemisphere (the parietal, premotor and prefrontal areas), regardless of whether the left or right hands were used. Furthermore, although unilateral lesions are typically associated with deficits in movements of the contralateral side of the body, it has also been observed that lesions in the left, but usually not the right parietal cortex, may lead to apraxia where people are impaired in ipsilateral hand movements (Rushworth, et al., 1998).
Visuospatial attention, on the other hand, is predominantly lateralised to the right-hemispheric fronto-parietal network in most individuals (Cieslik, Zilles, Grefkes, & Eickhoff, 2011; De Schotten et al., 2011; Fling, et al., 2011). A diffusion tensor imaging study which employed tractography in order to examine the connectivity of these tracts demonstrated that this fronto-parietal network was larger in the right than the left hemisphere (Thiebaut de Schotten et al., 2011). In addition, out of the three tracts, the dorsal, middle and ventral superior longitudinal fasciculus, the latter was the one which showed the highest degree of right-hemispheric lateralisation. A novel and interesting finding was that the degree of anatomical lateralisation was correlated with asymmetry of performance on visuospatial attention tasks.

As noted, it has been proposed that motor programs for reaching and grasping an object are automatically activated once such an object is seen. A positron emission tomography (PET) study which investigated the potential involvement of motor components during object perception found that the perception of objects, irrespective of the task, was associated with left-hemispheric activations in the fronto-parietal areas, including the parietal lobe and inferior frontal gyrus (Grezes and Decety, 2002). This suggests that viewing objects goes along with the activation of motor programs to reach and grasp them. Similarly, activations at the subcortical level were found in the right putamen and right caudate nucleus, structures which are part of the basal ganglia, involved in action selection (this study will be discussed further in chapter 7).

To date, one neuroimaging study has explored the neural correlates of the object-size effect, i.e. the influence of action relevant intrinsic object properties
on motor responses (Grezes, Tucker, Armony, Ellis, & Passingham, 2003). This fMRI study was a replication of the Tucker and Ellis (2001) object-size study described above. The behavioural object-size compatibility effects were replicated, and functional activations were observed in a left-hemispheric fronto-parietal network, namely the anterior parietal, dorsal premotor and inferior frontal cortex (Grezes et al., 2003), again supporting the proposal that viewing objects activates associated motor programs for reaching and grasping. (This study will be discussed in further detail in chapter 7). Thus, together, while there are only few studies testing it, the evidence available to date suggests that viewing objects indeed activates affordances in the same left-hemispheric networks as actual reaching and grasping.

2.3 Objectives and thesis overview

The main objective of this thesis is to investigate age-related changes in visuomotor integration in healthy younger and older individuals as measured by object affordance effects (the object-orientation effect and the object-size effect). To the author’s knowledge, there have been no previous investigations into age-related differences in neither the object-orientation effect nor the object-size effect. Let us briefly summarise the previously reviewed evidence on which our hypothesis and investigations will be based.

(1) A series of behavioural investigations have documented that action relevant object properties may automatically potentiate actions associated with those objects. In other words, intrinsic object features,
such as orientation or size, facilitates the specific motor actions required to interact with that object, despite them being task-irrelevant.

(2) The main alternative account to the object affordance hypothesis is that of the attentional-orienting hypothesis in which it is suggested that visual asymmetry of the experimental stimuli results in attentional shifts to the most salient and/or behaviourally relevant location (e.g. handle) of the object. Consequently, according to this view, object affordance effects are merely a form of spatial compatibility effect rather than the effect arising from the actions that the objects afford.

(3) There is evidence to suggest that older adults, in a similar manner to Parkinson's patients, have difficulties in resisting entrainment by visual stimuli and that they become more reliant on information in their environment to support behaviour. Conceivably, this increased reliance on external stimuli would result in age-related increases in the size of compatibility effects.

(4) The importance of the fronto-parietal network for visuomotor integration including reaching and grasping is well documented. Motor control and action is predominantly lateralised to a left-hemispheric fronto-parietal network whereas visuospatial attention is predominantly lateralised to the right-hemispheric fronto-parietal network.
(5) There is a substantial amount of research which has documented age-related degeneration of white matter integrity, particularly relating to the corpus callosum and age-related changes in microstructural integrity are well documented throughout the brain. Conceivably, these age-related neurophysiological changes impact on visuomotor integration and would result in age-related decreases of object affordance compatibility effects.

My main hypothesis is as follows: based on the presumption that successful visuomotor behaviour relies on fronto-parietal integration and that white matter integrity presumably is compromised to some extent in the older group, we predict that the older group will exhibit reduced object-size compatibility effects. Such findings, particularly if accompanied by age-related degeneration of white matter microstructural integrity, would be consistent with an account of ageing in which the decline of perceptual, cognitive and motor function is driven, at least in part, by a decline in neural/structural connectivity. An alternative to our account and prediction would be that the increased reliance on external stimuli in older adults would result in age-related increases in the size of spatial compatibility effects and/or object-orientation effects. Such findings would suggest that visuomotor processes as indexed by compatibility effects would primarily be due to older adults having difficulty in suppressing the irrelevant spatial information. Finally, we found it important also to address the main alternative account of object affordance effects; the attention-directing hypothesis (see below).
Four behavioural experiments and one neuroimaging study will address a number of questions related to visuomotor integration and potential age-related changes therein. Chapter 3 (experiment 1) will examine age-related differences in the object-size affordance effect using the same behavioural paradigm, grip devices and experimental stimuli as that of Tucker and Ellis (2001). Chapter 4 (experiment 2) will examine age-related differences in the object-orientation effect using the same behavioural paradigm and experimental stimuli as that of Galpin and colleagues (2011). More specifically, it will investigate the object-orientation affordance effect and the spatial-compatibility effect within the same study. Furthermore, it will examine whether the affordance and spatial effects arise from facilitation by compatible stimuli or interference from incompatible stimuli. Chapter 5 (experiments 3 and 4) will examine object-size affordance effects in younger individuals, using a new stimulus set which was created in order to address the most prominent alternative explanations for the affect, the spatial and attention-directing hypothesis specifically. The final experiment is a neuroimaging experiment which combines behavioural data (chapter 6) functional MRI data (chapter 7) and diffusion tensor imaging, DTI data (chapter 8). It will examine age-differences in object-size affordance effects and its neural substrates, including indices on microstructural integrity, using the same stimulus set which was employed in experiments 3 and 4. As we propose that potential age-related differences in object affordance effects may have, at least in part, a neurophysiological basis, this final experiment will seek to elucidate whether such age effects, if present, may be in fact be attributed to age-related neurophysiological changes. The final chapter (chapter 9) will include an
experimental summary and offer a few recommendations for further investigations as well as a discussion of the implications that the empirical findings of the current thesis may have on our understanding of healthy ageing and visuomotor integration.
Chapter 3

Experiment 1. Are there age-differences in object-size affordance effects?

To date, to the author’s knowledge, there has been no research investigating age-related differences in object affordance effects (neither object-orientation nor object-size compatibility effects) in healthy younger and older individuals. The study presented here was conducted as an initial exploration of potential age-related differences, using the same bi-manual stimulus-response compatibility paradigm as well as the same precision and power grip response devices as that of Tucker and Ellis (2001, experiment 5 – described in further detail below).

The first study to employ the precision and power grip devices used in all but one experiment in this thesis was that of Ellis and Tucker (2000) (for further details and pictures of the grip devices, please see the method section of the current chapter). Their stimulus set consisted of 40 commonly known objects, half of which would normally be grasped with a precision grip (i.e. with the distal phalanges of the index finger and thumb), and the other half would normally be grasped with a power grip (i.e. with the phalanges of the fingers opposing the palmar surface). The stimuli were real objects which were placed in a box with a one-way viewing screen. At the onset of each trial a light came on which made the object visible to participants and after 700 ms a low pitch or high pitch sounded to which participants were required to make a response
(half of whom responded with a precision grip to a high tone and power grip to a low tone and vice versa). A uni-manual setup was used, i.e. all participants held both the precision and power grip device in their right hands. Despite the sizes of the objects being irrelevant to the task, there was a highly significant object-size compatibility effect with responses to compatible objects (e.g. a precision grip to a small object) being executed faster than to incompatible objects (e.g. a precision grip to a large object). The authors termed this potentiation of the grasping component ‘micro-affordance’.

Tucker and Ellis (2001) conducted a series of experiments to further investigate the observed object-size compatibility effect (Ellis and Tucker, 2000). Participants were asked to categorise commonly known objects as either manufactured or natural by making either precision or power grip responses. Within each category, half of the objects were compatible with a precision grip (e.g. a screw) and half were compatible with a power grip (e.g. a hammer). The first experiment used real objects, the remaining four used colour photographs presented on a computer monitor. Their study primarily used a uni-manual setup where both the precision grip and power grip were held in the right hand. Only one of their presented series of experiments (experiment 5) used a bi-manual setup in which half of the participants held the precision grip in their right hand and power grip in their left hand in the first block and swapped the devices to the opposite hands half way through the experiment (and vice versa for the other half of participants). Although the sizes of the objects were irrelevant to the task, highly significant object-size compatibility effects were observed also in these experiments; responses were executed faster to
compatible objects than to incompatible objects. In addition, using a bi-manual setup where a full power grip could be used resulted in similar, if not larger effects than a uni-manual setup. These experiments thus provided support for the notion that the action relevant object properties (in these cases size) influenced reaction times despite being task irrelevant.

The main objective of the current study was to investigate, for the first time, whether there were any potential age-related differences in the object-size compatibility effect in healthy younger and healthy older individuals, using the same behavioural paradigm, grip devices and experimental stimuli as that of Tucker and Ellis (2001, experiment 5) described above. We predicted a significant object-size compatibility effect to be observed also in the present study. Furthermore, based on the presumption that successful visuomotor behaviour rely on fronto-parietal integration and that white matter integrity presumably is compromised to some extent in the older group, it was predicted that the older group would exhibit a reduced object-size compatibility effect.

3.1 Method

Participants

Twenty-eight healthy younger adults (4 men and 24 women aged 19-30 years, \( M = 24 \)), and twenty-eight healthy older adults (9 men and 19 women aged 65-75 years, \( M = 69 \)) participated in this study. All participants gave informed consent prior to beginning the tasks, and all were naïve as to the purpose of the study. All participants were right-handed, as assessed by the short version of
The Edinburgh Handedness Inventory (EHI; Oldfield, 1971), had normal or corrected to normal vision, normal motor function and no history of neurological disorder or stroke (by self-report). In the group of younger participants, 26 had a minimum of 12 years of education, the remaining two had between 9-12 years of education. In the group of older participants, 15 had a minimum of 12 years of education, the remaining 13 had between 9-12 years of education.

Materials and apparatus

Participants were seated in front of a computer monitor, holding two response devices, one in each hand. The response devices mimicked power and precision grips (see figure 3.1). The power grip device was a plastic cylinder, 11 centimetres long and with a diameter of 3 cm, and had a pressure switch inserted at the top. The precision grip device was a pressure switch measuring 1 cm square and 4 mm thick. The switches clicked when pressed. Participants held the power grip between the fingers and surface of the palm, and the precision grip between their index finger and thumb. Their hands were resting on a table in front of their body mid-line, and the viewing distance was approximately 60 centimetres. E-prime (version 2.0) software (Schneider, Eschman, & Zuccolotto, 2002) was used for stimulus presentation on a 20 inch monitor with a resolution of 1680 by 1050 pixels. Participants’ handedness was assessed using the amended short version of the Edinburgh Handedness Inventory (EHI; Oldfield, 1971). Participants’ cognitive function was assessed using The Mini-Mental State Examination, a brief measure of memory and attention (MMSE; Folstein, Folstein, & McHugh, 1975).
Figure 3.1. The power grip (left) and precision grip (right) devices.

**Stimuli**

The experimental stimuli were the same as those used in Grezes et. al. (2003) (see figure 3.2, listed in appendix 3A). The stimuli were colour photographs of 40 commonly known objects; 20 natural objects and 20 manufactured objects, and within each category half of the objects were small (normally grasped with a precision grip, such as a strawberry and a paperclip) and the other half large (normally grasped with a power grip, such as a banana and a hammer). The stimuli subtended approximately 3.6 to 31 degrees in visual angle, and all stimuli were presented on a black background which filled the rest of the screen.
Figure 3.2. Example of large and small objects within the natural and manufactured categories.

**Procedure**

Participants were asked to categorise the objects as either natural or manufactured by pressing the appropriate device. Half the participants were asked to press the precision grip for natural objects and the power grip for manufactured objects, and half received the opposite instructions. These response mappings, to which participants were randomly allocated, remained the same within participants throughout the experiment. In each of the two response mappings, half of the participants held the precision grip in their right hand and power grip in their left hand in the first block (and vice versa for the other half), and swapped the devices to the opposite hand for the second block. This arrangement is referred to as hand mapping. On each trial, a fixation cross
appeared at the centre of the screen for 1 second followed by the target object
which remained in view until a response had been made or until 2 seconds had
elapsed. There were 320 trials in total, 160 in each block, and participants
received 20 practice trials before each of the two blocks. In the practice trials,
participants heard a beep if they responded incorrectly.

3.2 Results

The Edinburgh Handedness Inventory, (EHI), and The Mini-Mental
State Examination, (MMSE)

All participants were classified as right-handed when calculated in accordance
with the standard cut-off points of the EHI, (Oldfield, 1971); (-100 to -40 = left-
handed, -40 to +40 = ambidextrous, and +40 to +100 = right-handed). For the
younger group, the mean handedness score was $M = 93.36$, ($SD = 14.14$) and for
the older group $M = 93.04$ ($SD = 12.07$). All participants scored greater than 26
on the MMSE, thus indicating normal cognitive function (Folstein et al., 1975)
($M_{younger} = 29.32$, $SD = 1.02$, $M_{older} = 28.71$, $SD = 1.27$).

Error rates

In addition to the 28 younger and 28 older participants whose data are included
in the analysis, an additional 6 participants took part in the study but their data
was discarded from the final sample. Of these 6 participants, 2 older
participants were unable to complete the experiment due to arthritis and the
remaining 4 participants (2 younger, 2 older) were excluded due to error rates
exceeding 10 percent. For the remaining participants, error trials, totalling 1.82 %
(2.44 % for the younger group, and 1.19 % for the older group) were excluded from the analysis. As in the original study, reaction times more than 2 SDs from each participant’s average RT, totalling 4.25 % (4.62 % for the younger group, and 3.88 % for the older group), were also excluded from analysis.

Response times – main analysis

The means from the remaining data were analysed using a mixed factorial analysis of variance (ANOVA). The two between-subjects factors were age group (younger, older) and response mapping (1. natural = precision grip, manufactured = power grip or 2. natural = power grip, manufactured = precision grip). The three within-subjects factors were hand mapping (hand mapping 1. precision grip right hand and power grip left hand, and hand mapping 2. precision grip left hand, power grip right hand), grip type (precision or power grip), and object size (small or large).

The ANOVA revealed three highly significant main effects; grip type, object size and age. Precision responses ($M = 558$) were faster than power responses ($M = 586$), $F(1,54) = 38.25, p < .001, \eta^2_p = .424$. Participants responded faster to large objects ($M = 566$) than small objects, ($M = 579$), $F(1,54) = 43.16, p < .001, \eta^2_p = .454$. The younger participants were significantly faster than the older participants, ($M = 520$ and $M = 625$ for the younger and older group, respectively), $F(1,54) = 23.63, p < .001, \eta^2_p = .312$. Thus, the older group responded, on average, 105 ms slower than the younger group.

Of more interest was the finding that there was a significant compatibility effect reflected by the significant interaction between grip type and object size, $F(1,54)$
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= 54.91, \( p < .001, \eta_{p}^{2} = .514 \). Participants responded faster with both precision and power grips to compatible objects than incompatible objects, (see figure 3.3).

![Figure 3.3. Main analysis. Mean RTs for both age groups combined by grip type (precision or power grip) and object size (small or large). Bars show standard errors.](image)

There was a significant interaction between hand mapping and grip type, \( F(1,54) = 6.51, p = .014, \eta_{p}^{2} = .111 \); the RT difference between precision and power grips were larger in hand mapping 1 \((M = 36)\) than HM 2 \((M = 21)\). There was a significant three-way interaction between grip type, object size and response mapping, \( F(1,54) = 4.13, p = .047, \eta_{p}^{2} = .074 \); the compatibility effect was approximately 13 ms in RM 1 and 22 ms in RM 2. Of more interest was the finding that the compatibility effect differed between hand mappings as demonstrated by the significant three-way interaction between grip type, object size, and hand mapping, \( F(1,54) = 5.22, p = .026, \eta_{p}^{2} = .091 \). In hand mapping 1
(HM 1), the overall compatibility effect was approximately 22 ms and in hand mapping 2 (HM 2) it was approximately 13 ms.

Of most interest, however, was the finding that although the interaction between grip type, object size and age-group was not significant, \( F(1,54) = .226, p = .637, \eta^2_p = .004 \), the four-way interaction between hand-mapping, grip type, object size and age-group was significant, \( F(1,54) = 5.03, p = .029, \eta^2_p = .088 \), thus indicating a significant difference in the response patterns for the two age-groups in the two hand-mappings (see further step down analyses below the errors analysis). None of the other main effects or interactions were significant, for all \( F < 2.9 \).

**Errors analysis**

Incorrect responses were entered into an ANOVA. There was a significant main effect of age, \( F(1,49) = 6.64, p = .013, \eta^2_p = .119 \), with the older group making fewer errors than the younger group. There was also a significant effect of grip type, \( F(1,49) = 23.65, p < .001, \eta^2_p = .326 \), in that more errors were made when responding with power grips. Finally, there was a significant interaction between grip type and age group, which revealed a larger proportion of power grip errors in the younger group than in the older group, \( F(1,49) = 5.32, p = .025, \eta^2_p = .098 \). Unlike the main RT analysis, there was no effect of compatibility, i.e. participants did not make significantly more errors in incompatible conditions, but the patterns followed the RTs, \( F(1,49) = 1.84, p = .181, \eta^2_p = .036 \). No other main effects or interactions were significant.
Step down analysis – hand mappings

As the four-way interaction in the main analysis was significant (suggesting age-differences in the compatibility effect across the two hand-mappings), and since it has been observed that the compatibility effect is larger when precision grips are made with the right hand and power grip with the left hand as opposed to the opposite hand mapping (Vainio, Ellis, & Tucker, 2006), supplementary analyses were carried out to explore this further, as well as whether the size of the compatibility effect differed between the two age groups for each hand mapping.

Two ANOVAs were carried out, one for each hand mapping (mapping 1. precision grip in the RH / power grip LH, and mapping 2. precision grip LH / power grip RH). As in the main analysis, the remaining within-subjects factors were grip type (precision or power grip), and object size (small or large). The between-subjects factor of age was included, but since the between-subjects factor of response mapping did not approach significance in the main analysis, that factor was left out of the following analysis. For both hand mappings, the same three main effects as the main analysis were significant; grip type, object size and age, and like in the main analysis, both also revealed a significant interaction of grip type and object size.

For hand mapping 1 (Precision RH / Power LH), precision responses ($M = 559$) were faster than power responses ($M = 594$), $F(1,54) = 36.04$, $p < .001$, $\eta^2_p = .400$. Participants responded faster to large objects ($M = 570$) than small objects, ($M = 583$), $F(1,54) = 17.58$, $p < .001$, $\eta^2_p = .246$. The younger participants were significantly faster than the older participants, ($M = 519$ and
$M = 634$ for the younger and older group, respectively), $F(1,54) = 22.36, p < .001, \eta^2_p = .293$. As in the main analysis, there was a significant interaction between grip type and object size $F(1,54) = 61.92, p < .001, \eta^2_p = .534$, reflecting the compatibility effect.

Of most interest was the finding that in mapping 1, there was also a significant interaction of grip type, object size and age group, $F(1,54) = 4.03, p = .050, \eta^2_p = .069$, revealing an overall smaller compatibility effect in older group. Indeed, for the younger group, precision responses to small objects were significantly faster ($M = 497$) than to large objects ($M = 510$) (two-tailed t-test, $P = .019$), and power grip responses to large objects were significantly faster ($M = 514$) than to small objects ($M = 556$), (two-tailed t-test, $P < .001$). For the older group, there was no significant difference in RT between small ($M = 611$) and large objects ($M = 616$) when making precision grip responses (two-tailed t-test, $P = .520$), but power grip responses to large objects ($M = 639$) were significantly faster than to small objects ($M = 667$), (two-tailed t-test, $P < .001$) (see figure 3.4, upper and lower panel for the younger and older group, respectively). Thus, in mapping 1, the overall object-size compatibility effect was approximately 27 ms for the younger group, whilst the overall compatibility effect for the older group was approximately 16 ms.
Figure 3.4. Mean RTs for the younger group (upper panel) and the older group (lower panel) in hand-mapping 1 (precision right hand / power left hand) by grip type (precision or power grip) and object size (small or large). Bars show standard errors.

For hand mapping 2 (Precision LH / Power RH), precision responses ($M = 558$) were faster than power responses ($M = 579$), $F(1,54) = 16.21, p < .001, \eta^2_p = .231$. Participants responded faster to large objects ($M = 562$) than small objects, ($M = 575$), $F(1,54) = 27.23, p < .001, \eta^2_p = .335$. The younger participants were significantly faster than the older participants, ($M = 521$ and $M = 616$ for the younger and older group, respectively), $F(1,54) = 20.14, p < .001, \eta^2_p = .272$. There was a significant interaction between grip type and object size.
$F(1,54) = 13.72$, $p = .001$, $\eta^2_p = .203$, reflecting the object-size compatibility effect. Unlike mapping 1, however, there was no interaction between grip type, object size and age-group, $F(1,54) = .952$, $p = .334$, $\eta^2_p = .017$.

![Bar chart](image1)

![Bar chart](image2)

**Figure 3.5.** Mean RTs for the younger group (upper panel) and the older group (lower panel) in hand-mapping 2 (precision left hand / power right hand) by grip type (precision or power grip) and object size (small or large). Bars show standard errors.

In sum, whilst the overall compatibility effect was very similar for the two age groups in the main analysis (approximately 18 msec and 16 msec for the younger and older group, respectively), there was a significant four-way interaction which indicated age-differences in compatibility effects across the
two hand mappings. Further analyses revealed significant age-differences in the size of the compatibility effect in hand-mapping 1 (27 ms for the younger group and 16 ms for the older group), but not in hand-mapping 2 (10 ms for the younger group and 16 ms for the older group).

3.3 Discussion

This initial exploration of age-related differences in the object-size compatibility effect produced three major findings; 1) the crucial compatibility effect was observed, 2) the size of the compatibility effect differed between hand-mappings, and 3) there were age differences in the size of the compatibility effect between hand mappings which supported our prediction of reduced compatibility effects in the older group.

Consistent with predictions, the results of this study corroborated previous findings of highly significant object-size compatibility effects with responses being faster to compatible objects than incompatible objects for both precision and power grip responses.

In addition, although it was not of any interest to our hypothesis and hence did not form part of our predictions, the results of the main RT analysis provided evidence that the size of the compatibility effect differed between hand-mappings. As our predicted age-differences were modulated by hand mapping, it is worth looking into this a bit further. In the present study there was an overall larger compatibility effect (approximately 22 ms) in hand mapping 1 (where participants held the precision grip in the right hand and power grip in
their left hand) than the opposite mapping (approximately 13 ms). Analyses in the original study (Tucker, & Ellis, 2001) were collapsed across hand-mappings so whether this effect was also present in that study is unknown.

Most other studies using the precision and power grip devices have used a uni-manual setup, so there is a general lack of evidence as regards the potential effect of hand mappings upon the object-size compatibility effect. There is one study, however, that specifically investigated manual asymmetries using the same precision and power grip devices with the same hand mappings as used here (Vainio, et al., 2006). Virtually all people prefer using one hand to the other when making skilled movements. In right-handed individuals, the left hand would typically take on a stabilising function whilst the right hand would be used to carry out the finer manipulation of objects (Napier, 1956). Consequently, Vainio and colleagues (2006) had hypothesised that the right hand would show superiority over the left hand for precision grips, thus leading to manual asymmetries. Their study differed from the present one in that it was a study of visually primed grasping; participants were presented with task-irrelevant prime objects and the explicit task was to respond to a target arrow that appeared superimposed over the prime. The computer generated 3D prime objects were either precision grip compatible (ball, cone and cylinder shapes) or power grip compatible (cylinder or capsule shapes). These objects appeared standing vertically and were therefore equally compatible with a right or left-handed grasp. Half of the participants held the precision grip in the right hand and power grip in the left hand and vice versa for the other half of the participants (hence, here hand mapping was a between-participants factor in
contrast to the present and previous (Tucker and Ellis, 2001) studies. Their main analysis revealed the crucial object size by grip type interaction, reflecting the predicted object-size compatibility effect. In addition, the compatibility effected also interacted with hand mapping, and the step-down analyses performed on each hand mapping separately revealed a significant compatibility effect for hand mapping 1 but not for hand mapping 2, thus supporting their predictions. We shall refer to hand mapping 1 (precision grip right hand, power grip left hand) as the preferred hand mapping. Furthermore, a second experiment replicated the right hand bias for small objects and left hand bias for large objects when the grip devices were replaced with simple left hand and right hand button presses (Vainio et al., 2006). Consequently, it was suggested by the authors that these results combined indicated the presence of manual asymmetries as well as a left-hemispheric specialisation for precision grips and right-hemispheric specialisation for power grips.

In sum, consistent with earlier findings (Vainio et al., 2006), results of our main analysis provided evidence of larger compatibility effects in the preferred hand mapping. Whereas Vainio and colleagues (2006) study found that the object-size compatibility effect was present only in the preferred hand-mapping and absent in the opposite mapping, our additional analysis broken down by hand-mapping did provide evidence of a significant object-size compatibility effect in both hand-mappings. Consequently, results of the present study provided support to the theory proposed by Vainio and colleagues.

However, the primary objective of this experiment was an investigation into whether there were any potential age-related differences in the object-size
compatibility effect. In short, based on the presumption that successful visuomotor behaviour rely on fronto-parietal integration and that white matter integrity presumably is compromised to some extent in the older group, we predicted reduced compatibility effects in the older group. Although the interaction between grip type, object size and age group was not significant, the four-way interaction including these three factors as well as hand mapping was significant. More specifically, consistent with our predictions of reduced compatibility effects for the older group, the step down analyses revealed a smaller compatibility effect for the older group (16 ms) than for the younger group (27 ms) in the preferred hand mapping. Whether this age-related reduction in the object-size compatibility effect may indeed be attributed to age-related neurophysiological changes in the visuomotor system is still speculative, considering that there have been no previous age-related investigations into either the object-orientation effect or the object-size effect in healthy ageing. We investigated this further in our functional MRI experiment (including behavioural data collected in the scanner) and DTI analyses which will be presented in subsequent sections (chapter 6 onwards).

As the age-difference in the compatibility effect was modulated by hand mapping whilst the overall compatibility effect was similar for the two age groups in the main analysis, an alternative interpretation may be that these results combined suggest a presence of a manual asymmetry in grasping that diminishes with age. Although motor asymmetries in younger adults are well documented, manual asymmetries in grasping have only been reported once using the same paradigm and grip devices as the present study, and only in
younger individuals (Vainio et al., 2006). Handedness is established in early childhood and remains stable throughout life (Raw, Wilkie, Culmer, & Mon-Williams, 2012). Age-related decline in manual proficiency, however, is well-documented on several different levels, such as general and pinch strength, bi-manual coordination, and older adults requiring extra time to manipulate objects (Kalish, Wilimzig, Kleibel, Tegenthoff, & Dinse, 2006). Nevertheless, there is less evidence of how advancing age effects hand dominance and asymmetries of hand use (Kalish, et al., 2006). As older adults have had decades of manual practice, one might expect that older adults would exhibit motor asymmetries that might even be more pronounced than in younger adults, but it is unclear whether the age-related decline in manual proficiency modifies the tendency towards motor asymmetries seen in younger adults (Raw et al., 2012). Others have suggested that as older adults have a more inactive lifestyle, the performance and ability of the dominant hand will decrease relative to the non-preferred hand, thus leading to an overall reduction in hand asymmetries (Kalish et al., 2006). One study specifically tested hand dominance and asymmetries of hand use in a group of 60 adults ranging from 20 to 90 years of age (Kalish, et al., 2006). A wide variety of both practical tests and questionnaires were administered and assessed, amongst others, motor performance of precision and speed of movement. An additional experiment was conducted in which accelerometer-sensors were employed in order to obtain objective measures of hand use in everyday actions (Kalish et al., 2006). In addition to a general task-dependent decline in motor performance with age, they found that older adults exhibited a more balanced hand performance compared to the young who showed more pronounced right-hand advantages.
This shift was caused by an age-related decline in right hand performance. The accelerometer test corroborated these findings in that the frequency of hand use shifted from a clear right-hand preference to a more balanced hand use in older adults in everyday activities. In contrast, another study which investigated potential age-differences in reaching found that whilst there was evidence of an asymmetry reduction in older adults, it was due to improved left hand performance rather than declines in right hand performance (Przybyla, Haaland, Bagesteiro, & Sainburg, 2011). To summarise, in general, the fairly limited amount of behavioural studies that have investigated hand dominance and asymmetries of hand use in older adults have employed very different tasks and methodologies. Although the general findings seem to suggest that there may be age-related reductions in manual asymmetries, the underlying reasons are unclear, including whether they may be caused by a decline in right-hand performance or improvement in left hand performance. In any way, these reductions are consistent with the reduced asymmetries observed in the present study.

Secondary findings worth mentioning included effects of grip type and object size. Precision grips were executed faster than power grips. This finding was to be expected as a pinch grip between index finger and thumb would presumably be faster to execute than a whole-hand grip between the fingers and surface of the palm. Responses to large objects were executed faster than to small objects, the likely explanation being that the larger objects are more visually salient and easier to categorize visually.
In sum, the results of this first investigation into potential age-differences in the object-size compatibility effect provided evidence of age-related decreases in the size of the compatibility effect, as predicted. Compatibility effects were observed in both hand mappings, and the age-difference was modulated by hand mapping in such a way that the older group, relative to the younger group, exhibited a reduced object-size compatibility effect in the preferred hand mapping. The potential effect of hand mapping upon the object-size compatibility effect will be explored further in experiments 3 and 4 using the same paradigm and grip devices, but a different stimulus set. Whether age-differences may be attributed to age-related neurophysiological changes will be further investigated in our behavioural and functional MRI as well as DTI experiments. First, however, an investigation of age-related differences in object-orientation affordance effects versus spatial compatibility effects and the locus of these effects (facilitation versus interference), will follow.
Chapter 4

Experiment 2. An exploration of age-differences in object-orientation effects versus spatial compatibility effects as well as the locus of these effects

As discussed in chapter 2, it is well established that the spatial location of an object influences reaction times despite being task-irrelevant (the so-called Simon effect, or spatial compatibility effect). It was also noted that older adults (in a similar manner to Parkinson’s patients), have been shown to have difficulties in resisting entrainment by visual stimuli. Furthermore, the few studies which have examined age-related differences in spatial compatibility effects suggest that older adults may be more affected by, and have greater difficulty in suppressing the irrelevant spatial information, which results in the size of spatial compatibility effects being up to 1.5 – 2 times that of younger individuals (Pick, & Proctor, 1999; Proctor et al., 2005; Van der Lubbe, & Verleger, 2002). Following from this, it would also imply that effects in older adults would be assumed to arise primarily from interference effects from incompatible stimuli. Of particular relevance for the current study is the finding that these age-related increases have been found to be particularly pronounced when both the relevant and irrelevant stimulus dimensions are presented within the same modality (Proctor et al., 2005), as is the case in the present study.
In addition to object location, reaction times to visual stimuli have also been demonstrated to be affected by the action relevant features contained within the object: the affordance effect discussed in the previous chapter. These affordance effects have been shown to occur in an independent manner to the spatial compatibility effects and two response codes can be activated, and, to some extent, summated; one pertaining to object location and one pertaining to type of grasp (Symes, Ellis, & Tucker, 2005).

Poliakoff and colleagues (Poliakoff, Galpin, Dick, Moore, & Tipper, 2007) investigated spatial and affordance effects within the same design in a group of Parkinson’s patients and age-matched controls. The action-relevant stimuli (the affording stimuli), were lateralised, graspable door handles oriented towards the left or the right, and the spatial stimuli were located in the same position, but were abstract bar stimuli intended to generate only spatial compatibility effects. The control group showed a larger affordance than spatial compatibility effect. Parkinson’s patients also showed affordance and spatial compatibility effects but, unlike controls, there was no significant difference between stimulus types. This supports a dissociation between the two types of effects in controls, but not the Parkinson’s patients.

A later study (Galpin, Tipper, Dick, & Poliakoff, 2011) expanded on this study by also including a baseline from which to measure whether the spatial and affordance effects were driven by facilitation by compatible stimuli or interference from incompatible stimuli. Furthermore, this study included three different stimulus onset asynchronies (SOAs), and participants were required to respond to a colour change of the object after 0 ms, 500 ms, or 1000 ms. As in
the earlier study, there was a highly significant compatibility effect. Consistent with the earlier study (Poliakoff et al., 2007), there was not a larger compatibility effect for the affording compared to spatial stimuli for the Parkinson's patients. The age-matched healthy controls did show a larger affordance than spatial effect, but only at the 500 ms SOA. In controls, the affordance effect was driven mainly from facilitation by compatible stimuli and the spatial effect was driven mainly by interference from incompatible stimuli. In Parkinson's patients, both the spatial and affordance effects were driven mainly by facilitation.

Galpin and colleagues (Galpin et al., 2011) kindly shared the experimental stimuli used in this study to allow us to extend this work in a group of healthy younger and older individuals. There were two main reasons for replicating this particular study; firstly, it allowed comparisons of spatial versus affordance compatibility effects within the same study (and potential age-differences therein). Secondly, it was the first study, to our knowledge, which included a baseline stimulus allowing an investigation of facilitation and interference effects in affordance and spatial effects. These are important aspects that need further examination due to the previously discussed literature, according to which an alternative prediction to ours would follow; namely an age-related increase in compatibility effects (at least as regards spatial-compatibility effects at that is the only of the two effects where age-related differences have previously been investigated). Furthermore, it would also follow that effects in the older group would be expected to arise primarily from interference effects. The procedures of the original study were adhered to, and identical data
analyses were performed (with the exception of the inclusion of one additional analysis of affordance versus spatial effects broken down by age group), in order to allow direct comparison with the earlier study.

4.1 Method

Participants

Thirty-six healthy younger adults (17 men and 19 women aged 19-30 years, \( M = 22 \)), and thirty-six healthy older adults (12 men and 24 women aged 63-79 years, \( M = 70 \)) participated in this study. All participants gave informed consent prior to beginning the tasks and all were naive as to the purpose of the study. One younger participant was ambidextrous and the remaining participants right-handed, as assessed by the short version of The Edinburgh Handedness Inventory (Oldfield, 1971). No participants were colour-blind, and all had normal or corrected to normal vision, normal motor function and no history of neurological disorder or stroke (by self-report). In the group of younger participants, 34 had a minimum of 12 years of education, the remaining two had between 9-12 years of education. In the group of older participants, 24 had a minimum of 12 years of education, the remaining 12 had between 9-12 years of education.

Materials and apparatus

E-prime (version 2.2) software (Schneider et. al., 2002) was used for stimulus presentation on a 20 inch monitor with a resolution of 1680 by 1050 pixels. Responses were collected on a serial-response box. Participants’ handedness
was assessed using the amended short version of the Edinburgh Handedness Inventory (EHI; Oldfield, 1971). Participants’ cognitive function was assessed using The Mini-Mental State Examination (Folstein et. al., 1975), and the two-subtest form of the Wechsler Abbreviated Scale of Intelligence, (WASI; Wechsler, 1999).

**Stimuli**

The experimental stimuli were kindly shared by Galpin, Tipper, Dick, & Poliakoff (2011). No changes to the original stimuli files were made, hence stimuli for the affordance condition were images of a door handle including the hinge (see figure 4.1.A below for photos of the stimuli). The hinge was presented in the centre of the screen and the handle extended from the centre of the screen diagonally downwards. The stimuli in the spatial condition were generated from the affordance stimuli; the hinge was removed, the handle was divided into 6 equal spherical segments and the shading misaligned in order to remove the appearance of an object but retain the same lateralised spatial position as the affordance stimuli. In both the affordance and spatial conditions, the stimuli extended from the centre of screen, approximately 6.9 cm horizontally and 6.4 cm vertically towards the bottom of the screen, and half were oriented towards the right, half towards the left. Finally, a centrally presented baseline condition was included from which to measure facilitation or interference effects. The stimuli used in the baseline condition were generated from the same 6 spheres; one sphere was presented centrally and the remaining 5 spheres around it in a circle. To prevent asymmetries of shading
unintentionally drawing attention to either side of the stimulus, stimuli were presented horizontally flipped for half of the trials.

**Procedure**

Participants were seated in front of a computer monitor with their index fingers resting on the extreme left and extreme right buttons of a serial-response box positioned on a table in front of their body mid-line. The viewing distance was approximately 60 centimetres. Each trial began with a black fixation cross on a white background which remained on screen for 2000 ms. In order to assess the development of compatibility effects over time, three stimulus onset asynchronies (SOAs) were included; 0 ms, 500 ms, and 1000 ms. Consequently, in two conditions, the fixation cross was followed by a silver stimulus object which changed colour to either green or blue after a delay of either 500 ms or 1000 ms. In the third (the 0 ms) condition, the silver stimulus did not appear, rather, the coloured stimulus appeared immediately in either green or blue. Participants’ explicit task was to respond to the stimulus colour that the object either appeared in, or changed to, making a button press with one index finger for one colour and the other index finger for the other colour (for the structure of a trial, see figure 4.1.B). The mapping between response hand and colour were counterbalanced between participants.
Figure 4.1. A) The three stimulus conditions. B) The structure of a trial.

In half of the trials, the task-irrelevant orientation was compatible with the hand of response (i.e. the hand typically used to operate a handle of this orientation in addition to being spatially compatible), in half incompatible. The coloured image remained on screen until participants made a response or until 1700 ms had elapsed. Feedback was presented for 2000 ms following erroneous responses; “Too early, please wait for the colour change” if participants responded before the object had changed colour, “Incorrect” if they responded with the wrong hand, and “No response” when the 1700 ms had elapsed.

Three separate blocked conditions were run once each; one with door handles presented laterally (affordance condition), one with lateral stimuli intended not to generate affordances but which retained the same lateralised position as the affordance condition in order to preserve spatial-compatibility effects (spatial condition), and one with centrally presented stimuli which had no compatibility with response hand (baseline condition). The order of the three experimental conditions was counterbalanced across participants as in the original study.
(Galpin et al., 2011). Combined with the 2 response mappings, this produced 6 possible versions with 6 participants allocated to each. There were 12 possible trial types in each condition; orientation (left, right), colour (green, blue), SOA, (0 ms, 500 ms, and 1000 ms). The affordance and spatial conditions began with a practice session of 24 trials and were followed by the respective experimental blocks which consisted of 192 trials (each trial type was presented 16 times in random order). In the baseline condition there were only 12 practice trials and 96 experimental trials due to the orientation factor not being applicable in this condition.

4.2 Results

The Edinburgh Handedness Inventory, (EHI), The Mini-Mental State Examination, (MMSE), and Wechsler Abbreviated Scale of Intelligence, (WASI).

All participants were right-handed apart from one younger participant who was classified as ambidextrous when calculated in accordance with the standard cut-off points of the EHI; (-100 to -40 = left-handed, -40 to +40 = ambidextrous, and +40 to +100 = right-handed). For the younger group, the mean handedness score was $M = 89.81$, ($SD = 16.87$) and for the older group $M = 90.67$ ($SD = 11.85$). All participants scored greater than 26 on the MMSE, thus indicating normal cognitive function ($M$ younger = 29.34, $SD = 1.10$, $M$ older = 28.97, $SD = 1.03$). To obtain an assessment of general intellectual functioning, the two-subtest form of the Wechsler Abbreviated Scale of Intelligence, (WASI), which is comprised of one verbal and one nonverbal test, was administered. Both age-
groups were classified as having average scores; \( M \) younger = 108.69, (\( SD = 9.61 \)) \( M \) older = 114.52 (\( SD = 8.01 \)).

**Error rates**

Three younger participants did not comply with instructions, one participant's error rates exceeded 10 percent, and two older participants were unable to complete the experiment due to arthritis. These six participants were removed from the sample and replaced, thus a total of 36 younger and 36 older participants’ data were included in the analysis. Error trials, totalling 2.05 % (3.13 % for the younger group, and 0.99 % for the older group) were excluded from the analysis. Reaction times more than 3 standard deviations (SDs) from each participant’s average RT were also excluded from analysis (0.01 % for both age groups).

**Response times - main analysis**

The means from the remaining data were analysed using a mixed factorial analysis of variance (ANOVA). The between-subjects factor was age group (younger, older), and the three within-subjects factors were stimulus type (affordance, spatial), compatibility (compatible, incompatible) and SOA (0 ms, 500 ms, and 1000 ms). Greenhouse-Geisser values are reported where it was necessary to correct for violations of sphericity.

The ANOVA revealed three highly significant main effects; age, compatibility, and SOA. The younger group of participants (\( M = 450 \)) were significantly faster than the older group (\( M = 568 \)), \( F(1,70) = 42,423, p < .001, \eta^2_p = .377 \). As in the original study, a highly significant effect of compatibility was observed due to
participants responding faster when the stimulus orientation and hand of response were compatible ($M = 497$) versus incompatible ($M = 521$), $F(1,70) = 82.160, p < .001, \eta^2_p = .540$. Also consistent with previous results, a large effect of SOA was obtained due to slower RTs at the 0 ms SOA ($M = 579$) than at the 500 ms SOA ($M = 480$), which in turn was longer than the RTs at the 1000 ms SOA ($M = 468$), $F(1,70) = 497.050, p < .001, \eta^2_p = .877$.

There was an interaction between SOA and age-group, $F(1,70) = 11.433, p < .001, \eta^2_p = .140$. Within-subjects contrasts revealed that there were significant differences between young and old for the 0 ms versus 500 ms SOAs, $F(1,70) = 20.722, p < .001, \eta^2_p = .228$, and also for the 500 ms versus 1000 ms, $F(1,70) = 16.978, p < .001, \eta^2_p = .195$, but not for the 0 ms versus 1000 ms, $F(1,70) = 3.143, p = .081, \eta^2_p = .043$. Overall, younger participants’ RTs were more directly affected by SOA than older participants’ RTs.

Unlike the original study there was no main effect of stimulus type; affording stimuli ($M = 507$) did not elicit significantly faster RTs than spatial stimuli ($M = 511$), $F(1,70) = .869, p = .335, \eta^2_p = .012$. There was a significant interaction between stimulus type and SOA, $F(1,70) = 5.133, p = .011, \eta^2_p = .068$. Within-subjects contrasts revealed significant differences between affording and spatial stimuli for the 0 ms versus 500 ms, $F(1,70) = 4.880, p = .030, \eta^2_p = .065$, and the 0 ms versus 1000 ms, $F(1,70) = 10.124, p = .002, \eta^2_p = .126$, but not for the 500 ms versus 1000 ms, $F(1,70) = .063, p = .803, \eta^2_p = .001$. In other words, participants responded faster to affording stimuli than spatial stimuli in the 500 ms and 1000 ms condition, but not in the 0 ms condition. This pattern did not interact with age-group.
There was also a significant interaction between compatibility and SOA, $F(1,70) = 14.003, p < .001, \eta^2_p = .167$. The factorial within-subjects contrasts revealed significant decreases in the size of the compatibility effect from the 0 ms to the 500 ms, $F(1,70) = 16.685, p < .001, \eta^2_p = .192$, and from the 0 ms to the 1000 ms, $F(1,70) = 19.574, p < .001, \eta^2_p = .219$, but not from the 500 ms to the 1000 ms, $F(1,70) = 1.524, p = .221, \eta^2_p = .021$. Thus, the overall compatibility effects decreased with increasing SOAs (44 ms, 22 ms, and 17 ms respectively), which is consistent with the original study (41 ms, 29 ms and 22 ms, respectively). This effect did not interact with age-group.

Even though both age-groups showed an overall larger effect for affording stimuli (27 ms and 28 ms for the younger and older group, respectively), than for spatial stimuli (18 ms and 25 ms for the younger and older group) as would be expected, these differences in effect magnitudes were not statistically significant, $F(1,70) = 2.783, p = .100, \eta^2_p = .038$. No other main effects or interactions were significant, for all, $F < 1.8$.

**Affordance versus spatial compatibility effects:**

As in the original paper (Galpin et al., 2011), pre-planned comparisons were carried out to explore potential differences between the compatibility effects for the affording and spatial stimuli at each SOA for each age-group (see Figure 4.2 below). First, two separate ANOVAs, one for each age group, were carried out. For the younger group there was an effect of stimulus type upon the compatibility effect, $F(1,34) = 4.776, p = .036, \eta^2_p = .120$, reflecting a larger compatibility effect for affording than spatial stimuli. For the older group there was no significant difference in effect magnitudes for affording versus spatial...
stimuli, $F(1,34) = .262, p = .612, \eta^2_p = .007$. There was, however, a hint of an effect when split by SOA, as evidenced by the interaction between stimulus type, compatibility and SOA approaching significance in the older group, $F(1,34) = 3.810, p = .059, \eta^2_p = .098$.

The pre-planned comparisons supported both of these findings; the paired samples t-tests revealed that for the younger group, in the 0 ms condition, the affording stimuli produced larger compatibility effects than did the spatial stimuli, $t(35) = 1.758, p = .044$. The affordance and spatial compatibility effects did not differ at the 500 ms or 1000 ms SOA; $t(35) = 1.078, p = .145$, and $t(35) = 1.388, p = .087$, respectively. For the older group, there was no difference between the affording and spatial stimuli at the 0 ms, 500 ms or 1000 ms SOA; $t(35) = 1.494, p = .072$, $t(35) = -.393, p = .349$, and $t(35) = -.645, p = .262$, respectively. These results therefore provide evidence for a dissociation of affordance and spatial compatibility effects for the younger group, but not for the older group (see figure 4.2). The original study found a dissociation in the controls but not the Parkinson’s patients (Galpin et al., 2011).
Response times compared to baseline:

In order to assess whether the observed compatibility effects arose from facilitation from compatible stimuli or interference from incompatible stimuli, each participant's performance in the affordance and spatial condition was compared to their performance in the baseline condition. We labelled this as the baseline-difference score. Each participant's average RTs for the compatible and incompatible stimuli in each condition and each SOA were subtracted from
each participant’s average baseline RT. Thus, a positive score would indicate RTs faster than baseline stimuli. Figure 4.3 shows the result of this analysis, collapsed across SOA.

These results indicated that for the younger participants, the compatibility effect in both the affordance and spatial conditions were driven mainly by interference from incompatible stimuli. For the older participants, results indicated that the spatial compatibility effect was also driven mainly by interference whereas the affordance compatibility effect was driven both by interference by incompatible stimuli and facilitation by compatible stimuli (see figure 4.3).
Figure 4.3. Mean RTs for compatible and incompatible conditions collapsed across SOA, compared to the baseline stimuli for both age-groups and for both the affordance (AFF) and spatial (SPA) conditions. Positive scores indicate RTs faster than baseline (x-axis). * Indicates RTs being significantly different to baseline.

Following procedures of the original paper (Galpin et al., 2011), pre-planned one-sample t-tests were carried out on the baseline-difference scores for each age group at each SOA (see table 4.1 below). In the affordance condition, for the younger group, incompatible stimuli resulted in slower RTs at the 0 ms and 500 ms SOA, whereas RTs to compatible stimuli did not significantly differ from
baseline. In the spatial condition incompatible stimuli led to slower RTs at the 0 ms SOA only, and compatible stimuli did not significantly differ from baseline.

For the older group incompatible stimuli in the affordance condition led to slower RTs at the 0 ms SOA and RTs to compatible stimuli were significantly faster than baseline for both the 500 ms and 1000 ms SOA. For the spatial condition incompatible stimuli resulted in significantly slower RTs at all three SOAs whilst compatible stimuli did not significantly differ from baseline.

Table 4.1

Results of one-sample t-tests comparing response times subtracted from baseline RTs for each condition for the younger and older group. A positive t-value indicates RTs faster than baseline.

<table>
<thead>
<tr>
<th></th>
<th>0 msec</th>
<th>500 msec</th>
<th>1000 msec</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Younger group</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Affordance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Compatible</td>
<td>.133, p = .895</td>
<td>1.239, p = .224</td>
<td>1.827, p = .076</td>
</tr>
<tr>
<td>Incompatible</td>
<td>-4.524, p &lt; .0005*</td>
<td>-2.155, p = .038*</td>
<td>-1.197, p = .239</td>
</tr>
<tr>
<td>Spatial</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Compatible</td>
<td>.597, p = .555</td>
<td>.806, p = .426</td>
<td>.330, p = .744</td>
</tr>
<tr>
<td>Incompatible</td>
<td>-2.701, p = .011*</td>
<td>-1.400, p = .170</td>
<td>-1.324, p = .194</td>
</tr>
<tr>
<td><strong>Older group</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Affordance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Compatible</td>
<td>.687, p = .496</td>
<td>2.617, p = .013*</td>
<td>2.072, p = .046*</td>
</tr>
<tr>
<td>Incompatible</td>
<td>-4.312, p &lt; .0005*</td>
<td>-3.31, p = .742</td>
<td>-1.63, p = .872</td>
</tr>
<tr>
<td>Spatial</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Compatible</td>
<td>-.323, p = .749</td>
<td>.785, p = .438</td>
<td>.715, p = .480</td>
</tr>
<tr>
<td>Incompatible</td>
<td>-3.712, p = .001*</td>
<td>-2.241, p = .031*</td>
<td>-2.082, p = .045*</td>
</tr>
</tbody>
</table>

* Indicates it is significantly different from baseline (p < .05)

**Errors analysis**

Incorrect responses were subjected to an ANOVA using the same between- and within-subjects factors as for the response time analysis with the proportion of errors as the dependent variable. As per the main RT analysis, there was a highly significant effect of compatibility, F(1,70) = 34.38, p < .001, η²p = .329 due to participants making significantly more errors in incompatible conditions,
thus providing support for the trends found in the RT data. There was also an effect of age, F(1,70) = 20.61, p < .001, \( \eta^2_p = .227 \), with the older group making significantly fewer errors than the younger group.

Similar to the RT data, there was also an effect of SOA, F(1,70) = 29.32, p < .001, \( \eta^2_p = .295 \), due to number of errors decreasing significantly with increasing SOAs, and SOA also interacted with age in that the reduction in proportion of errors was more prominent for the younger group from the 0 ms to 500 ms compared to the older group, F(1,70) = 6.30, p = .014, \( \eta^2_p = .083 \). There was an interaction between compatibility and SOA, F(1,70) = 20.20, p < .001, \( \eta^2_p = .224 \), with the proportion of errors being most prominent in the 0 ms incompatible condition. Unlike the RT data there was a significant interaction between age group and compatibility, F(1,70) = 15.63, p < .001, \( \eta^2_p = .182 \), with the compatibility effect being larger for the younger group.

Finally, there was a significant three-way interaction between age group, compatibility and SOA, F(1,70) = 5.38, p = .023, \( \eta^2_p = .071 \). This effect was not observed in the main RT analysis. The proportion of errors was larger in incompatible conditions in all three SOAs, with the highest level observed in the 0 ms incompatible condition for both age groups. For the younger group there was a linear decline in the error rates with increasing SOAs, whereas for the older group error rates were similar across the last two SOAs. As for the amount of errors to compatible objects they were virtually identical over the three SOAs for both age groups.
4.3 Discussion

We examined firstly, whether there were any age differences in affordance and spatial compatibility effects in healthy younger and healthy older individuals and secondly, whether there were any age differences in the locus of the effects, i.e. whether affordance and spatial compatibility effects arose from facilitation by compatible stimuli or interference from incompatible stimuli.

Results of the main analysis were largely consistent with the original study of Galpin and colleagues (2011). The most noteworthy results emerged in the lower-level analyses of the time course, which suggested a dissociation between affordance and spatial compatibility effects in the younger group but not the older group. Of equal importance were the findings from the baseline comparison which allowed an investigation of facilitation versus interference effects as these indicated that the processes eliciting the affordance and spatial compatibility effects differ with age. More specifically, in the younger group both effects were driven mainly by interference. In the older group, the spatial effect was driven mainly by interference whereas the affordance effect was due to both facilitation and interference.

A highly significant effect of compatibility was observed due to participants responding faster when the stimulus orientation and hand of response were compatible versus incompatible. Although a review of the (rather limited) investigations into age-related differences in spatial-compatibility effects (Proctor et al., 2005) suggested that the effect magnitude is typically 1.5 - 2 times larger for older individuals (and also that age-differences are particularly
pronounced when both the relevant and irrelevant dimensions are presented within the same stimulus, as in the present study), results of our main analysis provided no evidence to this effect. Consequently, our results did not support the notion that older adults were differentially affected by the irrelevant spatial information.

In the main analysis both age groups showed an overall larger affordance than spatial effect although the differences in effect magnitudes were not significant. Our additional analysis which investigated this effect broken down by age group, revealed a statistically larger compatibility effect for affording than spatial stimuli for the younger group. This effect was not present for the older group albeit there was a hint of an effect when split by SOA. The pre-planned comparisons investigating compatibility effects for each of the stimulus types at each SOA revealed a somewhat different pattern of results compared to the original study in terms of time course. The original study found a dissociation between the affording and spatial stimuli for the control group, but only for the 500 ms SOA, and found no differences the Parkinson group. Our study, in contrast, found evidence of larger affordance than spatial effects for the younger group only in the 0 ms SOA. Our results, therefore, provided evidence for a dissociation of affordance and spatial compatibility effects in the younger age group, but found no differences in the older group.

One reason for the weak effects might be that a colour-discrimination task was used. The earlier Parkinson’s study (Poliakoff et al., 2007) which employed a shape discrimination task (bars versus door handles) did find a larger compatibility effect for controls for the affording stimuli than the spatial stimuli
at what was, effectively, a 0 ms SOA. The lack of a larger affordance than spatial effect in the 0 ms condition in the later study (Galpin et al., 2011) was suggested by the authors to be due to the change from a shape discrimination to a colour discrimination task. This would be consistent with previous findings as using low-level visual features for response selection, such as colour, tend to produce much smaller compatibility/affordance effects (e.g. Symes, Ellis, & Tucker, 2005; Vainio, Ellis, & Tucker, 2007).

Of most relevance to the present study is a series of experiments by Tipper and colleagues (Tipper, Paul, & Hayes, 2006) who employed both a shape and a colour discrimination task within the same paradigm and used almost identical stimuli to those of the Parkinson’s studies (half of the participants responded to the shape of door handles, the other half to the colour of door handles). They did not employ stimulus onset asynchronies, so it was effectively a 0 ms SOA. The shape discrimination task produced highly significant compatibility effects whereas the colour discrimination task produced no significant compatibility effects. The authors (Tipper et al., 2006) argued that the property of the object which is attended is crucial for the action affordances to be induced. More specifically, an object’s shape is relevant for interacting with it, its colour is not. Thus, these results would appear to support the account that when using low-level visual features (such as a colour discrimination task), the lack of compatibility effects might be attributed to insufficient time to form an object representation as suggested by Symes and colleagues (Symes et al., 2005). This view would imply, however, that a colour categorisation task is resolved faster than other categorisation tasks. There are a few important things to note in this
regard. In Symes and colleagues’ study (Symes et al., 2005), the reaction times of the colour categorisation task were indeed much faster than the object categorisation tasks. This was not the case for Tipper and colleague’s study; here both the colour and shape discriminations were resolved around the same time. Hence, this account cannot directly explain the presence of a compatibility effect in the (door handle) shape discrimination task and lack of same in the (door handle) colour discrimination task, but instead seems to support the authors’ suggestion that the property of the object which is attended is crucial. Similarly, in the present study, participants were required to attend to object colour in both the affordance and spatial conditions and both discriminations were resolved around the same time, so again, this line of argument would not explain the presence of larger affordance than spatial effects. In light of the present findings with both the slowest reaction times and the strongest dissociations being observed in the 0 ms condition, speed of processing may have an impact on compatibility/affordance effects. However, despite the slowest reaction times also being observed in the 0 ms condition in the original study (Galpin et al., 2011) there was no evidence of a dissociation in this condition, hence there are no obvious reasons for these discrepancies in terms of the time-course of dissociation between affording and spatial stimuli.

Tipper and colleagues (Tipper et al., 2006) re-ran the shape discrimination task with bar stimuli which were identical to the door handle stimuli except for the removal of the hinge/door attachment component and therefore should not, according to the authors, be perceived as a door handle. Consequently, the experimental stimuli in this condition were almost identical to the spatial
stimuli employed in the present study. It should be noted though, that whereas the stimuli were rotated 45 degrees from horizontal in the present and the two Parkinson’s studies, this was only the case for half of the objects in Tipper and colleagues study - the other half were presented horizontally. This condition produced no significant compatibility effects. Although these three experiments by Tipper and colleagues are very similar to the present study (and the foregoing two Parkinson’s studies, self-evidently), the results are not necessarily/generally comparable to those of the present study. Considering previous evidence, one might, as a minimum, have expected a spatial-compatibility effect in the bar shape discrimination task. The most likely explanation is that in contrast to the present and the Parkinson’s studies where the hinge was presented in the centre of the screen and the handles extended laterally (and the spatial stimuli were in the same location), in Tipper’s and colleague’s study all stimuli were presented centrally. Hence, the horizontally presented bar stimuli would be equally graspable with either hand and therefore not be expected to evoke spatial compatibility effects. Contrary to centrally presented bars, the door handle stimuli used in the first experiment would be expected to evoke stronger left and right-handed grasps. Thus, in contrast to the earlier Parkinson’s study which did find both affordance and spatial effects (Poliakoff et al., 2007), the lack of a spatial-compatibility effect for this particular study (the bar shape discrimination task), may be explained by the location and orientation of the presented stimuli. In sum, despite the similarities of these four studies, both in terms of the employed paradigms and the experimental stimuli, the results are clearly equivocal. Further research is
needed in order to clarify both age differences in dissociation of affordance and spatial effects as well as their time-course.

As for the locus of the effects (facilitation by compatible stimuli or interference from incompatible stimuli), there is an important thing to keep in mind when discussing these results. It was mentioned earlier that results from the younger group were mainly due to interference effects – this is to say that effects could only be demonstrated for interference effects, but not for facilitation effects. This, evidently, does not necessarily mean that the effect was not also driven by facilitation, only that it could only be demonstrated for interference effects. Results of the present study indicated that for the older group, the spatial effect was driven mainly by interference whereas the affordance effect was due to both facilitation by compatible stimuli and interference from incompatible stimuli. The results of the older group were therefore comparable to those of the control group in the original study (Galpin et al., 2011), with the only difference being that for the control group the affordance effect was due to facilitation only. Taken together with results of the earlier study (Galpin et al., 2011), the results of the younger group and the Parkinson’s group were markedly different. As already mentioned, in the younger group the compatibility effects in both the affordance and spatial conditions were driven by interference from incompatible stimuli. In the Parkinson’s group, both the affordance and spatial effects were driven by facilitation by compatible stimuli. Thus, in other words, taken together with the results of the earlier study, the locus of the effects in the young group and the Parkinson’s group appear to arise from opposite sources and the patterns of results from the older groups
were somewhere in-between with both facilitation and interference effects occurring. This was an interesting finding in light of the evidence which suggests that older adults (in a similar manner to Parkinson's patients), have difficulties in resisting entrainment by visual stimuli and that they become more reliant on information in their environment to support behaviour.

Presumably, if older adults (and Parkinson’s patients) have difficulties in resisting entrainment by visual stimuli and as a consequence are more affected by the irrelevant stimulus dimension, one would expect the following; firstly, age-related increases in the size of compatibility effects (of which we found no evidence), and secondly, that compatibility effects (at least spatial-compatibility effects as mentioned above), would arise from interference effects. Interestingly, results of the two older groups suggested that spatial effects were indeed resulting mainly from interference effects. Thus, when looking at the locus of spatial-compatibility effects in the older groups alone, results would seem to lend some support to the ‘entrainment’ theory. However, when also looking at the results of the younger group in which both effects (spatial and affordance) could only be demonstrated to arise from interference effects, the picture becomes less clear. This is further thwarted by the finding that in the Parkinson’s group, both effects could only be demonstrated to arise from facilitation. Neither of these results fit well with the ‘entrainment’ theory.

In sum, when it comes to the locus of the effects, taken together with results of the earlier study, results are not unequivocal. It remains an important area for further investigations as external cues have been found to benefit Parkinson’s patients in appropriate movement selection and enhance reaching movements.
(Oliveira, Gurd, Nixon, Marshall, & Passingham, 1997). Thus, further research may elucidate which types of external stimuli may facilitate or interfere with movements in individuals with and without Parkinson's disease and hence may be fruitful in establishing training interventions which may be of potential therapeutic benefit.

The following chapter will address the main alternative account of object affordance effects; the attention-directing hypothesis.
Chapter 5

Experiments 3 and 4. Is the object-size effect real – or are results confounded by spatial / attentional factors?

It has been debated whether object affordance effects genuinely arise from visual objects automatically activating associated motor programmes (McBride, Boy, Husain, & Sumner, 2012). Anderson, Yamagishi, and Karavia (2002) pointed out that the stimuli used in affordance studies have generally been asymmetrical. They noted that this asymmetry is likely to induce attentional bias and furthermore, often the most visually salient part of the object has also been the graspable part of the object. Hence they argued that the object orientation effects may be due to attentional shifts to the most salient and/or behaviourally relevant location (e.g. handle) of the object rather than arising from the actions that the objects afford. These are valid points and although they are arguably more relevant for object orientation studies than object size studies, the attention-directing hypothesis cannot be ruled out as a plausible alternative to the affordance hypothesis when using visually asymmetric objects.

In addition, the individual stimuli used in previous studies have usually been very dissimilar (both in terms of general visual similarity, colours and the sizes of the objects within each category). After a number of trials, participants may have been able to make the categorical distinction based on some other object property, for example colour. For example, if a participant notices that a
pomegranate is the only red stimulus in the entire set, then presumably it would be faster to categorise than when having to attend to the object more carefully in order to be able to decide whether it is a pomegranate or a cricket ball. Furthermore, some of the objects used in previous experiments have been less ideal as they were arguably not entirely innocuous if to be picked up like that in real life (being horizontally flipped for half of the trials) - e.g. a sharp trowel, a chisel and a garden fork.

For these reasons, in an attempt to address these problems and to exert tighter experimental control, it was decided to create a new stimulus set from scratch as none of the freely available databases had experimental stimuli which satisfied our criteria for as tight experimental control as we required. The new stimulus set consisted of 36 objects, half of which were edible, half of which were inedible (and within each category half of the objects were small and the other half large). It was decided to change the categorisation task from natural/manufactured to edible/inedible in order to simplify procedures. More importantly, all objects were spherical (or as close as possible to spherical using an edible and inedible category), and all were matched in pairs across category for size and colour. For example, within the large category there was a matched pair of a pomegranate and a cricket ball, and within the small category there was a matched pair of a small Ferrero Rocher chocolate and a pine cone (for example pictures of the objects, see figure 5.1 in the method section). Presenting spherical objects centrally should make it clearer whether the object-size effect can in fact be attributed to automatic motor activation of grip-type compatible responses as it has been suggested previously (e.g. Tucker, &
Ellis, 2001), as spatial - and hence also the attention-directing attributes are ruled out as potential confounds.

As the intention was to use this new stimulus set in the fMRI experiment, using such tight experimental control in terms of the stimuli being matched across category for both shape, size, and colour could have several additional advantages, some of which are relevant for our fMRI study and some of which could be advantageous for future investigations. The stimuli used in experiment 1 for example, extended from approximately 3.6 to 31 degrees of visual angle. In the present stimulus set the small stimuli extended approximately 1.5 - 3 degrees visual angle whereas the large stimuli extended approximately 6 - 8 degrees visual angle. The human visual system has a retinotopic organisation. In simple terms, this means that every location in visual space is mapped to a particular location of the visual cortex and vice versa, i.e. for each voxel in the visual cortex there is a corresponding region of the visual field (see e.g. Liu, Ashida, Smith, & Wandell, 2006). Consequently, using spherical objects presented centrally (and which are also matched for size and colour), should minimise eye movements and would most probably result in visual cortex activations being much more similar across categories, making it easier to tease apart specific effects of interest without them being confounded by aspects not intended to have any impact/influence. For example, within the large category, there was a matched pair of pomegranate and cricket ball (compared to for example a hammer and potato in experiment 1) – in both cases participants would respond with a precision grip to one and power to the other. As a result,
the visual similarity of the former should make it easier to look at the effect of
for example grip type in isolation with minimal interfering factors.

As only younger participants took part in these two studies, no predictions in
terms of age effects upon the compatibility effect could be made - consequently,
the only prediction was that this novel stimulus set would produce significant
object-size compatibility effects.

The method and results sections of experiment 3 will be presented first, then
the method and results sections of experiment 4. Finally, we shall revert to a
joint discussion of both experiments.

5.1 Method – Experiment 3

Participants

Thirty-five healthy younger adults (all female, aged 18-24 years, \( M = 19 \))
participated in this study. All participants were undergraduate psychology
students, had a minimum of 12 years of education and received course credit
for participation. Participants signed up for the study online, and participation
was restricted to right-handed individuals only and also to individuals who had
not previously taken part in either experiment one or two. All gave informed
consent prior to beginning the tasks, and were naïve as to the purpose of the
study. All participants had normal or corrected to normal vision, normal motor
function and no history of neurological disorder or stroke (by self-report).
**Materials and apparatus**

The response devices used were the same power and precision grip devices described in experiment 1. As in experiment 1, the participants were seated in front of a computer monitor holding one device in each hand, their hands resting on a table in front of their body mid-line, and the viewing distance was approximately 60 centimetres. E-prime (version 2.0) software (Schneider et al., 2002) was used for stimulus presentation on a 20 inch monitor with a resolution of 1680 by 1050 pixels.

The categorisation task was changed from natural/manufactured to edible/inedible in order to simplify procedures. After having completed the computer experiment, participants were given a folder with colour photos of the experimental stimuli and a questionnaire which asked them to write down what the objects were and if they were edible or not.

**Stimuli**

The stimuli (listed in appendix 5.A) were colour photographs of 36 commonly known objects; 18 edible objects and 18 inedible objects, and within each category half of the objects were small (normally grasped with a precision grip) and the other half large (normally grasped with a power grip). All objects were spherical (or as close as possible to spherical using an edible and inedible category), and all were matched in pairs across category for size and colour, as previously discussed (see figure 5.1. below).
Figure 5.1. Example of two sets of matched stimuli across category.

The procedure for creating the stimuli files was as follows; first the objects were placed on a white table and pictures taken using a Nikon D80 which was fixed on a tripod in order to have the same viewing and lighting angle as well as distance to the objects. Next the stimuli were edited in pairs using Adobe photoshop CS5. The hue and saturation of the objects were edited to match each other as closely as possible whilst maintaining a natural appearance. The objects, including their shadow, were then extracted using the magnetic lasso tool and superimposed on a photo of a wooden table (taken using the same angle and camera settings). The centre of the object was placed in the centre of the screen, and the back edge of the table was visible. This was set up in such a way that when participants saw the finalised stimuli on the screen, it would appear to be a similar viewing angle as if the object had been placed on a table in front of them within reaching distance. Furthermore, the size in which the
object appeared on the screen corresponded to the actual, real-life size of the object placed within reaching distance. Finally, all the objects’ shadows were edited so they appeared in the same shade for all objects. The reason for this somewhat cumbersome exercise was that had the photos been taken whilst the objects were placed on the wooden table, the zoom distance would inevitably vary between objects in order to get the object in focus. Hence, the structure/grain of the table top would vary between objects, which in turn would mean that when appearing on the screen it would seem as if they were not the same viewing distance. The small objects subtended approximately 1.5 to 3 degrees in visual angle, and the large objects 6-8 degrees in visual angle. The wooden table top filled out the rest of the screen (apart from the small area above the back edge of the table which was included to provide distance and size cues). On each trial, a fixation cross which was superimposed on the same wooden table top, appeared at the centre of the screen for 800 ms followed by the target object which remained in view until a response had been made or until 2 seconds had elapsed.

Procedure

In this experiment participants were asked to categorise the objects as either edible or inedible (rather than natural/manufactured) by pressing the appropriate device. There were 576 trials in total, 288 in each block, and participants received 36 practice trials before each of the two blocks. In each of the two experimental blocks, each stimulus was presented 8 times in a random order. The procedure was otherwise identical to that of experiment one; half the participants were asked to press the precision grip for edible objects and
the power grip for inedible objects, and half received the opposite instructions. These response mappings, to which participants were randomly allocated, remained the same within participants throughout the experiment. In each of the two response mappings, half of the participants held the precision grip in their right hand and power grip in their left hand in the first block (and vice versa for the other half), and swapped the devices to the opposite hand for the second block. This arrangement is referred to as hand mapping.

5.2 Results – experiment 3

Error rates

In addition to the 35 participants whose data are included in the analysis, an additional 14 participants took part in the study but their data were excluded; 4 participants did not follow instructions and the remaining 10 were due to error rates exceeding 10 percent. For the 35 participants included in the analysis, error trials (totalling 5.29 %) were excluded from the analysis, as were trials with reaction times more than 3 SDs from each participant’s average RT (1.52 %).

Response times – main analysis

The means from the remaining data were analysed using a mixed factorial analysis of variance (ANOVA). The between-subjects factor was response mapping (1. edible = precision grip, inedible = power grip or 2. edible = power grip, inedible = precision grip). The three within-subjects factors were hand mapping (hand mapping 1. precision grip right hand and power grip left hand,
and hand mapping 2. precision grip left hand, power grip right hand), grip type (precision or power grip), and object size (small or large).

The ANOVA revealed two highly significant main effects; grip type and object size. Precision responses ($M = 572$) were faster than power responses ($M = 614$), $F(1,33) = 106.46, p < .001, \eta^2_{p.} = .763$. Participants responded faster to large objects ($M = 580$) than small objects, ($M = 607$), $F(1,33) = 111.29, p < .001, \eta^2_{p.} = .771$. The main effects of response mapping and hand mapping were not significant, $F(1,33) = .38, p = .541, \eta^2_{p.} = .011$ and $F(1,33) = .23, p = .636, \eta^2_{p.} = .007$, respectively.

More importantly there was a highly significant compatibility effect, $F(1,33) = 30.27, p < .001, \eta^2_{p.} = .478$, reflected by the interaction between grip type and object size. This reveals that compatible grips were generally faster than incompatible grips. This was further confirmed by follow up t-tests. Power grip responses to large objects were faster ($M = 591$) than to small objects ($M = 638$) (two-tailed t-test, $t = 8.82, p < .001$). There were no significant differences between precision grip responses to small objects ($M = 575$) and large objects ($M = 569$), (two-tailed t-test, $t = 1.40, p = .171$), see figure 5.2). Hence, the overall compatibility effect was approximately 21 ms.
There was also a significant interaction between grip type and response mapping, $F(1,33) = 36.92, p < .001, \eta^2_p = .528$. In response mapping 1 (RM1) (where participants responded with precision grips to edible objects and power grips to inedible objects), there was a larger RT difference between precision grips ($M = 566$) and power grips ($M = 633$), than in RM 2, precision grips ($M = 578$) and power grips ($M = 595$).

Finally, there was a significant three-way interaction between object size, grip type and response mapping, $F(1,33) = 6.64, p = .015, \eta^2_p = .167$, which suggested that compatibility effects were larger in one response mapping than the other. Indeed, the average RT for compatible objects were ($M = 585$) in RM1 and ($M = 581$) in RM2, and the average RT for incompatible objects were ($M = 615$) in HM1 and ($M = 593$) in HM2. Thus, the overall compatibility effect was
30 ms in RM1 and 12 ms in RM2. None of the other main effects or interactions were significant, for all $F < .99$.

**Errors analysis**

Incorrect responses were entered into an ANOVA, which revealed significant effects for hand mapping, object size, grip type, and an interaction between object size and grip type. There was no effect of hand mapping in the RT analysis, but the errors analysis revealed that participants made more errors in hand mapping 2 than in the ‘preferred’ hand mapping 1, $F(1,33) = 23.01 \ p < .001, \eta^2_p = .411$. In line with the RT analysis, there was a significant effect of object size, $F(1,33) = 49.36 \ p < .001, \eta^2_p = .599$; participants made more errors when responding to small objects, and participants also made more errors when responding with power grips, $F(1,33) = 12.38 \ p = .001, \eta^2_p = .273$. Finally, also in line with the RT analysis, there was a significant effect of compatibility as demonstrated by the significant interaction between object size and grip type, $F(1,33) = 6.20 \ p = .018, \eta^2_p = .158$, i.e. participants made significantly more errors in incompatible conditions thus providing support for the effects found in the RT data. No other main effects or interactions were significant.

The method and results sections of experiment 4 will be presented next, after which we shall return to a joint discussion of experiments 3 and 4.
5.3 Method – experiment 4

Participants

Seventeen healthy younger adults (13 female, 4 male, aged 18-25 years, $M = 19.94$) participated in this study. Apart from this, all other participant specifics and selection/exclusion criteria remained the same as those of experiment 3.

Materials and apparatus

In experiment 3, the number of participants excluded on the basis of error rates exceeding 10 percent, as well as the information obtained from the object-questionnaire, made it apparent that some participants were not familiar with some of the objects. Consequently, in this experiment participants were given the folder with colour photos of the experimental stimuli before completing the computer experiment. They were asked to name the objects and whether they were edible or not. If incorrect, they were told what the objects were (and if in doubt, whether they were edible or not). Other than this, the response devices, apparatus and experimental set-up were the same as that of experiment 3.

Stimuli and procedure

The experimental stimuli and procedure was identical to experiment 3.
5.4 Results – experiment 4

**Error rates**

Two participants were excluded from the analysis due to error rates exceeding 10 percent. For the 17 participants whose data are included in the analysis, error trials (totalling 4.60 %) were excluded from the analysis, as were trials with reaction times more than 3 SDs from each participant’s average RT (1.58 %).

**Response times – main analysis**

The analysis set-up was identical to that of experiment 3. The means from the remaining data were analysed using a mixed factorial analysis of variance (ANOVA), and the between-subjects factor was response mapping (1. natural = precision grip, manufactured = power grip or 2. natural = power grip, manufactured = precision grip). The three within-subjects factors were hand mapping (hand mapping 1. precision grip right hand and power grip left hand, and hand mapping 2. precision grip left hand, power grip right hand), grip type (precision or power grip), and object size (small or large).

As was the case for experiment 3, the two main effects of grip type and object size were highly significant. Precision responses ($M = 602$) were faster than power responses ($M = 640$), $F(1,15) = 27.49$, $p < .001$, $\eta^2_{p.} = .647$. Participants responded faster to large objects ($M = 613$) than small objects, ($M = 629$), $F(1,15) = 12.034$, $p = .003$, $\eta^2_{p.} = .445$. The main effects of response mapping and
hand mapping were not significant, $F(1,15) = .51, p = .487, \eta^2_{p.} = .033$ and $F(1,15) = .02, p = .882, \eta^2_{p.} = .002$, respectively.

As in experiment 3, there was a highly significant compatibility effect, $F(1,15) = 40.49, p < .001, \eta^2_{p.} = .730$, reflected by the interaction between grip type and object size. Thus, compatible grips were generally faster than incompatible grips and this was further confirmed by follow up t-tests. Power grip responses to large objects were faster ($M = 617$) than to small objects ($M = 661$), (two-tailed t-test, $t = 6.68, p < .001$). Precision grip responses to small objects were slightly faster ($M = 595$) than to large objects ($M = 609$), (two-tailed t-test, $t = -2.09, p = .053$). (see figure 5.3). Hence, the overall compatibility effect was 29 ms.

![Figure 5.3. Main analysis. Mean RTs by grip type (precision or power grip) and object size (small or large).](image)

There was also a significant interaction between grip type and response mapping, $F(1,15) = 9.67, p = .007, \eta^2_{p.} = .392$. In response mapping 1 (RM1)
(where participants responded with precision grips to edible objects and power grips to inedible objects), there was a larger RT difference between precision grips ($M = 603$) and power grips ($M = 664$), than in RM 2, precision grips ($M = 601$) and power grips ($M = 617$). All the results for experiment 4 presented thus far are therefore in line with those of experiment 3.

Finally, the only result that differed to experiment 3 was the presence of a significant interaction between object size and hand mapping, $F(1,15) = 9.65, p = .007, \eta^2_p = .392$. There was a larger RT difference between HM 1 and HM 2 when responding to small objects ($M = 624$ and $M = 634$, for HM 1 and HM 2, respectively), than when responding to large objects ($M = 617$ and $M = 610$ for HM 1 and HM 2, respectively). None of the other main effects or interactions were significant, for all, $F < 2.3$.

**Errors analysis**

Incorrect responses were entered into an ANOVA which revealed significant main effects for object size, grip type and response mapping. Furthermore, there were significant interactions between response mapping and grip type, object size and grip type, and a three-way interaction between response mapping, hand mapping and object size.

As was the case for experiment 3, there was a significant effect of object size, $F(1,15) = 18.47, p = .001, \eta^2_p = .552$; participants made more errors when responding to small objects, and participants also made more errors when responding with power grips, $F(1,15) = 34.68, p < .001, \eta^2_p = .017$. Unlike experiment 3, participants made more errors in response mapping 1 (RM 1)
than in RM 2, \( F(1,15) = 4.62 \ p = .048, \eta^2_p = .235 \), and the significant interaction between response mapping and grip type revealed a larger proportion of power grip errors in RM 1 than RM 2, \( F(1,15) = 6.95 \ p = .019, \eta^2_p = .317 \).

More importantly, in line with both the RT analysis and the errors analysis in experiment 3, there was a significant effect of compatibility as demonstrated by the interaction between object size and grip type, \( F(1,15) = 12.82 \ p = .003, \eta^2_p = .461 \), i.e. participants made more errors in incompatible conditions thus providing support for the effects found in the RT data.

Unlike experiment 3 where participants made more errors in HM 2 than the preferred HM 1, in this experiment there was no significant effect of hand mapping, \( F(1,15) = .86, p = .367, \eta^2_p = .054 \). Finally, there was a significant three-way interaction between object size, hand mapping and response mapping, \( F(1,15) = 8.08 \ p = .012, \eta^2_p = .350 \). In RM 1, the proportional reductions in errors for large objects compared to small objects were similar for both hand mappings (reductions by about a third). In RM 2, the numbers of errors were almost identical for small and large objects in HM2, whereas in HM 1 the number of errors to small objects were over double that of large objects.

5.5 Discussion – experiments 3 and 4

A new experimental stimulus set was created in an attempt to eliminate the potentially confounding factors in previously used stimuli sets. Creating a stimulus set that consisted purely of spherical, centrally presented objects (which, in addition, were also matched across category for colour and size)
would allow a dismissal of the spatial Simon (1969) and attention-directing hypotheses as alternative explanations to the object affordance hypothesis.

Thus, the main objectives of these two studies were to investigate whether this new stimulus set would produce the recurrently observed object-size compatibility effects which, in turn, would provide strong evidence in favour of the object-size affordance hypothesis, and secondly, to ensure that the stimulus set was usable for the intended purposes before employing it in the MRI scanner.

The number of participants excluded on the basis of excessive error rates in the first experiment as well as the object questionnaire, made it apparent that some participants were not familiar with some of the objects. This was quite surprising, but highlighted that this was an issue that needed to be addressed. Consequently, in the second experiment, participants were shown the experimental stimuli before completing the computer experiment to ensure all participants were aware of what all of the objects were. Other than this change, which reduced the number of excluded participants due to excessive error rates to a normal level, these two studies were identical.

Most importantly, as for the main effect of interest in these experiments, there was a highly significant compatibility effect in both experiments. Overall, responses to compatible objects were faster than to incompatible objects. Interestingly, the sizes of the observed compatibility effects (21 and 29 ms for experiment 3 and 4, respectively), were somewhat larger numerically than what is usually observed, which tends to be in the region of 10-15 ms, sometimes up to 20 ms. The fact that the results of both of these studies
corroborated previous findings of affordance/object-size compatibility effects using this novel stimulus set, is crucial. As previously discussed, most affordance studies, both those investigating the object-orientation effect and object-size effect, have used asymmetrical objects. Consequently, some of the main criticisms have been that rather than the intrinsic object properties potentiating associated action plans, that the effects may instead be caused by either a simple spatial compatibility effect (spatial Simon effect) and/or be biased by attentional effects. The novel stimulus set which was employed in the present two studies was created in an attempt to address these criticisms. More specifically, as all of the objects were spherical and presented centrally, it rules out both the spatial and attentional orienting effects as alternative explanations. Thus, the results of these two studies provide strong evidence in favour of the object-size affordance hypothesis.

As discussed in chapter 3, the potential effect of hand mapping upon the object-size compatibility effect was not of any particular interest for our hypothesis. However, in experiment 1 the main effect of interest (the effect of age upon the compatibility effect), interacted with hand mapping. Recall from experiment 1 that whereas there was a difference in the size of the compatibility effect between hand mappings in the younger group (approximately 27 ms in the preferred hand-mapping versus 10 ms in the opposite mapping), they were absent in the older group (approximately 16 ms in both hand-mappings). Similarly, the one study reported so far, which had the specific purpose of investigating whether the object-size compatibility effect differs between hand mappings (Vainio et al., 2006) only tested younger individuals and found the
same pattern of results as our study (i.e. significant compatibility effects in hand mapping 1, whereas the effect was absent in hand mapping 2).

Importantly, the present two experiments also tested only younger participants where one would expect the difference between hand mappings, if present, to be most pronounced – yet, there was no hint of an effect of hand mapping upon the compatibility effect in either experiment. Although the sizes of the compatibility effects in both experiments were slightly larger numerically (but not statistically) in the preferred hand mapping 1 than hand mapping 2, the RT difference was small (approximately 2-3 ms).

Thus, the results from the few studies which have included hand mapping as a main factor are diverging and inconclusive. However, as the stimulus set used in the present two experiments is the one that will be used in the fMRI study, the lack of an effect of hand mapping upon the compatibility effect in younger individuals have led us to the conclusion that hand mapping will be excluded as a factor in the fMRI experiment, and that only the preferred hand mapping will be investigated. Needless to say that the scanning costs are substantial and funds limited, so optimising statistical power by excluding factors which are not of any particular interest also needed to be taken into account. In the light of the findings of experiment 1, deciding to exclude hand mapping 2 from the fMRI study would have been problematic had we had reason to expect an effect of hand mapping upon the compatibility effect in the younger but not the older group, but the present results renders this no longer a concern.

The behavioural data collected in the scanner will be presented next.
Chapter 6

Experiment 5. Age-differences in object-size effects – behavioural MRI data

As we have proposed that potential age-related differences in object affordance effects may have, at least in part, a neurophysiological basis, it was necessary to undertake a neuroimaging study which allowed an assessment of potential age-differences on the neurophysiological level alongside behavioural measures. This final neuroimaging experiment combines behavioural data (presented in the current chapter), functional MRI data (chapter 7), and diffusion tensor imaging data (chapter 8).

There were only a few changes to the experimental procedure of the behavioural MRI experiment (the behavioural data collected in the scanner), compared to experiments 3 and 4 discussed in the previous chapter (for full details see method section). For easy reference, the most important changes were as follows; a genetic algorithm was used to generate stimulus-presentation sequences with the purpose of optimising the experimental fMRI design (Wager, & Nichols, 2003). Hence, there were two fixed stimulus-presentation sequences in the present experiment as opposed to the stimuli being presented in random order. In this experiment all participants held the precision grip in their right hand and power grip in their left hand. Thus, only the ‘preferred’ hand mapping (HM1) was included, the reason being that there was no hint of an effect of hand mapping upon the compatibility effect in
experiments 3 and 4. The fixation cross (superimposed over the wooden table) used previously, was now also included as a baseline stimulus to which no response was required. The baseline stimulus was included for the purposes of functional MRI data analysis as was a black screen after each stimulus presentation. The experiment was divided into four runs / blocks to allow participants a rest in between and to communicate with the experimenter, if needed. Based upon the results of our previous investigations, for the two main contrasts of interest we predicted (1) an object-size compatibility effect, and (2) that the compatibility effect would be smaller for the older group than the younger group.

6.1 Method

Participants

Eighteen healthy younger adults (11 females, 7 males aged 20-36 years, \( M = 25.53 \)) and fourteen healthy older adults (6 females, 8 males aged 62-76 years, \( M = 67.29 \)) participated in this study. Participants were recruited by various methods, for instance via a presentation at an event held by University of the Third Age and advertisements on Plymouth University’s website. All participants went through strict MRI safety screening processes in accordance with the Peninsula Magnetic Resonance Research Centre’s regulations and filled out the research consent form for MRI scanning prior to beginning the tasks. All participants were right-handed, as assessed by the short version of The Edinburgh Handedness Inventory (EHI; Oldfield, 1971), and all had normal cognitive function as assessed by The Mini-Mental State Examination, (MMSE,
Folstein et al., 1975). Furthermore, all had normal or corrected to normal vision, normal motor function and no history of neurological disorder or stroke (by self-report).

**Materials and apparatus**

The study was carried out using a 1.5T Philips Gyrosocan Intera Scanner in the Peninsula MR Research Centre, University of Exeter. The precision- and power-grip response devices used in previous experiments were modified so that they were MRI compatible, without it impacting on their shape or size. Participants were shown the colour photos of the experimental stimuli before completing the experiment, and asked to name the objects and whether they were edible or not. If incorrect, they were told what the objects were (and if in doubt, whether they were edible or not). E-prime (version 2.0) software (Schneider et al., 2002) was used for stimulus presentation. The stimuli were projected onto a screen which was visible to participants via a small mirror placed above their eyes. If needed, participants were equipped with MRI compatible glasses.

**Genetic algorithm**

Two different stimulus-presentation sequences were generated using a genetic algorithm (GA) for experimental fMRI design optimisation (Wager, & Nichols, 2003). The reason for creating two models instead of just one was to reduce the likelihood of any factor being inadvertently optimised over another. The GA allows optimisation of a randomised event-related design by maximising statistical power when the objective is detecting one or more contrasts across different event types (Wager, & Nichols, 2003). The GA constructs random
designs according to the specified parameters, builds design matrices, test them, and ‘interbreeds’ the best of them. It iterates this process until the best design is found (or until the specified maximum amount of time is reached). The output is a sequence of event types to be presented at specified times during the experiment.

The models were created using the following parameters: The number of conditions was set to 5, i.e. the four experimental conditions and the baseline condition, and all were weighted equally at 0.2 each. The scan length was set to 350 seconds and number of runs to 4 (each TR was 2.8 seconds and there were 125 stimuli presentations in each of the 4 runs). The number of iterations was set to 100,000 of 300 designs each, over a maximum time of 12 hours. The high-pass filter length was set to 120 seconds. The order of counterbalancing was set to 2, meaning that the GA used use second-degree counterbalancing (i.e. one-back and two-back counterbalancing). The vector of weights which specifies the importance of the objectives of the study was: 1) counterbalancing was set to 0.2, 2) contrast detection efficiency was set to 1, 3) HRF shape estimation efficiency was set to 0.3 and 4) maintenance of input frequencies for each trial type was set to 0.7 (the weights do not have to sum to 1 in this instance). As contrast detection was optimised, the GA will attempt to create ‘mini-blocks’ of the same event types in the event-related design. The potential predictability that could arise from such ‘mini-blocks’ was counteracted by specifying a maximum number of 5 repeats of the same type of stimuli. This specific value is a hard constraint meaning that design vectors that do not meet this criterion are excluded from further consideration (Wager, & Nichols, 2003). The five contrasts of interest which were entered into the GA were: 1) task versus
baseline, 2) compatible > incompatible, 3) incompatible > compatible, 4) precision grip > power grip, 5) power grip > precision grip. The contrast efficiencies were multiplied by the following weights; 0.5, 1, 1, 0.5, 0.5, respectively, before computing overall design fitness. The two GA outputs specified which event type to present at each point in time but not the specific identity of the stimulus. Hence, in order to randomise the order of the particular objects within each of the individual stimuli categories, the stimuli in each of the four experimental conditions were entered into ‘Research Randomizer’ (version 4.0, Urbaniak, & Plous, 2013) in blocks of nine. These numeric outputs where then merged with the outputs of the GA, producing two different stimulus-presentation sequences. Finally, these sequences were combined with each of the two response mappings.

**Stimuli and procedure.**

The stimuli were the same as those used in experiment 3 and 4. Contrary to previous experiments, all participants held the precision grip in their right hand and power grip in their left hand. Participants were asked to categorise the objects as either edible or inedible by pressing the appropriate device. Half the participants were asked to press the precision grip for edible objects and the power grip for inedible objects, and half received the opposite instructions. These response mappings, to which participants were randomly allocated, remained the same within participants throughout the experiment. The experiment was divided into four runs, each of which contained 100 stimulus presentations and 25 baseline stimulus presentations. The baseline stimulus was the fixation cross superimposed on the wooden table top used in previous
experiments. Each TR was 2800 ms, thus, on each trial, the stimulus (experimental stimulus or baseline stimulus) appeared on the screen for 2000 ms and remained on the screen for the entire 2000 ms even after a response had been made. This was followed by a black screen presented for 800 ms.

6.2 Results

**The Edinburgh Handedness Inventory, (EHI), and The Mini-Mental State Examination, (MMSE)**

All participants were classified as right-handed when calculated in accordance with the standard cut-off points of the EHI, (Oldfield, 1971). For the younger group, the mean handedness score was $M = 95.11$ and for the older group $M = 93.00$. All participants scored greater than 26 on the MMSE, thus indicating normal cognitive function (Folstein et al., 1975) ($M$ younger = 29.83 and $M$ older = 29.43).

**Error rates**

In addition to the 32 participants whose data are included in the analysis, an additional 9 older participants took part in the study but their data were excluded both from the behavioural analysis and the functional MRI analysis. For three participants there was a malfunction of the grip devices so no behavioural data was collected. Two participants were excluded due to excessive movement in the scanner and one did not follow instructions. The last three participants were excluded on the basis of their error rates exceeding 20 percent. It was decided to increase the acceptable error rate for participant
inclusion to 20 percent (compared to 10 percent for the earlier studies) to account for higher error rates in the novel scanning condition. Four participants (two young and two old) had error rates between 10-20 percent, for the rest of the participants it was below 10 percent. For the 32 participants included in the analysis, error trials (totalling 6.56 %) were excluded from the analysis as was reaction times more than 3 SDs from each participant’s average RT (0.82 %).

**Response times – main analysis**

The means from the remaining data were analysed using a mixed factorial analysis of variance (ANOVA). The two between-subjects factors were age group (younger, older), response mapping (1. natural = precision grip, manufactured = power grip or 2. natural = power grip, manufactured = precision grip). The two within-subjects factors were grip type (precision or power grip), and object size (small or large).

The ANOVA revealed three highly significant main effects; grip type, object size, and age. Precision responses ($M = 1051$) were faster than power responses ($M = 1166$), $F(1,30) = 42.30, p < .001, \eta^2_p = .602$. Participants responded faster to large objects ($M = 1085$) than small objects, ($M = 1133$), $F(1,30) = 55.64, p < .001, \eta^2_p = .665$. The younger participants responded significantly faster than the older participants, ($M = 988$ and $M = 1229$ for the younger and older group, respectively), $F(1,30) = 23.95, p < .001, \eta^2_p = .461$. Thus, the older group responded, on average, 241 ms slower than the younger group. It is evident that the mean RTs for both the younger and older participants were much slower in this experiment than in previous experiments. This was most likely due both to
the novel scanning situation and to the unavoidable presentation limitations in
the scanner. Hence, the apparent size and resolution of the stimuli was
somewhat less optimal compared to the laboratory studies (experiments 3 and
4), and the visual similarity of the objects would add to the time required to
make the categorical distinction. The main effect of response mapping was not
significant, $F(1,30) = .009, p = .924, \eta^2_{p} = .000$.
Importantly, there was no effect of compatibility, $F(1,30) = 2.30, p = .141, \eta^2_{p}$
= .076, as the interaction between grip type and object size was not significant.
However, the interaction between grip type, object size and age group was
significant, $F(1,30) = 5.60, p = .025, \eta^2_{p} = .167$, suggesting a difference in the
compatibility effect between age groups (see figure 6.1, below). To explore this
further, two separate step-down analyses were performed, one for each age
group. For the younger group, there was a highly significant effect of object size,
$F(1,16) = 47.62, p < .001, \eta^2_{p} = .748$, with participants responding faster to large
objects. The effect of grip type was also highly significant, $F(1,16) = 22.28, p$
< .001, $\eta^2_{p} = .582$, with participants responding faster with precision grips.
Finally, and most importantly, there was a significant compatibility effect,
$F(1,16) = 7.92, p = .012, \eta^2_{p} = .331$, reflected by the object size by grip type
interaction. For the older group, there was also a highly significant effect of
object size, $F(1,12) = 19.84, p = .001, \eta^2_{p} = .623$, with participants responding
faster to large objects. The effect of grip type was also highly significant, $F(1,12)$
= 19.28, $p = .001, \eta^2_{p} = .616$, with participants responding faster with precision
grips. Importantly, in the older group the compatibility effect was not
significant, $F(1,12) = .36, p = .558, \eta^2_{p} = .029$. The between-subjects main effect
of response mapping was not significant for either age group, $F < 1.54$. 
Figure 6.1. Mean RTs for the younger group (upper panel) and the older group (lower panel) by grip type (precision or power grip) and object size (small or large). Bars show standard errors.

The compatibility by age interaction (figure 6.1 above), shows that the pattern of responses were otherwise similar for the two age groups; both age groups responded faster to compatible objects when responding with power grips and slower to compatible objects when responding with precision grips. The response patterns were further examined using follow up t-tests. For the
younger group, precision responses to small objects \((M = 955)\) were significantly slower than to large objects \((M = 932)\) (two-tailed t-test, \(t = 3.65, p = .002\)), and power responses to large objects \((M = 1004)\) were significantly faster than to small objects \((M = 1060)\) (two-tailed t-test, \(t = 3.67, p < .001\)). For the older group, precision responses to small objects \((M = 1188)\) were also significantly slower than to large objects \((M = 1128)\) (two-tailed t-test, \(t = 3.84, p = .002\)), and power responses to large objects \((M = 1274)\) were also significantly faster than to small objects \((M = 1327)\) (two-tailed t-test, \(t = 4.43, p = .001\)). Thus, the overall object-size compatibility effect was approximately 17 ms for the younger group. The overall compatibility effect for the older group, on the other hand, was negative and approximately -4 ms, i.e., the older group responded, on average, faster to incompatible objects than to compatible objects. None of the other interactions were significant, for all, \(F < 3.7\).

**Errors analysis**

Incorrect responses were entered into the same ANOVA model as the response times. There was a significant main effect of object size, \(F(1,30) = 20.66, p < .001, \eta^2_p = .408\), with more errors being made when responding to small objects. The main effect of grip type was also significant, \(F(1,30) = 5.06, p = .032, \eta^2_p = .144\), with more errors being made when responding with power grips. None of the other main effects or interactions were significant, for all, \(F < 2.69\). For the main contrasts of interest (compatibility and compatibility by age) the interaction patterns followed those of the RT data with more errors being made in incompatible conditions compared to compatible conditions.
6.3 Discussion

The most important findings of this experiment were twofold, firstly the lack of an overall significant object-size compatibility effect and secondly, the presence of an age-effect upon the compatibility effect which supported our prediction of reduced compatibility effects in the older group.

Inconsistent with previous results, the first of the main contrasts of interest, the object-size compatibility effect, was not significant. In other words, overall participants did not respond faster to compatible objects than to incompatible objects. This finding was unexpected as all of our previous experiments had documented highly significant compatibility effects, including the two that used the same stimulus set.

There was, however, a significant interaction between age group, grip type and object size, which suggested the presence of an age-difference in the size of the compatibility effect. The step-down analysis which investigated the compatibility effect separately for each age group revealed a significant compatibility effect for the younger group (17 ms), but not the older group (-4 ms). Recall that in experiment 1 the age, grip type and object size interaction was not significant, however, in that experiment the compatibility effect was modulated by hand mapping. The step-down analysis revealed a significant age-difference in the size of the compatibility effect in hand mapping 1 (27 ms for the younger group and 16 ms for the older group). The present experiment only investigated this hand mapping. Hence, the present patterns of results of larger
compatibility effects for the younger group compared to the older group are consistent with that of experiment 1 and our predictions.

In the present experiment the average RTs were much slower for both age groups than (we had) previously observed. This suggests that the slowing down of response times may have been caused, in part, by the fact that the resolution and apparent size of the objects would have been less optimal (compared to the laboratory conditions) due to the inevitable presentation limitations in the scanner. Arguably, it is fair to assume that the older group may have been more affected by this aspect, particularly for the smaller objects, due to general poorer visual acuity and the fact that many more older than younger participants needed to wear the MRI compatible glasses (that were less suited to their individual needs than their regular glasses). The data did not back up such a speculation, however, as there was no direct evidence that object size affected response times for younger versus older participants differentially, and similarly, the error data showed no evidence to this effect either. Consequently, the slowing of reaction times for both age groups is more likely to result from a combination of factors, namely the novel scanning situation, the less ideal viewing conditions and the visual similarity of the objects. Reasonably, these factors combined would entail that additional time would be required in order to make the categorical distinction of the objects’ edibility. Furthermore, the fact that the objects were matched across categories for both shape, size, and colour may very well have accentuated this aspect.

There is a substantial amount of evidence to suggest that spatial compatibility effects decrease with increasing reaction times in the Simon task, and also in
other tasks which induce conflicting responses, such as the Stroop and Eriksen flanker tasks (Ridderinkhof, van den Wildenberg, Wijnen, & Burle, 2004). These findings are revealed in delta plots, for example, in which the compatibility effect is plotted as a function of response speed. Typically, the compatibility effect levels off with increasing reaction times. These observations have contributed to the formulation of the activation-suppression hypothesis (Ridderinkhof, 2002), which posits that the selective inhibition of the irrelevant stimulus features takes time to build up, and therefore only becomes efficient after a given amount of time. There are only a couple of object affordance studies, to the author’s knowledge, in which distributional analyses have been performed (Symes, Ellis, & Tucker, 2005; Tucker & Ellis, 2001). According to these two studies, there is some evidence that the object affordance effect may follow a different time course to those of spatial compatibility effects. More specifically, in one of these studies, the object affordance effect appeared to increase with increasing reaction times (Tucker & Ellis, 2001). The other paper (Symes, et al., 2005) reported distributional analyses of the object-orientation effect in two experiments; one experiment showed that the effect reduced slightly over the reaction time distribution whereas the other increased. Crucially though, in this latter observation, responses were made with the feet rather than hands and is therefore not very informative for the present purposes. Consequently, taken together it seems plausible that the substantial increase in reaction times may be the reason for the lack of compatibility effect in the group as a whole, and for the weaker effects in both age-groups. In sum, there was an effect of age upon the compatibility effect, and consistent with predictions, the size of the effect was smaller for the older than the younger
group. After the following section in which the results of the functional MRI data will be presented, we will return to a joint discussion of the behavioural and functional data.
Chapter 7
Experiment 5. Age-differences in object-size effects – functional MRI data

To date, there has been one previous neuroimaging study which has investigated the neural correlates of the object-size effect using a similar behavioural paradigm and grip devices as the present study. As we do, it investigated the influence of action relevant intrinsic object properties on motor responses which were either compatible or incompatible with the actions afforded by the observed objects, (Grezes, Tucker, Armony, Ellis, & Passingham, 2003). Grezes and colleagues (2003) replicated the behavioural study conducted by Tucker and Ellis (2001) (i.e. the same experimental paradigm and stimuli as our experiment 1) using functional magnetic resonance imaging (fMRI). Their fMRI study, which tested 12 young participants, replicated the behavioural object-size compatibility effects observed in the original study (Tucker & Ellis, 2001). Activations were observed in a left-hemispheric fronto-parietal network, namely the parietal, dorsal premotor and inferior frontal cortex (Grezes et al., 2003). They analysed brain-behaviour correlations, and found that the amplitude of the blood oxygenation level dependant (BOLD) signal correlated with the difference in reaction time; the larger the reaction time difference between compatible and incompatible trials (i.e. the larger the object-size effect), the stronger the activations in these areas. The authors suggested that this could potentially be resulting from greater
competition between the action which was afforded by the object and that required by the explicit task (Grezes et al., 2003).

Grezes and Decety (2002) used Positron emission tomography (PET) to explore the potential involvement of motor components during object perception in a variety of tasks, in all of which participants were presented with familiar, graspable objects. It was found that the perception of objects, irrespective of the task, versus viewing of non-objects, lead to a regional cerebral blood flow (rCBF) increase in the inferior parietal lobe, posterior cingulate gyrus, inferior frontal gyrus, occipito-temporal junction - all in the left hemisphere. Activations at the subcortical level were found in the right putamen and right caudate nucleus, structures which are part of the basal ganglia, involved in action selection. The authors suggested that the simultaneous activation of these common sets of cortical areas (which included parietal and premotor areas which are known to be involved with the control of object-related actions), could be interpreted as involvement of motor representations in object perception. Similar observations of activations in brain regions involved in motor representations (such as premotor, left-hemispheric parietal as well as the right cerebellum), during object perception has been observed in several other studies, both when participants prepare to act and when they imagine acting upon objects (for a meta-analysis see e.g. Grezes and Decety, 2001). Thus, these studies have provided support for the notion that the perception of objects automatically potentiates associated motor programmes.

In one of the tasks in the PET study (Grezes and Decety, 2002), participants were required to judge whether the objects were upright or inverted by making
a keyboard response (i.e. it was the same paradigm which was employed by Tucker and Ellis (1998) discussed previously). In addition to the common sets of cortical areas that were active irrespective of the task, activations for the upright/inverted categorical decision task included a number of right-hemispheric areas. Cortical activations included the right anterior cingulate gyrus, the middle and inferior frontal gyrus, middle temporal gyrus and the temporo-parietal junction. Subcortical activations were observed in the right putamen. Some researchers have suggested that areas which are part of the dorsal attention network, the right temporo-parietal junction in particular, facilitates attentional re-orienting by promoting interhemispheric connectivity between the intraparietal sulci, as demonstrated by dynamic causal modelling (DCM) analyses of fMRI data (Cieslik, Zilles, Grefkes, & Eickhoff, 2011; Cieslik, Zilles, Kurth, & Eickhoff, 2010). As both the PET (upright/inverted task) and fMRI (natural/manufactured task) studies employed similar categorisations tasks and stimuli, it is perhaps somewhat surprising that the former involved both left and right-hemispheric activations whereas the latter involved only a left-hemispheric network. The reason for these apparent discrepancies may be due to the different analyses which were employed. The fMRI study employed regression analyses, looking for areas in which activity correlated with the size of the compatibility effect. The PET study employed differential contrasts, reporting areas of task-related activity (i.e. areas in which activity was higher for the task relative to baseline conditions). In both of these experiments orientation was task-irrelevant (but action relevant), whereas in the dynamic causal modelling studies the task was a stimulus-response compatibility proper experiment, i.e. participants are instructed to respond to object location in
either a congruent or incongruent manner depending on task condition, which may influence dynamic interactions differentially.

As discussed in previous chapters, one of the main reasons for creating a new stimulus set which consisted only of centrally presented spherical objects (which were also matched for size and colour) was to address the attention-directing hypothesis, which suggests that the object-size and the object-orientation effects are merely a form of spatial compatibility effect (Anderson et al., 2002; Cho, & Proctor, 2013). Consequently, by using spherical, centrally presented objects, one would expect much less involvement of the right-hemispheric attentional network in the present experiment. Instead, based upon the aforementioned activations in left-hemispheric motor areas during object perception, as well as the previously reviewed literature, our predictions for the functional MRI data included (1) activity related to object affordance effects in a predominantly left-hemispheric fronto-parietal network (and right-hemispheric subcortical activations within the cerebellum and basal ganglia) and (2) that this task-related activity/effect would differ between young and old. More specifically, as we predicted a reduced effect in the older group and since the regression analysis discussed above found that larger object-size compatibility effects were associated with stronger activations, we predict larger activations for the younger than the older group for the contrasts of compatibility. Although no specific predictions were made for the contrasts of grip type as it was not central to our hypothesis, on the basis of the previously reviewed literature on more general age differences in functional activation
patterns in motor tasks, one might expect increased activations for the older group, both ipsilaterally and contralaterally for the contrasts of grip type.

7.1 Method

Functional MRI data acquisition and pre-processing.

The functional MRI data acquisition was carried out using a 1.5T Philips Gyroscan Intera Scanner in the Peninsula MR Research Centre, University of Exeter. The imaging parameters were as follows; Echo-Planar Imaging (EPI) sequence with repetition time (TR) = 2800 ms, echotime (TE) = 45 ms, flipangle = 90 degrees, 36 slices with a 0.4 mm gap. The order of acquisition was interleaved (first odd, then even), the acquisition voxel size = 3 x 3 x 3.5 mm and the reconstruction voxel size = 2.5 x 2.5 x 3.5 mm, and field-of-view (FOV) = 240 mm. A high-resolution structural scan was also acquired in the same session with the following parameters; 3D gradient echo sequence with TR = 25 ms, TE = 4 ms, flipangle = 30 degrees, 160 slices with no gap. The acquisition voxel size = 0.9 x 0.9 x 1.8 mm and the reconstruction voxel size = 0.9 x 0.9 x 0.9 mm, and FOV = 230 mm. Data pre-processing and all subsequent analyses were carried out using The Oxford Centre for Functional Magnetic Resonance Imaging of the Brain (FMRIB’s), software library (FSL; www.fmrib.ox.ac.uk/fsl).

The fMRI data analyses were carried out using FEAT (fMRI Expert Analysis Tool), which is part of the FSL software package. Data pre-processing included motion correction using MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002). MCFLIRT is an automated tool for linear (affine) brain image registration, and
involves aligning each image in the functional time series with a common reference image, in this case the middle volume. The interleaved slice timing correction was applied in order to shift each voxel’s time series by an appropriate fraction of the TR as subsequent analyses processes assumes that all slices were acquired half way through each TR.

The structural image was skull stripped using the Brain Extraction Tool (BET; Smith, 2002). During visual inspection of each participant’s brain extracted image, it became obvious that whereas the default fractional intensity threshold of 0.5 produced good results for all the younger participants, this was not the case for 6 of the 14 older participants. For one participant, the residual eye voxels in the brain extracted image needed to be removed. In the remaining 5 cases, the automated BET had removed too much brain matter, almost certainly due to increased age-related cerebral atrophy. Reducing the fractional intensity threshold causes the overall segmented brain to become larger and furthermore, there is also an option to use a vertical gradient in the fractional intensity threshold. BET was re-run using a combination of these two parameters for each of the five participants until an acceptable result was achieved.

The main reason for spatially smoothing the data is to improve the signal to noise ratio (Poldrack, Mumford, & Nichols, 2011). If noise varies randomly from voxel to voxel then spatially blurring the data should cancel out noise (as the blurring is essentially a local averaging). In contrast, activations that are larger in spatial extent than the chosen size of the smoothing kernel should be much less affected and the underlying signal thus retained (Jezzard, Matthews, & Smith, 2009). In this experiment, spatial smoothing was carried out using a
Gaussian kernel of full-width-half-maximum (FWHM) of 6.0 mm, a commonly-applied value which is close to the thickness of cortical tissue. Thus, the chosen kernel size was slightly larger than the voxel size of 2.5 x 2.5 x 3.5 mm.

Temporal filtering/smoothing can be low-pass (removing high-frequency noise) or high-pass (removing low-frequency noise). The default high-pass temporal filtering option was applied to remove slowly varying, low-frequency artefacts, such as cardio-respiratory effects and linear trends. This default high-pass temporal filtering option uses a local fit of a straight line (Gaussian-weighted) to give a smooth response. In addition, a high-pass filter cut-off value (in seconds) which controls the longest temporal period that will be allowed, must be specified. The command line utility ‘cutoffcalc’ was run in order to obtain an estimate of a sensible cut-off value for the particular model in question, which in this case was 90 seconds. ‘Pre-whitening’ was also applied; it involves a local autocorrelation correction instead of low-pass filtering, and this step is highly recommended in designs of this type for the first-level time series analysis in order to make the statistics valid and to improve estimation efficiency (Woolrich, Ripley, Brady, & Smith, 2001).

Statistical analysis of single subject fMRI data

The blood oxygenation level dependant (BOLD) signal

Neuronal activity requires additional oxygen supply which results in an increase in blood flow, the so-called hemodynamic response. The blood supply is larger than what is needed by the cells to replenish the oxygen levels, hence the activity-related increase in regional blood flow leads to a surplus of local
blood oxygen. The fMRI signals depend on this change in local concentration of oxygenated haemoglobin. Although the neuronal activity following an experimental manipulation may only last a few milliseconds, the hemodynamic response function (HRF) last approximately 16 seconds. In some cases, an initial dip occurring around 0-2 seconds is observed. The signal peak occurs at around 4-6 seconds post stimulus onset. The maximum observed amplitude (the peak height) of the HRF is around 5 percent for primary sensory stimulation (Poldrack, et al., 2011). The HRF returns to baseline around 12 – 18 seconds, sometimes involving a relatively long post-stimulus undershoot, but the amplitude of this undershoot is generally negligible compared to the signal evoked by the experimental manipulation.

**Statistical modelling**

This section explains the model which was set up in order to be able to assess the degree to which the BOLD signal from each voxel corresponds to the experimental manipulation. In this experiment we used a mass univariate approach, meaning that each voxel’s time-course is analysed separately.

The functional data was modelled as one continuous run so each participant’s four functional runs were concatenated into one 4D data file. Our model consisted of four separate explanatory variables, EVs (or regressors), one for each stimulus type; small compatible (SC), small incompatible (SI), large incompatible (LI) and large compatible (LC). Small and large refers to the object sizes. Compatibility refers to whether the grip type required by the explicit task was compatible with the object. For example, in the response mapping in which participants were asked to press the precision grip for edible objects and the
power grip for inedible objects, SC was a small edible object requiring a precision grip response, hence it was compatible. SI was a small inedible object and the response a power grip, hence it was incompatible. Likewise, LI was a large edible object but the response a precision grip (hence incompatible), and LC was a large inedible object and hence compatible. Each of the four regressors (or EVs) specified the occurrence of each of the different types of events for trials in which participants responded correctly. In addition to the four EVs, one confound EV (error regressor) was also included in the model. This error regressor specified the occurrence of trials in which participants made erroneous responses. The data were modelled as single linear regressors in which events of interest (the four EVs and the error regressor) were modelled by a boxcar function (using a custom 1-entry per volume) of the duration of one TR.

Parameter estimates give an estimate of the amplitude of the activation of a particular voxel over time according to the specified contrasts. The five contrasts of interest which had been identified when setting up the genetic algorithm were included, namely; 1) task versus baseline, 2) compatible > incompatible, 3) incompatible > compatible, 4) precisiongrip > powergrip, 5) powergrip > precisiongrip. In the regions-of-interest (ROI) analysis the contrasts for object size were also included; 6) small versus baseline and 7) large versus baseline. Activations for the different explanatory variables (i.e. different conditions) can be compared to each other by performing contrasts of parameter estimates (COPE’s) (Jezzard et al., 2009). So for example, 2)
compatible > incompatible identifies the voxels where activations are greater for compatible conditions than for incompatible conditions.

The stimulus timing files were convolved with a gamma function. This function acts as a proxy for the hemodynamic response function (HRF) and the convolution blurs and delays the box car waveform in an attempt to create a shape that more accurately reflects the shape of the BOLD signal (as described in more detail above). Temporal filtering was applied as it is recommended (Smith, 2002) to apply the same temporal filtering to the model as that which was applied to the data. A temporal derivative was also added which produces a new waveform in the model which is slightly shifted in time, and allows a better model fit and reduces unexpected noise. Finally, each participant’s brain extracted image was registered/aligned to the standard brain coordinate system of MNI152 (Montreal Neurological Institute).

**Statistical inference**

Typically there are thousands of voxels in the brain, hence, using the conventional significance value of \( p < .05 \) will lead to a substantial amount of false positives – this so-called problem of multiple comparisons is a crucial issue and needs to be addressed by statistical thresholding. In this experiment, the method of cluster-level inference was employed. Cluster-level inference typically consists of two stages (Woo, Krishnan, & Wager, 2014). First, a cluster-forming threshold is specified and groups of voxels which are above this threshold are retained. Second, a cluster-level extent threshold (measured in units of contiguous voxels) is determined using Gaussian Random Field Theory – thus, a cluster of a particular size is deemed exceedingly rare/unlikely to be
stemming from chance, and consequently the cluster, as a whole, is deemed statistically significant. The cluster-forming threshold used in the analyses presented here were $Z > 2.3$ (equals $p < 0.01$) for the lower-level analyses (i.e. single subject analyses) and either $Z > 2.3$ or $Z > 1.8$ (equals $p < 0.03$) for the higher-level (i.e. group) analyses. Reducing the cluster-forming threshold favours clusters of large spatial extent and low intensity, whereas increasing the cluster-forming threshold would result in clusters being broken up into a larger number of smaller clusters. It should be noted that the cluster-forming threshold used at the lower-levels is only used for inferences at that level, and similarly, the threshold specified at the higher-level is only relevant for the higher-level results. Once the clusters have been defined using the $Z$ statistic threshold, the probability of these clusters are tested against a set threshold which in all the analyses presented here was set to $p < 0.05$, corrected for the whole brain.

7.2 Results

**Statistical analysis of multi subject fMRI data**

A total of four higher-level group analyses were run; two across-group averages (one-sample t-tests) and two unpaired two-group difference (two-sample unpaired t-tests). These higher-level analyses were carried out using FLAME (FMRIB’s Local Analysis of Mixed Effects). All analyses were carried out using cluster-level inference and a correction for multiple comparisons using $p < .05$ at the whole brain levels. Labels for regions of activations were determined by
reference to the Juelich Histological Atlas and the MNI structural Atlas using the FSL ‘atlasquery’ command.

**Across-group analysis 1**

In the first across-group average analysis a cluster-forming threshold of $Z > 2.3$ (equals $p < 0.01$) was employed.

For the differential contrasts of compatibility (compatible > incompatible and incompatible > compatible), the analysis produced no significant areas of activations.

The contrast of precisiongrip > powergrip produced two clusters of activations, one cortical and one subcortical. Cortical activations were observed in the superior parietal lobe, primary somatosensory cortex, secondary somatosensory cortex, primary motor cortex, and premotor cortex (all in the left hemisphere). Subcortical activations were observed in the cerebellum (in the right hemisphere). See figure 7.1 and table 7.1 for cluster extent and local maxima.
Figure 7.1. Results of across-groups analysis 1 for the contrast of grip type (precisiongrip > powergrip). The clusters surpass a statistical threshold of $p < 0.05$ corrected for the whole brain. The cluster is overlaid onto the MNI152 template.

The contrast of powergrip > precisiongrip produced 3 clusters of activations, two of which were very extensive and extended over both hemispheres. Cortical activations included inferior parietal lobe, superior parietal lobe, primary somatosensory cortex, secondary somatosensory cortex, primary motor cortex, premotor cortex and inferior frontal gyrus. Extensive activations were observed in the left cerebellum (and to a lesser extent also in the right hemisphere). See figure 7.2 and table 7.1 for cluster extent and local maxima. L and R refers to left
and right hemisphere, respectively, and the X, Y and Z coordinates are in MNI space. For the two extensive clusters, the hemisphere in which activations were more extensive is listed first.

Figure 7.2. Results of across-groups analysis 1 for the contrast of grip type (powergrip > precisiongrip). The clusters surpass a statistical threshold of $p < 0.05$ corrected for the whole brain. The cluster is overlaid onto the MNI152 template.
Table 7.1.

Across-group analysis 1

<table>
<thead>
<tr>
<th></th>
<th>X (mm)</th>
<th>Y (mm)</th>
<th>Z (mm)</th>
<th>Max Z</th>
<th>Cluster extent (voxels)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Precisiongrip &gt; Powergrip</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SPL, S1, S2, M1, P1</td>
<td>L -46</td>
<td>-20</td>
<td>50</td>
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<td>-16</td>
<td>4.84</td>
<td>501</td>
</tr>
<tr>
<td>Powergrip &gt; Precisiongrip</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<tr>
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<td>-16</td>
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<td>30327</td>
</tr>
<tr>
<td>IFG</td>
<td>L -58</td>
<td>10</td>
<td>2</td>
<td>4.27</td>
<td>1474</td>
</tr>
</tbody>
</table>

Abbreviations: IPL = Inferior parietal lobe, SPL = Superior parietal lobe, S1 = Primary somatosensory cortex, S2 = Secondary somatosensory cortex, M1 = Primary motor cortex, P1 = Premotor cortex, IFG = inferior frontal gyrus. L and R refers to left and right hemisphere. X, Y and Z coordinates are in MNI space. All clusters surpass a statistical threshold of \( p < 0.05 \) corrected for the whole brain.

As the main contrast of interest (compatibility) had produced no significant areas of activations, two regions-of-interest (ROIs) were created (one precisiongrip ROI and one powergrip ROI) in order to investigate the effect of object size within each of those two ROIs.

Creating Regions-of-interest (ROI)

The output of the differential contrasts of precisiongrip > powergrip and powergrip > precisiongrip from the across-group analysis 1 using clusters determined by \( Z > 2.3 \) and a corrected cluster significance threshold of \( p < 0.05 \) were used to create two regions-of-interest (ROIs).

The differential contrast of powergrip > precisiongrip had produced widespread bi-hemispheric activations. In order to limit/reduce the regions for
the ROI analyses, the output was first thresholded using clusters determined by $Z > 4.5$. FSL’s tool ‘cluster’ was used to create an index of the clusters surviving this threshold. This procedure effectively limits our analysis to the peaks of the activations and yielded 16 different clusters. The six largest clusters (four cortical and two subcortical) had voxel sizes ranging from 92 to 3516 and $Z$-max of 5.92 to 6.83. Each of the six clusters were binarised and a cluster mask created. Using fslmaths, these six cluster masks were combined into one mask which then formed the powergrip > precisiongrip ROI.

As the differential contrast of precisiongrip > powergrip had produced defined regions of activation, the cluster index was created without carrying out any additional thresholding. This procedure yielded two different clusters, one cortical and one subcortical with a voxel size of 501 – 2429 and $Z$-max of 4.84 to 5.59. These two clusters were then used to create the precisiongrip > powergrip ROI as per the above described procedures.

**Regions-of-interest (ROI) analyses**

FSL’s featquery tool was used to extract percent signal change for the conditions of object size (the contrasts of parameter estimates for small and large) within the two grip type ROIs. These values were analysed using an ANOVA with the factors of ROI (precisiongrip > powergrip and powergrip > precisiongrip) and object size (small, large). Of main interest was the question of whether there was an effect of object size within the ROIs. There was, however, no evidence to this effect as the main effect of object size was not significant, $F(1,31) = 2.434, \ p = .129, \ \eta^2_p = .073$. The main effect of ROI approached significance, $F(1,31) = 4.087, \ p = .052, \ \eta^2_p = .116$, with the average
percent signal change being higher for the powergrip > precisiongrip ROI ($M = .216$) than the precisiongrip > powergrip ROI ($M = .188$).

Figure 7.3. Average percent signal change for the conditions of object size (small, large) and ROIs (precisiongrip > powergrip and powergrip > precisiongrip). Bars show standard errors.

Across-group analysis 2

Reducing the cluster-forming threshold favours activations of weaker signal intensity and larger spatial extent. Hence, a second across-group analysis with a cluster-forming threshold of $Z > 1.8$ (equals $p < 0.03$) was run in order to investigate whether areas of activation would be present for the contrast of interest (compatibility) when employing a relaxed set of criteria. However, as per the previous across-group analysis, this analysis produced no evidence of significant activations for the contrasts of compatibility either.
**Between-groups analysis 1**

In the first between-group analysis a cluster-forming threshold of $Z > 2.3$ was employed. Neither the compatibility by age interactions nor the grip type by age interactions produced any significant areas of activations. Consequently, for the same reasons described earlier, a second analysis was run.

**Between-groups analysis 2**

In the second between-group analysis a lower cluster-forming threshold of $Z > 1.8$ was employed. All surviving clusters surpass $p < 0.05$ corrected for the whole brain. This analysis produced a significant result for the compatibility by age interaction. More specifically, the contrast of compatible $>$ incompatible produced larger activations for the younger group than the older group. Activations were observed in the posterior division of the left cingulate cortex (and to a lesser extent also in the right cingulate cortex) as well as along the association tracts connecting the cingulate cortex; the cingulum and superior longitudinal fasciculus. There was also some evidence of activations in the caudate, the anterior intra-parietal sulcus and the superior parietal lobe. The other contrast of compatibility (incompatible $>$ compatible) did not show evidence of larger activations for the younger than the older group. See figure 7.4 which displays the age-related differences in the differential contrast of compatible $>$ incompatible in axial, coronal and sagittal views. Images are displayed in neurological convention meaning that the left side of the image corresponds to the left hemisphere. Cluster extent and local maxima are available in table 7.2.
Figure 7.4. Results of between-groups analysis 2 for the differential contrast of compatibility (compatible > incompatible). Voxels in which activations were larger for the younger than the older group are displayed in green in axial, coronal and sagittal views. The cluster surpass a statistical threshold of \( p < 0.05 \) corrected for the whole brain. The cluster is overlaid onto the MNI152 template.

For the contrasts of grip types there were significant areas of activations for the grip type by age interaction. The powergrip > precisiongrip produced two clusters in which activations for the older group were larger than for the younger group. The subcortical cluster was located in the cerebellum (left hemisphere) and the right-hemispheric cortical cluster was comprised of the premotor cortex, the primary motor cortex and the primary somatosensory cortex (see table 7.2 for cluster extent and local maxima).

Table 7.2.
Between-groups analysis 2.

<table>
<thead>
<tr>
<th></th>
<th>X (mm)</th>
<th>Y (mm)</th>
<th>Z (mm)</th>
<th>Max Z</th>
<th>Cluster extent (voxels)</th>
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<tbody>
<tr>
<td><strong>Compatible &gt; Incompatible</strong></td>
<td></td>
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</tr>
<tr>
<td>Cingulate cortex</td>
<td>L</td>
<td>Y &gt; 0</td>
<td>-12</td>
<td>-48</td>
<td>2.92</td>
</tr>
</tbody>
</table>

|                     |        |        |        |       |                         |
| **Powergrip > Precisiongrip** |         |        |        |       |                         |
| Cerebellum          | L      | 0 > Y  | 0      | -56   | 3.08                    | 1213                  |
| P1, M1, S1          | R      | 0 > Y  | 26     | -16   | 3.1                     | 1139                  |

Abbreviations: P1 = Premotor cortex, M1 = Primary motor cortex, S1 = Primary somatosensory cortex
L and R refers to left and right hemisphere. X, Y and Z coordinates are in MNI space. All clusters surpass a statistical threshold of \( p < 0.05 \) corrected for the whole brain.
7.3 Discussion

In the present experiment we used event-related fMRI to investigate the neural correlates of the behavioural object-size compatibility effect observed in previous experiments. Based upon the results of previous neuroimaging studies, we predicted areas of activity related to object affordance in a predominantly left-hemispheric fronto-parietal network and subcortical activations within the cerebellum and basal ganglia. Furthermore, as an effect of age upon the compatibility effect was predicted from the behavioural data (in line with previous findings), one might expect this age-difference also to be reflected in the functional activation patterns. In this section, the results of the functional data will be discussed (first the across-group effects, then the between-groups effects), along with a discussion of how these results relate to the results of the behavioural data collected in the scanner (presented in the previous chapter).

To briefly summarise, the main findings of the functional data were as follows; firstly, contrary to predictions, neither the first across-group analysis nor the second exploratory across-group analysis produced significant areas of activations related to the object-size compatibility effect in the group as a whole. As for the differential contrasts of grip type, the patterns of activity were consistent with what was expected. The first between-groups analysis did not produce any significant areas of activations, neither for the compatibility by age nor the grip type by age interactions. The second exploratory between-groups analysis did show an effect of age upon the compatibility effect, more specifically the contrast of compatible > incompatible produced larger
activations for the younger than for the older group, primarily in the left posterior cingulate cortex. For the contrast of grip type, the power > precision contrast produced two clusters in which activations were larger for the older than the younger group; the subcortical cluster was located in the left cerebellum and the cortical cluster comprised the premotor cortex, the primary motor cortex and the primary somatosensory cortex (all in the right hemisphere).

**Across-group effects**

In the first across-group average analysis a cluster-forming threshold of \( Z > 2.3 \) was employed. The differential contrast of compatibility produced no significant areas of activation. The precision > power contrast produced cortical activations in a number of areas, including the primary motor cortex, the premotor cortex, the primary and secondary somatosensory cortex and the superior parietal lobe – all in the left hemisphere. Subcortical activations were observed in the right cerebellum. As precision actions were always carried out with the right hand, these activations were exactly in line with what would be expected, namely lateralised to the left hemisphere cortically and ipsilateral activity in the cerebellum. The power > precision contrast produced extensive cortical as well as subcortical activations. Cortical activations were observed in the same areas as the other grip type contrast (i.e. primary motor cortex, the premotor cortex, the primary and secondary somatosensory cortex and the superior parietal lobe). In addition, there were activations in the inferior parietal lobe. Crucially though, in this power > precision contrast, the cortical activations were predominantly right-hemispheric. Similarly, subcortical
activations were observed in the cerebellum, primarily in the left hemisphere and, to a lesser extent, in the right cerebellum. As power actions were always carried out with the left hand, again, this is the pattern that would be expected.

As the first of the main contrasts of interest, compatibility averaged over both groups, had produced no significant areas of activation an additional ROI analysis was conducted. However, this analysis did not provide any evidence of an effect of object size within each of the ROIs that captured the parietal and premotor activation foci in the prior studies (Grezes & Decety, 2002; Grezes et al., 2003). Consequently, in order to explore whether an effect of compatibility would be present when employing a relaxed set of criteria, a second exploratory across-group analysis with a Z-threshold of 1.8 was run. Reducing the cluster-forming threshold favours activations of weaker signal and larger spatial extent. However, this analysis also did not produce any evidence of significant activations for compatibility either.

Consequently, the present across-group analyses of the functional data did not show evidence of activity related to the contrast of compatibility that would be common to both age groups. As the behavioural data also did not support our predictions of a significant object-size compatibility effect overall, these behavioural and functional data are consistent with each other (but note that step down analyses revealed a significant object-size compatibility effect for the younger, but not the older group – see below for further discussion). One possible explanation for why this experiment failed to replicate previous findings of highly significant compatibility effects (including the two fMRI ‘pilot’ studies, i.e. experiments 3 and 4) is due to the much slower RTs in the scanner -
the reason for this slowing probably resulted from a combination of factors, as discussed in the previous chapter. The one the study which has used the same paradigm and grip devices in the scanner (Grezes et al., 2003), found significant compatibility effects on the behavioural level. Importantly though, the RTs in that study were almost twice as fast as the present study. Similarly, the RTs in the two fMRI 'pilot' studies which documented highly significant compatibility effects were also almost twice as fast. These findings together thus support the notion that processing times may be crucial in the compatibility effect. From an evolutionary perspective, the advantage of automatic activation of motor responses from the perception of affordances would appear to be present in the speed and immediacy of the effect rather than a gradual build-up (see e.g. Philips and Ward, 2002). Furthermore, it is consistent with the findings that visuomotor processing in the dorsal stream is transient, which has been said to be crucial for any system involved in action control, which seems a sensible suggestion (Tucker, & Ellis, 2001). As for the results of their functional data analysis (Grezes et al., 2003), it does not allow a direct comparison to the present results due to the different analyses which were performed. Rather than across-group averages which compare two experimental conditions directly, they reported regression analyses which sought to establish areas of activations which co-varied with the effect of compatibility. Similar regression analyses (although performed on DTI data and not functional data which evidently does not allow for a direct comparison either), will be presented in the following chapter.
**Between-groups effects**

As for the between-groups analyses, the first between-groups analysis did not produce any significant areas of activation, neither for the compatibility by age or grip type by age interactions. Consequently, it was decided to perform a second exploratory analysis which employed a relaxed set of criteria, (i.e. a cluster-forming threshold of $Z > 1.8$), which provided evidence of an age-difference for the second main contrast of interest, the compatibility by age interaction. The contrast of compatible > incompatible showed larger activations for the younger than the older group primarily in the posterior division of the left cingulate cortex and, to a lesser extent, also in the right posterior cingulate cortex. There were some indications, as evidenced by the ‘atlasquery’ command, that this cluster of activation also extended into areas along the association tracts connecting the cingulate, as previously noted. However, the output by atlasquery can be rather low from a probabilistic point of view. Furthermore, there may be difficulties and/or uncertainties in pinpointing the exact anatomical locations from the statistical maps in smaller clusters. Consequently, appropriate caution must be taken in the interpretation of results - not only regarding featquery results, but the results of this exploratory analysis in general - particularly when taking into account the very liberal threshold employed in this analysis.

Thus, contrary to predictions, there was very limited evidence of activation associated with the object-size compatibility effect in fronto-parietal areas. Although there was some indication from the exploratory analysis that age-differences may be present in the posterior cingulate cortex, (PCC), it is worth
bearing in mind that the PCC is not typically associated with a particular type of task - instead it is a key node in the default mode network (DMN). The DMN is a network that is active during rest and which is rapidly deactivated during a wide range of tasks which require externally directed attention, at least in healthy younger adults (Buckner, Andrews-Hanna, & Schacter, 2008). There are, however, a number of studies of healthy ageing which have demonstrated that posterior cingulate (PCC) function changes in older age, for example, functional connectivity to other regions have been shown to decrease, which in turn is associated with cognitive impairment (Andrews-Hanna, Snyder, Vincent, Lustig, Head, & Raichle, 2007). In conditions of externally directed attention, the magnitude of deactivation of the DMN is strongly coupled with increases in cognitive load in younger adults (Sing, & Fawcett, 2008), whereas in older adults a failure of appropriate deactivation has been demonstrated (Prakash, Heo, Voss, Patterson, & Kramer, 2012). This lack of appropriate deactivation has been associated with inefficient cognitive function (e.g. Sambataro et al., 2010; Spreng, & Schacter, 2012). Results of the present analysis may not necessarily arise from age-related changes within the PCC itself though. Recall the mention of the cortical disconnection hypothesis discussed earlier, which states that changes in cortical activation patterns may instead result from changes in white matter tracts connecting cortical regions. There is in fact evidence to suggest that age-related changes in PCC are correlated with changes in white matter tracts connecting the PCC (and DMN), which could potentially be an underlying reason for the present observations (Andrews-Hanna et al., 2007). It is also possible that this between-groups result may be noise due to the lowered threshold. Consequently, with that in mind, our functional MRI results were,
unfortunately, not particularly informative regarding visuomotor processes and potential age-related changes therein, but may be a reflection of other processes, for example attentional processes.

Although not central to our hypothesis, the between-groups analysis also provided evidence of a grip type by age interaction with the older group showing larger activations for the power grip in the ipsilateral cerebellum and contralateral motor areas. This finding is largely consistent with the age-related changes in functional activation patterns during motor tasks; there was an increase in the magnitude of activation as observed previously, but there was no evidence of increased activation in ipsilateral motor cortical regions. Consequently, the present results did not support previous findings of reduced interhemispheric inhibitory function with age.

As this is the first investigation of age-differences in the object-size compatibility effect using neuroimaging, there are no previous findings to which to the present set of results can be compared (and different analyses were employed in the earlier study which complicates direct comparisons). It was, however, somewhat surprising that there was rather limited evidence of activation related to the object-size effect in fronto-parietal areas. However, this is difficult to compare to the prior studies. Although an across-group analysis was apparently performed in the earlier study (Grezes et al., 2003), only the results of the regression analysis was reported. In hindsight, rather than optimising statistical power of our event-related design by making use of the genetic algorithm for improved contrast detection (Wager, & Nichols, 2003), it may have been more optimal to have restricted the functional analyses to pre-
defined ROIs in order to have optimised statistical power. However, as the present investigation was the first of its kind, that approach would have implied defining ROIs based upon related types of studies, which in turn may have resulted in other problematic issues. Instead, Thus, the same reasoning formed the basis for the functional analyses as for the DTI analyses, namely that whole-brain analyses were preferred over pre-specified ROI analyses due to the limited amount of research (whether behavioural or neurophysiological) on the relationship between healthy ageing and visuomotor functions. In sum, further research is needed in order to clarify whether the temporal resolution of fMRI is sufficient to capture potentially transient affordance-related activations of motor programmes or whether methods which provide much finer temporal information, such as electroencephalography (EEG), is better suited.
Chapter 8
Experiment 5. Age-differences in object-size effects – diffusion tensor imaging data

Diffusion Tensor Imaging (DTI) is a recent non-invasive MRI technique which allows investigation white matter integrity. Conventional MRI allows assessment of brain structural and volumetric information whereas DTI adds valuable information regarding cerebral microstructural integrity. As previously mentioned, most DTI studies on healthy aging have focussed on the two global measures of integrity; fractional anisotropy and mean diffusivity. The overall pattern which has emerged is that healthy aging is associated with declines in fractional anisotropy and increases in diffusivity measures. There is continued debate as to whether age-related changes in white matter microstructural integrity is characterised by anterior-posterior and superior-inferior gradients of higher-to-lower vulnerability (Salat, 2011; Sexton, Walhovd, Storsve, Tamnes, Westlye, Johansen-Berg, & Fjell, 2014).

The relationship between age-related changes in white matter physiology and higher-level cognitive functions has been studied extensively. How these changes impact on lower level perceptual and motor components is less well understood, however, an increasing number of studies have begun to elucidate the neural substructures associated with motor control in healthy ageing (Fling, Peltier, Bo, Welsch & Seidler, 2011; Seidler et al., 2010). Age-related declines in motor function / motor performance deficits appear to result from age-related
changes seen throughout the central and peripheral nervous systems as well as deterioration of the neuromuscular system (Seidler et al., 2010). Several studies have demonstrated significant relationships between white matter integrity and motor performance, more specifically, intact/undisrupted white matter integrity correlates with better motor performance (e.g. Sullivan, Rose, Rohlfing, & Pfefferbaum, 2009; Sullivan, Rohlfing, & Pfefferbaum, 2010; Zahr, Rohlfing, Pfefferbaum, & Sullivan, 2009 – this will be discussed in further detail below).

There are several different DTI indices, each of which is believed to be sensitive to different aspects of white matter physiological properties. DTI makes use of the fact that 90 percent of protons in the body are located in water molecules and that movement of the hydrogen molecules varies between tissue types (Mori, & Tournier, 2014). In biological tissue, water tends to diffuse along a preferential axis, for example, in white matter, the diffusion of water molecules is constrained by the axon sheath, which makes diffusion less restricted along the axon (this is called anisotropic diffusion, i.e. directionally dependent) (Soares, Marques, Alves, & Sousa, 2013). In grey matter, diffusion is usually less anisotropic. In cerebrospinal fluid (CSF), water molecules can move freely in all directions, called isotropic diffusion. DTI requires quantification by mathematical computation of a tensor. The tensor is a three-dimensional ellipsoid and thus requires at least six different gradient directions during acquisition. The tensor has three eigenvectors (V1, V2, V3) which define the orientation of the principle axis of the ellipsoid and three eigenvalues (λ1 +λ2 +λ3) which define the shape of the ellipsoid (Mori, & Tournier, 2014). The
primary eigenvalue ($\lambda_1$) is the longest of the three axes and is referred to as axial (longitudinal) diffusivity, (AD). AD is thought to reflect axonal integrity. In terms of investigations into how advanced age impacts on white matter integrity, AD is the DTI metric which has shown the most diverse results with both age-related increases and decreases observed in different regions of the brain (Barrick, Charlton, Clark, & Markus, 2010). The secondary and tertiary eigenvalues ($\lambda_2$ and $\lambda_3$, respectively) are the axons which are perpendicular to the primary axis and therefore reflect radial (transverse) diffusivity, (RD). Radial diffusivity is in fact an average of the two non-primary eigenvalues (($\lambda_2 + \lambda_3$) /2)). RD is thought to reflect myelin integrity, more specifically, RD increases with demyelination and furthermore, changes in axonal density may also influence RD (Chanraud, Zahr, Sullivan, & Pfefferbaum, 2010). The average of all three eigenvalues (($\lambda_1 + \lambda_2 + \lambda_3$) /3)) is referred to as mean diffusivity, (MD), or the apparent diffusion coefficient. MD is a measure of overall water diffusion. It is sensitive to necrosis, amongst other things, and consequently tends to increase with age due to increased diffusion in extracellular tissue due to age-related atrophy (Alexander et al., 2011; Bennett, et al., 2010). The final diffusion parameter called fractional anisotropy (FA) is one of the most widely reported diffusion parameters as it is a good overall measure of microstructural integrity – it is, however, less informative to the type of microstructural change compared to the other parameters (Alexander, Lee, Lazar, & Field, 2007). FA is determined by the degree to which the primary eigenvalue dominates the two non-primary eigenvalues, and it is thus a measure of orientational preference within a voxel (Chanraud et al., 2010). As for FA, age-related decreases in
integrity would manifest as a lower FA, and this arguably the most frequently reported DTI measure of age-related change in microstructural integrity.

Most DTI studies have primarily focused on the global measures of integrity; FA and MD. However, as animal research indicated that AD and RD may be selectively sensitive to specific properties of neural changes, an increasing number of ageing studies have included AD and RD and consequently, the more frequently used measures are increasingly examined in relation to AD and RD which provides a much more detailed picture (Bennett, et al., 2010). For example, a longitudinal study investigating DTI measures as potential biomarkers for Alzheimers disease found that RD and FA may be providing stage-specific information (i.e. how far the disease has progressed), whereas AD and MD may provide state-specific information (i.e. changes in AD and MD are the first abnormalities to occur, but remains relatively stable subsequently) (Acosta-Cabronero, Alley, Williams, Pengas, & Nestor, 2012).

Recently, Inano and colleagues (Inano, Takao, Hayashi, Abe, & Ohtomor, 2011) investigated age-related differences in FA, AD, and RD and this study had what is likely to be the largest sample-size to date in this particular field (857 participants, aged 24-84 years of age). In addition to the frequently reported age-related decreases in FA, the results suggested that more generally speaking, age-related decreases in microstructural integrity are more strongly associated with myelin sheath degeneration / demyelination (as measured/indicated by increases in RD) than with axonal damage/injury (as measured by increases in AD) (Barrick et al., 2010; Irvine, & Blakemore, 2006).
The relationship between white matter physiological properties, such as myelination, and the speed of nerve conduction is well established; increased myelination results in faster conduction and consequently faster reaction times, and it has been suggested that individual differences in reaction times may be explained by differences in degrees of myelination (Liston, Watts, Tottenham, Davidson, Niogi, Ulug, & Casey, 2006; Tuch, Salat, Wisco, Zaleta, Hevelone, & Rosas, 2005). Sullivan and colleagues (Sullivan et al., 2010) reported that fine finger movement scores were positively correlated with FA in the internal and external capsules which are regions interconnecting the striatum/basal ganglia and motor cortical regions. In addition, increased RD in the cerebellum was associated with slower finger movement. Zahr and colleagues (Zahr et al, 2009) examined a group of younger and older individuals on a range of neuropsychological tests, and found that for the motor component, higher FA in the anterior and posterior callosum (the genu and splenium), the uncinate fasciculus and the fornix was associated with better motor performance. Unfortunately, although the motor component was only one of three main points of focus of this study, the superior longitudinal fasciculus was not included in their pre-specified ROIs which is somewhat surprising considering its considerable relevance for fronto-parietal integration as it interconnects both occipital, parietal, temporal and frontal regions.

A very recent study (Sexton, Walhovd, Storsve, Tamnes, Westlye, Johansen-Berg, & Fjell, 2014 ) was the first, according to the authors, to report both longitudinal measures of the timescale as well spatial distribution of age-related white matter changes in healthy adults across the lifespan. Their study included data
from over 200 participants aged 20-84 and incorporated quantification of annual changes in measures of all four diffusion / anisotropy measures. Consistent with previous cross-sectional studies (Bennett et al., 2010; Burzynska, Preuschhof, Bäckman, Nyberg, Li, Lindenberger, & Heekeren, 2010), results indicated that age-related decline appears to be relatively stable until the fifth decade followed by an accelerated annual decline in fractional anisotropy and increases in diffusivity (AD, RD, and MD). Furthermore, all of these results supported a superior-inferior gradient of higher-to-lower vulnerability (Sexton et al., 2014). There have only been a few other longitudinal DTI studies to date, and only one of these studies included AD and RD in addition to FA (Barrick et al., 2010). Generally, all of the white matter ROIs exhibited increases in AD and RD and decreases in FA, however, changes were not uniform as inconsistent patterns of both increases and decreases in AD were observed. In addition, results suggested that the longitudinal age-related changes in white matter integrity were apparent across the whole brain and that the prefrontal areas were not differentially affected. Furthermore, only their Tract Based Spatial Statistics (TBSS) analyses (see below for further explanation) were sufficiently sensitive to detect longitudinal changes in all of the parameters as these were not evident with either 1D, 2D, 3D or ROI analyses, apart from a few regions in which changes were particularly substantial.

Due to the relatively limited amount of research on the connection between healthy ageing, visuomotor functions and white matter integrity, whole-brain brain analyses of DTI parameters were employed in the present study rather
than using pre-specified ROIs. The primary objectives of including DTI metrics in the present MRI study were two-fold. The first objective was to quantify potential age-differences in white matter integrity. For this purpose, Tract Based Spatial Statistics (TBSS) was employed (Smith, Jenkinson, Johansen-Berg, Rueckert, Nichols, Mackay, & Behrens, 2006). TBSS is a recent technique which attempts to avoid the morphometric differences that might result from using the older and more conventional whole-brain voxel-wise analyses by using a ‘mean skeleton’ which represents the centres of the white matter tracts which are common to all participants, and thus avoids the pitfalls caused by partial voluming in which extra-tract voxels are included in analysis. Whole-brain TBSS analyses were carried out for each of the four anisotropy and diffusion parameters (FA, AD, RD, and MD) as they are sensitive to different physiological properties. The second objective concerned the question of whether, provided age-differences in white matter integrity were present, those age-differences would be reflected in, or impact on the size of the behavioural measure of the compatibility effect. White matter sub-serves intra- and interhemispheric communication, hence, if white matter connectivity is compromised, then this may affect behavioural measures of visuo-motor integration. For this purpose, TBSS regression analyses of the diffusion parameters against the compatibility effect were performed.
8.1 Method

Diffusion Tensor Imaging data acquisition and pre-processing

The Diffusion Tensor Imaging (DTI) data acquisition was carried out using a 1.5T Philips Gyroscan Intera Scanner in the Peninsula MR Research Centre, University of Exeter. The imaging parameters were as follows; Spin-Echo sequence (SE) with repetition time (TR) = 9543 ms, echotime (TE) = 66 ms, flipangle = 90 degrees, and 36 slices with a 0.4 mm gap. The order of acquisition was interleaved ascending (first odd, then even), the acquisition voxel size = 2.33 x 2.33 x 3 mm, the reconstruction voxel size = 1.75 x 1.75 x 3 mm, and field-of-view (FOV) = 224 mm. An image with no diffusion weighting (b0) was also acquired. Diffusion Tensor Imaging data was analysed using FSL’s Diffusion Toolbox (FDT, Behrens et al., 2003) and Tract-Based Spatial Statistics (TBSS, Smith et al., 2006).

In order to be able to run TBSS, the following preprocessing steps were performed; the data were corrected for distortions and subject movement using eddy current correction, the brain was skull stripped using FSL’s BET tool and a mask created from the b0 image (the first, un-weighted volume). Subsequently, the diffusion tensor model was fit to the data at each brain voxel using the ‘dtifit’ tool within FDT. This produced fractional anisotropy (FA), mean diffusivity (MD) and axial diffusivity (AD) images for each individual. The AD is the primary eigenvalue (diffusion parallel to the axon fibers). The radial diffusivity (RD), which is the average of the two non-primary eigenvalues (diffusion perpendicular to the axon fibers), was calculated using ‘fslmaths’. The MD is the
average of all three eigenvalues. As discussed above, the global measures of FA and MD have been widely reported, FA being a measure of overall microstructural integrity and MD a measure of overall water diffusion which is sensitive to necrosis. AD is thought to reflect axonal integrity, and RD myelin integrity.

Voxelwise analysis of FA, AD, RD, and MD using Tract-Based Spatial Statistics

Tract-Based Spatial Statistics (TBSS) was employed to perform whole-brain statistical analysis of white matter tracts. TBSS involved spatially normalising each individual’s FA image to the standard 1x1x1 mm MNI (Montreal Neurological Institute) template and combining them into a single 4D file. The mean of all FA images were then projected onto a skeleton which represents the centre of white matter tracts common to all participants. This mean FA skeleton was thresholded at FA > 0.2 in order to avoid partial voluming.

In the same manner, each of the MD, AD, and RD data were also spatially normalised to the MNI152 template and combined into 4D files. For MD, AD, and RD, the 4D files were projected onto the original mean FA skeleton by using the original FA data’s projection vectors. Those 4D FA, MD, AD and RD skeletonised images were then fed into voxelwise statistics, allowing an investigation of age differences in white matter integrity - more specifically, the resulting statistical maps specify which skeleton voxels are significantly different between the two groups. For these purposes, a design matrix (containing contrasts of younger > older and older > younger) was created and tested using FSL’s ‘randomise’ tool with the number of random permutations
set to 5000. Threshold-Free Cluster Enhancement (TFCE) was applied to enhance areas for analysis and all resulting statistical maps were corrected for multiple comparisons using family-wise error (FWE) and thresholded at $p < .05$.

**TBSS regression analyses of the diffusion parameters against the compatibility effect**

In order to investigate whether the four different diffusion parameters (FA, AD, RD, and MD) were correlated with the behavioural measures of the compatibility effect, regression analyses were performed. To this effect, a single-group average analysis with the additional covariate of compatibility effect was conducted. Each participant’s overall compatibility effect was demeaned and entered into design matrix in which both positive and negative correlations were also included. Voxelwise analyses of each of the four demeaned diffusion parameters were regressed against the compatibility effect using the tool 'randomise'. The number of random permutations were set to 5000, and as per the previous voxelwise analyses, TFCE was employed and the resulting statistical maps were corrected for multiple comparisons using FWE and thresholded at $p < .05$.

**8.2 Results**

**Age related differences in FA, AD, RD and MD**

All of the four between-group voxelwise analyses of global DTI indices, i.e. Fractional Anisotropy, Axial Diffusivity, Radial Diffusivity and Mean Diffusivity,
produced significant results, (please see figure 8.1, 8.2, 8.3, and 8.4, respectively). Labels for regions of statistical difference were determined by reference to the MNI structural Atlas, the Juelich Histological Atlas, and the JHU white-matter tractography atlas. All images are displayed in neurological convention meaning that the left side of the image corresponds to the left hemisphere.

TBSS results for the group contrast of fractional anisotropy are displayed in figure 8.1. FA was arguably the one of the four parameters where age-differences were most pervasive, both in terms of brain regions affected and local spatial extent. Age-related decreases in FA were observed in the commissural fibres; the entire corpus callosum apart from the most posterior part of the splenium and the hippocampal commissure (the commissure of fornix). Pervasive changes were observed in most of the association fibres, namely the inferior and superior longitudinal fasciculus, the uncinate fasciculus and occipito-frontal fasciculus, the optic radiation, the cingulum and the fornix bilaterally. There were also age-related decreases in FA in the caudate, the thalamus and the anterior thalamic radiation. There were no voxels in which FA was lower for the younger group than the older group.
Figure 8.1. TBSS results for age-related reductions in Fractional Anisotropy. The statistical maps (thresholded at TFCE and $p < 0.05$) are overlaid onto the MNI152 template.

TBSS results for the group contrasts of axial diffusivity are displayed in figure 8.2. AD was the only one of the four diffusion parameters where both of the differential contrasts (younger > older and older > younger) produced statistically significant maps. Overall, however, there were many more brain areas in which AD was higher for the younger than the older group, than the reverse. AD was higher for the older than the younger group only in the central
regions, more specifically in the fornix and thalamus bilaterally. In contrast, AD was higher for the younger than the older group in parts of the anterior and central corpus callosum, the inferior and superior longitudinal fasciculus, the occipito-frontal fasciculus, the cortico-spinal tract, the optic radiation, the cingulum and cerebellum.

Figure 8.2. TBSS results for age-related differences in Axial Diffusivity. Voxels in which AD is higher for the younger than the older group are displayed in blue. Voxels in which AD is higher for the older than the younger group are displayed in red. The statistical maps (thresholded at TFCE and $p < 0.05$) are overlaid onto the MNI152 template.
TBSS results for the group contrast of radial diffusivity are displayed in figure 8.3. The statistical map showed widespread age-related increases in RD in a number of white matter structures bilaterally. As for major white matter tracts, age-related increases in RD were observed all regions of the corpus callosum apart from the most posterior part of the splenium. Additionally, RD increases were observed in the superior and inferior longitudinal fasciculus, the inferior occipito-frontal fasciculus and the optic radiation as well as along the entire anterior cingulate/commissure. There were also increases in RD in the fornix and thalamus bilaterally. There were no voxels in which RD was higher for the younger group than the older group.
Figure 8.3. TBSS results for age-related increases in Radial Diffusivity. The statistical maps (thresholded at TFCE and $p < 0.05$) are overlaid onto the MNI152 template.

TBSS results for the group contrast of mean diffusivity are displayed in figure 8.4. The statistical map showed widespread age-related increases in MD in a number of white matter structures bilaterally, with the most prominent increases in MD being present in central and anterior regions. Age-related changes were observed in the entire corpus callosum although the splenium was relatively preserved in relation to more anterior sections. Furthermore
there were MD increases along the entire anterior cingulate, the inferior occipito-frontal fasciculus, the fornix, the caudate and thalamus bilaterally. There were no voxels in which MD was higher for the younger group than the older group.

Figure 8.4. TBSS results for age-related increases in Mean Diffusivity. The statistical maps (thresholded at TFCE and $p < 0.05$) are overlaid onto the MNI152 template.
In sum, there were age related decreases in FA and age related increases in MD and RD. As for AD, there were regions in which AD was higher for the younger group and other regions where AD was higher for the older group.

**TBSS regression analyses**

None of the four voxelvise regression analysis of FA, MD, AD, and RD against the compatibility effect produced any significant results. In other words, in the group as a whole, there were no brain voxels in which there was a significant correlation between the behavioural measure of compatibility and the four diffusion parameter measures.

**8.3 Discussion**

Whole-brain statistical analyses of the DTI data were carried out using TBSS in order to quantify potential age differences in the four diffusion metrics, each of which are sensitive to different physiological properties. The results provided evidence for significant age-related differences in FA, AD, MD and RD.

TBSS voxel-wise regression analyses of the four diffusion parameters against the compatibility effect were also performed; however, none of those produced any significant results. Thus, there was no evidence that the observed age-related changes in microstructural integrity as measured by the anisotropy and diffusion parameters correlated with the behavioural measure of compatibility.

As noted previously, the majority of studies have focussed on the global measures of FA and MD as markers for age-related changes in microstructural integrity. A frequently reported finding has been an anterior-posterior gradient
whereby fractional anisotropy is lower in anterior relative to posterior regions and similarly, diffusivity is higher in anterior relative to posterior regions. It has been noted though, that the majority of studies supporting this anterior-posterior gradient has been based primarily on studies of the corpus callosum (Sullivan et al., 2010). Furthermore, it has also been proposed that age-related decreases in microstructural integrity may be characterised by a superior-inferior gradient whereby anisotropy is lower and diffusivity higher in superior relative to inferior regions (Sexton et al., 2014; Sullivan et al., 2010). The recent longitudinal study (Sexton et al., 2014) was, according to the authors, the first to report continuous superior-inferior gradients in all four metrics. However, although results clearly favoured a superior-inferior gradient, the authors still encouraged cautious interpretation of results in terms of gradient theories as discrepancies may, to some extent, reflect different methodologies rather than the anatomy itself.

In the present study, FA was the parameter in which the most pervasive age-related changes were observed, both in terms of global extent and local spatial extent. Pervasive age-related decreases in FA were observed in all of the major white matter tracts, including the corpus callosum (facilitating inter-hemispheric communication), and intra-hemispheric association tracts connecting occipital, parietal, temporal and frontal regions. Our results provided no apparent indication of an anterior-posterior gradient of age-related decreases in FA. Age-related decreases were also observed in subcortical structures which are involved in voluntary movement and relaying sensory and motor signals to the cortex (the caudate, thalamus and thalamic radiation).
There was no evidence of a superior-inferior gradient, if anything age-related decreases in FA were more pervasive in central and inferior regions in comparison to superior regions.

When it comes to MD which is an indicator of sensitive to necrosis, however, our results provided evidence of age-related increases in MD which were more apparent in central and anterior regions, thus supporting the anterior-posterior gradient hypothesis. Overall age-related changes in MD were nowhere near as extensive as those of FA but, as was the case for FA, the subcortical structures involved in movement and sensory-motor transformations were also affected. Also in the case of MD there was no evidence in favour of a superior-inferior gradient, if anything age-related increases were more extensive in central and inferior regions.

RD increases with demyelination. The pattern of age-related changes in RD was similar to that of FA with widespread age-related increases in RD observed in all major inter- and intra-hemispheric white matter tracts. Age-related changes in RD were not quite as extensive as that observed for FA, neither globally nor locally. The TBSS results of RD did not support either an anterior-posterior or a superior-inferior gradient of age-related increases in RD. Rather, age-related increases in RD would appear to be more prominent in inferior than in superior regions.

AD is believed to reflect axonal integrity. As previously noted, measures of AD with increasing age are complex and have been found to show both age-related increases and age-related decreases. Results of our analyses were consistent with those previous findings – AD was the only of the four measures in which
both of the differential contrasts produced significant results. Areas where AD was higher for the older than younger group were limited to the fornix and thalamus. The finding of higher AD in the fornix thus replicated earlier findings (Burzynska et al., 2010; Inano et al., 2011; Zahr, Rohlfing, Pfefferbaum, & Sullivan, 2009). In contrast, AD was higher for the younger than the older group in most of the inter- and intra-hemispheric white matter tracts as well as the cerebellum, and was slightly more predominant in inferior regions. Interestingly, the substantial extent of age-related decreases in AD seems to contradict the previously reported general pattern of age-related increases in diffusivity. However, as researchers have only recently begun to include measures of AD and RD in addition to FA, findings are still very much equivocal. According to Bennett and colleagues (Bennett et al., 2010) two patterns of age-differences in diffusivity have emerged from the earlier studies that have included AD and RD; in one pattern, age-related decreases in FA are accompanied by increases in RD but not AD, in the second pattern, age-related decreases in FA are accompanied by increases in both RD and AD. At first glance, the present findings of widespread age-related decreases in AD appear to be inconsistent with these previously observed patterns. It is worth keeping in mind that different statistical analyses and approaches have often been employed, so although the various different methodologies are equally valid, it frequently leads to difficulties in comparing results to previous findings. For instance, a number of studies have looked for age-differences in pre-specified ROIs rather than whole-brain analyses. This is an important point as all DTI metrics, both anisotropy and diffusion metrics, have been found to be characterised by substantial regional variations (Sexton et al., 2014). Other
studies have employed whole-brain statistical analyses as per the present study, but have then only analysed diffusivity measures in the clusters which showed age-differences in FA. One study (Bennett et al., 2010) which used this approach found that, in addition to the two patterns reported above, a third pattern was also observed. This showed that clusters with significant age-related decreases in FA both had higher RD and lower AD in older versus younger adults. This third pattern is consistent with our findings, although in the present study whole-brain analyses were employed for each of the metrics in an independent manner from other metrics. Consequently, had the present study first identified the regions in which age-related decreases in FA were observed and then subsequently limited the investigations of diffusion parameters to those regions, different patterns of diffusivity may have emerged. For instance, the age-difference in AD in the cerebellum would not have emerged had this approach been taken.

Bennett and colleagues (Bennett et al., 2010) noted that (at the time of publication), only a total of nine other DTI studies of healthy ageing had included AD and RD in the assessment of age-differences and, furthermore, the finding of increases in RD along with decreases in AD had only been reported a couple of times. One of these studies (Burzynska et al., 2010) interpreted this particular pattern as an indication of axonal loss and gliosis, whereas Bennett et al. (2010) suggested that age-related decreases in AD may be caused by disrupted macrostructural orientation, caused, amongst other things, by microstructural variables such as demyelination and axonal shrinkage.
To conclude, although the present study found evidence of age-related decreases in microstructural integrity in several regions known to be essential for motor performance/action selection, such as the basal ganglia substructures, the four voxel-wise regression analyses of the individual DTI parameters against the behavioural measures of the compatibility effect found no evidence of any correlations.

Regarding the question of the extent to which microstructural integrity in healthy ageing is characterised by an anterior-posterior gradient, the only metric which provided evidence to this effect in the current study was that of MD. As for the superior-inferior gradient theory, the present results indicated that for all of the four metrics, age-related changes were more prominent in inferior relative to superior regions. These results are in contrast to previously reported cross-sectional studies and a recent longitudinal study which have documented higher susceptibility of age-related degeneration in superior than inferior regions (Salat, 2011; Sexton et al., 2014; Sullivan et al., 2010). It is important to keep in mind that there are still a very limited number of DTI studies of healthy ageing which have incorporated all four DTI metrics and most have employed different methodologies (e.g. whole-brain voxel-based/whole-brain TBSS/ROI analyses and vary quite substantially in terms of number and characteristics of participants. In addition, although DTI studies can provide very detailed information about microstructural integrity, they cannot elucidate which individual neural substrates contribute to DTI metrics smaller than the voxel size which is usually in the region of 1-3mm. Hence, in order to further clarify which specific neural substrates (e.g. degree of myelination, fibre
orientation and axonal damage) may be the underlying reason for these observations, future studies would benefit from employing higher resolution DTI combined with techniques that can assess microstructure at the cellular level, such as magnetic resonance spectroscopy (Bennett et al., 2010). Regardless, DTI is widely applicable in both health and disease and accumulating evidence is likely to provide valuable information as to the ‘normal’ ageing processes of the brain and aid in disease detection and then perhaps intervention at an earlier stage than was previously possible.
Chapter 9
General discussion

9.1 Experimental summary

The main objective of this thesis was to explore age-related changes in visuomotor integration (in healthy younger and older individuals) as measured by object affordance effects (the object-orientation effect and the object-size effect). To the author’s knowledge, these paradigms have never been employed before in the study of healthy ageing. This final chapter offers a summary of the four behavioural experiments and one neuroimaging study (which combined behavioural, functional MRI and DTI data) that were carried out. Furthermore, recommendations for further investigations will be made. Finally, the implications that the empirical findings of the current thesis may have on our understanding of healthy ageing and visuomotor integration will be discussed.

Object-orientation effects:

Experiment 2 (chapter 4) was the only experiment, which investigated the object-orientation effect. More specifically, it was an investigation into the object-orientation affordance effect and the spatial-compatibility effect within the same study, and it also included a baseline condition which allowed an assessment of whether effects were driven by facilitation or interference. Thus, this experiment included three conditions; an affordance condition (door handles), a spatial condition (6 spheres presented in the same location as the
door handle stimuli), and a baseline condition (the same 6 spheres presented centrally). Furthermore, it was also the only study which was built on previous evidence from an older group (as a healthy, age-matched control group in Galpin and colleagues’ study). The procedures of the earlier study on Parkinson’s patients (Galpin et al., 2011) were adhered to and identical analyses performed in order to allow direct comparison with their study.

Both age groups showed an overall larger effect for affording stimuli than for spatial stimuli although the differences in effect magnitudes were not statistically significant. Our additional analysis, which investigated this effect broken down by age group revealed a larger compatibility effect for affording than spatial stimuli for the younger group, whereas for the older group there was only a slight hint of an effect when split by SOA. Thus, the results of our study provided evidence of a dissociation of affordance and spatial effects (i.e. larger affordance than spatial effects) only in the younger group. The original study found evidence of a dissociation in healthy controls (but not the Parkinson’s group).

The second objective of this study was to examine whether the effects arose from facilitation by compatible stimuli or interference from incompatible stimuli. Such an investigation was relevant due to the previously discussed literature, which suggests that older adults, in a similar manner to Parkinson’s patients, have difficulties in resisting entrainment by visual distractors. Conceivably, (in direct contrast to our predictions of age-related decreases in compatibility effects), this increased reliance on external stimuli would result in an age-related increase in the size of compatibility effects, in line with previous
(although limited) demonstrations of age-related increases in spatialcompatibility effects (Gazzaley, 2013). However, our results did not find any evidence of age-related increases in neither the object-orientation effect nor the spatial-compatibility effect. Furthermore, one might expect that difficulties in resisting entrainment by visual distractors would entail that compatibility effects would be driven by interference effects. However, taken together with the results of the original study (Galpin et al, 2011), results suggested that the locus of the effects for the two healthy older groups appeared to be due to both facilitation and interference, whereas the locus of the effects in the young group and the Parkinson’s group arose from different sources (interference in the young group and facilitation in the Parkinson’s group).

**Object-size effects:**

Experiment 1 (chapter 3), investigated age-differences in the object-size compatibility effect, using the same behavioural paradigm, grip devices and experimental stimuli as that of Tucker and Ellis (2001). Participants were asked to categorise commonly known objects (e.g. a hammer), as being natural or manufactured by making precision and power grip responses. Consistent with predictions, the results of this study corroborated previous findings of highly significant object-size compatibility effects. Importantly, the findings also included an age-related decrease in the size of the compatibility effect (in the ‘preferred’ hand-mapping). As the age-related difference was modulated by hand mapping, these results may point towards a manual asymmetry in grasping specialisation – left for holding and right for manipulating – that diminishes with age.
For experiments 3 and 4 (chapter 5), a new stimulus set which consisted of spherical objects, which were matched across category for size and colour, was created. The main reason for creating this new stimulus set was to address the attention-directing hypothesis (Anderson et al., 2002; Cho & Proctor, 2013), which suggests that affordance effects are merely a form of spatial compatibility effect. By using spherical, centrally presented objects, spatial – and hence also attention-directing attributes – are ruled out as potential confounds. Consequently, the finding that both experiments 3 and 4 revealed highly significant object-size compatibility effects was crucial in that it provided strong evidence in favour of the object-size affordance hypothesis by ruling out the most important alternative explanations of the effect, the spatial and attention-directing hypotheses specifically. In contrast to Experiment 2, neither of these experiments suggested that the object-size effect was modulated by hand mapping in younger individuals, where one would expect the effect, if present, to be most pronounced.

The final neuroimaging experiment combined behavioural data (chapter 6) functional MRI data (chapter 7) and diffusion tensor imaging, DTI data (chapter 8). For the across group effects, this experiment failed to replicate previous findings of highly significant compatibility effects on the behavioural level. Similarly, the functional imaging data showed no evidence of activation common to both age groups for the contrasts of compatibility. As such, for the across-group analyses, the behavioural and functional data were consistent with each other, and we proposed that the most likely explanation for the lack
of compatibility effect in the group as a whole, and for the weaker effects in both age-groups was due to the much slower reaction times in the scanner.

For the between-group effects, the step down analysis of the behavioural data revealed a significant object-size effect for the younger group whereas this effect was absent for the older group. In contrast to predictions, the functional data showed limited evidence of activation related to the object-size effect in fronto-parietal areas. Instead, in the exploratory analysis which employed a relaxed threshold, the contrast of compatible > incompatible showed larger activations for the younger than the older group, primarily in the posterior division of the left cingulate cortex. As the task complexity increased in incompatible conditions, perhaps due to the increased demands of selecting a response incompatible with the observed object, the posterior cingulate cortex was deactivated in the young, but not the old. These patterns of activity were consistent with previous findings whereby older adults demonstrate a lack of appropriate deactivation which, in turn, has been associated with inefficient processing (e.g. Buckner et al., 2008; Spreng, & Schacter, 2012).

For the diffusion tensor imaging (DTI) data, we performed whole-brain analyses in order to investigate age-related differences in white matter microstructural integrity for all of the four diffusion metrics; fractional anisotropy, mean diffusivity, axial diffusivity, and radial diffusivity (FA, MD, AD, and RD, respectively). Results corroborated previous findings of pervasive age-related decreases in fractional anisotropy and age-related increases in mean diffusivity. For both of these metrics, age-related differences were also observed in subcortical structures which are involved in voluntary movement
and relaying sensory and motor signals to the cortex, (such as the caudate and thalamus). There is very limited healthy ageing research to date which has included analyses of axial and radial diffusivity. We found evidence of widespread age-related increases in radial diffusivity, whereas axial diffusivity showed both age-related increases and decreases. In addition, from each of the four DTI metrics, we sought to establish whether the measures of microstructural integrity correlated with the behavioural measures of compatibility effects, but there was no evidence to this effect.

9.2 Implications of the current thesis and recommendations for further investigations

Visuomotor integration is of fundamental importance in our everyday lives; we continually move around in, and interact with objects in our environment. Despite this being such a fundamental aspect of the human existence, there is still limited research into how healthy ageing affects these aspects. Advancing our knowledge in this area is becoming increasingly important due to the speed at which the world’s population is growing, as well as the rapid increase in the proportion of older adults (www.un.org/esa/population). The empirical work presented in this thesis offers several novel findings.

For the object-orientation study, the most interesting novel finding was that (taken together with results of the earlier study, Galpin et al., 2011), the locus of the effects in the two healthy older groups appeared to arise from both facilitation and interference effects. This was an interesting finding in light of the previously discussed evidence which suggests that older adults (in a similar
manner to Parkinson’s patients), have difficulties in resisting entrainment by visual distractors. Following from this, one might expect that the influence of the task-irrelevant stimulus dimension (orientation) would influence older adults to a larger extent than younger individuals. In accordance with such a view, although the evidence is limited, there are a few studies on ageing and the spatial compatibility effect which seem to suggest that older adults may be more affected by, and have greater difficulty in suppressing the task-irrelevant spatial information which results in larger spatial compatibility effects (Pick, & Proctor, 1999; Proctor et al., 2005; Van der Lubbe, & Verleger, 2002). However, contrary to these earlier findings, we found no evidence of age-related increases (or decreases) in either the object-orientation affordance effect or spatial compatibility effect, which seems to suggest that the older group were not proportionally disadvantaged by the irrelevant stimulus dimension.

Another consequence of older adults having difficulties in resisting entrainment by visual distractors (in a similar manner to Parkinson’s patients), would presumably entail that compatibility effects would be driven by interference effects. However, our results did not support such speculation. In fact, only in the younger group did results suggest that effects were caused by interference effects, and similarly, results of the Parkinson’s group in the earlier study (Galpin et al., 2011) were due to facilitation. Consequently, both the earlier results and our results run counter to such proposition. As discussed earlier, external stimuli have been shown to effect movements both positively and negatively in people with Parkinson’s disease. Consequently, further investigations of the dynamics of these aspects and how they change over the
lifespan is necessary, and may clarify which types of external stimuli facilitate successful visuomotor behaviour in healthy ageing and in Parkinson’s disease, and may be fruitful in establishing training interventions and / or visual markers to aid movement.

Importantly, our novel investigations into age-related changes in object-size affordance effects supported our predictions of age-related reductions in the effect, both when using asymmetrical and centrally presented, spherical stimuli. Experiments 3 and 4 had provided strong evidence in favour of the object-size affordance hypothesis, which posits that intrinsic object features, such as size, facilitates the specific motor actions required to interact with that object, despite them being task-irrelevant. Using the same stimulus set, we further examined whether these effects would be detectable as functional activation in the neural networks which are considered crucial to visuomotor integration, and whether age-related changes in those same networks would compromise visuomotor integration. Results showed very limited evidence of activation related to the object-size compatibility effect in fronto-parietal areas. Instead, it seemed that increasing task complexity was associated with the failure of deactivation of the posterior cingulate cortex in older adults and therefore, perhaps, less focussed attention towards the demanding external task. This would be consistent with previous findings in other types of tasks, but we emphasised that appropriate caution should be taken in the interpretation of the results of this analysis due to the liberal threshold. All in all, our functional MRI results were not particularly informative regarding the processes of visuomotor integration and any age-related changes therein. It still begs the
question as to why there was such limited evidence of not only age-differences, but activation related to the object-size effect generally, in fronto-parietal areas. It is possible, that the temporal resolution of fMRI is not sufficient to capture potentially transient affordance-related activations of motor programmes, and that methods providing much finer temporal information, such as EEG, is better suited. Our novel stimulus set would be ideally suited for such further explorations of the object-size effect for the same reasons mentioned earlier, i.e. ruling out spatial, and hence attention-directing factors.

In addition, the results of experiment 1 (which used non-symmetrical stimuli) indicated that there might be a manual asymmetry in grasping (left for holding, right for manipulating) which diminishes with age. This would be consistent with previous findings of age-related reductions in hand dominance and asymmetries of hand use, although the mechanisms whereby this occurs are still not clear. As discussed previously, an earlier study has documented manual asymmetries in visually primed precision and power grips in young participants (Vainio et al., 2006). Furthermore, a second experiment replicated the right hand bias for small objects and left hand bias for large objects when the grip devices were replaced with simple left hand and right hand button presses (Vainio et al., 2006). Consequently, it was suggested by the authors that these results indicated the presence of manual asymmetries as well as a left-hemispheric specialisation for precision grips and right-hemispheric specialisation for power grips. However, as previously discussed, neither our experiment 3 nor experiment 4 (which used spherical, centrally presented stimuli) found evidence of manual asymmetries in the object-size compatibility
effect in younger individuals where one would expect the effect, if present, to be most pronounced. So whilst the results of experiment 1 provided support for the theory proposed by Vainio and colleagues, the following experiments 3 and 4 did not. In sum, due to the very limited number of studies which have included hand mapping as a factor, and which have provided diverging results, it is not possible to draw any conclusions regarding manual asymmetries in grasping, or any age-related changes therein, without further investigations and clarifications.

Our DTI analyses of age-related differences in white matter microstructural integrity yielded several interesting findings. Due to the limited amount of research which has investigated the connection between healthy ageing, visuomotor functions and white matter integrity, we employed whole-brain analyses rather than pre-specified ROIs, and we did so for all four (FA, MD, AD, and RD) diffusion metrics. Some previous investigations have limited their investigations of other diffusion parameters to regions in which age-related decreases in fractional anisotropy were observed – had the same approach been taken in the present study, some of our observations of age-related differences in diffusivity would have gone unnoticed. Only very few DTI studies on healthy ageing have also included axial and radial diffusivity, but this is likely to change in the near future as the inclusion of all four metrics provides a more comprehensive understanding as each are sensitive to different microstructural physiological properties. The advancement of techniques that can assess microstructure at the cellular level, such as magnetic resonance spectroscopy, combined with the recent discovery that these DTI metrics may serve as
potential biomarkers in Alzheimer’s disease, are likely to fuel the application of DTI in general as well as the inclusion of all metrics further.

One of the most pervasive theories regarding age-related changes in white matter integrity is that of the anterior-posterior gradient (and to a lesser extent, also the superior-inferior gradient). Interestingly, for the anterior-posterior gradient theory, the only metric which provided evidence to this effect, was that of mean diffusivity. As for the superior-inferior gradient theory, our results for all four metrics seemed to suggest the exact opposite, i.e. that the age-related changes were in fact more prominent in inferior, relative to superior regions. The most likely reason for these seemingly diverging results may in fact be down to the quite substantial differences in the employed methodologies. For example, as pointed out by Sullivan and colleagues (2011), a number of studies that have seemingly corroborated previous findings of the anterior-posterior gradient have been based upon analyses of specific tracts/ROIs rather than whole brain analyses. Hence, whilst it may be the case that specific white matter regions (the corpus callosum in particular as it has been studied extensively), tend to show this gradient, it may not be true for other regions. Consequently, it might be wise to take a cautious approach when it comes to analysing results in terms of gradient theories.

To conclude, our novel investigations into potential age-related differences in object affordance effects provided evidence of age-related reductions in the size of the object-size compatibility effect, as predicted. However, despite these behavioural manifestations of age-differences, as well as widespread age-related microstructural changes throughout the brain, including areas central to
visuomotor performance, results of our neuroimaging study did not provide direct evidence that those age-related changes in the object-size compatibility effect could in fact be attributed to neurophysiological changes as we had predicted. We proposed that the temporal resolution of fMRI may not be sufficient to capture potentially transient affordance-related activations of motor programmes. Furthermore, we suggested that our novel stimulus set (which provided strong support for the object-size compatibility effect by ruling out the most prominent alternative explanations for the effect), would be ideally suited for further explorations using methods which provide much finer temporal resolution.

A crucial question remains, namely the extent to which this affects older individuals in their daily lives. This is difficult to predict based upon studies conducted in the lab and in the scanner. Hence, future research would benefit from a multidisciplinary approach, for example by including human factors research and cutting edge technological platforms which would allow investigations of visuomotor behaviour in virtual, realistic or real world settings. Combining such methodologies with experimental and neuroimaging findings would further elucidate which factors impact on visuomotor behaviour, either positively or negatively, and would enhance the development of interventions which could improve the lives of an aging population.
Appendices

Appendix 3A: The experimental stimuli used in experiment 1 (chapter 3).

<table>
<thead>
<tr>
<th>Precision grip compatible objects:</th>
<th>Power grip compatible objects:</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Natural</strong></td>
<td><strong>Manufactured</strong></td>
</tr>
<tr>
<td>Bean</td>
<td>Bolt</td>
</tr>
<tr>
<td>Berries</td>
<td>Clip</td>
</tr>
<tr>
<td>Cherry tomato</td>
<td>Hook</td>
</tr>
<tr>
<td>Chilli</td>
<td>Key</td>
</tr>
<tr>
<td>Garlic</td>
<td>Paperclip</td>
</tr>
<tr>
<td>Green grape</td>
<td>Pin</td>
</tr>
<tr>
<td>Mushroom</td>
<td>Screw</td>
</tr>
<tr>
<td>Pea pod</td>
<td>Tag</td>
</tr>
<tr>
<td>Rosehip</td>
<td>Teaspoon</td>
</tr>
<tr>
<td>Strawberry</td>
<td>Tweezers</td>
</tr>
</tbody>
</table>
Appendix 5A: The experimental stimuli used in experiments 3, 4 and 5 (chapters 5-6).

<table>
<thead>
<tr>
<th>Precision grip compatible objects:</th>
<th>Power grip compatible objects:</th>
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</thead>
<tbody>
<tr>
<td><strong>Edible</strong></td>
<td><strong>Inedible</strong></td>
</tr>
<tr>
<td>Ferrero rocher</td>
<td>Pomegranate</td>
</tr>
<tr>
<td>Gooseberry</td>
<td>Lemon</td>
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<tr>
<td>Garlic bulb</td>
<td>Orange</td>
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<tr>
<td>Radish</td>
<td>Onion brown</td>
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<tr>
<td>Brussel sprout</td>
<td>Onion white</td>
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<tr>
<td>Hazel nut</td>
<td>Grapefruit</td>
</tr>
<tr>
<td>Cherry</td>
<td>Apple</td>
</tr>
<tr>
<td>Olive</td>
<td>Melon</td>
</tr>
<tr>
<td>Blueberry</td>
<td></td>
</tr>
<tr>
<td><strong>Edible</strong></td>
<td><strong>Inedible</strong></td>
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<tr>
<td></td>
<td>Pomegranate</td>
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<td></td>
<td>Lemon</td>
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<td>Onion brown</td>
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<td>Onion white</td>
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<td></td>
<td>Grapefruit</td>
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<tr>
<td></td>
<td>Apple</td>
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<td></td>
<td>Melon</td>
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<td></td>
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<tr>
<td></td>
<td>Cricket ball</td>
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<tr>
<td></td>
<td>Tennis ball</td>
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<tr>
<td></td>
<td>Foam tennis ball</td>
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<tr>
<td></td>
<td>Ball of string</td>
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<td></td>
<td>8 ball</td>
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<td>Baseball</td>
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<td>Croquet ball</td>
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<tr>
<td></td>
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</tr>
<tr>
<td></td>
<td>Foam ball</td>
</tr>
</tbody>
</table>


A copy of the publication (Linnet, & Roser, 2012) can be found on the following pages.